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Decapod Crustacean Phylogenetics

edited by

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The Evolution of Mating Systems in Decapod Crustaceans

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ABSTRACT

The mating systems of decapod crustaceans are reviewed and classified according to general patterns of lifestyles and male–female relations. The scheme employs criteria that focus on ecological, life history, and social determinants of both male and female behavior, and by these criteria nine types of mating systems are distinguished: (1) Short courtship: Both males and females are free-living (= not symbiotic with other organisms), and copulation occurs after brief behavioral interactions between a male and a female. (2) Precopulatory guarding: A male guards a mature female one to several days before copulation; both males and females are generally free-living. (3) Podding: In some large-size decapods, aggregations consisting of an extremely large number of individuals are formed, and mating occurs inside those aggregations. (4) Pair-bonding: In many symbiotic and some free-living species, males and females are found in a heterosexual pair and are regarded as having a monogamous mating system. They may live on or inside other organisms such as sponges, corals, molluscs, polychaetes, sea urchins, ascidians, and algal tubes. (5) Eusocial: In some sponge-dwelling snapping shrimps, a colony of shrimps contains a single reproductive female and many small individuals that apparently never breed. (6) Waving display: In many intertidal and semi-terrestrial crabs inhabiting mudflats or sandy beaches, males conduct visual displays that include species-specific dances to attract females. (7) Visiting: In some hapalocarcinid crabs, females are sealed inside a coral gall, and the male crab normally residing outside the gall is assumed to visit the gall for mating. (8) Reproductive swarm: In some pinnotherid crabs, mating occurs when a female is a free-swimming instar before she enters her definitive host. (9) Dwarf male mating: In some anomuran sand crabs, an extremely small male attaches near the gonopore of a free-living female.

1 INTRODUCTION

Decapod crustaceans are a large and diverse assemblage of animals. In most decapods, the sexes live separately and pair briefly as adults. Pairs are formed after a brief display, the sexes remain together for a relatively short period, the sexes separate after copulation, and the females assume all further parental duties such as selecting suitable habitat for egg incubation, aeration, and cleaning (Salmon 1983). However, recent discoveries of often-conspicuous behavior and male–female relations among decapods have shown that their mating system is highly diverse and is sometimes quite similar to mating systems of other animals such as birds, mammals, reptiles, and insects (see Shuster & Wade 2003; Duffy & Thiel 2007 for a review).

As claimed by Emlen & Oring (1977) in their classic work on the relationships among ecological factors, sexual selection, and the evolution of mating system, sexual selection is the driving force that underlies the evolution of male–male competition and female choice. However, ecological factors apparently contribute to the evolution of mating systems as well as to behavioral and morphological differences between the sexes. From this point of view, much study has been conducted recently on the evolution of the mating system of decapods (see section 2 below).

In this paper, I describe the diversity of mating systems of decapods in an attempt to recognize and classify their general patterns from the viewpoints of the ecological, life history, and social determinants of both male and female behavior. Historically, there are two ways of describing mating systems (Shuster & Wade 2003). The first is in behavioral ecology, where mating systems are usually described in terms of the number of mates per male or female, such as monogamy, polygyny, and polyandry. The second is in terms of the genetic relationships between mating males and females, such as random mating, negative assortative mating (outbreeding), and positive assortative mating (inbreeding). My approach to describing mating systems of decapods is a "recognition of general pattern" approach, a kind of a combination of these two approaches that captures variation in the relationship between male and female, from promiscuity to monogamy, as well as the relationship between male guarding and the female tendency to settle down in certain places or to aggregate, and the complex nature of eusociality.

Terminology generally follows Duffy & Thiel (2007). Additionally, some basic terms are redefined here, because these terms are sometimes used in more or less different ways according to taxa, including birds, mammals, and fish:

- **Monogamy** (= pair bonding): One male and one female have an exclusive mating relationship.
- **Polygamy**: One or more males have an exclusive relationship with one or more females. Three types are recognized: **polygyny**, where one male has an exclusive relationship with two or more females; **polyandry**, where one female has an exclusive relationship with two or more males; and **polygynandry**, where two or more males have an exclusive relationship with two or more females (the numbers of males and females need not be equal, and, in vertebrate species studied so far, the number of males is usually fewer).
- **Promiscuity**: Any male within the group mates with any female.
- **Eusociality**: Multigenerational (cohabitation of different generations), cooperative colonies with strong reproductive skew (reproductive division of labor, usually a single breeding female) and cooperative defense of the colony (after Duffy 2003).
- **Symbiosis**: Here defined simply as dissimilar organisms living together.

2 HISTORY OF STUDY

The first important review of decapod mating systems was Hartnoll's (1969) publication on brachyuran crabs. He distinguished two types of mating systems. "Soft-female mating" was defined as copulation occurring immediately after molting of the female, usually preceded by a lengthy pre-molt courtship behavior including precopulatory guarding by the male. "Hard-female mating" was defined as mating in which the female copulates during the intermolt stage after a relatively brief courtship behavior.

Through their intensive study of the harlequin shrimp *Hymenocera picta*, Wickler & Seibt (see Reference 16 in Appendix I, Table 10) found that these shrimp form stable heterosexual pairs based on individual recognition by chemical cues at a distance. Wickler & Seibt discussed several similar hypotheses, independently developed in research on crustaceans and humans, for the evolution of monogamy and other mating systems. Individual recognition in the monogamous mating system was intensively studied in the banded shrimp *Stenopus hispidus* by Johnson (1969, 1977).

The report by Emlen & Oring (1977) was influential for studies on crustacean mating systems. They classified the mating system into the following categories:

1. Monogamy
2. Polygyny (subdivided into 2a, resource defense polygyny; 2b, female (or harem) defense polygyny; and 2c, male dominance polygyny (further subdivided into 2c-1, explosive breeding assemblages, and 2c-2, leks))

3. Rapid multiple clutch polygamy
4. Polyandry (subdivided into 4a, resource defense polyandry; and 4b, female access polyandry)

Ridley (1983) intensively reviewed the precopulatory mate guarding behavior in various groups of animals including tardigrades, crustaceans, arachnids, and anurans, and discussed its evolution.

Work on the behavior of the fiddler crabs (genus *Uca*) has contributed greatly to our understanding of the mating systems of brachyuran crabs. These studies include the works of H.O. von Hagen (e.g., von Hagen 1970), J. Crane (e.g., Crane 1975), J. Christy and his coworkers (e.g., Christy et al. 2003a, b), M. Salmon and his coworkers (e.g., Salmon & Hyatt 1979), P. R. Y. Backwell and her coworkers (e.g., Backwell et al. 2000), M. Murai and his coworkers (e.g., Murai et al. 2002), and T. Yamaguchi (e.g., Yamaguchi 2001a, b). Based on the studies of *Uca* and other brachyurans, as well as other decapods, Salmon (1983) reported the diversity of behavioral interactions preceding mating in decapods, and he defined some of the consequences of these interactions in terms of sexual selection, courtship behavior, and mating systems. The book edited by Reback & Dunham (1983), which included Salmon's (1983) work, was a landmark in the study of decapod behavior.

Christy (1987) reviewed the mating systems of brachyuran crabs and classified them, according to modes of competition among males for females, into three major categories and eight subcategories, as follows.

1. Female-centered competition, including: 1a, defense of mobile females following free search; 1b, defense of sedentary females following a restricted search; 1c, capture, carrying, and defense of females at protected mating sites; and 1d, attraction and defense of females at protected mating sites
2. Resource-centered competition, including: 2a, defense of breeding sites; and 2b, defense of refuges
3. Encounter rate competition, including: 3a, neighborhoods of dominance; and 3b, pure search and interception

In their book on crustacean sexual biology, Bauer & Martin (1991) introduced developments in various fields and taxa of crustacean research, including studies on sex attraction, sex recognition, mating behavior, mating system, and structure and function associated with insemination. Bauer and his coworkers have extensively studied the mating behavior, mating system, and hermaphroditism of shrimps (e.g., see Bauer 2004 for a review).

Through their intensive studies on the mating system of the spider crab *Inachus* and of the extended maternal care of semi-terrestrial grapsid crabs of Jamaica, Diesel and his coworker revealed examples of highly specialized mating and social systems in these crabs (see Diesel 1991; Diesel & Schubart 2007 for reviews).

Thiel and his students have conducted intensive research on the mating system of rock shrimps (see Reference 6 in Appendix I, Table 4) and symbiotic anomuran crabs (e.g., Baeza & Thiel 2003). Based on these studies, Thiel & Baeza (2001) and Baeza & Thiel (2007) reviewed factors affecting the social behavior of marine crustaceans living symbiotically with other invertebrates. Similarly, Correa & Thiel (2003) reviewed mating systems in caridean shrimp and their evolutionary consequences for sexual dimorphism and reproductive biology. The book by Duffy & Thiel (2007) on the evolutionary ecology of social and sexual systems of crustaceans is a monumental landmark that synthesizes the state of the field in crustacean behavior and sociobiology and places it in a conceptually based, comparative framework. The relatively recent discovery of eusociality in snapping shrimp by Duffy has opened the door to a new field in social and mating systems of decapods (see Duffy 2007 for a review; see also sections 3.5 *Eusocial type* and 4.5 *Evolution of the eusocial type* below for further explanation).

Asakura (1987, 1990, 1993, 1994, 1995, 1998a, 1998b, 1999, 2001a, b, c), Imazu & Asakura (1994, 2006), and Nomura & Asakura (1998) reported mating systems and various aspects of sexual differences in the ecology and behavior of hermit crabs and other decapods.

3 TYPES OF MATING SYSTEMS

3.1 *Short courtship type*

This type is generally seen in species whose males and females are free living, that is, not symbiotic with other organisms (Appendix 1, Tables 1, 2). Copulation occurs after a short courtship behavior by the male, or copulation occurs just after brief behavioral interactions between a male and a female. This type of courtship includes very different groups of decapods, from the most primitive group (dendrobranchiate shrimps) to groups specialized for certain habitats such as freshwater crayfishes, intertidal hermit crabs, and semi-terrestrial and terrestrial brachyuran crabs. It is perhaps the most widely seen mating system in decapods.

No intensive aggressive behavior between males (for a female) has been reported in species of dendrobranchiate shrimps of the families Penaeidae and Sicyoniidae, caridean shrimps of the families Palaemonidae, Hyppolytidae, and Pandalidae, or anomuran sand crabs of the family Hippidae. In these species, females are generally similar in size to, or larger than, males. On the other hand, strong aggressive interaction is seen between males in freshwater crayfish species of all three families (Astacidae, Parastasidae and Cambaridae) as well as in brachyuran crabs of the Grapsoidea and Gecarcinidae. In these species, the male body and weaponry (chelipeds) are generally larger than the female.

Among decapods exhibiting this mating system are species whose females molt before copulation (Appendix 1, Table 1) and those whose females do not molt before copulation (Appendix 1, Table 2). In species inhabiting terrestrial and semi-terrestrial habitats, females generally copulate in the hard shell condition; these species include land hermit crabs of the genus *Coenobita* and brachyuran crabs of the Grapsoidea and Gecarcinidae.

In penaeid shrimp, the molting condition of copulating females is determined according to the type of thelycum. The thelycum is the female genital area, i.e., modifications of female thoracic sternites 7 and 8 (sometimes including thoracic sternite 6) that are related to sperm transfer and storage. A female with externally deposited spermatophores is said to have an "open thelycum," which is formed by modifications of the posterior coxae and sternites to which the spermatophores attach. Primitive dendrobranchiate shrimps, including species of the families Aristeidae, Solenoceridae, Benthesicymidae, and the penaeid genus *Litopenaeus,* have open thelyca. In these species, females copulate in the hard shell condition. On the other hand, a "closed thelycum" refers to sternal plates that may (1) enclose a noninvaginated seminal or sperm receptacle, (2) cover a space that leads to spermathecal opening, or (3) form an external shield guarding the spermathecal openings. In the most advanced groups, including the penaeoid genera *Fenneropenaeus, Penaeus, Farfantepenaeus, Melicertus, Marsupenaeus, Trachypenaeus,* and *Xiphopenaeus*, females have closed thelyca. In these species, females molt just before copulation. Since no significant difference is seen in mating behavior between the open thelycum species and the closed thelycum species, Hartnoll's (1969) rule, which predicts a lengthy pre-molt courtship behavior associated with soft-female mating and a relatively brief courtship behavior with hard-female mating, does not hold in the case of the penaeid shrimps.

A sperm plug, which is believed to preclude subsequent insemination by other males, is known in some species of *Farfantepenaeus, Marsupenaeus, Metapenaeus,* and *Rimapenaeus* (Appendix 1, Table 3).

In all the above-mentioned taxa, copulation generally continues only for several minutes. After mating, the male separates from the female and presumably goes on to search for other females.

The habitat of species that exhibit this mating system varies, ranging from terrestrial through intertidal to deep water.

3.2 *Precopulatory guarding type*

This mating system also is generally seen in species whose males and females are free living (Appendix 1, Table 4). A male guards a mature female for one to several days before copulation. Generally, males aggressively fight for a female using their cheliped(s) and sometimes also the ambulatory pereopods. In some species, females always molt prior to mating and copulation; in other species, females may or may not molt prior to copulation. There are two types of guarding: (1) contact guarding of hermit crabs and brachyuran crabs, in which a male grasps part of the appendages, the body, or the shell (in the case of hermit crabs) of a mature female, and (2) non-contact guarding, as exhibited in *Macrobrachium* shrimps and *Homarus* lobsters, in which a male keeps a female without grasping her. After mating, postcopulatory guarding by a male for a female is sometimes observed (Appendix 1, Table 5). However, after postcopulatory guarding, or just after copulation, the male and female separate so that both may later mate with other individuals. Generally, in this mating system, the body size of males is larger than that of females, or weaponry (chelipeds) is more developed in males than in females.

Species of the river prawn genus *Macrobrachium* are well known for the extremely long chelipeds in males. A male guards a female for one to several days before copulation and fights with other males using these chelipeds. In some species, such as *M. australiense*, a male has a nest (a saucer-shaped depression on the bottom), beckons a female to the nest, and guards and copulates with her in the nest. In the American lobster *Homarus americanus*, a male guards a female in his shelter, which is dug under rocks, boulders, or eelgrass, and the cohabitation of a male and a female lasts from one to three weeks.

In hermit crabs of the genus *Diogenes* (Diogenidae) and in many species of the family Paguridae, all of which have unequal chelipeds in terms of both size and morphology, a male grasps the rim of the shell inhabited by a mature female by the minor cheliped, guards her for one to several days before copulation, and fights with other males approaching him using the major cheliped. In crab-shaped anomurans, the male *Paralithodes brevipes* conducts both pre-copulatory and post-copulatory guarding. The male claims a female by grasping her chelae or legs with his chelae, or he covers the female with his body. Similarly, the male *Hapalogaster dentata* grasps a female with his left chela and covers the female with his body; these guarding behaviors occur one to three days before copulation.

In the brachyuran crab *Corystes cassivelaunus* (Corystidae), the male carries the female in his chelae, and, while stationary, holds one or both of the female's chelae in his own and holds her carapace close to his sternum. Such behavior continues up to several days before copulation. In species of the Cancridae and Portunidae, males carry the pre-molt female with her carapace or sternum held against the sternum of the male for a period of days; after this period the male releases the female so that she molts, and copulation occurs shortly after the molting. In many species in these two families, the male continues to carry the female after copulation in the pre-molt position until her integument has partially hardened. Sperm plugs, which are regarded as being produced by the males to block the females' genital duct to preclude subsequent insemination by other males (Diesel 1991), also are often reported for species of these families (Appendix 1, Table 6). In *Menippe mercenaria* (Xanthidae), the male guards the entrance to the burrow occupied by the pre-molt female, and they copulate as soon as the female molts. In species of the Majidae and Cheiragonidae, the male guards the female before copulation in a manner similar to what is seen in the Cancridae and Portunidae, where the male grasps the ambulatory pereopods, chelipeds, or body of the female.

Species that exhibit this mating system are from the intertidal through shallow water to deep waters, but they are not found in terrestrial or semi-terrestrial environments.

3.3 *Podding*

In large decapods inhabiting shallow waters, an aggregation consisting of an extremely large number of individuals in certain places is called a "pod." Podding is regarded as a type of behavior that is optional and that is associated with different stages in the species' life history, such as molting, mating, and the incubation period (Appendix 1, Table 7). The pod is also called a "heap" or "mound," according to the locality and/or the species.

The function of the pod may vary depending on the condition of the specimens within it (such as level of maturity, sex, intermolt stage) and possibly on changes in habitat condition, such as water temperature and presence of predators (Sampedro & González-Gurriarán 2004). However, as listed in Appendix 1, Table 7, pods in some species have the function of facilitating mating, so I will treat this as a special kind of mass mating in some species.

Stevens (2003) and Stevens et al. (1994), reporting more than 200 pods with a total of 100,000 crabs of the majid *Chionoecetes bairdi* in an area of only 2 ha off Kodiak Island in Alaska in 1991, observed that the formation of the pods and mating synchronized with the spring tide. Similar observations were made for another majid, *Hyas lyratus*, by Stevens et al. (1992), who reported large aggregations during the mating season from off Kodiak Island. They found 200 mating pairs (males grasping females) among 2000 individuals in one pod. The majid crab *Loxorhynchus grandis*, distributed along the east coast of North America, often forms large aggregations numbering hundreds of animals. The aggregation is composed of crabs of both sexes, and the function is thought to be the attraction of males for mating (Hobday & Rumsey 1999). DeGoursey & Auster (1992) reported large mating aggregations in another majid crab, *Libinia emarginata*, in April and May 1989. Many mating pairs were found in the aggregations, and the percentage of ovigerous females among all females increased from 26% on 1 May to 100% on 14 May. Males paired with females were significantly larger than unpaired males, while the paired and unpaired females were not significantly different in size. Carlisle (1957) monitored a pod consisting of 60–80 individuals of the majid crab *Maja squinado* in shallow waters in the English Channel; 20 were adult males and the rest were juvenile males and females in equal amounts. He observed crabs molting inside the pod and mating between intermolt males and postmolt females, which led him to conclude that the main purpose of podding is to provide protection for newly molted soft crabs against predators and to facilitate mating. However, later behavioral observations by Hartnoll (1969) indicated that copulation occurs between a male and a female in the intermolt stage. Furthermore, Sampedro & González-Gurriarán (2004) found that the gonads of females in the pods were in an early stage of development (= not fully matured) and that the spermathecae were empty, suggesting to them that mating of this species occurs in deeper waters.

In crab-shaped anomurans, large pods of the red king crab *Paralithodes camtschaticus* are well known in the northern Pacific Ocean, with each pod consisting of thousands of crabs in the 2-4 year class (juveniles). Aggregations of adult red king crabs (ovigerous females) also were reported and are thought to be related to mating (Stone et al. 1993), but detailed surveys have not been conducted. Dense aggregations of the southern king crab *Lithodes santolla* have been reported from Chile (South America); however, the crabs forming these aggregations are juveniles, so this behavior is not thought be related to mating (Cardenas et al. 2007).

In summary, podding is known only in large species distributed in temperate or boreal waters in both the Pacific and Atlantic oceans.

3.4 *Pair-bonding type*

Many species of decapods, in particular those that are symbiotic with other animals, have been reported as "found in a heterosexual pair" (Appendix 1, Tables 8–12). Most of these are considered to have a monogamous mating system, which is well known in birds and mammals. In species whose males engage in mate-guarding, temporal heterosexual pairing occurs, where the pair is formed when the female is close to molting or spawning a new batch of unfertilized eggs, and the mate-guarding males abandon the females soon after the eggs are fertilized. However, in pair-bonding species, males cohabit with females, independent of their reproductive status or of the stage of development of the brooded embryos. Nevertheless, the observations for the monogamous nature of these pair-bonding species are often only anecdotal, and how long the pair remains together, and with whom they mate, is rarely recorded. Some well-documented studies include the formation of stable pairing and individual recognition (individuals in a pair can recognize each other as mates), as in the case of the banded shrimp *Stenopus hispidus* (Reference 8 in Appendix 1, Table 10), the scarlet cleaner shrimp *Lysmata debelius* (Reference 12 in Appendix 1, Table 10), and the harlequin shrimp *Hymenocera picta* (Reference 16 in Appendix 1, Table 10).

Detailed observations of the monogamous nature of pairing have been made for several species of snapping shrimps, for example, *Alpheus angulatus* (Reference 97 in Appendix 1, Table 9), *Alpheus heterochaelis* (Reference 99 in Appendix 1, Table 9), *Alpheus armatus* (Reference 28 in Appendix 1, Table 9), and *Alpheus roquensis* (Reference 31 in Appendix 1, Table 9), as well as for the pontoniid shrimp *Pontonia margarita* (Reference 45 in Appendix 1, Table 8), the deep-water sponge-dwelling shrimp *Spongicola japonica* (Reference 1 in Appendix 1, Table 10), a porcelain crab *Polyonyx gibbesi* (Reference 11 in Appendix 1, Table 11), and several species of coral crabs of the genus *Trapezia* (References 2–14 in Appendix 1, Table 12). Many pair-bonding species are known in caridean shrimps of the subfamily Pontoniinae and family Alpheidae, "cleaner" shrimps of the families Stenopodidae and Spongicolidae, crab-shaped anomurans (family Porcellanidae), and brachyuran crabs of the family Trapeziidae.

Most of these species are symbiotic with other animals or live in special habitats. Host animals for these species include sponges, sea anemones, black corals, reef-building corals, gastropods, opistobranch molluscs, bivalves, polychaetes, crinoid feather stars, sea stars, sea urchins, sea cucumbers, and ascidians. The special habitats include gastropod shells used by large hermit crabs; tubes of polychaetes such as *Chaetopterus*; soft, web-like tubes consisting of filamentous algae, sponges, and other debris built by shrimp themselves; burrows excavated in hard dead corals; burrows of gobiid fish; and burrows of the thalassinidean shrimp genus *Upogebia*. However, free-living species are also known, such as stenopodid shrimps inhabiting rocky subtidal zones and many alpheid shrimp species inhabiting rock crevices or found under rubble, around large algae, or in burrows of their own in mudflats and other soft bottoms.

The following generalizations can be made for almost all of these species. They are territorial, and they cooperatively defend their habitats (hosts, special habitats, and burrows) against other conspecific or non-conspecific animals. Thus, the mating system of these species is termed "resource-defense monogamy." The pairs are size-matched (– size-assortative pairing); there is strict preference exerted by either sex for mates of a particular size relative to themselves. Baeza (2008) proposed two possible explanations for this phenomenon in his study on pontoniid shrimps symbiotic with bivalves:

1. The two sexes might choose large individuals of the opposite sex as sexual partners and host companions. In males, a preference for large females should be adaptive, as female size is positively correlated with fecundity in shrimps. In females, sharing a host with a large male might result in indirect benefits (i.e., good genes) or direct benefits (increased protection against predators or competitors).
2. Choice of a certain-size partner could also be a consequence of constraints in the growth rates of shrimps dictated by host individuals. Space limitations for shrimps in hosts are suggested by the tight relationship between shrimp and host size, and by the fact that hosts harboring solitary or no shrimps were among the small hosts.

These species tend to display low sexual dimorphism in weaponry in terms of cheliped size and morphology and often in body size. This is in contrast to the large sexual differences in mate-guarding species in which the weaponry is much more developed and where body size is often much larger in males than in females. Regarding body size, there is a tendency in pair-bonding shrimp for the male to be slightly smaller, in terms of body length, and much more slender than its mate female; in trapeziid crabs the male is often slightly larger than his female mate.

The bathymetric distribution of species with this mating system is generally from intertidal to shallow water, but a few groups of species, such as those of the Spongicolidae, inhabit deep water.

3.5 *Eusociality type*

Until the discovery of the eusocial shrimp *Zuzalpheus regalis* (as *Synalpheus regalis*) (Duffy 1996), eusociality was recognized only among social insects, including ants, bees, and wasps (Hymenoptera) and termites (Isoptera); in gall-making aphids (Hemiptera); in thrips (Thysanoptera); and in two mammal species, the naked mole rat (*Heterocephalus glaber*) and the damaraland mole rat (*Cryptomys damarensis*). *Zuzalpheus regalis* lives inside large sponges in colonies of up to >300 individuals, with each colony containing a single reproductive female. Direct-developing juveniles remain in the natal sponge, and allozyme data indicate that most colony members are full siblings. Larger members of the colony, most of whom apparently never breed, defend the colony against heterospecific intruders (Duffy 1996).

Following this initial discovery, Duffy and his coworkers have found several other species of *Zuzalpheus* exhibiting monogynous, eusocial colony organization in the western Atlantic (Appendix 1, Table 13). In the Indo-west Pacific region, Didderen et al. (2006) found a colony of a sponge-dwelling alpheid shrimp, *Synalpheus neptunus neptunus*, with one large ovigerous female or "queen" together with many small individuals, indicating a eusocial colony organization (Appendix 1, Table 13).

Some 20 species of symbiotic decapod species have been reported as found in a group (Appendix 1, Tables 14–15). Among them, examples of *Synalpheus* and *Zuzalpheus* exhibited more than 100 individuals in one aggregation, and, in particular in the case of *Zuzalpheus brooksi,* more than 1000 individuals were recorded from one sponge. These aggregations are regarded either as having a non-social structure (Thiel & Baeza 2001) or with the social structure totally unknown.

3.6 *Waving display type*

In many species of the crab families Ocypodidae, Dotillidae, and Macrophthalmidae, and in species of the genus *Metaplax* of the family Varunidae (formerly subfamily Varuninae in the Grapsidae *sensu lato*), males perform waving displays using the chelipeds. As in many other territory advertisement signals in animals, this behavior is commonly thought to have the dual function of simultaneously repelling males and attracting females (e.g., Salmon 1987; Crane 1975). These species typically live in mudflats, tidal creeks, sandbars, and mangrove forests, and each individual has its own burrow with a small territory around it. They often occur in huge numbers, with thousands of individuals living in small, adjacent territories, and with males and females living intermixed. The burrow serves various functions, including a refuge during high tide, an escape from predators, and the site of mating, oviposition, and incubation.

The behavior and mating systems of fiddler crabs (genus *Uca*, Ocypodidae) have been intensively studied (see references in History of Study, above). There are species whose males defend burrows from which they court females and species whose males wander from their burrows and court females on the surface (Christy 1987). For the former group of species, the following generalization is possible (based mainly on P. Backwell and coworkers; see references in History of Study, above). Males wave their enlarged claw, and, when a female is ready to mate (i.e., she matures), she leaves her own burrow and wanders through the population of waving males. The female visits several males before selecting a mate, and a visit consists of a direct approach to the male. Before copulation, both individuals enter the male's burrow, and two behavioral patterns are known: the male enters his burrow first and the female follows him in, or it happens in the reverse order, i.e., the female enters first. The male then gathers up sand or mud to plug the burrow entrance. Mating occurs in the burrow. On the following day, the male emerges, reseals the burrow entrance with the female still underground, and leaves the area. The female remains underground for the following few weeks while she incubates her eggs.

In addition to waving displays, males of some fiddler crab species employ acoustic signals to attract females. In these species, males attract females during the day first by waving and then by producing sounds just within their burrows. At night, the males produce sounds at low rates, but when touched by a female they increase their rate of sound production (Salmon & Atsaides 1968).

Many species of ocypodid crabs build sand structures next to their burrows, some of which function to attract females for mating, such as pillars (*Uca*: Christy 1988a, b), hoods (*Uca*: Zucker 1974, 1981; Christy et al. 2002, 2003a, b), mudballs (*Uca*: Oliveira et al. 1998), and pyramids (*Ocypode*: Linsenmair 1967; Hughes 1973).

3.7 *Visiting type*

An interesting mating system has been suggested for coral gall crabs (family Cryptochiridae), which inhabit cavities in scleractinian corals in (usually) shallow water. However, the information is still anecdotal, based on ecological observations on *Hapalocarcinus marsupialis*, *Troglocarcinus corallicola*, and *Opecarcinus hypostegus* (Potts 1915; Fize 1956; Kropp & Manning 1987; Takeda & Tamura 1981; Hiro 1937; Kotb & Hartnoll 2002; Carricart-Ganivet et al. 2004). In *H. marsupialis* and *T. corallicola*, the male crab normally resides outside the gall, which was constructed by the female, and is thought to visit the gall of the female for mating. The males and females apparently show promiscuity, and male–male aggressive behavior for a female has not been reported. The female is much larger than the male and in some species has a soft body with a very large abdomen. On the other hand, the male is usually hard, with a small abdomen. Geographical distribution includes mostly the tropics (see Wetzer et al. this volume).

In *Opecarcinus hypostegus,* couples were found sharing cavities; ovigerous females and males are recorded inhabiting adjoining cavities on colonies of *Siderastrea stellata* corals (Carricart-Ganivet et al. 2004). This species may have a mating system different from the above.

3.8 *Reproductive swarm type*

This mating system is reported only in pinnotherid crabs that are considered parasitic or co-inhabiting with other animals, including bivalves, gastropods, sea slugs, chitons, polychaetes, echinoderms, burrowing crustaceans, and sea squirts (Cheng 1967; Gotto 1969). In several species of these crabs, mating occurs, or is thought to occur, when the female is in the free-swimming stage before she enters into her definitive host (Appendix 1, Table 16).

The following generalization is possible for these species. Adult females have a soft, membranous carapace, and generally each one lives by itself within its host animal. These females produce broods of planktonic larvae. After development, the larvae metamorphose into the "invasive stage" crab, which is morphologically similar to the later swimming stage in having a flattened shape and ambulatory legs with dense setae adapted for swimming. Following this stage is a stage designated as "prehard"; these crabs invade, and live in, the host invertebrate animals. The crab at this stage is soft, resembling the later posthard stage. These crabs grow and mature into small adults of both sexes and leave their host to join mating swarms in open water. This stage is called the "hard stage," swimming stage, or copulation stage, and it is characterized by a hard body, swimming legs densely fringed with setae, and a thick fringe of setae along the front of the carapace. They copulate at this stage, and, in all reported species (see Appendix 1, Table 16), females copulate in the hard shell condition. After copulation, each female enters the host animal, but the male dies. The female becomes soft and grows much larger in the host, and later the female produces eggs fertilized by sperm from her single mating.

This is a kind of mass mating, with males and females showing promiscuity. In the copulation stage, no intensive aggressive behavior between males for females has been reported. The males in this stage are slightly larger than the females, and the morphology is similar between the sexes. After the female enters the host animal, the female becomes soft and grows much larger and stouter. The species with this mating system are found generally from intertidal to shallow water where their host invertebrates occur. In some pinnotherid species, adult crabs are found in a heterosexual pair in the host animal, although life history and mating systems of these species are mostly unknown.

3.9 *Neotenous male type*

Extremely small, neotenous males exist in some species of anomuran sand crabs (genus *Emerita*) inhabiting wave-exposed sandy beaches in tropical and temperate waters (Appendix 1, Table 17). In these species, the males become sexually mature soon after their arrival on the beach as a megalopa. When copulating, a male attaches near one of the female's gonopores, which are located on the coxae of the third pereopods. Surprisingly, the size of the neotenous males is similar to, or smaller than, those coxae.

Protandric hermaphroditism is described in detail in *Emerita asiatica* as it relates to neotenous males (Subramoniam 1981). The neotenous males occur at 3.5 mm carapace length (CL) and above, whereas females acquire sexual maturity at 19 mm CL. The neotenous males, as they continue to grow, gradually lose male functions and reverse sex at about 19 mm CL. In the CL range of 19–22 mm, the male's gonad consists of inactive testicular and active ovarian portions. Androgenic glands, active in the neotenous males, show signs of degeneration in the larger males and disappear in the intersexuals.

The male separates from the female after copulation. Aggressive behavior between males is not reported. As opposed to the female, the neotenous male shows a general simplicity of appendages associated with its small size. Among decapods, this phenomenon is known only in species of *Emerita*.

4 EVOLUTION OF MATING SYSTEMS IN DECAPODA

4.1 *Introduction*

It is apparent from the above that similar mating systems have evolved independently in different taxa at different times; i.e., convergent evolution is widespread. Species in ecologically similar habitats often display patterns that are strikingly comparable. Here I discuss the possible origin and evolutionary pathway of each mating system and compare them with those of other animals.

4.2 *Evolution of the short courtship type and the precopulatory type*

These two mating systems are most dominant among decapods. The mode of life is often quite similar; both males and females are free living (not symbiotic with other organisms), and after mating the male soon separates from the female. However, the habitat is sometimes different; in terrestrial and freshwater species, only the short courtship type has been reported. Therefore, a question arises as to why some groups of species have evolved the prolonged precopulatory mate guarding, whereas others have not.

Precopulatory mate guarding is known in a very broad range of taxa such as tardigrades, crustaceans, arachnids, and anurans (Parker 1974; Ridley 1983; Conlan 1991). It is thought to evolve when male–male competition for females is strong enough and female receptivity is restricted in time (Parker 1974; Jormalainen 1998), or even if receptivity is not time-limited but the guarding costs are low enough (Yamamura 1987). Guarding should be beneficial to the male, if the expected fitness gain achieved by guarding is greater than that expected by continuing to search for other females (Parker 1974). Thus, the optimal guarding duration for the male is determined by the encounter rate of females and the costs of guarding relative to those of searching (Yamamura 1987). The cost of guarding for males includes decreased mobility and feeding (Adams et al. 1985, 1991; Robinson & Doyle 1985), an increase in predation risk while guarding (Verrel 1985; Ward 1986), increased energetic costs associated with carrying females (Sparkes et al. 1996; Plaistow et al. 2003), and an increase in fighting costs through male–male conflict (Benesh et al. 2007; Yamamura & Jormalainen 1996). Additionally, a long guarding time decreases future opportunities to mate with other females (Benesh et al. 2007).

Pelagic dendrobranchiate and caridean shrimps are primarily swimmers, and possibly for that reason they have not evolved prolonged, elaborate behavioral interactions before copulation. However, the above-mentioned energetic cost hypothesis (Sparkes et al. 1996; Plaistow et al. 2003) may be applicable; for males of these species, carrying a swimming female for a long duration requires much more energy than in benthic species. In fact, all species exhibiting a prolonged precoulatory guarding period are benthic species.

In all freshwater crayfish studied, the mating system includes a short courtship without a lengthy precopulatory guarding, even though they have a benthic lifestyle and male–male aggression is often common. They may live in their burrows separately, or underneath boulders or heaps of fallen leaves, and these habitats are quite similar to, or virtually the same as, those of shrimps of the genus *Macrobrachium*. Why males of *Macrobrachium* adopt a precopulatory guarding strategy whereas male crayfish do not is not known.

A similar question arises in intertidal and shallow water decapods. For example, intertidal hermit crab species exhibiting precopulatory guarding have a tendency toward vastly unequal chelipeds, with a well-developed major cheliped particularly in males, who use it for fighting with other males during guarding. Such species include those of the genera *Pagurus* (Paguridae) and *Diogenes* (Diogenidae). On the other hand, species of *Paguristes* have small and similar right and left chelipeds and execute short courtship mating; males do not aggressively fight with other males. Species of *Calcinus,* which conduct short courtship type mating, often have vastly unequal chelipeds, with the well-developed major cheliped similar to those species that display precopulatory guarding. However, males of *Calcinus* species do not aggressively fight with each other during mating. Further study is needed to clarify the relationship between mating behavior and morphology.

In land hermits and land brachyurans, the above-mentioned predation risk hypothesis (Verrel 1985; Ward 1986) may be applicable to those species where mating system is the short-courtship type with hard-female mating. Male–male aggression is common in these taxa, but they have never evolved precopulatory guarding. Prolonged guarding may carry the risk of attack by visual predators such as birds in a terrestrial environment. In these taxa, a strong connection exists between a prolonged precopulatory guarding and soft-female mating as well as between a short courtship and hard-female mating. When marine species adapted to land, the former mating system might have been lost and changed to the latter, i.e., from soft-female to hard-female, to avoid desiccation and to deal with the large and often unpredicted fluctuations in availabilities of females in a terrestrial environment.

The evolution of sperm plugs in species of short-courtship type (penaeid shrimps) and precopulatory type (brachyuran crabs) is interesting. The sperm plug has virtually the same function as the copulation plug (= copulatory plug, mating plug) in mammals (rodents, bats, monkeys, koala), reptiles (snakes and lizards), insects (butterflies, ants, dragonflies, and stinkbugs), spiders, and acanthocephalan worms (Smith 1984). These plugs, secreted by the male after mating, serve to block the female tract for some time to prevent further mating by other males.

4.3 *Evolution of the podding type*

Why many animal species (e.g., insects, fish, birds, and herbivorous mammals) group together is one of the most fundamental questions in evolutionary ecology. It is believed that strong selective pressures lead to aggregation rather than to a solitary existence in most of these groups. These pressures include protection against predators, increased foraging efficiency, increased ease of assessing potential mates, and increased information exchange about the location of food (Barta & Giraldeau 2001). Similarly, various ecological reasons for the formation of pods have been proposed, including protection during molting, location of mates, aiding in food capture, and protection from predation (see References in Appendix 1, Table 7). Why some species evolved aggregating behavior and others did not is unknown.

4.4 *Evolution of the pair-bonding type*

Heterosexual pairing behavior ("social monogamy," Gowaty 1996; Bull et al. 1998; Gillette et al. 2000; Wickler & Seibt 1981) has evolved many times in a broad range of animal taxa, including mammals, birds, reptiles, amphibians, fish, insects, and crustaceans. For example, a colony of scleractinian coral sometimes yields a pair of goby fish, alpheid shrimps, and trapeziid crabs. Researchers interested in social system evolution must look for ecological and physiological factors (beyond basic sexual differences) that may make social monogamy selectively advantageous to individual males and/or females. Of particular interest are factors that may consistently correlate with such behavior across taxonomic groups. Several hypotheses for the evolution of social monogamy have been developed [see also Mathews (2002b), Baeza (2008), Baeza & Thiel (2007) for a review], as follows.

Biparental care hypothesis: Kleiman (1977) argued that the advantages of monogamy in mammals can lead to social monogamy. The hypothesis also implies that both males and females would suffer significantly reduced or zero fitness if they did not cooperate in caring for the offspring. However, this is not the case for marine decapods, where only the females care for the fertilized eggs and where neither parent cares for the larvae.

Extended mate guarding hypothesis: If males are under selection to guard females for some time before, during, and/or after courtship and mating, they may be forced into partner-exclusive behavior by some other factor, such as female dispersion (Kleiman 1977; Wickler & Seibt 1981) or female–female aggression (Wittenberger & Tilson 1980). In other words, monogamy can result from males guarding females over one or multiple reproductive cycles, because the female's synchronous receptivity, density, or abundance relative to males renders other male mating strategies (pure searching) less successful (Parker 1970; Grafen & Ridley 1983).

Territorial cooperation hypothesis: The fact that most monogamous species are territorial leads to this hypothesis. Territoriality correlates in various ways with social system evolution (Emlen & Oring 1977; Hixon 1987), and cooperation in territorial defense can lead to individual advantages in social groups or pairs (Brown 1982; Davies & Houston 1984; Fricke 1986; Clifton 1989, 1990; Farabaugh et al. 1992). In other words, males and females benefit by sharing a refuge (a territory) as heterosexual pairs because, for example, the risk of being evicted from the territory by intruders decreases (Wickler & Seibt 1981).

Recent intensive behavioral studies in various species shrimps have supported the predictions of the mate-guarding and/or territorial cooperation hypotheses (e.g., in *Hymenocera picta*, Wickler & Seibt 1981; *Alpheus angulatus*, Mathews 2002a, b, 2003; and *Alpheus heterochelis*, Rahman et al. 2002, 2003).

Another hypothesis about social monogamy (Baeza & Thiel 2007) concerns species symbiotic to other organisms (= host). Baeza & Thiel predicted that monogamy evolved when hosts are small enough to support few individuals and are relatively rare, and when predation risk away from the hosts is high. Under these circumstances, movements among hosts are constrained, and monopolization of hosts is favored in males and females due to their scarcity and because of the host's value in offering protection against predators. Because spatial constraints allow only a few adult symbiotic individuals to cohabit in/on the same host, both adult males and females would maximize their reproductive success by sharing "their" dwelling with a member of the opposite sex. This hypothesis was supported by Baeza's (2008) intensive study on a heterosexual pair of *Pontonia margarita*, a species symbiotic to the pearl oyster.

However, as mentioned before, most of observations for this mating system are anecdotal, and further detailed study is needed to clarify actual conditions of monogamous features of those species.

4.5 *Evolution of the eusocial type*

Hypotheses explaining how eusociality has evolved include Trophallaxis Theory (Roubaud 1916), Parental Manipulation Theory (Michener & Brothers 1974), Superorganism Theory (Reeve & Hölldobler 2007), and Inclusive Fitness Theory (Hamilton 1964a, b), of which the last one is most widely accepted. According to the Inclusive Fitness Theory, eusociality may evolve more easily in species exhibiting haplodiploidy, which facilitates the operation of kin selection. Although eusocial mole rats and termites exhibit diploidy, they display high levels of inbreeding by living as a family in a single burrow, such that colony members share more than 50% of their genes, and therefore the same model is considered to apply to these species and also to eusocial *Zuzalpheus* shrimps, in which all members of a colony share a single sponge.

4.6 *Evolution of the waving display type*

As compared to terrestrial species, courtship in aquatic species may be short and may not involve elaborate visual signaling (display) by the males; in aquatic species, chemical or visual cues are more important stimuli. In species of several genera of semi-terrestrial (= upper intertidal) decapods including *Uca* and other ocypodid crabs, visual signalling for prolonged periods is common, and sounds are often emitted by males to "call" females from their burrows to the surface for mating. Salmon & Atsaides (1968) presented ecological arguments to account for these differences in terms of optimal strategy of distance communications in the terrestrial and aquatic environments. Most aquatic decapods are nocturnally active and cryptic and live in an acoustically noisy environment, and this situation virtually eliminates all but the chemical channel for effective distance communication. On the other hand, visual and acoustic signals are effective in terrestrial species and are well developed in most terrestrial animals such as insects, birds, mammals, and also ocypodid and other terrestrial and semi-terrestrial decapods, probably because of the greater visibility in the terrestrial environment.

Waving displays seen in a variety of semi-terrestrial crabs is a case of convergent evolution (Kitaura et al. 2002). Grapsid crabs of the genus *Metaplax* conduct waving displays like species of the ocypodid crab genera *Uca*, *Macrophthalmus*, *Scopimera*, and *Dottila* (Kitaura et al. 2002). Species of *Metaplax*, unlike other grapsid crabs, which generally live along rocky shores, live in mud flats and burrow into the mud like many ocypodids. Salmon & Atsaides (1968) proposed the following factors as advantageous for the evolution of visual signaling in semi-terrestrial crabs: the substrate, which is flat and relatively free from the vegetational obstructions and other discontinuities; diurnal activity of the crabs; and the feeding proximity to their shelters, which leads crabs to live in aggregations so that social contacts are frequent. Therefore, it is assumed that habitat similarity between *Metaplax* and ocypodid crabs resulted in convergent evolution of these displays.

A recent molecular phylogenetic analysis suggested that even the waving display in *Uca* has multiple origins (Sturmbauer et al. 1996). Indo-west Pacific *Uca* species have simpler reproductive social behaviors, are more marine, and were thought to be ancestral to the behaviorally more complex and more terrestrial American species. It was also thought that the evolution of more complex social and reproductive behavior was associated with the colonization of the higher intertidal zones. However, Sturmbauer et al. (1996) demonstrated that species bearing the set of "derived traits" are phylogenetically ancestral, suggesting an alternative evolutionary scenario: the evolution of reproductive behavioral complexity in fiddler crabs may have arisen multiple times during their evolution, possibly by co-opting of a series of other adaptations for high intertidal living and antipredator escape.

This mating system is quite similar to male-territory-visiting polygamy (Kuwamura 1996) in fish, in which many examples are known in intertidal or shallow species; males have a burrow or a territory, and, when a mature female approaches a male, the male changes the color of part of his body and/or conducts species-specific courtship displays, after which the female enters the burrow or territory of the male and spawns (e.g., Miyano et al. 2006). In these fish species, males are brilliantly colored, as are male *Uca* species.

4.7 *Evolution of the visiting type*

A widely recognized tendency among various kinds of animals is that females live in a particular place and have a narrow home range, whereas males have a comparatively wider home range (Clutton-Brock et al. 1982). This "visiting type" mating system (seen in cryptochirid crabs) probably has evolved as one extremity of this tendency, with females living in a very specialized habitat (inside coral galls).

4.8 *Evolution of the reproductive swarm type*

Surprisingly, the function of the reproductive swarm in pinnotherid crabs is very similar to that of the nuptial flight (mating swarm) in ants (Insecta, Formicidae), and indeed their life history is quite similar. In most species of ants, breeding females and males that mature in their mothers' nest have wings and, during the breeding season, fly away from their nests and form swarms. Mating occurs during this period, and the males die shortly afterward. The surviving females land, and each female digs a burrow for the new nest. As eggs are laid in the burrow, stored sperm, obtained during their single nuptial flight, is used to fertilize all future eggs produced.

In the pinnotherids, crabs first grow in their host animals (vs. ants in their initial burrow). Then the crabs with swimming setae leave the hosts and swarm (vs. ants with wings fly away from their nests and conduct the nuptial flight). Mating occurs during this period (in ants, too), after which the female crabs enter the hosts, whereas the males die just after the mating (vs. the female ants make burrows of their own, with males dying just after the mating). As in the case of the ants, the female crabs reproduce by fertilizing their eggs with sperm from a single mating.

4.9 *Evolution of the neotenous male type*

The miniaturization of male mole crabs in the anomuran genus *Emerita* coupled with neoteny is similar to "dwarf males" (parasitic males, complemental males, miniature males), which are tiny males often attached to females. This condition has evolved in various groups of animals, including thoracican barnacles (Yamaguchi et al. 2007), acrothoracican barnacles (Kolbasov 2002), the oyster *Ostrea puelchanas* (Castro & Lucas 1987; Pascual 1997), epicaridean isopods (Mizoguchi et al. 2002), an echiuran *Bonellia* (Berec et al. 2005), anglerfish (Lophiiformes) (Pietsch 2005), blanket octopus (Tremoctopodidae), argonauts (Argonautidae), football octopus (Ocythoidae), and a deeper water octopus *Haliphron atlanticus* (Alloposidae) (Norman et al. 2002). The evolutionary cause for these phenomena has not been fully studied. The neoteny of male *Emerita* is considered to be one rather radical evolutionary solution to the problem of keeping the male and female together in the harsh and turbulent surf zone environment (Salmon 1983; Subramoniam & Gunamalai 2003).

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APPENDIX 1

Table 1. Species of the short courtship type, in which females molt before copulation (= soft-female mating *sensu* Hartnoll 1969).

DENDROBRANCHIATA

Penaeidae: *Marsupenaeus japonicus* (1), *Melicertus kerathurus* (2), *Melicertus brasiliensis* (3), *Melicertus paulensis* (4), *Farfantepenaeus aztecus* (5), *Fenneropenaeus merguiensis* (6), *Penaeus monodon* (7), *Penaeus semisulcatus* (8), *Trachypenaeus similis* (9), *Xiphopenaeus* sp. (10)*,

Sicyoniidae: *Sicyonia dorsalis* (11), *Sicyonia parri* (12), *Sicyonia laevigata* (13)

PLEOCYEMATA

Caridea

Palaemonidae: *Palaemonetes vulgarus* (14), *Palaemonetes varians* (15), *Palaemonetes pugio* (16), *Palaemon serratus* (17), *Palaemon elegans* (18), *Palaemon squilla* (19)

Alpheidae: *Athanus nitescens* (20), *Alpheus dentipes* (21)

Hippolytidae: *Heptacarpus picta* (22), *Heptacarpus paludicola* (23)

Pandalidae: *Pandalus dana* (24), *Pandalus platyceros* (25), *Pandalus borealis* (26)

Crangonidae: *Crangon crangon* (27), *Crangon vulgaris* (28)

Astacidea

Nephropidae: *Nephrops norvegicus* (29)

Palinuridea

Palinuridae: *Jasus lalandii* (30)*

Anomura

Hippidae: *Emerita asiatica* (31), *Emerita analoga* (32)

Diogenidae: *Calcinus latens* (33), *Calcinus seurati* (34), *Clibanarius tricolor* (35), *Clibanarius antillensis* (36), *Clibanarius zebra* (37), *Paguristes cadenati* (38), *Paguristes tortugae* (39), *Paguristes anomalus* (40), *Paguristes hummi* (41), *Paguristes oculatus* (42)

*Hard-female mating was rarely reported in addition to the soft-female mating. References: (1) Hudinaga (1942 as *Penaeus japonicus*), (2) Heldt (1931 as *Penaeus caramote*), (3) Brisson (1986), (4) de Saint-Brisson (1985), (5)–(6) Aquacop (1977), (7) Primavera (1979), Aquacop (1977), (8) Browdy (1989), (9)–(10) Bauer (1991), (11) Bauer (1992, 1996), (12)–(13) Bauer (1991), (14) Burkenroad (1947), Bauer (1976), (15) Antheunisse et al. (1968), Jefferies (1968), (16) Berg & Sandifer (1984), Bauer & Abdalla (2001), Caskey & Bauer (2005), (17) Nouvel & Nouvel (1937), Forster (1951), Bauer (1976), (18) Hoglund (1943), (19) Hoglund (1943), Bauer (1976), (20) Nouvel & Nouvel (1937), (21) Volz (1938), (22) Bauer (1976), (23) Bauer (1979), (24) Needler (1931), (25) Hoffman (1973), (26) Carlisle (1959), (27) Nouvel (1939), (28) Lloyd & Young (1947), Havinga (1930), Bodekke et al. (1991), (29) Farmer (1974), (30) von Bonde (1936), Silberbauer (1971), McKoy (1979), (31) Menon (1933), Subramoniam (1979), (32) MacGinitie (1938), Efford (1965), (33) Hazlett (1972), (34) Hazlett (1989), (35)–(36) Hazlett (1966), (37) Hazlett (1966, 1989), (38)–(42) Hazlett (1966).

Table 2. Species of the short courtship type, in which females do not molt before copulation (= hard-female mating *sensu* Hartnoll 1969).

DENDROBRANCHIATA

Penaeoidea: *Litopenaeus vannanmei* (1), *Litopenaeus setiferus* (2), *Litopenaeus stylirostris* (3), *Litopenaeus schmitti* (4)

PLEOCYEMATA

Astacidea

Astacidae: *Pacifastacus trowbridgii* (5), *Pacifastacus leniusculus* (6), *Austropotamobius pallipes* (7), *Austropotamobius italicus* (8), *Austropotamobius torrentium* (9), *Astacus astacus* (10), *Astacus leptodactylus* (11)

Parastacidae: *Cherax quadricarinatus* (12)

Cambaridae: *Orconectes nais* (13), *Orconectes limosus* (14), *Faxonella clypeata* (15), *Orconectes rusticus* (16), *Orconectes propinquus* (17), *Orconectes virilis* (18), *Orconectes inermis inermis* (19), *Orconectes pellucidus* (20), *Cambarus blandingi* (21), *Cambaroides japonicus* (22), *Cambarus immunis* (23), *Procambarus alleni* (24), *Procambarus clarkii* (25), *Procambarus hayi* (26)

Palinuridea

Palinuridae: *Panulirus homarus* (27)*, *Panulirus argus* (28)*, *Panulirus longipes cygnus* (29)

Anomura

Diogenidae: *Calcinus verilli* (30), *Calcinus laevimanus* (31), *Calcinus seurati* (32), *Calcinus elegans* (33), *Calcinus hazletti* (34), *Calcinus laurentae* (35)

Coenobitidae: *Birgus latro* (36), *Coenobita perlatus* (37), *Coenobita clypeatus* (38), *Coenobita compressus* (39)

Brachyura

Leucosiidae: *Philyra scabriuscula* (40), *Ebalia tuberosa* (41)

Xanthidae: *Lophopanopeus bellus* (42), *Lophopanopeus diegensis* (43), *Paraxanthias taylori* (44), *Pilumnus hirtellus* (45), *Xantho incisus* (46), *Nanopanope sayi* (47), *Eurypanopeus depressus* (48), *Panopeus herbstii* (49)

Majidae: *Microphrs bicornutus* (50), *Pisa tetraodon* (51), *Pugettia gracilis* (52), *Pugettia producta* (53), *Pleistacantha moseleyi* (54), *Macrocheira kaempferi* (55)

Grapsoidea: *Aratus pisonii* (56), *Cyclograpsus punctatus* (57), *Cyclograpsus integer* (58), *Cyclograpsus insularum* (59), *Cyclograpsus lavauxi* (60), *Eriocheir sinensis* (61), *Eriocheir japonicus* (62), *Goniopsis cruentata* (63), *Grapsus grapsus* (64), *Leptograpsus variegatus* (65), *Hemigrapsus nudus* (66), *Hemigrapsus crenulatus* (67), *Hemigrapsus oregonensis* (68), *Hemigrapsus sexdentatus* (69), *Pachygrapsus crassipes* (70), *Pachygrapsus gracilis* (71), *Pachygrapsus marmoratus* (72), *Gaetice depressus* (73), *Geograpsus lividus* (74), *Geosesarma percaccae* (75), *Plagusia chabrus* (76), *Planes minutus* (77), *Armases ricordi* (78), *Sesarma reticulatum* (79), *Sesarma bidentatum* (80), *Sesarma verleyi* (81), *Sesarma rectum* (82), *Sesarma eumolpe* (83), *Armases cinereum* (84), *Armases angustipes* (85), *Armases curacaoense* (86), *Helice crassa* (87)

Gecarcinidae: *Gecarcoidea natalis* (88), *Gecarcoidea lateralis* (89), *Cardisoma guanhumi* (90), *Cardisoma armatum* (91)

Table 2. continued.

*Soft-female mating was rarely reported in addition to the hard-female mating. References: (1) Yano et al. (1988), Misamore & Browdy (1996), Palacios et al. (2003), (2) Misamore & Browdy (1996), (3) Aquacop (1977), (4) Bueno (1990), (5) Mason (1970a, b), (6) Lowery & Holdich (1988), Stebbing et al. (2003), (7) Ingle & Thomas (1974), Brewis & Bowler (1985), Carral et al. (1994), Villanelli & Gherardi (1998), (8) Galeotti et al. (2007), Rubolini et al. (2006, 2007), (9) Laurent (1988), (10) Cukerzis (1988), (11) Köksal (1988), (12) Barki & Karplus (1999), (13) Pippit (1977), (14) Schone (1968), Holdich & Black (2007), (15) Smith (1953), (16) Berrill & Arsenault (1982), Snedden (1990), Simon & Moore (2007), (17) Tierney & Dunham (1982), (18) Bovbjerg (1953), Rubenstein & Hazlett (1974), Tierney & Dunham (1982), (19)–(20) Bechler (1981), (21) Pearse (1909), (22) Kawai & Saito (2001), (23) Tack (1941), (24) Bovbjerg (1956), Mason (1970a, b), (25) Ameyaw-Akumfi (1981), Corotto et al. (1999), (26) Payne (1972), (27) Berry (1970), Heydon (1969), (28) Sutcliffe (1952, 1953), Kaestner (1970), Lipcius et al. (1983), Lipcius & Hernkind (1987), (29) Chittleborough (1976), Sheard (1949), (30)–(35) Hazlett (1972), (36) Helfman (1977), (37) Page & Willason (1982), (38) Dunham & Gilchrist (1988), (39) Contreras-Garduño et al. (2007), (40) Naidu (1954), (41) Schembri (1983), (42)–(43) Knudsen (1960, 1964), (44)–(46) Bourdon (1962), (47)–(49) Swartz (1976a, b), (50) Hartnoll (1965a), (51) Vernet-Cornubert (1958a), (52) Knudsen (1964), (57) Boolootian et al. (1959), Grigg personal communication in Hartnoll (1969), Knudsen (1964), (54) Berry & Hartnoll (1970), (55) Arakawa (1964), (56) Warner (1967, 1970), (57) Broekhuysen (1941), (58) Hartnoll (1965b), (59)–(60) Brockerhoff & McLay (2005a, b), (61) Hoestlandt (1948), Peters et al. (1933), (62) Kobayashi & Matsuura (1994), (63) Schone & Schone (1963), Warner (1967, 1970), (64) Kramer (1967), Schone & Schone (1963), (65) Brockerhoff & McLay (2005a, b, c), (66) Knudsen (1964), (67) Yaldwyn (1966b), Brockerhoff (2002), (68) Knudsen (1964), (69) Brockerhoff & McLay (2005a, b, c), (70) Bovbjerg (1960), Hiatt (1948), (71) Brockerhoff & McLay (2005a, b), (72) Vernet-Cornubert (1958b), (73) Fukui (1991, 1994), (74) Hartnoll (1969), (75)–(77) Brockerhoff & McLay (2005a, b), (78) Warner (1967 as *Sesarma ricordi*), (79) Seiple & Salmon (1982), (80)–(81) Hartnoll (1969), (82) von Hagen (1967), (83) Hartnoll (1969), (84) Seiple & Salmon (1982 as *Sesarma cinereum*), (85) Hartnoll (1969 as *Sesarma angustipes*), (86) Hartnoll (1969 as *Sesarma curacaoense*), (87) Nye (1977), Beer (1959), Brockerhoff & McLay (2005a, b), (88) Hicks (1985), (89) Abele et al. (1973), Klassen (1975), Bliss et al. (1978), (90) Gifford (1962), Henning (1975), (91) Ameyaw-Akumfi (1987).

Table 3. Penaeid shrimp species in which a sperm plug has been reported.

Penaeidae	
Rimapenaeus similis	(1)
Farfantepenaeus aztecus	(2)
Rimapenaeus constrictus	(3)
Marsupenaeus japonicus	(4)
Metapenaeus joyneri	(5)

References: (1) Bauer & Min (1993 as *Trachypenaeus similis*), (2) Bauer & Min (1993), (3) Costa & Fransozo (2004), (4) Fuseya (2006), (5) Miyake (1982).

Table 4. Species of the precopulatory guarding type, in which males guard females before copulation. S = species in which females molt before copulation. H = species in which females do not molt before copulation. V = species in which both types (S and H) have been reported. ? = molting condition has not been reported.

CARIDEA

Palaemonidae: *Macrobrachium amazonicum* [S](1), *Macrobrachium rosenbergii* [S](2), *Macrobrachium austoraliense* [S](3), *Macrobrachium nipponense* [S](4), *Macrobrachium longipes* [S](5)

Rhynchocinetidae: *Rhynchocinetes typus* [H](6)

ASTACIDEA

Homaridae: *Homarus americanus* [V](7)

ANOMURA

Diogenidae: *Diogenes pugilator* [S](8), *Diogenes nitidimanus* [V](9), *Dardanus punctulatus* [?](10), *Calcinus tibicen* [S?](11)

Paguridae: *Pagurus miamensis* [V](12), *Pagurus pygmaeus* [V](13), *Pagurus bonairensis* [H](14), *Pagurus marshi* [S](15), *Pagurus bernhardus* [S](16), *Pagurus cuanensis* [H](17), *Pagurus anachoretus* [H](18), *Pagurus alatus* [H](19), *Pagurus marshi* [S](20), *Pagurus nigrofascia* [S](21), *Pagurus lanuginosus* [V](22), *Pagurus prideauxi* [H](23), *Pagurus hirsutiuculus* [S](24), *Pagurus maculosus* [?](25), *Pagurus minutus* [V](26), *Pagurus filholi* [V](27), *Pagurus gracilipes* [?](28), *Pagurus middendorffii* [H](29), *Pagurus nigrivittatus* [V](30), *Anapagurus chiroacanthus* [V](31), *Anapagurus breriaculeatus* [V](32), *Pylopagurus* sp. *sensu* Hazlett (1975)[H](33)

Lithodidae: *Paralithodes camtschaticus* [S](34), *Paralithodes brevipes* [S](35), *Lithodes maja* [S](36), *Lithodes santolla* [S](37), *Paralomis granulose* [S](38), *Hapalogaster dentata* [S](39)

BRACHYURA

Leucosiidae: *Philyra laevis* [H](40)

Majidae: *Chionoecetes opilio* [S](41), *Chionoecetes bairdi* [S](42), *Macropodia longirostris* [S](43), *Macropodia rostrata* [S](44)

Hymenosomatidae: *Halicarcinus* sp. [S](45), *Hymenosoma orbiculare* [S](46)

Cancridae: *Cancer gracilis* [S](47), *Cancer irroratus* [S](48), *Cancer magister* [S](49), *Cancer oregonensis* [S](50), *Cancer pagurus* [S](51), *Cancer productus* [S](52), *Cancer borealis* [S](53), *Cancer antennarius* [S](54)

Cheiragonidae: *Telmessus cheiragonus* [S](55), *Erimacrus isenbeckii* [S](56)

Corystidae: *Corystes cassivelaunus* [H](57)

Portunidae: *Callinectes sapidus* [S](58), *Carcinus maenas* [S](59), *Macropipes holsatus* [S](60), *Ovalipes ocellsatus* [S](61), *Portunus pelagicus* [S](62), *Portunus sanguinolentus* [S](63), *Portunus puber* [S](64), *Portunus trituberculatus* [S](65), *Scylla serrata* [S](66)

Xanthidae: *Menippe mercenaria* [S](67)

Table 4. continued.

References: (1) Guest (1979), (2) Bhimachar (1965), Rao (1967), Ra'anan & Sagi (1985), Kuris et al. (1987), (3) Ruello et al. (1973), Lee & Felder (1983), (4) Ogawa et al. (1981), Mashiko (1981), (5) Shokita (1966), (6) Correa et al. (2000, 2003), Hinojosa & Thiel (2003), Correa & Thiel (2003a, b), Díaz & Thiel (2003), Thiel & Hinojosa (2003), Díaz & Thiel (2004), Thiel & Correa (2004), van Son & Thiel (2006), Dennenmoser & Thiel (2007), (7) Herrick (1909), Templeman (1934, 1936), McLeese (1970, 1973), Hughes & Matthiessen (1962), Aiken & Waddy (1980), Waddy & Aiken (1981), Aiken et al. (2004), (8) Bloch (1935), Hazlett (1968), (9) Asakura (1987), (10) Matthews (1956), (11)–(13) Hazlett (1966), (14)–(17) Hazlett (1968), (18) Hazlett (1968), Hazlett (1975), (19) Hazlett (1968), (20) Hazlett (1975), (21)–(22) Wada et al. (2007), (23) Hazlett (1968), (24) MacGinitie (1935), (25) Imazu & Asakura (2006), (26) Imazu & Asakura (2006), Wada et al. (2007), (27) Imafuku (1986), Goshima et al. (1998), Minouchi & Goshima (1998, 2000), Wada et al. (2007), (28) Imazu & Asakura (2006), (29) Wada et al. (1996, 1999), (30) Wada et al. (2007), (31)–(32) Hazlett (1968), (33) Hazlett (1975), (34) Marukawa (1933), Powell & Nickerson (1965a, b), Gray & Powell (1966), Wallace et al. (1949), McMullen (1969), Matsuura & Takeshita (1976), Takeshita & Matsuura (1989), (35) Wada et al. (1997, 2000), Sato et al. (2005a, b), (36) Pike & Williamson (1959), (37)–(38) Lovrich & Vinuesa (1999), (39) Goshima et al. (1995), (40) Schembri (1983), (41) Watson (1972), (42) Paul (1984), Donaldson & Adams (1989), (43)–(44) Hartnoll (1969), (45) Lucas personal communication in Hartnoll (1969), (46) Broekhuysen (1955), (47) Knudsen (1964), (48) Chidchester (1911), Elner & Elner (1980), Elner & Stasko (1978), Haefner Jr. (1976), (49) Bulter (1960), Cleaver (1949), Snow & Nielsen (1966), (50) Knudsen (1964), (51) Edwards (1966), (52) Knudsen (1964), (53) Elner et al. (1985), (54) Knudsen (1960), (55) Kamio et al. (2000, 2002, 2003), (56) Sasaki & Ueda (1992), (57) Hartnoll (1968), (58) Childchester (1911), Churchill (1919), Hay (1905), Gleeson (1980), Ryan (1966), Gleeson et al. (1984), Christofferson (1970), Teytaud (1971), Jivoff & Hines (1998), (59) Broekhuysen (1936, 1937), Cheung (1966), Childchester (1911), Spalding (1942), Veillet (1945), Williamson (1903), Berrill (1982), Berrill & Arsenault (1982), Jensen (1972), (60) Broekhuysen (1936), (61) Childchester (1911), (62) Delsman & de Man (1925), Broekhuysen (1936), Fielder & Eales (1972), (63) George (1963), Ryan (1966, 1967a, b), Christofferson (1970, 1978), (64) Duteutre (1930), (65) Oshima (1938), (66) Hill (1975), (67) Binford (1913), Cheung (1968), Savage (1971), Porter (1960), Wilber (1989).

Table 5. Duration of guarding time in selected species of decapod crustaceans.

Species	Precopulatory guarding time	Female condition when copulating	Postcopulatory guarding time	Refere
ANOMURA				
Lithodidae				
Paralithodes brevipes	9–84 hrs (mean 38.9±24.9 hrs)	Soft	?	(1)
Paralithodes brevipes				
3 males & 3 females	32.1±44.1 hrs	Soft	?	(2)
1 male & 5 females	15.1+20.1 hrs	Soft	?	(3)
Hapalogaster dentata	2–3 days	Soft	?	(4)
BRACHYURA				
Cancridae				
Cancer pagurus	3–21 days	Soft	1–12 days	(5)
Canner irroratus	4.5 days	Soft	5 days	(6)
Carcinus maenas				
1 male & 1 female	2–16 days	Soft	0–1.5 days	(7)
2 or 3 males – 1 female	3–10 days	Soft	1–3.5 days	(8)
Majidae				
Chionoecets bairdi	1–12 days	Various	?	(9)
Chionoecets opilio	7–9 days	Soft	8 hrs	(10)
Cheiragonidae				
Telmessus cheiragonus	11.8 ± 5 SD days	Soft	4.0 ± 6.6 hrs	(11)
Corystidae				
Corystes cassivelaunus	Up to several days	Hard	0	(12)

References: (1) Wada et al. (1997), (2)–(3) Wada et al. (2000), (4) Goshima et al. (1995), (5) Edwa (1966), (6) Elner & Elner (1980), (7)–(8) Berrill & Arsenault (1982), (9) Donaldson & Adams (19 (10) Watson (1972), (11) Kamio et al. (2003), (12) Hartnoll (1968).

Table 6. Brachyuran crab species, in which a sperm plug has been reported.

Cancridae	
Cancer magister	(1)
Cancer irroratus	(2)
Cancer pagurus	(3)
Geryonidae	
Geryon fenneri	(4)
Portunidae	
Callinectes sapidus	(5)
Carcinoplax vestita	(6)
Carcinus maenas	(7)
Macropipus holsatus	(8)
Ovalipes ocellsatus	(9)
Portunus sanguinolentus	(10)
Necora puber	(11)
Liocarcinus depurator	(12)
Cheiragonidae	
Telmessus cheiragonus	(13)
Eriphiidae	
Eriphia smithii	(14)

References: (1) Oh & Hankin (2004), (2) Childchester (1911), (3) Edwards (1966), (4) Hinsch (1988), (5) Childchester (1911), Wenner (1989), Johnson & Oito (1981), Jivoff (1997), (6) Doi & Watanabe (2006), (7) Broekhuysen (1936, 1937), Spalding (1942), (8) Broekhuysen (1936), (9) Childchester (1911), (10) George (1963), (11) González-Gurriarán & Freire (1994), Norman & Jones (1993), (12) Abelló (1989), (13) Kamio et al. (2003), (14) Tomikawa &Watanabe (1990).

Table 7. Species found in large aggregations called a "pod," "heap," or "mound."

Species	Number of crabs in each aggregation	Reference
ANOMURA		
Lithodidae		
Paralithodes camtschaticus	1000 or more	(1)
Lithodes santolla	70 ind·m-2 or more	(2)
BRACHYURA		
Majidae		
Maja squinado	22-50,000 or more	(3)
Chionoecetes bairdi	100,000s	(4)
Hyas lyratus	2,000	(5)
Loxorhynchus grandis	100s	(6)
Libinia emarginata	5,000?	(7)

References: (1) Dew (1990), Dew et al. (1992), Powell & Nickelson (1965a, b), Powell et al. (1973), Zhou & Shirley (1997), Stone et al. (1993), (2) Cardenas et al. (2007), (3) Baal (1953), Le Sueur (1954), Carlisle (1957), Sampedro & González-Gurriarán (2004), (4) Stevens (2003), Stevens et al. (1994), (5) Stevens et al. (1992), (6) Debelius (1999), Hobday & Rumsey (1999), (7) DeGoursey & Auster (1992), Hinsch (1968).

Table 8. Species of the Pontoniinae reported as "found in pair." Species of shrimps with [host animals in brackets] are listed according to the phyla of the host animals (large capitals).

PORIFERA

Apopontonia dubia [*Spongia* sp.](1), *Onycocaris amakusensis* [*Callyspongia elegans*](2), *Onycocaris oligodentata* [purplish sponge](3), *Onycocaris spinosa* [small sponge](4), *Onycocaridella prima* (5)[*Mycale sulcata*], *Onycocaridella monodoa* (= *Onycocaris monodoa*) [*Pavaesperella hidentata*](6), *Onycocaridites anornodactylus* [sponge] (7), *Orthopontonia ornatus* [*Jaspis stellifera*](8), *Periclimenaeus stylirostris* [sponge](9), *Typton dentatus* [*Reniera* sp.](10)

CNIDARIA

Antipatharia

Dasycaris zanzibarica [black coral, sea whips](11)

Actiniaria

Periclimenes brevicarpalis [*Cryptodendron adhaesivum*](12), *Periclimenes colemani* [*Asthenosoma intermedium*](13), *Periclimenes ornatus* [*Entacmaea quadricolor, Heteroactis malu, Parasicyonis actinostroides*](14)

Scleractinia

Anapontonia denticauda [*Galaxea fascicularis*](15), *Coralliocaris superba* [*Acropora tubicinaria* and other 15 spp. of *Acropora*](16), *Jocaste lucina* [*Acropora tubicinaria*](17), *Jocaste japonica* [*Acropora* sp., *Acropora humilis, Acropora variabilis, Acropora tubicinaria, Acropora nasuta*](18), *Ischnopontonia lophos* [*Galaxea fascicularis*](19), *Periclimenes lutescens* (20), *Periclimenes koroensis* [*Fungia actiniformis*](21), *Philarius imperialis* [*Acropora* sp., *Acropora millepora*](22), *Vir euphyllius* [*Euphyllia* spp.](23), *Vir philippinensis* [*Plerogyra sinuosa*](24)

Scleractinia [in network of fissures on surface of faviid coral]

Ctenopontonia cyphastreophila [*Cyphastrea microphthalma*](25)

Scleractinia [forming galls or bilocular cyst in corals]

Paratypton siebenrocki [*Acropora hyacinthus* and other 6 spp. of *Acropora*](26)

MOLLUSCA

Opistobranchia

Periclimenes imperator [*Hexabranchus marginatus*](27)

Bivalvia

Anchistus demani [*Tridacna maxima*](28), *Anchistus miersi* [*Tridacna squamosa, Tridacna maxima*](29), *Anchistus pectinis* [*Pecten* sp., *Pecten albicans*], *Anchistus custos* [*Pinna saccata, Pinna* sp.](31), *Chernocaris plaunae* [*Placuna placenta*](32), *Conchodytes biunguiculatus* [*Pinna bicolor*](33), *Conchodytes meleagrinea* [*Meleagrina margaritifera*](34), *Conchodytes monodactylus* [*Pecten* sp., *Atrina* sp.](35), *Conchodytes nipponensis* [*Pinna* sp., *Pecten laquetus, Atrina japonica*](36), *Conchodytes tridacnae* [*Tridacna maxima*](37), *Bruceonia ardeae* (= *Pontonia ardeae*)[*Chama pacifica*](38), *Pontonia domestica* [*Atrina seminuda, Atrina rigida, Pinna muricata*](39), *Pontonia mexicana* [*Pinna cornea, Pinna rigida, Atrina seminuda*](40), *Ascidonia miserabilis* (= *Pontonia miserabilis*)[*Spondylus americanus*](41), ?*Ascidonia miserabilis* (as ?*Pontonia miserabilis*)[*Spondylus americanus*](42), *Pontonia pinnae* [*Pinna rugosa, Atrina tuberculosa*](43), *Pontonia pinnophylax* [*Pinna rudis, Pinna nobilis*](44), *Pontonia margarita* [*Pinctada mazatlanica*](45), *Platypontonia hyotis* [*Pycnodonta hyotis*](46)

Table 8. continued.

ECHINODERMATA

Crinoidea: Comatulida

Palaemonella pottsi [*Comanthina schlegelii, Comanthus briareus, Stephanometra briareus*](47), *Parapontonia nudirostris* [*Tropiometra afra, Himerometra robustipinna*] (48), *Periclimenes alegrias* [*Lamprometra palmata, Lamprometra klunzingeri, Stephanometra spicata*](49), *Periclimenes attenuatus* [*Comaster multifidus*](50), *Periclimenes novaecaledoninae* [*Lamprometra klunzingeri*](51)

Echinoidea

Tuleariocaris holthuisi [*Astropyge radiata*](52), *Tuleariocaris zanzibarica* [*Astropyge radiata, Diadema setosum*](53)

CHORDATA

Ascidiacea: compound ascidian

Periclimenaeus diplosomatis [*Diplosoma ?rayneri*](54), *Periclimenaeus serrula* [*Leptoclinoides incertus*](55), *Periclimenaeus tridentatus* [unidentified ascidian](56), *Ascidonia flavomaculata* (= *Pontonia flavomaculata*)[*Ascidia mentula, Ascidia mammillata, Ascidia involuta, Ascidia interrupta*](57), *Odontonia sibogae* (= *Pontonia sibogae*)[*Styela whiteleggei, Pyura momus, Rhopalaea crassa*](58)

Ascidiacea: solitary ascidian

Dasella ansoni [*Phallusia depressiuscula*](59)

References: (1) Bruce (1983a), (2)–(4) Fujino & Miyake (1969), (5)–(6) Bruce (1981a), (7) Bruce (1987), (8) Bruce (1982), (9) Bruce & Coombes (1995), (10) Bruce & Coombes (1995), Bruce (1980a), (11) Gosliner et al. (1996), (12) Bruce & Svoboda (1983), (13) Bruce (1975), (14) Bruce & Svoboda (1983), Omori et al. (1994), (15) Bruce (1967), (16)–(17) Bruce (1980b), (18) Bruce (1974, 1980b, 1981c), (19) Bruce (1980b, 1981c), Bruce & Coombes (1995), (20) Bruce (1981c), Bruce & Coombes (1995), (21) Bruce & Svobboda (1984), (22) Bruce & Coombes (1995), (23) Martin (2007), (24) Bruce & Svoboda (1984), (25) Bruce (1979), (26) Bruce (1980a, b), (27) Bruce (1972a, 1976a), Bruce & Svoboda (1983), Strack (1993), (28) Bruce (1972a), (29) Bruce (1972a), Debelius (1999), (30) Bruce (1972a), Fujino & Miyake (1967), (31) Bruce (1972a, 1989), Hipeau-Jacquotte (1973), (32) Bruce (1972a), (33) Bruce (1972a), Hipeau-Jacquotte (1973), (34) Bruce (1973), (35)–(36) Bruce (1972a), (37) Bruce (1974), (38) Bruce (1981b), Fransen (2002), (39) Bruce (1972a), Courtney & Couch (1981), Fransen (2002), (40) Bruce (1972a), Criales (1984), Fransen (2002), (41) Fransen (2002), (42) Criales (1984), (43) Bruce (1972a), (44) Debelius (1999), Richardson et al. (1997), (45) Baeza (2008), (46) Hipeau-Jacquotte (1971), (47) Bruce & Coombes (1995), Bruce (1989), (48) Bruce (1992), (49) Bruce (1986), Bruce & Coombes (1995), (50) Bruce (1992), (51) Bruce & Coombes (1995), (52)–(53) Bruce (1967), (54) Bruce (1980b), (55) Bruce & Coombes (1995), (56) Bruce & Coombes (1995), (57) Monniot (1965), Millar (1971), Fransen (2002), (58) Bruce (1972b), Fransen (2002), (59) Bruce & Coombes (1995).

Table 9. Species of the Alpheidae reported as "found in pair." Species of shrimps with [host animals in brackets] are listed according to the phyla of host animals (large captals) with higher taxa or habitat when known.

PORIFERA

Synalpheus bituberculatus [sponge](1), *Synalpheus hastilicrassus* [sponge](2), *Synalpheus jedanensis* [sponge](3), *Synalpheus streptodactylus* [sponge](4), *Synalpheus theano* [sponge](5), *Synalpheus fossor* [sponge](6), *Synalpheus harpagatrus* [sponge](7), *Synalpheus nilandensis* [sponge](8), *Synalpheus tumidomanus* [sponge](9), *Zuzalpheus androsi* [*Hyattella intestinalis*](10), *Synalpheus couitere* [sponge](11), *Zuzalpheus bousfield* [*Hymeniacidon* spp.](12), *Zuzalpheus carpenteri* [*Aeglas* spp.](13), *Zuzalpheus goodei* [*Xestospongia wiedenmayeri, Pachypellina podatypa*](14), *Zuzalpheus paraneptunus* [*Hyattella intestinalis, Oceanapia* sp.](15), *Zuzalpheus ruetzleri* [*Hymeniacidon* cf. *caerulea*](16), *Zuzalpheus sanctithomae* [*Hymeniacidon caerulea* etc.](17), *Alpheus parvirostris* [sponge](18), *Alpheus alcyone* [sponge](19), *Alpheus* aff. *eulimene**[sponge](20), *Alpheus paralcyone* [sponge](21), *Alpheus spongiarum* [sponge] (22)

CNIDARIA

Scyphozoa: Coronatae

Synalpheus modestus (23), *Synalpheus* aff. *modestus sensu* Nomura & Asakura (1998) [*Stephanoscyphus racemosus*](24)

Anthozoa: Gorgonacea

Synalpheus iphinoe [*Solenocaulon* sp.](25), *Synalpheus trispinosus* [gorgonacean](26)

Anthozoa: Alcyonacea

Synalpheus neomeris [*Dendronephthya*](27)

Anthozoa: Actiniaria

Alpheus armatus [*Bartholomea annulata*](28), *Alpheus immaculatus* [*Bartholomea annulata*](29), *Alpheus polystuctus* [*Bartholomea annulata*](30), *Alpheus roquensis* [*Heteractis lucida*](31)

Anthozoa: Scleractinia

Alpheus lottini [reef coral, *Pocillopora*](32), *Alpheus ventrosus* (33), *Synalpheus charon* [*Pocillopora*, reef coral](34), *Synalpheus scaphoceris* [*Madracis decactis*](35), *Racilius compressus* [*Galaxea fascicularis*](36)

Anthozoa: Scleractinia (in fissures on massive coral)

Alpheus deuteropus [*Asteropora, Porites, Acropora, Montipora, Pavona*](37)

Anthozoa: Scleractinia (coral borer, in dead coral head)

Alpheus saxidomus (38), *Alpheus simus* (39), *Alpheus schmitti* (40), *Alpheus idiocheles* (41), *Alpheus colluminaus* (42)

ANNELIDA

Polychaeta

Alpheus sulcatus [*Eurythoe complanata*](43)

CRUSTACEA

Shell used by hermit crab

Aretopsis amabilis [*Dardanus sanguinolentus, Dardanus megistos, Dardanus guttatus, Dardanus lagopodes, Clibanarius eurysternus, Calcinus latens*](44), *Aretopsis manazuruensis* [*Aniculus miyakei*](45)

In burrow of thalassinidean shrimps

Betaeus longidactylus [*Upogebia pugettensis*](46), *Betaeus harrimani* [*Upogebia pugettensis*](47), *Betaeus ensenadensis* [*Upogebia pugettensis*] (48)

In burrow of mantis shrimp

Athanas squillophilus [*Oratosquilla oratoria*](49)

Table 9. continued.

ECHINODERMATA

Crinoidea: Comatulida

Synalpheus carinatus [crinoids](50), *Synalpheus comatularum* [*Comanthus timorensis*](51), *Synalpheus demani* [criniod](52), *Synalpheus stimpsoni* [*Comaster multibrachiatus, Comaster multifidus, Comaster gracilis, Comaster alternans*](53), *Synalpheus odontophorus* [crinoid](54)

Echinoidea

Athanas indicus [*Echinometra mathaei*](55)

ECHIURA

Athanopsis rubricinctuta [*Ochetostoma erythrogrammon*](56), *Betaeus longidactylus* [*Urechis* sp.](57)

"PISCES" [in burrow of goby fish]

Alpheus bellulus [*Tomiyamichthys* spp, *Amblyeleotris* spp.](58), *Alpheus purpurilenticularis* [*Amblyeleotris steinitzi*], (59) *Alpheus rapacida* [*Myersina* spp., *Vanderhorstia* spp., *Mahidoria* spp.], (60) *Alpheus rapax* [*Cryptocentrus* spp.](61)

ALGAE TUBE

Alpheus frontalis [tube of filamentous blue-green algae such as *Microcoelus* spp.](62), *Alpheus bucephalus* [tube of pure algae or algae with sponges and other material](63), *Alpheus brevipes* [tube of red filamentous alga](64), *Alpheus clypeatus* [tube of red filamentous alga *Acrochaetium*](65), *Alpheus pachychirus* [tube of algae](66)

FREE LIVING [crack of rock, under rubble, around large algae, burrow in mudflat]

Alpheopsis chilensis (67), *Alpheus normanni* (68), *Alpheus euphrosyne richardsoni* (69), *Alpheus strenuus cremnus* (70), *Alpheus diadema* (71), *Alpheus architectus* (72), *Alpheus amirantei* (73), *Alpheus bisincisus* (74), *Alpheus brevicristatus* (75) (might be commensal with goby?), *Alpheus edwardsii* (76), *Alpheus* aff. *gracilipes** (77), *Alpheus heeia* (78), *Alpheus* aff. *heeia**(79), *Alpheus* aff. *leviusculus* sp. 1*(80), *Alpheus* aff. *leviusculus* sp. 2*(81), *Alpheus lobidens* (82), *Alpheus* aff. *lobidens* sp. 1*(83), *Alpheus* aff. *lobidens* sp. 2*(84), *Alpheus* aff. *lobidens* sp. 3*(85), *Alpheus malleodigitus* (86), *Alpheus miersi* (87), *Alpheus obesomanus* (88), *Alpheus pacificus* (89), *Alpheus* aff. *pacificus* (90), *Alpheus paradentipes* (91), *Alpheus parvirostris* (92), *Alpheus polyxo* (93), *Alpheus serenei* (94), *Alpheus suluensis* (95), *Alpheus tenuipes* (96), *Alpheus angulatus* (97), *Alpheus armillatus* (98), *Alpheus heterochaelis* (99), *Alpheus floridanus* (100), *Alpheus inca* (101), *Metalpheus paragracilis* (102)

Table 9. continued.

**sensu* Nomura & Asakura (1998). References: (1) Banner & Banner (1975), Nomura & Asakura (1998), (2)–(5) Nomura & Asakura (1998), (6) Didderen et al. (2006), (7) Banner & Banner (1975), (8)–(9) Nomura & Asakura (1998), (10) Rios & Duffy (2007), (11) Nomura & Asakura (1998), (12) Rios & Duffy (2007), (13) Macdonald III et al. (2006), Rios & Duffy (2007), (14)–(17) Rios & Duffy (2007), (18) Banner & Banner (1982), (19)–(27) Nomura & Asakura (1998), (28) Knowlton (1980), Knowlton & Keller (1982, 1983, 1985), Criales (1984), (29)–(31) Knowlton (1980), Knowlton & Keller (1982, 1983, 1985), (32) Vannini (1985), Nomura & Asakura (1998), Abele & Patton (1976), Tsuchiya & Yonaha (1992), (33) Patton (1966), (34) Patton (1966), Nomura & Asakura (1998), (35) Dardeau (1984, 1986), (36) Bruce (1972c), (37) Banner & Banner (1983), (38) Fischer & Meyer (1985), Fischer (1980), (39)–(40) Werding (1990), (41) Kropp (1987), Nomura & Asakura (1998), (42) Banner & Banner (1982), Nomura & Asakura (1998), (43) Banner & Banner (1982), (44) Bruce (1969), Banner & Banner (1973), Kamezaki & Kamezaki (1986), (45) Suzuki (1971), (46)–(48) MacGinitie (1937), (49) Hayashi (2002), (50) Bruce (1989), (51) Banner & Banner (1975), (52) Bruce (1989), Nomura & Asakura (1998), (53) Nomura & Asakura (1998), Van den Spiegel et al. (1998), (54) Nomura & Asakura (1998), (55) Gherardi (1991), (56) Anker et al. (2005), Berggren (1991), (57) MacGinitie (1935), (58) Miya & Miyake (1969), Nomura & Asakura (1998), Nomura (2003), (59) Macnae & Kalk (1962), Karplus (1979), Nomura (2003), (61) Macnae & Kalk (1962), Nomura (2003), (62) Fishelson (1966), Banner & Banner (1982), (63) Banner & Banner (1982), Nomura & Asakura (1998), (64)–(65) Banner & Banner (1982), (66) Cowles (1913), Banner & Banner (1982), (67) Boltana & Thiel (2001), (68) Nolan & Salmon (1970), (69)–(70) Banner & Banner (1982), (71)–(75) Nomura & Asakura (1998), (76) Nomura & Asakura (1998), Jeng (1994), (77)–(96) Nomura & Asakura (1998), (97) Mathews (2002a, b, 2003, 2006, 2007), Mathews et al. (2002), (98) Mathews et al. (2002), (99) Nolan & Salmon (1970), Schein (1975), Obermeier & Schmitz (2003a, b), Rahman et al. (2001, 2002, 2003, 2005), Schmitz & Herberholz (1998), Dworschak & Ott (1993), (100) Dworschak & Ott (1993), (101) Boltana & Thiel (2001), (102) Nomura & Asakura (1998).

Table 10. Species of shrimps other than Pontoniinae and Alpheidae reported as "found in pair." Species of shrimps with [host animals in brackets] are listed according to the phyla of host animals (large capitals) with higher taxa or habitat when known.

SPONGICOLIDAE

PORIFERA

Spongicola japonica [*Euplectella oweni*](1), *Spongicola venusta* [*Euplectella aspergillum*](2), *Spongicola levigata* [*Euplectella oweni*?](3), *Spongiocaris semiteres* [hexactinellid sponge], (4) *Spongicoloides iheyaensis* [Euplectellidae & Hyalonematidae](5), *Globospongicola spinulatus* [hexactinellid sponge *Semperella* sp.](6)

FREE LIVING

Microprosthema validum (7)

STENOPODIDAE

FREE LIVING

Stenopus hispidus (8), *Stenopus scutellatus* (9), *Stenopus tenuirostris* (10), *Stenopus zanzibaricus* (11)

HIPPOLIYTIDAE

FREE LIVING

Lysmata debelius (12), *Lysmata grabhami* (13)

CNIDARIA

Actiniaria, Scleractinia

Thor amboinensis (14)

GNATHOPHYLLIDAE

ECHINODERMATA

Holothuroidea

Pycnocaris chagoae [*Holothuria cinerascens*](15)

Asteroidea

Hymenocera picta [prey on sea star](16)

References: (1) Saito et al. (2001), (2) Miyake (1982), Hayashi & Ogawa (1987), (3) Hayashi & Ogawa (1987), (4) Bruce & Baba (1973), (5) Saito et al. (2006), (6) Komai & Saito (2006), (7) Davie (2002), (8) Johnson (1969, 1977), Castro & Jory (1983), Zhang et al. (1998), Yaldwyn (1964, 1966a), (9) Debelius (1999), (10) Bruce (1976b), (11) Gosliner et al. (1996), (12) Rufino & Jones (2001), Gosliner et al. (1996), (13) Wirtz (1997), Debelius (1999), (14) Stanton (1977), (15) Bruce (1983b), (16) Seibt & Wickler (1972, 1979, 1981), Wickler & Seibt (1970, 1972, 1981), Seibt (1973a, b, 1974, 1980), Wasserthal & Seibt (1976), Wickler (1973), Kraul & Nelson (1986), Fiedler (2002).

Table 11. Species of Thalassinidea and Anomura reported as "found in pair." Species with [host animals or habitat in brackets] are listed according to the phyla of host animals (in capitals) with higher taxa or habitat where known.

THALASSINIDEA
Axiidae
FREE LIVING
Axiopsis serratifrons [in burrow in sediments with a higher content of coral rubble](1)
Laomediidae
FREE LIVING
Axianassa australis [in burrow in mud flat](2)
Callianassidae
"PISCES"
Neotrypaea affinis [burrow of blind goby *Typhlogobius californiensis*](3)
FREE LIVING
Neotrypaea gigas [burrow in mud](4)
Upogebiidae
PORIFERA
Upogebia synagelas [*Agelas sceptrum*](5)
CNIDARIA: Scleractinia
Pomatogebia rugosa [inside live colony of *Porites lobata*](6), *Pomatogebia operculata* [inside live coral colony](7), *Upogebia corallifora* [inside dead coral colony](8)
FREE LIVING
Upogebia pugettensis [U- or Y-shaped burrow in mudflat](9), *Upogebia affinis* [burrow in mud](10)

ANOMURA
Porcellanidae
CNIDARIA
Gorgonacea
Aliaporcellana telestophila [*Solenocaulon*](11)
Pennatulacea
Porcellanella haigae [*Cavernularia* sp.](12)
Actiniaria
Neopetrolisthes oshimai [*Soichactis* spp.](13), *Neopetrolisthes maculatus* [*Stychodactyla*](14), *Neopetrolisthes alobatus, Neopetrolisthes spinatus* [*Heteroactis malu*](15)
ANNELIDA
Polychaeta [in tube of large polychaete species]
Polyonyx macroheles [*Chaetopterus variopedatus*](16), *Polyonyx quadriungulatus* [*Chaetopterus variopedatus*](17), *Polyonyx transversus* [*Chaetopterus* sp.](18), *Polyonyx vermicola* [*Sasekumaria selangora*](19), *Polyonyx bella* [*Chaetopterus variopedatus*](20), *Polyonyx gibbesi* [*Chaetopterus variopedatus*](21), *Polyonyx utinomii* [*Chaetopterus* sp.](22), *Heteropolyonyx biforma* [*Chaetopterus* sp.](23), *Polyonyx biunguiculatus* [*Chaetopterus* sp.](24)
CRUSTACEA [in shell being used by hermit crab]
Porcellana cancrisocialis [*Petrochirus californiensis, Dardanus sinistripes, Aniculus elegans, Paguristes digueti*](25), *Porcellana paguriconviva* [*Petrochirus californiensis, Dardanus sinistripes, Aniculus elegans, Paguristes digueti*](26)
ECHINODERMATA
Echinoidea
Clastotoechus vanderhorsti [*Echinometra lucunter*](27), *Clastotoechus vanderhorsti* [*Echinometra lucunter*](28)
Asteroida
Minyocerus angustus [*Luidia, Astropecten, Tethyaster*](29)

Table 11. continued.

FREE LIVING
Pachycheles rudis [underside of stone, basal portion of large algae](30)
Galatheidae
ECHINODERMATA
Crinoidea
Galathea inflata [*Comanthus parvicirrus, Comaster schlehelii*](31)

References: (1) Dworschak & Ott (1993), (2) Coelho & Rodrigues (1999), Coelho (2001), (3)–(4) Meinkoth (1981), (5) Williams (1987), (6) Fonseca & Cortés (1998), (7) Kleeman (1984), Williams & Ngoc-Ho (1990), Coelho & Rodrigues (1999), Coelho (2001), (8) Williams & Scott (1989), (9) Jensen (1995), (10) Meinkoth (1981), (11) Ng & Goh (1996), (12) Nakasone & Miyake (1972), (13) Seibt & Wickler (1971), (14) Debelius (1984), (15) Osawa & Fujita (2001), (16) Gray (1961), (17) Kudenov & Haig (1974), (18) McNeill & Ward (1930), (19) Ng & Sasekumar (1993), (20) Hsueh & Huang (1998), (21) Rickner (1975), Williams (1984), Grove & Woodin (1996), (22)–(23) Osawa (2001), (24) Macnae & Kalk (1962), (25) Glassell (1936), Parente & Hendrickx (2000), Williams & McDermott (2004), (26) Parente & Hendrickx (2000), Williams & McDermott (2004), (27) Werding (1983), (28) Werding (1983), Schoppe (1991), (29) Werding (1983), Gore & Shoup (1968), (30) Meinkoth (1981), (31) Fujita & Baba (1999).

Table 12. Species of brachyuran crabs reported as "found in pair." Species of crabs with [host animals in brackets] are listed within family or superfamily according to the phyla of host animals (in capitals) with higher taxa or habitat where known.

XANTHIDAE
CNIDARIA: Scleractinia
Cymo andreossyi [*Pocillopora*](1)

TRAPEZIIDAE
CNIDARIA
Scleractinia: *Pocillopora*
Trapezia areolata (2), *Trapezia corallina* (3), *Trapezia cymodoce* (4), *Trapezia dentata* (5), *Trapezia digitalis* (6), *Trapezia ferruginea* (7), *Trapezia flavomaculata* (8), *Trapezia guttata* (10), *Trapezia intermedia* (11), *Trapezia rufopunctata* (12), *Trapezia tigrina* (13), *Trapezia wardi* (14)
Antipatharia
Quadrella maculosa [*Antipathes*] (15), *Quadrella* spp. [*Cirrhipathes abies, Antipathes* spp.](16), *Quadrella reticulata* [*Antipathes* sp.](17)

TETRALIIDAE
CNIDARIA
Scleractinia: Acropora
Tetralia fulva (18), *Tetralia nigrolineata* (19), *Tetralia rubridactyla* (20)

CARPILIIDAE
FREE LIVING
Carpilius corallinus (21)

Table 12. continued.

PINNOTHERIDAE
ANNELIDA
Polychaeta [in tube of large polychaetes]
Pinnixa tubicola [terebellids and chaetopterids, *Eupolymnia heterobranchia, Amphitrite* sp., *Eupolymnia heterobranchia, Neoamphitrite rohusta, Thelepus crispus, Chaetopterus variopedatus*](22), *Pinnixa chaetopterana* [*Chaetopterida* spp. *Chaetopterus variopedatus, Amphitrite ornata*](23), *Pinnixa transversalis* [*Chaetopterus variopedatus*](24)
MOLLUSCA
Bivalvia
Pinnixa faba [*Tresus capax, Tresus nuttalli*](25), *Pinnixa littoralis* [*Tresus capax*](26)
Gastropoda [inside mantle cavity]
Orthotheres turboe [*Turbo* sp.](27), *Orthotheres haliotidis* [*Haliotis asinina, Haliotis squamata*](28)
SIPUNCULA & ECHIURA
Mortensenella forceps [*Ochetostoma erythrogrammon*](29)
ECHINODERMATA
Echinoidea
Dissodactylus mellitae [*Mellita quinguiesperforata, Echinarachnius parma, Encope michelini*](30), *Dissodactylus crinitichelis* [*Mellita sexiesperforata*](31)
Holothuroidea
Holotheres halingi (= *Pinnotheres halingi*) [*Holothuria scarba*](32), *Holotheres semperi* (= *Pinnotheres semperi*)[*Holothuria fursocinerea, Holothuria scabra*](33)
BURROWS OF OTHER ANIMALS
Scleroplax granulata [burrow of echiuroid *Urechis caupo,* mud shrimps *Neotrypaea californiensis, Neotrypaea gigas, Upogebia pugettensis, Upogebia macginiteorum*](34)

GRAPSOIDEA
"REPTILIA": Testudines
Planes minutus [loggerhead sea turtle *Caretta caretta*, inanimate flotsam](35)
ECHINODERMATA
Echinoidea
Percnon gibbesi [*Diadema antillarum*](36)

References: (1) Castro (1976), Guinot (1978), Miyake (1983), (2) Miyake (1983), Tsuchiya & Yonaha (1992), Tsuchiya & Taira (1999), (3) Patton (1966), Miyake (1983), Huber (1985), Gotelli et al. (1985), Castro (1996), (4) Patton (1966), Tsuchiya & Yonaha (1992), Tsuchiya & Taira (1999), (5) Patton (1966), Huber (1985), (6) Patton (1966), Preston (1973), Huber (1985, 1987), Huber & Coles (1986), Tsuchiya & Taira (1999), (7) Patton (1966), Preston (1973), Abele & Patton (1976), Finney & Abele (1981), Miyake (1983), Adams et al. (1985), Huber & Coles (1986), Castro (1978, 1996), Tsuchiya & Taira (1999), (8) Patton (1966), Preston (1973), Miyake (1983), (9) Gotelli et al. (1985), Castro (1996), (10) Miyake (1983), Tsuchiya & Yonaha (1992), Tsuchiya & Taira (1999), (11) Preston (1973), Huber & Coles (1986), Huber (1987), (12)–(13) Huber (1985), (14) Preston (1973), Miyake (1983), Huber & Coles (1986), (15) Shih & Mok (1996), (16) Tazioli et al. (2007), (17) Castro (1999), (18) Vytopil & Willis (2001), (19)–(20) Sin (1999), (21) Laughlin (1982), (22) Hart (1982), Wells (1928), Garth & Abbott (1980), Zmarzly (1992), (23) Gray (1961), Grove & Woodin (1996), Grove et al. (2000), McDermott (2005), (24) Baeza (1999), (25) Pearce (1965, 1966a), Hart (1982), Zmarzly (1992), (26) Pearce (1966a), Zmarzly (1992), (27) Sakai (1969), (28) Geiger & Martin (1999), (29) Anker et al. (2005), (30) Bell & Stancyk (1983), Bell (1984), George & Boone (2003), (31) Telford (1978), (32) Hamel et al. (1999), (33) Ng & Manning (2003), (34) Anker et al. (2005), Campos (2006), (35) Dellinger et al. (1997), Frick et al. (2000, 2004, 2006), Carranza et al. (2003), (36) Hayes et al. (1998).

Table 13. Eusocial species. All species found inhabiting cavity of sponge.

Alpheidae	
Zuzalpheus rathbunae [sponge]	(1)
Zuzalpheus elizabethae (= *Synalpheus "rathbunae* A")[*Lissodendoryx*]	(2)
Zuzalpheus "paraneptunus small" [sponge]	(3)
Zuzalpheus regalis [*Xestospongia* etc.]	(4)
Zuzalpheus filidigitus [*Xestospongia* etc.]	(5)
Zuzalpheus chacei [*Aeglas, Hyattella* etc.]	(6)
Zuzalpheus elizabethae [*Lissodendoryx* etc.]	(7)
Synalpheus neptunus neptunus [sponge]	(8)

References: (1) Duffy (2003), (2) Duffy (1996c, 2003), Morrison et al. (2004), (3) Duffy et al. (2000), Duffy (2003), (4) Duffy (1996a, b), Duffy et al. (2002), Rios & Duffy (2007), (5) Duffy (1996c), Duffy & Macdonald (1999), Rios & Duffy (2007), (6) Chace (1972), Duffy (1998), Rios & Duffy (2007),(7) Duffy (1996c), Morrison et al. (2004), Rios & Duffy (2007),(8) Didderen et al. (2006).

Table 14. Species found in small groups. Species with [host animals] are listed, according to the phyla of host animals (large capitals) with higher taxa or habitat. One group consists of fewer than 20 individuals on a single host (species, host, number of individuals found, and reference).

CARIDEA	
CNIDARIA	
Scyphozoa	
Periclimenes holthuisi [*Cassiopei*]	Max. 8 (various sizes and sexes)(1)
Actiniaria	
Periclimenes holthuisi [sea anemone]	Several individuals (2)
Periclimenes tenuipes [*Megalactis, Cryptodendron*]	Max. 6 (various sizes and sexes)(3)
Periclimenes longicarpus [*Entacmaea*]	Max. 7 (various sizes and sexes)(4)
Periclimenes anthophilus [*Condylactis gigantea*]	Up to 9 (5)
Scleractinia	
Thor marguitae[*Porites andrewsi*]	10 (2 ♂, 5 ov. ♀, 2 non-ov. ♀, 1 juv.)(6)
Jocaste japonica [*Acropora divaricata*]	15 (5 ♂, 6 ov. ♀, 3 non-ov. ♀, 1 juv.)(7)
Periclimenes holthuisi [corals]	Several individuals (8)
Periclimenes pederosoni [*Antipathe*]	7 (2 ♂, 3 ov. ♀, 2 non-ov. ♀)(9)
Anapontonia denticauda [*Galaxea*]	5 (1 ♂, 1 ♀, 3 juv.)(10)
ECHINODERMATA	
Echinoidea	
Gnathophylloides mineri [*Tripneustes ventricosus*]	Up to 13, with females greatly outnumbering males (11)
GALATHEOIDEA	
CNIDARIA	
Scleractinia	
Lissoporcellana spinuligera [*Solenocaulon*]	7 (1 ♂, 3 ov. ♀, 3 juv.)(12)
CRUSTACEA: shell used by hermit crab	
Porcellana sayana [*Dardanus, Petrochirus, Paguristes*]	Max. 11 (several ♂, several ov. ♀)(13)

Table 14. continued.

BRACHYURA	
MOLLUSCA	
Bivalvia	
Pinnixa faba [*Tresus*]	More than 3 (1 ♂, 1 ♀, few juv.)(14)

References: (1) Bruce & Svoboda (1983), (2) Coleman (1991), (3)–(4) Bruce & Svoboda (1983), (5) Nizinski (1989), (6) Bruce (1978), (7) Bruce (1981b), (8) Coleman (1991), (9) Spotte (1996), (10) Bruce (1967), (11) Patton et al. (1985), (12) Ng & Goh (1996), (13) Gore (1970), (14) Haig & Abbott (1980).

Table 15. Species found in large groups. Species with [host animals] are listed, according to the phyla of host animals (large capitals) with higher taxa or habitat. One group consists of more than 20 individuals on a single host.

CARIDEA	
PORIFERA	
Synalpheus dorae [*Reiniere*]	136 (all ♂)(1)
Synalpheus streptodactylus [sponge]	105 (68 ♂, 37 ov. ♀, several non- ov. ♀)(2)
Synalpheus crosnieri [sponge]	147 (144 ♂, 3 ♀)(3)
Synalpheus paradoxus [sponge]	112 (110 ♂, 2 ♀), 132 (130 ♂, 2 ♀)(4)
Zuzalpheus brooksi [sponge]	10s to 1000s (5)
Zuzalpheus idios [*Hymeniacidon* etc.]	Several 10s (including many ov. ♀ & juv.)(6)
Zuzalpheus pectiniger [*Spheciospongia*]	Few 100s (7)
CNIDARIA	
Scyphozoa	
Latreutes anoplonyx [*Nemopilema nomurai*]	More than 100 (8)
Scleractinia	
Coralliocaris macrophthalma [*Acropora hyacinthus*]	24 (including 16 ♀)(9)
Fennera chacei [*Pocillopora*]	Max. 49 (all adults) (10)
Periclimenes toloensis [*Lytocarpus philippinensis*]	110 (including 43 ov. ♀)(11)
ECHINODERMATA	
Periclimenes affinis [*Heterometra magnipinna*]	64 (including 16 ov. ♀)(12)
Periclimenes meyeri [*Nemaster grandis*]	Max. 25 (various sizes and sexes)(13)

References: (1) Bruce (1988), (2) Banner & Banner (1975, 1982), (3) Banner & Banner (1983), (4) Banner & Banner (1982), (5)–(7) Rios & Duffy (2007), (8) Hayashi et al. (2003), (9) Bruce (1977), (10) Gotelli et al. (1985), (11)–(12) Bruce & Coombes (1995), (13) Criales (1984).

Table 16. Selected species of pinnotherid crabs (and their hosts) in which life history has been studied.

MOLLUSCA	
Bivalvia	
Fabia subquadrata [*Modiohis niodiolus*]	(1)
Tumidotheres maculatus (= *Pinnotheres maculatus*) [*Mytilus edulis, Argopecten irradians* etc.]	(2)
Pinnotheres ostreum [*Crassostrea virginica, Mytilus edulis*]	(3)
Pinnotheres pisum [*Mytilus edulis* etc.]	(4)
Pinnotheres taichungae [*Laternula marilina*]	(5)
Pinnotheres bidentatus [*Laternula marilina*]	(6)
ANNELIDA: Polychaeta	
Tritodynamia horvathi [in tube of *Loimia verrucosa*]	(7)

References: (1) Pearce (1962, 1966b), (2) Pearce (1964), Williams (1984), (3) Christensen & Mc-Dermott (1958), (4) Atkins (1926), Christensen (1958), Hartnoll (1972), Williams (1984), (5) Hsueh (2003), (6) Hsueh (2001a, b), (7) Matsuo (1998, 1999), Takahashi et al. (1999).

Table 17. Species in which neotenous males have been reported.

ANOMURA	
Hippidae	
Emerita brasiliensis	(1)
Emerita asiatica	(2)
Emerita emeritus	(3)
Emerita holthuisi	(4)
Emerita talpoida	(5)
Emerita rathbunae	(6)

References: (1) Delgado & Defeo (2006, 2008), (2) Subramoniam (1981), (3)–(4) Subramoniam & Gunamalai (2003), (5)–(6) Efford (1967).

APPENDIX 2:

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