

Chapter 4

SYMBIOSIS OF SEA ANEMONES AND HERMIT CRABS IN TEMPERATE SEAS

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ABSTRACT

Symbiosis, according to its initial meaning, refers to the biological interaction between two organisms living in close association. However, this definition is rather controversial, with the term being often used generically, since the outcome can vary across a continuum from negative to positive interactions. Symbiosis is a widespread phenomenon in temperate marine communities, and the association between sea anemones and hermit crabs belongs to the most common cases, being a familiar example of mutualism. In these latter specific cases of interactions gastropod shells are involved as prerequisite, since they provide both refuge for hermit crabs and substratum for the settlement of sea anemones; thus, shell resource availability is crucial for the establishment of this particular type of symbiosis. Within this context the present study aims to integrate the results of various studies to provide a general review about the symbiotic interactions of sea anemones and hermit crabs in temperate seas, addressing the following issues: (1) clarify the relevant terminology, which is differently interpreted by various authors; (2) provide a general description of the sea anemone - hermit crab association, as most studies examine separately the species involved and not the symbiosis as a whole; (3) assess the diversity and distribution of sea anemone - hermit crab associations in temperate seas, also incorporating gastropod shells and their availability, which although crucial, has been only little investigated; (4) address the behavioural patterns of both symbionts for the establishment of the symbiosis, including as well the behavioural plasticity of hermit crab related to shell resource utilization, and (5) report relevant information about co-evolution of the participant species, referring to the existing hypotheses on the evolution of the symbiosis, underlining its importance.

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Symbiosis: Meaning and Relevant Terminology Considering the Specific Case of Sea Anemones - Hermit Crabs

In nature very few species, if any, live separated; almost all species depend on other to gain vital resources, such as habitat, food and protection. This dependency among species has been very early recognized from biologists under the concepts of biotic interactions and symbiosis. The term symbiosis was coined originally by Anton de Bary in 1879 in his study about lichens, to mean any association between different species, with the implication that the organisms are in persistent contact, but that the relationship does not need to be advantageous to all participants (see Douglas, 2010). Thus, according to its initial meaning, symbiosis refers to the biotic interaction between two organisms living in close association; the latter phrase differentiates symbionts from simply interacting species. However, this definition is rather controversial, since the outcome of interactions can vary across a continuum from negative to positive results, and among participant species. Moreover, the term has often been used generically and its meaning has frequently been deviated from the original definition. The subsequent proposition of additional definitions and the lack of agreement for a specific one within the scientific community have further complicated the strength of this term; similar problems can be found for many other, widely applicable, terms in the field of marine ecology (see Dauvin et al., 2008).

After the first definition of symbiosis, very little awareness about the term, as defined subject, existed between biologists and up to 1950s; the phenomenon has been encountered as scattered among organisms and very little research was in progress, almost exclusively covering terrestrial associations (see Smith, 2001 for a thorough review of symbiosis research trends over the last century). Thereafter, and especially after 1970s, symbiosis research advanced incorporating many topics and including major marine taxa, such as sponges, corals and sea anemones. Symbiotic procedures are thought to be less diverse and widespread in aquatic domain (Smith, 2001), despite the recognition of their prominent role in particular marine ecosystems, such as coral reefs in tropics, and shallow benthic communities in temperate seas (Grutter and Irving, 2007).

Considering all the above the first task of this study is to thoroughly revise and clarify the relevant terminology, which is differently interpreted by various authors, focusing on the marine domain and the specific case of interactions between closely associated sea anemones and hermit crabs.

As Smith (2001) clearly pointed “there is still no clear and universally agreed definition of symbiosis, even though it is 130 years after de Bary devised the term”. Currently symbiosis is used under a wide range (Martin and Britayev, 1998) referring to all cases in which two species live in close association (Henry, 1966), although many researchers attempted to restrict the term to associations where partners mutually benefit (Rhode, 1981) or alternatively and more sophisticated defined, symbiosis refers to intimate mutualism involving direct supply of nutrients or other resources between physiologically integrated species (Grutter and Irving, 2007). Proving benefit existence is highly problematic since, at least in some associations, the partner’s cost surpasses any hypothetical benefit. Douglas (1994) rejected mutual gains and suggested the acquisition of a novel metabolic capability from one partner as the basis of symbiosis. However, this concept is complex as the gain is strictly connected with metabolism, although practically applicable to some specific cases of

interactions between bacteria and plants or metazoans (e.g. symbiotic zooxanthellae and corals or sea anemones). This fact, together with the largely unknown nature of species interactions, hinders the general acceptance of the latter idea and enhances the generic sense of the term.

As mentioned earlier, symbiosis constitutes a rather loose term up to date, which includes a wide range of interactions that cover the specific cases of: (i) parasitism, i.e. when the symbiosis is advantageous to one partner at the expense of the other, (ii) commensalism, i.e. when the symbiosis is advantageous to one partner without harming the other, and (iii) mutualism, i.e. when the symbiosis is reciprocally advantageous to both partners; these cases are symbolized as follows +/-, +/-, +/+, respectively (Martin and Britayev, 1998; Bruno et al., 2003; Patzner, 2004). Apart from parasitism which is interpreted as a negative interaction (at least for one partnership) symbiosis is also described under the terms of facilitative or positive interactions (Stachowicz, 2001). The latter terms are becoming of increasing applicability in the scientific audience as they give a more precise description about the nature of species interactions and thus, a trend to replace the more generically defined symbiosis is evolving (Stachowicz, 2001; Grutter and Irving, 2007). A clear distinction, however, among the above cases of symbiosis is not always evident, because many factors define the nature of these interactions, such as the degree of association between the species and their specialization, its necessity for the species survival, the temporal pattern, and the life stage at which interaction occurs (Martin and Britayev, 1998). Considering all the above it seems rather reasonable to adopt the latter authors' opinion suggesting the use of the term symbiosis as "stepping stone in helping to understand the real relationships in any particular association".

Symbiosis appears to be more common in tropical marine communities (Grutter and Irving, 2007); nevertheless, the phenomenon is widespread also in temperate seas with the association between sea anemones and hermit crabs belonging to the most common and widely acknowledged cases of mutualism (Williams and McDermott, 2004; Vafeiadou et al., 2011). More specifically, each case of symbiosis, including mutualism, can be categorized as: (i) obligate or facultative, in the first case partners may survive only in association and in the second, while benefiting from the presence of each other, they may also survive in absence of their partner (Boucher et al., 1982), (ii) direct or indirect, in the first case partners interact physically and in the second they benefit from the each other's presence without direct contact (Boucher et al., 1982), (iii) permanent or temporary, in the first case partners are living together during their whole life and in the second only in some phase of their life cycle (Martin and Britayev, 1998), and (iv) monoxenic, oligoxenic or polyxenic, in the first case the symbiont is associated with only one host, whereas in the other two cases few or several different host species are involved, respectively (Lom, 2001); the latter category is used only for parasitism.

Considering the particular case of symbiosis between sea anemones and hermit crabs, its development requires the involvement of a third part, i.e. gastropod shells, which provide both refuge for hermit crabs and substratum for the settlement of sea anemones. These tripartite associations were assigned as ecological triangles by Ross and Sutton (1963). Nevertheless, the term has been expanded and is currently used in the broad fields of ecology and environmental biology to describe interactions among three biotic or abiotic parameters (Styron, 1977; Kareiva, 1982; Xu et al., 2006). Taking into account its original description, the limited implementation from other authors (Chintiroglou, et al. 1992; Christidis et al., 1997), or even from the ones who suggested it (Ross 1974a, 1974b, 1979), and the doubt

concerning its validity, since gastropods do not actively participate in the association although their shells are vital for the development of the sea anemones - hermit crabs symbiosis (Vafeiadou et al., 2011), the term ecological triangle is abandoned at the present review.

Sea Anemones - Hermit Crabs Symbiosis: A General Description

The interaction of sea anemones and hermit crabs is one of the most familiar examples of symbiosis in temperate seas, interpreted as a typical case of mutualism. Considering symbiosis terminology (see above), this specific case can further be described as a clear paradigm of indirect, permanent, facultative, in most cases, mutualism. If we can expand the use of the terms monoxenic/oligoxenic/polyxenic which so far is used for parasitism, we assume most sea anemones as polyxenous symbionts, as they can be hosted by several different hermit crab species; however, this term is rather species-specific (see for example the case of the sea anemone *Adamsia obvolva* which associates only with the hermit crab *Sympagurus pictus* as a monoxenous symbionts).

Nevertheless, much discussion around this aspect has followed due to confusion through terms and suggestions by several authors; although sea anemone - hermit crab symbiosis had been considered as mutualism from early studies (Roughgarden, 1975; Hazlett, 1981; Ross, 1984; Brooks, 1989), it has only recently been characterized as facultative mutualism (Patzner, 2004; Williams and McDermott, 2004; Vafeiadou et al., 2011). With older studies using contradictory terminology, given that an exact description of the symbiotic relationship was missing, the kind of interaction should be re-examined, at least for some particular species. The interaction between the sea anemone *Adamsia palliata* and the hermit crab *Pagurus prideaux* for example had long been interpreted as a case of obligate commensalism, before the anemone species was proved first to live alone, without any association with hermit crabs, and second to live in association with other hermit crab species too (Ates, 1995). Even further, hermit crabs of some species may prey on their symbiotic sea anemones under starvation, or under increased sea anemone densities (Imafuku et al., 2000). Williams and McDermott (2004) in their review study on hermit crab symbiosis stress the difficulties of such categorization. There are some examples of species among cnidarians in association with hermit crabs that happen to feed on the eggs of hosts but the relationship had been previously described as commensalism, or other cases of temporal changes in the symbiotic nature of the relationship, i.e. switching from commensalism to mutualism or parasitism, depending on different environmental and biological factors.

In this aspect, a general description of the sea anemone - hermit crab symbiosis is presented below, encompassing all the relevant information included in the literature, as such to underline the importance of symbiosis for both participant species, and for marine ecosystems, respectively.

In the particular case of sea anemones - hermit crabs symbiosis, though, the presence of a third, indirect participant is required: gastropod shells. They constitute the linking part of the symbiosis, providing refuges for hermit crabs (to protect their abdomen part) and suitable substratum for the settlement of sea anemones (Conover, 1978; Brooks, 1989). Thus, shell availability is a crucial factor for the establishment of the symbiosis.

The development of the symbiotic interaction initiates by the detachment of sea anemones from the substratum and their placement on gastropod shells inhabited by hermit

crabs. A cooperation of both symbionts is necessary for the well-establishment of the symbiosis; however, some cases where symbiosis initiates by only one of the symbionts have also been reported. As such, hermit crabs detach sea anemones, using tactile stimulation, and actively transfer them on their shells (Brunelli, 1910; Cowles, 1919; Ross, 1970); in some cases with the cooperation of the sea anemones, which loosen their connection with the substratum to enhance their transfer (Ross, 1974a, 1974b; Lawn, 1976; McFarlane, 1976).

In particular, sea anemones are the only symbionts among cnidarians associated with hermit crabs which are actively hosted by them and not haphazardly fixed on the shells during larval settlement (Gusmão and Daly, 2010). In other cases, sea anemones do also transfer themselves on shells inhabited by hermit crabs, without aid of the latter, to establish a symbiotic relationship with them (Davenport et al., 1961; Ross, 1959, 1965; Ross and Sutton, 1961; see also section 4 for details in behavioural patterns).

The importance of symbiosis for both partners is diverse (Table 1). The hermit crab enforces its defence to predators, gaining protection via the sea anemone nematocysts (Brooks, 1989). As known, the main predators of hermit crabs are cephalopod molluscs (e.g. octopus) which are not resistant to the toxins excreted by the nematocysts of cnidarians (Ross, 1967, 1971; Brooks, 1991). As a result, hermit crabs actively host sea anemones on the gastropod shells they inhabit (Gusmão and Daly, 2010), evolving a whole behaviour towards the establishment of the symbiosis, including gathering increased number of anemones under predator pressure, or stealing anemones from other crabs (Ross and Boletzky, 1979; see also section 4 for details in behavioural patterns).

Table 1. Overview of the advantages and disadvantages of symbiosis for sea anemones and hermit crabs

	Hermit crabs	Sea anemones
Advantages	Protection from predators	Protection from predators
	Increased shell strength	Substratum availability
	Decreased energetic costs of changing/searching for shells	Increased feeding capacity (increased food resource exploitation)
	Prey on symbionts in case of starvation (only some species)	Increased dispersal Direct feeding by their host
Disadvantages	Increased energetic costs of carrying heavier shells	Predation by the host (only in specific cases)
	Increased intra- and inter-specific competition	

Additional benefits for the hermit crab may also derive from expansion of the anemone over the shell, forming a so called “living cloak” inhabited by the hermit crab, strengthening the shell in this way and thus, the crab’s structural defence (Faurot, 1910; Doumenc, 1975; Ross, 1984). Furthermore, sea anemones of the genus *Adamsia* form a chitin shell-like structure, known as carcinoecium, which probably gives further protection to the hermit crab while it grows, without the need of switching shells (Dunn et al., 1980; Gusmão and Daly

2010), as it has also been reported for the genus *Stylobates* in tropical seas (Dunn and Liberman, 1983; Fautin, 1987, 1992).

Protection against predators is a benefit for the sea anemones too, since symbiosis with hermit crabs ensures their mobility, in addition with their active defence by hermit crabs against animals which endeavour to prey on their symbiotic sea anemones (Brooks and Gwaltney, 1993). Moreover, sea anemones increase their dispersal capability via hermit crab mobility (Balss, 1924), gaining suitable substrata for their settlement (Nyblade, 1966; Riemann-Zürneck, 1994).

Increased exploitation of food sources by sea anemones has also been reported as a consequence of hermit crab mobility. For example, the sea anemones of the species *Calliactis parasitica* when settled on stable substrata (e.g. rocky) are able to exploit food supplies from only a limited area (ca. 0.5 m²/day), whereas they are able to move up to 20 m²/day due to symbiosis, thus, increasing their feeding potential (Stachowitsch 1979, 1980). Increased food supplies for the sea anemones can also derive from the food residuals of hermit crabs (Ross, 1960; Stachowitsch, 1979, 1980; Chintiroglou and Koukouras, 1991; Fautin, 1992). The exact position the sea anemones are placed on the shell has also proved to be important, as the closer they are to the shell aperture, and thus to the hermit crab, the more they benefit during its feeding (Balasch et al., 1977; Brooks, 1989); however, the sea anemone is often placed on the top of the shell, which may potentially increase their accessibility to suspended particulate organic matter from the water column. The anemones are usually oriented with their mouth below the shell aperture, to increase protection and allow their host to avoid changing shells when it grows (Ross, 1974b). Direct feeding of the sea anemones by their associated hermit crabs has also been mentioned in the literature (e.g. Wortley, 1863; Fox, 1965), being though a rather controversial possibility (Ross, 1974a).

Apart from the positive outcomes for both hermit crabs and sea anemones, the symbiosis has a great importance for biodiversity in marine benthic ecosystems, too. It is broadly known that gastropod shells that are inhabited by hermit crabs host also a variety of other organisms (epibiotic and endolithic), thus, formatting small biotic communities (Conover, 1979; Stachowitsch, 1980; Hazlett, 1984; McClintock, 1985; Caruso et al., 2003; Turra, 2003; Williams and McDermott, 2004).

Although gastropod abundance and distribution are important for the establishment of such micro-communities (McLean, 1983), hermit crabs have also a key-role. They prolong the presence of empty gastropod shells on the sea bottom by occupying them, avoiding their burial in soft sediments in the opposite situation (Conover, 1975, 1979), and thus, the shells can be available as substrata and colonized by a great diversity of organisms (McLean, 1983; Williams and McDermott, 2004). As a result, the abundance and distribution of hermit crabs, and the selection of shells, affect the abundance and distribution of a variety of organisms, which use the shells as micro-habitats. With respect to this function of hermit crabs, they had been characterized as allogenic ecosystem engineers, which are defined as these organisms able to transform biotic or abiotic substances from one physical situation to another (Jones et al., 1997; Gutiérrez et al., 2003; Jones and Gutiérrez, 2007).

Sea Anemones - Hermit Crabs Symbiosis: Diversity and Distribution Patterns

In the comprehensive review of hermit crab associated species, Williams and McDermott (2004) reported 37 species of sea anemones living as symbionts with hermit crabs, whereas [Gusmão \(2010\)](#) reduced the number of associate sea anemone species to 32. According to our revision a total of 35 valid sea anemone species belonging to 14 genera (*Adamsia*, *Aiptasia*, *Antholoba*, *Calliactis*, *Carcinactis*, *Gonactinia*, *Hormathia*, *Neoaipiasia*, *Paracalliactis*, *Paranthus*, *Sagartiogeton*, *Sagartiomorphe*, *Stylobates*, *Verrillactis*) and seven families (Actiniidae, Actinostolidae, Aiptasiidae, Gonactiniidae, Hormathiidae, Sagartiidae, Sagartiomorphidae) have been reported as hermit crab symbionts (see Table 2). The vast majority of those species belong to Hormathiidae family (22 valid species), whereas other three sea anemone species are under uncertain taxonomic status (i.e. *Paracalliactis mediterranea*, *P. japonica* and *Verrillactis guttata*). Hermit crabs of 41 species hosted sea anemones (Table 2); those species belong to 15 genera (*Anapagurus*, *Catapaguroides*, *Catapagurus*, *Clibanarius*, *Dardanus*, *Diacanthurus*, *Diogenes*, *Lophopagurus*, *Micropagurus*, *Oncopagurus*, *Paguristes*, *Pagurus*, *Parapagurus*, *Petrochirus*, *Sympagurus*) and three families (Diogenidae, Paguridae, Parapaguridae).

Overall, 68 different types of sea anemones - hermit crabs symbiosis, have been reported in the literature up to date. The hermit crab *Dardanus arrosor* appeared to host the larger diversity of sea anemones, i.e. seven species, followed by *Pagurus alatus*, *P. bernhardus*, *P. cuanensis* and *Paguristes eremita* that were found in symbiosis, each, with three different anemone species. The sea anemone *Calliactis polypus* is involved in symbiosis with eight hermit crab species, followed by *C. parasitica* that has been found on the shells of seven hermit crabs; *C. tricolor* and *Adamsia palliata* are associated with six hermit crabs, and *Verrillactis paguri* with five. The rest hermit crab and sea anemone species appeared to be more specialized as they have been reported associated with one or two different species.

Considering diversity of shell utilization, whether hermit crabs prefer the shells of specific gastropod species remains unknown (see also [Ates et al., 2007](#)), and in most cases the abundance of shells seems to be the major factor influencing shell utilization (Kellogg, 1976; Barnes, 1999). [Vafeiadou et al. \(2011\)](#) studying shell resource utilization of hermit crab species in symbiosis with *Calliactis parasitica* in the Mediterranean, reported that 53 different shells are occupied by the four hermit crabs: *Dardanus arrosor*, *D. calidus*, *Pagurus excavatus* and *Paguristes eremita*, associated with *C. parasitica* (Figure 1). All crabs utilized a large variety of discarded shells, although a preference for specific gastropods has also been suggested, at least for some species. For example *Pagurus excavatus* inhabits 17 different species, but in most cases it was found in *Bolinus brandaris* and *Galeodea echinophora* shells, while *Paguristes eremita* most frequently occupied *Hexaplex trunculus* and *B. brandaris* shells, although it is occasionally found in the shells of other 33 gastropod species (Vafeiadou et al., 2011). A selective behaviour of hermit crabs towards the size of shells has been suggested (Childress, 1972; Chintiroglou et al., 1992; Wada et al., 1997; Côté et al., 1998; Caruso et al., 2003); nevertheless, selectivity to shells of certain gastropod species remains doubtful and further research is necessary to elucidate relevant patterns.

Table 2. Taxonomic list and temperate zone distribution of sea anemone and hermit crab species reported to live in symbiosis; ? Refers to species under uncertain taxonomic status (participant species data based on Williams and Mc Dermott, 2004; taxonomic status checked with World Register of Marine Species; distribution data based on Fautin, 2008 and Ocean Biogeographic Information System)

Sea anemone species	Temperate zone distribution
Actiniidae	
<i>Stylobates aeneus</i> Dall, 1903	
<i>Stylobates cancrisocia</i> (Carlgren, 1928)	Indian
<i>Stylobates loisetteae</i> Fautin, 1987	
Actinostolidae	
<i>Antholoba achates</i> (Drayton in Dana, 1846)	SW Atlantic, SE SW Pacific
<i>Paranthus rapiformis</i> (Le Sueur, 1817)	NW SW Atlantic
Aiptasiidae	
<i>Aiptasia</i> sp.	
<i>Neoaipiasia commensali</i> Parulekar, 1969	
Gonactiniidae	
<i>Gonactinia prolifera</i> (Sars, 1835)	NE NW Atlantic, SE Pacific
Hormathiidae	
<i>Adamsia obvolva</i> Dally et al., 2004	NW Atlantic
<i>Adamsia palliata</i> (Muller 1776)	NE Atlantic, Mediterranean
<i>Adamsia sociabilis</i> Verrill, 1882	NW Atlantic
<i>Calliactis algoaensis</i> Carlgren 1938	Indian
<i>Calliactis argentacolorata</i> Pei, 1996	
<i>Calliactis conchiola</i> Parry 1952	SW Pacific
<i>Calliactis japonica</i> Carlgren, 1928	NW Pacific
<i>Calliactis parasitica</i> (Couch, 1842)	NE Atlantic, Mediterranean
<i>Calliactis polypores</i> Pei, 1996	NW Pacific
<i>Calliactis polypus</i> (Forsk., 1775)	NW Atlantic, NW SW NE SE Pacific, Indian
<i>Calliactis reticulata</i> Stephenson, 1918	SW Atlantic
<i>Calliactis tricolor</i> (Le Sueur 1817)	NW SW Atlantic
<i>Calliactis variegata</i> Verrill, 1869	SE Pacific
<i>Calliactis xishaensis</i> Pei, 1996	
<i>Hormathia coronata</i> (Gosse, 1858)	NE Atlantic, Mediterranean, Indian
<i>Paracalliactis consors</i> (Verrill, 1882)	N Atlantic
<i>Paracalliactis lacazei</i> Dechance and Dufaure, 1959	Mediterranean
<i>Paracalliactis mediterranea</i> Ross and Zamponi, 1982?	Mediterranean
<i>Paracalliactis michaelsarsi</i> Carlgren 1928	NE NW Atlantic
<i>Paracalliactis japonica</i> Carlgren 1928 ?	NW Pacific
<i>Paracalliactis rosea</i> Hand 1976	SW Pacific
<i>Paracalliactis sinica</i> Pei, 1982	NW Pacific
<i>Paracalliactis stephensoni</i> Carlgren 1928	NE Atlantic
<i>Paracalliactis valdiviae</i> Carlgren 1928	Indian

Sea anemone species	Temperate zone distribution
Sagartiidae	
<i>Carcinactis dolosa</i> Riemann-Zurneck, 1975	SW Atlantic
<i>Carcinactis ichikawai</i> Uchida, 1960	NW Pacific
<i>Sagartiogeton undatus</i> (Muller, 1788)	NE Atlantic, Mediterranean
<i>Verrillactis guttata</i> (Agassiz in Verrill, 1864)?	N Atlantic
<i>Verrillactis paguri</i> (Verrill, 1869)	NW SE Pacific, Indian
Sagartiomorphidae	
<i>Sagartiomorpha carlgreni</i> Kwietniewski, 1898	SW NW Pacific
Hermit crab species	
Diogenidae	
<i>Clibanarius erythropus</i> (Latreillei, 1818)	NE Atlantic, Mediterranean
<i>Clibanarius padavensis</i> De Mann, 1888	
<i>Clibanarius vittatus</i> (Bosc, 1802)	NW SW Atlantic
<i>Dardanus arrosor</i> Herbst, 1796	NE SE Atlantic, Indian, Mediterranean, NW SW Pacific
<i>Dardanus calidus</i> (Risso, 1827)	NE Atlantic, Mediterranean
<i>Dardanus deformis</i> (H. Milne Edwards, 1836)	SE SW Pacific, Indian
<i>Dardanus impressus</i> (De Haan, 1849)	NW Atlantic
<i>Dardanus lagopodes</i> (Forsk., 1775)	
<i>Dardanus pedunculatus</i> (Herbst, 1804)	NW SW SE Pacific, Indian
<i>Dardanus tinctor</i> (Forsk., 1775)	
<i>Dardanus venosus</i> (H. Milne Edwards, 1848)	NW SW Atlantic
<i>Diogenes custos</i> (Fabricius, 1798)	
<i>Diogenes edwardsii</i> (De Haan, 1849)	NW Pacific
<i>Diogenes</i> sp.	
<i>Paguristes eremita</i> (Linnaeus, 1767)	Mediterranean
<i>Paguristes subpilosus</i> (Henderson, 1888)	SW Pacific
<i>Petrochirus diogenes</i> (Linnaeus, 1767)	NW SW Atlantic
Paguridae	
<i>Anapagurus chiroacanthus</i> (Lilljeborg, 1856)	NE Atlantic, Mediterranean
<i>Anapagurus laevis</i> (Bell, 1846)	NE Atlantic, Mediterranean
<i>Catapaguroides fragilis</i> (Melin, 1939)	
<i>Catapagurus sharreri</i> A. Milne Edwards, 1880	NW Atlantic
<i>Diacanthurus rubricatus</i> (Henderson, 1888)	SW Pacific
<i>Lophopagurus lacertosus</i> (Henderson, 1888)	SE SW Pacific
<i>Micropagurus polynesiensis</i> (Nobili, 1906)	
<i>Pagurus alatus</i> Fabricius, 1775	NE Atlantic, Mediterranean
<i>Pagurus bernhardus</i> (Linnaeus, 1758)	NW NE SW SE Atlantic
<i>Pagurus cuanensis</i> Bell, 1846	NW NE Atlantic, Mediterranean
<i>Pagurus excavatus</i> (Herbst, 1791)	Mediterranean
<i>Pagurus forbesi</i> Bell, 1846	NE Atlantic, Mediterranean
<i>Pagurus impressus</i> (Benedict, 1892)	NW Atlantic

Hermit crab species	Temperate zone distribution
<i>Pagurus longicarpus</i> Say, 1817	NW Atlantic
<i>Pagurus pollicaris</i> Say, 1817	NW Atlantic
<i>Pagurus prideaux</i> Leach, 1815	NE Atlantic, Mediterranean Indian
Parapaguridae	
<i>Oncopagurus bicristatus</i> (A. Milne Edwards, 1880)	NW NE Atlantic
<i>Parapagurus pilosimanus</i> Smith, 1879	NE SE NW Atlantic, Mediterranean, Indian, NE NW Pacific
<i>Parapagurus</i> sp.	
<i>Sympagurus andersoni</i> (Henderson, 1896)	Indian
<i>Sympagurus dimorphus</i> (Studer, 1883)	SW SE Atlantic, Indian, SE SW Pacific
<i>Sympagurus dofleini</i> (Balss, 1912)	SE SW Pacific
<i>Sympagurus pictus</i> Smith, 1883	NW Atlantic
<i>Sympagurus trispinosus</i> (Balss, 1911)	SE SW Pacific, Indian



Figure 1. Sea anemone – hermit crab symbiosis: specimens of the sea anemone *Calliactis parasitica* in symbiosis with the hermit crab *Pagurus excavatus*, in Thermaikos Gulf (north Aegean Sea) using a *Bolinus brandaris* shell (above) and with *Dardanus calidus*, in Sifnos Island (Cyclades plateau, South Aegean Sea) using a *Phalium granulatum* shell (below).

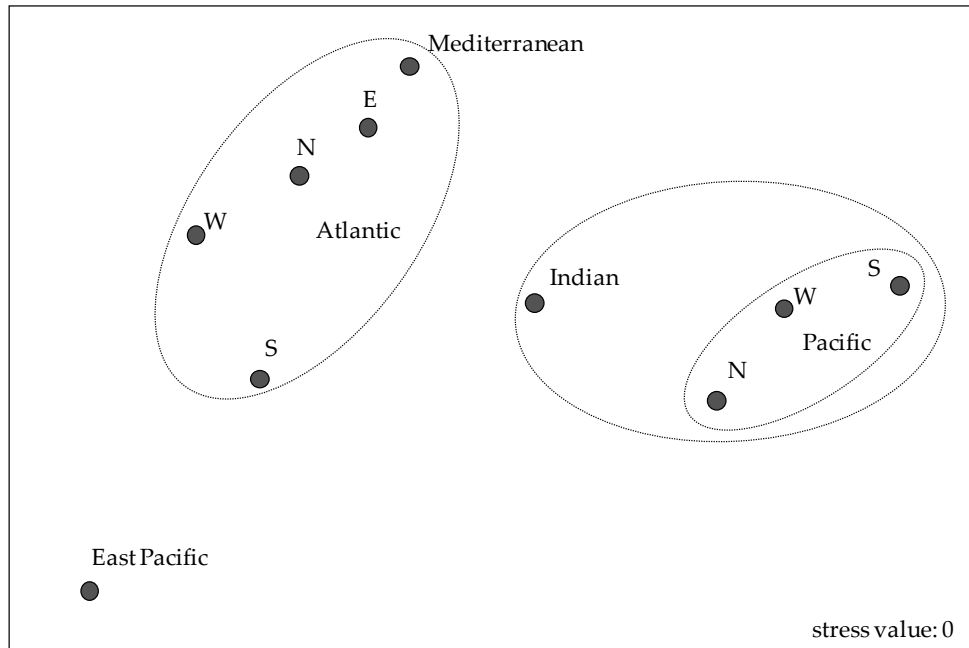


Figure 2. Temperate zone distribution of sea anemone - hermit crab symbiosis types as visualized by applying multi-dimensional scaling ordination via Bray-Curtis distances on presence – absence data (N = north, S = south, E = east, W = west).

Out of the 68 different types of sea anemones - hermit crabs symbiosis, 53 are distributed in temperate zones. Their biogeographic distribution, as visualized applying non-metric multidimensional scaling ordination via Bray-Curtis distances on presence – absence data (Figure 2), revealed the increased affinity in symbiotic types' composition between: (i) the Mediterranean and the Atlantic and (ii) within the Pacific Ocean with the exception of its eastern part, where very few such associations have been reported. The symbiotic types reported from the Indian Ocean (data from tropical zone excluded from the analysis) showed increased similarity with the Pacific group, although to a smaller degree (Figure 2).

These results conform to the findings of Ross (1974a) which documented that sea anemone - hermit crab symbiosis types cover mainly the circumtropical zone, extending also to some warm-temperate areas such as the Mediterranean Sea, and differ in their qualitative structure according to the geographic region in a global scale; accordingly the author claimed the existence of different zoogeographic zones. An analogous pattern has been revealed in a much smaller spatial scale, i.e. over the Aegean Sea (Vafeiadou et al., 2011). According to the latter authors, the symbiotic types, even when only one sea anemone species has been considered, followed a consistent pattern of spatial distribution according to the geographic areas studied. After considering the diversity of shell utilisation as well, a similar pattern emerged, concurring to the recently proposed latitudinal cline of shell resource utilisation by hermit crabs (Barnes, 2003). Therefore, this trend in the distribution of sea anemones - hermit crabs symbiosis types may be useful in biogeography studies.

Sea Anemones - Hermit Crabs Symbiosis: Manifested Behavioural Patterns

How beneficial symbiosis is for both sea anemones and hermit crabs has been already discussed (see section 2, general description of the symbiosis); nevertheless, specific behavioural patterns promoting their association exhibited by both symbionts, and verify once again its importance. Since the development of a symbiotic relationship depends on specific actions driven by particular behaviours of the participant species, behavioural patterns exhibited by sea anemones and hermit crabs (summarized in Table 3) are reported in this part, giving also examples of specific cases.

As aforementioned, the establishment of the sea anemones - hermit crabs symbiotic interaction is primarily based on hermit crabs for they detach sea anemones from their substrata, using tactile stimulation, and place them on the gastropod shells they inhabit (Brunelli, 1910; Cowles, 1919; Ross, 1970). Hermit crabs of the species *Dardanus arrosor*, known to host sea anemones of the species *Calliactis parasitica* in temperate seas, move the anemones by manipulating their base little by little, a behaviour performed, though, only by female individuals (Ross, 1967). Prior species recognition and selectivity by hermit crabs towards particular sea anemone species has been mentioned in the literature (Ross, 1974b; Brooks and Mariscal, 1986); however, such behaviour has not so far been confirmed by experimental results. On the other extreme, the hermit crab species *Pagurus alatus* does not facilitate the anemone transfer and settlement on the shell (Ross and Zamponi, 1982).

Table 3. Synopsis of the main behavioural patterns manifested by sea anemones and hermit crabs to enhance symbiosis; (?) refers to uncertain behaviours

Hermit crabs	Sea anemones
Detachment / transfer of sea anemones (using tactile stimulation)	Facilitation of its detachment by the hermit crab
Preference towards particular sea anemone species (?)	Active transfer on the shell without the participation of the host
Placement of increased number of sea anemones on the shell under predator presence	
Preference towards shells with increased number of sea anemones under predation stress	
Arrangement of sea anemones on the shell (balance, predation stress)	
Symmetric placement of sea anemones on the shell (?)	
Intra- and inter-specific competition for sea anemones	
Plasticity on shell selectivity patterns (depending on various factors and previous experience)	
Intra- and inter-specific competition for gastropod shells	

Active participation of the sea anemones during their detachment from the substratum by the hermit crabs is one of the most interesting behaviours in the symbiosis (Balasch and Mengual, 1974; Ross and Boletzky, 1979; Bach and Herrnkind, 1980). It has been reported

that sea anemones are loosening their connection with the substratum during their manipulation by hermit crabs to enhance their transfer on the shells (Ross, 1974b; Lawn, 1976; McFarlane, 1976). According to Ross (1979), although sea anemones move themselves from rocky substrata to attach on gastropod shells, they do not seem to actively change their shell substratum for another, but only when getting transferred by their host crab. Nevertheless, experiments revealed that they may transfer themselves by tentacle adhesion (followed by pedal disc attachment) to a shell inhabited by a hermit crab – without the active participation of it – under conditions of high predation risk for the latter, e.g. upon perception of mollusc presence (Davenport et al., 1961; Ross, 1959, 1965; Ross and Sutton, 1961). This particular behaviour has been observed in four species of the genera *Calliactis* and *Paracalliactis* (Gusmão and Daly, 2010) and has been characterized as one of the most complex behaviours of cnidarians (Ross, 1974b).

The perception of predator presence has as a result the active behaviour of hermit crabs too (Balasch and Mengual, 1974; Ross and Boletzky, 1979), which prefer to inhabit shells with more sea anemones, and/or place more sea anemones on their shell under increased density of predators, in comparison with predator absence circumstances (Balasch and Mengual, 1974; Ross and Boletzky, 1979; Brooks and Mariscal, 1986; Brooks, 1989). The placement of sea anemones on the shell is also influenced by predation stress, with anemones being typically placed close to the aperture of the shell, a key-position for better protection (Cutress and Ross, 1969; Brooks, 1988, 1991); though, the balance of the crab is first and foremost considered, with anemones being arranged in accordance with the center of gravity of the shells (Balasch et al., 1977; Brooks, 1989; Caruso et al., 2003).

Preference towards a symmetric placement of the sea anemones by hermit crabs has also been assumed, in particular for the species *Dardanus pedunculatus* living in symbiosis with *Calliactis tricolor* in reef ecosystems (Giraud, 2011). The author mentioned a consistent pattern, probably related to the balance of the shell, although this specific study does not use anemone weight distribution data. Additionally, this behaviour of non-random but symmetrical anemone placement by the hermit crab could be related to shell cover with sea anemones in a way to maximize protection, without necessarily needing a large number of them (Giraud, 2011) and thus, reducing the energy costs of the crab by carrying a heavier shell. Another remarkable behavioural pattern manifested by hermit crabs is their strategy for gathering more sea anemones, including intra- and inter-specific competition. Accordingly, they steal sea anemones from the shells of other hermit crabs (Mainardi and Rossi, 1969; Ross, 1974b, 1979), which sometimes might even be of the same species (Giraud, 2011). As an example, the hermit crab species *Dardanus arrosor* appears to dominate over *Pagurus excavatus* or *Paguristes eremita* when they occur at the same habitat, stealing their symbiotic anemones as a result of antagonism (Ross, 1979). The size of both the hermit crab (and in particular the size of its cheliped) and its shell are considered as the main factors for its competitive dominance (Giraud, 2011; Yasuda, 2011; Yoshino, 2011), giving the advantage to larger individuals and/or species.

In spite of its indirect benefit, gastropod shell selectivity by hermit crabs is a very important aspect for the well-establishment of the symbiosis, and should not be neglected from the behavioural patterns manifested by hermit crabs. Numerous studies have focused on shell selection behaviours of hermit crabs (e.g. Reese, 1962; Balasch and Cuadras, 1976; Fotheringham, 1976; Hazlett, 1978, 1984, 1992; Abrams, 1982; Dowds and Elwood, 1983, 1985; McClintock, 1985; Liszka and Underwood, 1990; Wada et al., 1997; Côté et al., 1998;

Hahn, 1998; Osorno et al., 1998). Experimental studies suggest gastropod mass, weight, total size (McClintock, 1985) and protective ability (see Reese, 1962), as the main factors that influence the selection by hermit crabs (Buckley and Ebersole, 1994). Intrinsic shell properties (e.g. shape, spines, center of gravity, shell axis) are other important features in shell selection by hermit crabs (Reese, 1963; Caruso and Chemello, 2009), influencing also the placement of sea anemones on the shell (Ross and Boletzky, 1979; Brooks, 1989).

According to Wada et al. (1997), the preferential shell size for a hermit crab depends on the growth rate of the latter. The same authors showed that hermit crabs tend to occupy larger shells in proportion with their size in the following cases: (i) when shell resource availability is restricted, (ii) when they are going to change their exoskeleton, and (iii) when the growth of their body size after the next moulting phase is expected to be large. On the contrary, the size of the gastropod shell may influence the rate of the hermit crab growth (Wada et al., 1997), a fact which illustrates the complexity of these associations. For instance, by selecting an oversized shell in proportion to its size, the hermit crab may on the one hand delay its searching for a larger shell during its growth, as to assure its further growth and reproduction (Childress, 1972; Wada et al., 1997; Côté et al., 1998), and on the other hand gain some advantage over antagonists; however, the energy cost is much higher. Occupying a shell that is too large could negatively affect growth and fecundity of the crab and its ability to protect itself from predators (Vance, 1972; Bertness, 1981; Elwood et al., 1995). Hermit crabs seem to select suitable shells not only with respect to their size but also regarding the environmental conditions, as for instance the strength of marine currents, showing a preference towards stronger/heavier shells under strong current conditions (Hahn, 1998), balancing the energetic constraints of carrying a heavier shell by increasing their protection.

Among the most important factors affecting the choice of an adequate shell by hermit crabs should also be considered their previous experience on shell selection, beginning from the early stage of their life (Gilchrist, 1985; Hazlett, 1992; Hahn, 1998; Gherardi, 2006). The preference hermit crabs show towards shells of specific gastropod species has been also discussed to be related to such previous experience (Reese, 1963; Elwood et al., 1979; Borjesson and Szelistowski, 1989). According to Hazlett (1992), individual hermit crabs can also adjust their preferences on shell size/type depending on recent shell availability experience. In spite of the importance of species-specific selectivity, whether such behaviours are typical, or exhibited only by some hermit crab species, or even only in particular cases related with shell availability, is very hard to be explicitly demonstrated, and thus remain uncertain.

An exceptional behaviour of hermit crabs, under conditions of limited shell resources, includes their fighting for a more suitable (better-fitting) gastropod shell than they already have (Abrams, 1982; Dowds and Elwood, 1983, 1985; Gherardi, 2006). These fights seem to either benefit both antagonists, as at the end they both gain a better shell than what they initially had, or only the stronger crab (Hazlett, 1978; Abrams, 1982). As a result of these competitions, or possibly of the lack of previous experience in shell selection, smaller hermit crabs usually end up carrying less suitable shells. The ability of larger crabs to obtain more suitable shells creates a pressure over smaller individuals to inhabit the remaining ones, without the possibility of selection; this behaviour is considered indicative of the crabs' "high social status", according to Balasch and Cuadras (1976).

Analogous behaviours have been confirmed by examining the biometric relationships between hermit crab weight and shell weight or total sea anemone biomass, for the species *D.*

calidus, *D. arrosor* and *P. excavatus* in symbiosis with *C. parasitica* in the Aegean Sea, SE Mediterranean (Vafeiadou et al., 2011). The results of this study revealed that smaller hermit crabs carry heavier shells and increased anemone biomass in proportion to their weight. Analogous observations have been previously reported by two other studies (Balasch and Cuadras, 1976; Chintiroglou et al., 1992) which examined the biometric relationships between the shell and the symbionts, referred as biometric indicators (e.g. shell weight / crab weight, shell and anemone weight / crab weight). Such biometric relationships are used to describe the ability of the crab to carry its shell and the latter's protective capacity, and their application, at the very end, can give an approximation of the functionality of the symbiosis.

Sea Anemones - Hermit Crabs Symbiosis: Co-Evolution of the Participant Species

Reciprocal altruism is among the first theories proposed to explain the evolution of mutualism; such an interaction can be developed and maintained when individuals interact by providing benefit to another in the expectation of future reciprocation, as in the case of marine cleaning behaviour (Trivers, 1971). Reciprocal altruism has been formalized in the iterated Prisoner's Dilemma game (two individuals that can defect or cooperate, receive a high payoff from defection independently of partner's behaviour but receive higher payoff if they cooperate than if both defect). Thereafter, other approaches also emerged, including by-product mutualism (partners act selfishly but a benefit results from their behaviour), pseudoreciprocity (at least one partner invests to cooperation), and biological market theory (partners exchange goods or commodities but differ in the degree of controlling them); for details on above concepts see Grutter and Irving (2007).

Sea anemones - hermit crabs mutualistic symbiosis is characterized by increased complexity being affected by a great variety of factors (e.g. shell resource availability, predation, behavioural patterns), as thoroughly discussed in previous sections. The development of the symbiosis depends on both members, as aforementioned (see previous section), with both sea anemones and hermit crabs exhibiting behavioural patterns enhancing their symbiosis. Therefore, their interaction constitutes a model case to examine species co-evolution under symbiosis, and in particular under mutualism.

Evolutionary aspects of hermit crab symbiotic interactions have been thoroughly investigated by Williams and Dermott (2004). According to the latter authors, and despite the poor representation of hermit crab exoskeletons in the fossil records, hermit crabs seem to have provided a new niche for epibiotic organisms in marine ecosystem during the middle Jurassic (Walker, 1992). Shell resource utilization by hermit crabs has been hypothesized to develop initially for refuge and protection of their abdomen which became decalcified when posterior pereopods and uropods were modified to fit the animal in shells and pleopods were placed on one side to maximize utilization of gastropod lumen during reproduction (McLaughlin, 1983).

The knowledge on the shared evolutionary history of sea anemones and hermit crabs remains limited and it is mostly based on behavioural patterns followed by the symbionts. Ross (1974a, 1983) in his pioneer work of sea anemone - hermit crab symbiosis

comprehensively studied evolutionary aspects, tried to elucidate possible drivers and hypothesized that the symbiosis evolved independently multiple times.

This latter hypothesis has been recently supported by molecular data presented by Gusmão and Daly (2010) who provided strong evidences of at least two independent origins of the sea anemones - hermit crab symbiosis, by constructing a phylogenetic tree of the sea anemone family Hormathiidae (a family that includes the vast majority of sea anemone genera having symbiotic interactions with hermit crabs).

Moreover, the widely accepted idea of close evolutionary relation among sea anemone genera symbiotic with hermit crabs, which has been assumed on the basis of common morphological and behavioral patterns, has been currently rejected on the basis of phylogenetic data; monophyly in the origin of the three symbiotic with hermit crabs sea anemone genera examined, i.e. *Calliactis*, *Adamsia* and *Paracalliactis*, has not been supported but evidences of paraphyly emerged (Gusmão and Daly, 2010). Accordingly, the reported similarities in morphology and behaviour of some sea anemone genera forming symbiotic interactions with hermit crabs is not due to shared evolutionary history but due to the necessary ways for the development and maintenance of symbiosis, as explicitly stated by Gusmão and Daly (2010).

Two main hypotheses have been suggested by Ross (1974a) to explain possible leading factors to the development of the sea anemones - hermit crabs symbiosis: (i) the “crab-driven” and (ii) the “shell-response” hypotheses which are driven by the behaviour of hermit crab and sea anemone, respectively, and have been subsequently adopted and analysed by other authors (Williams and Dermott, 2004; Gusmão and Daly, 2010).

According to the first hypothesis the initial establishment of the symbiosis is founded on hermit crabs behaviour of placing sea anemones on their residence shells to be protected, i.e. hidden from predators by camouflage, which, however, evolved afterwards to an actual mechanism of defence. Under this hypothesis a clear benefit emerges for the hermit crab increasing its fitness (Gusmão and Daly, 2010). According to the second hypothesis the development of the symbiosis is based on the sea anemone behaviour of shell mounting. In this case sea anemones firstly settled on living gastropod shells and later started also to utilize shells occupied by hermit crabs as the settlement of the anemone is stimulated by a shell factor stronger on alive than on discarded gastropod shells. Sea anemones, besides gaining novel habitat, benefit by transportation; thus settlement behaviour reinforced toward shells occupied by hermit crabs, since they are much more mobile than gastropods.

The most important evidence supporting the first hypothesis is that in most cases the symbiosis of sea anemones with a hermit crab is initiated under the activity of the crab, while sea anemones are more frequently found on shells occupied by crabs than on living gastropods, even in areas with dense gastropod populations. In favor of the second hypothesis is the exclusive presence of some anemones on living gastropods, such as the species *Allantactis parasitica* and *Hormanthia digitata*, the ability of some other anemones to actively move on gastropod shells, and the equal presence of some other species, e.g. *Calliactis conchiola*, on both living gastropods and shells occupied by hermit crabs (Hand, 1975). Whatever was the initial behavioural pattern stimulating the establishment of sea anemones - hermit crabs symbiosis, both patterns positively responded. Hermit crabs, after having their residence shells being occupied by sea anemones, started to benefit under their protection against predators, and evolved a specialized behaviour of actively enhancing anemone colonization of their shells. Sea anemones, after being picked up by the hermit crab,

started to benefit from transportation, and evolved a positive response to their stimulation by the crab, as Ross (1974b) showed with manipulative laboratory experiments (i.e. only those anemones that were previously symbiotic with hermit crabs responded to tactile stimulation by the latter). Overall, the limited number of sea anemones living on gastropods or inactive crabs (Gusmão and Daly, 2010) and the very strong pattern manifested by several hermit crabs of stealing sea anemones from other ones (Ross, 1979), argue against the “shell-response” hypothesis, which however, has been preferred to some extent by Ross (1974a).

Sea Anemones - Hermit Crabs Symbiosis: Summarized Conclusive Remarks

The sea anemones - hermit crabs symbiosis represents a clear example of mutualism, as it has reciprocal advantages for both symbionts. The partners' interaction is characterized by increased complexity as the establishment of the symbiosis depends on a large variety of factors such as shell resource availability, predation pressure and environmental constraints, and involves the cooperation of both participants in most cases. Well-developed behavioural patterns exhibited by both symbionts, including from the sea anemones' active transfer on shells inhabited by hermit crabs to the behavioural plasticity of crabs in view of shell utilization and gathering of sea anemones, determine the development of the symbiosis and confirm its importance for both participants, making them excellent models to examine species co-evolution under a mutual symbiotic context. Several species of sea anemones and hermit crabs frequently form symbiotic interactions in temperate marine environments providing benefits, not only to the directly involved partners, but also to other organisms, which colonize this complex biotic formation. Thus, through the intermingled processes of epibiosis and ecosystem engineering, sea anemones - hermit crabs symbiosis contribute to the diversity of marine benthic ecosystems by supporting diverse micro-communities.

References

- Abrams PA, 1982. Frequencies of interspecific shell exchanges between hermit crabs. *Journal of Experimental Marine Biology and Ecology* 61: 99-109.
- Ates RML, 1995. *Pagurus prideaux* and *Adamsia palliata* are not obligate commensals. *Crustaceana* 68: 522-524.
- Ates AS, Katagan T, Kocatas A, 2007. Gastropod shell species occupied by hermit crabs (Anomura: Decapoda) along the Turkish coast of the Aegean Sea. *Turkish Journal of Zoology* 31: 13-18.
- Bach CE, Herrnkind WF, 1980. Effects of predation pressure on the mutualistic interactions between the hermit crab *Pagurus pollicaris* Say, 1817 and the sea anemone *Calliactis tricolor* (Lesueur, 1817). *Crustaceana* 38: 104-108.
- Balash J, Mengual V, 1974. The behavior of *Dardanus arrosor* in association with *Calliactis parasitica* in artificial habitat. *Marine Behaviour and Physiology* 2: 251-260.
- Balash J, Cuadras J, 1976. Role of association with *Calliactis parasitica* (Couch) in social behaviour of *Dardanus arrosor* (Herbst). *Vie et Milieu* 26: 281-291.

- Balash J, Cuadras J, Alonso G, 1977. Distribution of *Calliactis parasitica* on gastropod shells inhabited by *Dardanus arrosor*. *Marine Behaviour and Physiology* 5: 37-44.
- Balss H, 1924. Über anpassungen und symbiose der Paguriden eine zusammenfassende ubersicht. *Zeitschriften Okologie Morphologie Tiere* 1: 752-792.
- Barnes DKA, 1999. Ecology of tropical hermit crabs at Quirimba Island, Mozambique: shell characteristics and utilisation. *Marine Ecology Progress Series* 183: 241-251.
- Barnes DKA, 2003. Local, regional and global patterns of resource use in ecology: hermit crabs and gastropod shells as an example. *Marine Ecology Progress Series* 246: 211-223.
- Bertness MD, 1981. The influence of shell-type on hermit crab growth rate and clutch size (Decapoda. Anomura). *Crustaceana* 40: 197-205.
- Borjesson DL, Szelistowski WA, 1989. Shell selection, utilization and predation in the hermit crab *Clibanarius panamensis* Stimpson in a tropical mangrove estuary. *Journal of Experimental Marine Biology and Ecology* 133: 213-228.
- Boucher DH, James S, Keeler KH, 1982. The ecology of mutualism. *Annual Review of Ecology and Systematics* 13: 315-347.
- Brooks WR, 1988. The influence of the location and abundance of the sea anemone *Calliactis tricolor* (Lesueur) in protecting hermit crabs from octopus predators. *Journal of Experimental Marine Biology and Ecology* 116: 15-21.
- Brooks WR, 1989. Hermit crabs alter sea anemone placement patterns for shell balance and reduced predation. *Journal of Experimental Marine Biology and Ecology* 132: 109-121.
- Brooks WR, 1991. Chemical recognition by hermit crabs of their symbiotic sea anemones and a predatory octopus. *Hydrobiologia*. 216-217: 291-295.
- Brooks WR, Mariscal RN, 1986. Population variation and behavioral changes in two pagurids in association with the sea anemone *Calliactis tricolor* (Lesueur). *Journal of Experimental Marine Biology and Ecology* 103: 275-289.
- Brooks WR, Gwaltney CL, 1993. Protection of symbiotic cnidarians by their hermit crab hosts: evidence for mutualism. *Symbiosis* 15: 1-13.
- Brunelli G, 1910. Osservazioni ed esperienze sulla simbiosi dei Paguridi e delle Attinie. *Atti della Accademia Nazionale dei Lincei, Classe si Scienze Fisiche, Matematiche e Naturali, Rendiconti* 19: 77-82.
- Bruno JF, Stachowicz JJ, Bertness MD, 2003. Inclusion of facilitation into ecological theory. *Trends in Ecology and Evolution* 18: 119-125.
- Buckley WJ, Ebersole JP, 1994. Symbiotic organisms increase the vulnerability of a hermit crab to predation. *Journal of Experimental Marine Biology and Ecology* 182: 49-64.
- Caruso T, Chemello R, 2009. The size and shape of shells used by hermit crabs: a multivariate analysis of *Clibanarius erythropus*. *Acta Oecologica* 35: 349-354.
- Caruso T, Falciai L, Zupo V, 2003. Decapoda Anomura Paguridea: morpho-functional relationships and influence of epibiotic anemones on shell use along a bathymetric cline. *Crustaceana* 76: 149-166.
- Childress JR, 1972. Behavioral ecology and fitness theory in a tropical hermit crab. *Ecology* 53: 960-964.
- Chintiroglou C, Koukouras A, 1991. Observations on the feeding habits of *Calliactis parasitica* (Couch, 1842) (Anthozoa, Cnidaria). *Oceanologica Acta* 14: 389-396.
- Chintiroglou C, Doumenc D, Koutsoubas D, 1992. Allométrie d'une nouvelle association entre le Décapode Anomure *Pagurus excavatus* (Herbst, 1791) et l'Actinie Acontiaire *Sagartiogeton undatus* (Müller, 1788). *Crustaceana* 62: 1-12.

- Christidis J, Chintiroglou C, Culley MB, 1997. A study of the populations of *Calliactis parasitica* (Couch, 1842) in symbiosis with anomuran decapods in Thermaikos Gulf (N. Aegean Sea). *Crustaceana* 70: 227-238.
- Conover MR, 1975. Prevention of shell burial as a benefit hermit crabs provide to their symbionts (Decapoda, Paguridae). *Crustaceana* 29: 311-313.
- Conover MR, 1978. The importance of various shell characteristics to the shell selection behavior of hermit crabs. *Journal of Experimental Marine Biology and Ecology* 32: 131-142.
- Conover MR (1979) Effect of gastropod shell characteristics and hermit crabs on shell epifauna. *Journal of Experimental Marine Biology and Ecology* 40: 81-94.
- Côté IM, Reverdy B, Cooke PK, 1998. Less choosy or different preference? Impacts of hypoxia on hermit crab shell assessment and selection. *Animal Behaviour* 56: 867-873.
- Cowles RP, 1919. Habits of tropical crustacean: III Habits and reactions of hermit crabs associated with sea anemones. *Philippine Journal of Science* 15: 81-90.
- Cutress CE, Ross DM, 1969. The sea anemone *Calliactis tricolor* and its association with the hermit crab *Dardanus venosus*. *Journal of Zoology* 158: 225-241.
- Dauvin J.C., Bellan G., Bellan-Santini D., 2008. The need for a clear and comparable terminology in benthic ecology. Part I. Ecological concepts. *Aquatic Conservation: Marine and Freshwater Ecosystems* 18: 432-445.
- Davenport D, Ross DM, Sutton L, 1961. The remote control of nematocyst discharge in the attachment of *Calliactis parasitica* to shells of hermit crabs. *Vie et Milieux* 12: 197-209.
- Douglas A.E., 1994. *Symbiotic interactions*. Oxford University Press, Oxford, New York.
- Douglas A.E., 2010. *The Symbiotic Habit*. Princeton University Press, Princeton, New Jersey.
- Doumenc D, 1975. Actinies bathyales et abyssales de l'océan Atlantique nord. Families des Hormathiidae (genres *Paracalliactis* et *Phelliactis*) et des Actinostolidae (genres *Actinoscyphia* et *Sicyonis*). *Bulletin de Musée Nationale de l'Histoire Naturelle* 287: 1-201.
- Dowds BM, Elwood RW, 1983. Shell wars: assessment strategies and the timing of decisions in hermit crab shell fights. *Behaviour* 85: 1-24.
- Dowds BM, Elwood RW, 1985. Shell wars II: the influence of relative size on decisions made during hermit crab shell fights. *Animal Behaviour* 33: 649-656.
- Dunn DF, Liberman MH, 1983. Chitin in sea anemone shells. *Nature* 221: 157-159.
- Dunn DF, Devaney DM, Roth B, 1980. Stylobates: a shell-forming sea anemone (Coelenterata, Anthozoa, Actiniidae). *Pacific Science* 34: 379-388.
- Elwood RW, McClean A, Webb L, 1979. The development of shell preference by the hermit crab *Pagurus bernhardus*. *Animal Behaviour* 27: 940-946.
- Elwood RW, Mark N, Dick JTA, 1995. Consequences of shell-species preferences for female reproduction success in the hermit crab *Pagurus bernhardus*. *Marine Biology* 123: 431-434.
- Faurot L, 1910. Etude sur les associations entre les Pagures et les Actinies; *Eupagurus prideauxi* Heller et *Adamsia palliata* Forbes, *Pagurus striatus* Latreille et *Sagartia parasitica* Cosse. *Archives de Zoologie Experimentale et Generale* 5: 421-486.
- Fautin DG, 1987. *Stylobates loisetteae*, a new species of shell-forming sea anemone (Coelenterata: Actiniidae) from Western Australia. *Proceedings of the California Academy of Sciences* 45, 1-7.
- Fautin DG, 1992. A shell with a new twist. *Natural History* 4: 50-57.

- Fotheringham N, 1976. Population consequences of shell utilization by hermit crabs. *Ecology* 57: 570-578.
- Fox HM, 1965. Confirmation of old observations on the behaviour of a hermit crab and its commensal sea anemone. *Annals and Magazine of Natural History* 13: 173-175.
- Gherardi F, 2006. Fighting behavior in hermit crabs: the combined effect of resource-holding potential and resource value in *Pagurus longicarpus*. *Behavioral Ecology and Sociobiology* 59: 500-510.
- Gilchrist SL, 1985. Ecology of juvenile hermit crabs shell use: Field and laboratory comparisons. *American Zoologist* 25: 60.
- Giraud C, 2011. Intraspecific competition, stealing and placement of the symbiotic sea anemone *Calliactis tricolor* by the hermit crab *Dardanus pedunculatus*. Student Research Papers, Fall 2011, UCB Moorea Class: Biology and Geomorphology of Tropical Islands, Berkeley Natural History Museum, UC Berkeley.
- Grutter AS, Irving AD, 2007. Positive interactions in marine communities. In: Conell SD, Gillanders BM (eds) *Marine Ecology*, Oxford, pp 110-137.
- Gusmão LC, 2010. Systematics and evolution of sea anemones (Cnidaria: Actiniaria: Hormathiidae) symbiotic with hermit crabs. *Doctorate Dissertation*, Ohio State University.
- Gusmão LC, Daly M, 2010. Evolution of sea anemones (Cnidaria: Actiniaria: Hormathiidae) symbiotic with hermit crabs. *Molecular Phylogenetics and Evolution* 56: 868-877.
- Gutiérrez JL, Jones CG, Strayer DL, Iribarne OO, 2003. Mollusks as ecosystem engineers: the role of shell production in aquatic habitats. *Oikos* 101: 79-90.
- Hahn DR, 1998. Hermit crab shell use patterns: response to previous shell experience and to water flow. *Journal of Experimental Marine Biology and Ecology* 228: 35-51.
- Hand C, 1975. Behaviour of some New Zealand sea anemones and their molluscan and crustacean hosts. *New Zealand Journal of Marine and Freshwater Research* 9: 529-538.
- Hazlett BA, 1978. Shell exchanges in hermit crabs: aggression, negotiation or both? *Animal Behavior* 26: 1278-1279.
- Hazlett BA, 1981. The behavioral ecology of hermit crabs. *Annual Review of Ecology and Systematics* 12: 1-22.
- Hazlett BA, 1984. Epibionts and shell utilization in two sympatric hermit crabs. *Marine Behaviour and Physiology* 11: 131-138.
- Hazlett BA, 1992. The effect of past experience on the size of shells selected by hermit crabs. *Animal Behaviour* 44: 203-205.
- Henry SM, 1966. *Symbiosis*. I Associations of microorganisms, plants and marine organisms. New York and London, Academic Press.
- Imafuku M, Yamamoto T, Ohta M, 2000. Predation on symbiotic sea anemones by their host hermit crab *Dardanus pedunculatus*. *Marine Freshwater Behaviour and Physiology* 33: 221-232.
- Jones CG, Gutiérrez JJ, 2007. On the purpose, meaning, and usage of the physical ecosystem engineering concept. In: Cuddington K, Byers JE, Wilson WC, Hastings A (eds) *Ecosystem Engineers*. Plant to protists, *Theoretical Ecology Series*, Academic Press, Elsevier, pp 3-24.
- Jones CG, Lawton JH, Shachak M, 1997. Positive and negative effects of organisms as physical ecosystem engineers. *Ecology* 78: 1946-1957.
- Kareiva P, 1982. Insects and Adaptions. *Science* 215: 658-659.

- Kellogg CW, 1976. Gastropod Shells: a potentially limiting resource for hermit crabs. *Journal of Experimental Marine Biology and Ecology* 22: 101-111.
- Lawn ID, 1976. The Marginal Sphincter of the Sea Anemone *Calliactis parasitica*. I. Responses of Intact Animals and Preparations. *Journal of Comparative Physiology* 105: 287-300.
- Liszka D, Underwood AJ, 1990. An experimental design to determine preferences for gastropod shells by a hermit crab. *Journal of Experimental Marine Biology and Ecology* 137: 47-62.
- Lom, J. 2001. *Protozoan Symbioses*. eLS.
- Mainardi D, Rossi AC, 1969. Relations between social status and activity toward the sea anemone *Calliactis parasitica* in the hermit crab *Dardanus arrosor*. Atti della Accademia Nazionale dei Lincei, Classe di Scienze Fisiche, Matematiche e Naturali, Rendiconti 47: 116-121.
- Martin D., Britayev T.A., 1998. Symbiotic polychaetes: review of known species. *Oceanography and Marine Biology an Annual Review* 36: 217-340.
- McClintock TS, 1985. Effects of shell condition and size upon the shell choice behavior of a hermit crab. *Journal of Experimental Marine Biology and Ecology* 88: 271-285.
- McFarlane ID, 1976. Two slow conduction systems co-ordinate shell-climbing behaviour in the sea anemone *Calliactis parasitica*. *Journal of Experimental Biology* 64: 431-445.
- McLaughlin PA, 1983. Hermit crabs—are they really polyphyletic? *Journal of Crustacean Biology* 3: 608-621.
- McLean R, 1983. Gastropod shells: a dynamic resource that helps shape benthic community structure. *Journal of Experimental Marine Biology and Ecology* 69: 151-174.
- Nyblade CF, 1966. The association between *Pagurus floridanus* (Benedict) and *Calliactis polypus* (Forsk.) *Journal of the Mississippi Academy of Sciences* 7: 232-241.
- Osorno JL, Fernández-Casillas L, Rodríguez-Juárez C, 1998. Are hermit crabs looking for light and large shells?: Evidence from natural and field induced shell exchanges. *Journal of Experimental Marine Biology and Ecology* 222: 163-173.
- Patzner RA, 2004. Associations with sea anemones in the Mediterranean Sea: a review. *Ophelia* 58: 1-11.
- Reese ES, 1962. Shell selection behaviour of hermit crabs. *Animal behaviour* 10: 347-360.
- Rhode K., 1981. The nature of parasitism. In: Australian Ecology Series: Ecology of marine parasites, H. Heatwole (ed), *University of Queensland Press*, 4-5.
- Riemann-Zórneck K, 1994. Taxonomy and ecological aspects of the Subarctic sea anemones *Hormathia digitata*, *Hormathia nodosa* and *Allantactis parasitica* (Coelenterata, Actiniaria). *Ophelia* 39: 197-224.
- Ross DM, 1959. The sea anemone (*Calliactis parasitica*) and the hermit crab (*Eupagurus bernhardus*). *Nature* 184: 1161-1162.
- Ross DM, 1960. The association between the hermit crab *Eupagurus bernhardus* (L.) and the sea anemone *Calliactis parasitica* (Couch). *Proceedings of the Zoological Society of London* 134: 43-57.
- Ross DM, 1965. Complex and modifiable behavior patterns in *Calliactis* and *Stomphia*. *American Zoologist* 5: 573-580.
- Ross DM, 1967. Behavioral and ecological relationships between sea anemones and other invertebrates. *Oceanography and Marine Biology: an Annual Review* 5: 291-316.

- Ross DM, 1970. The commensal association of *Calliactis polypus* and the hermit crab *Dardanus gemmatus* in Hawaii. *Canadian Journal of Zoology* 48: 351-357.
- Ross DM, 1971. Protection of hermit crabs (*Dardanus* spp.) from octopus by commensal sea anemones (*Calliactis* spp.). *Nature* 230: 401-402.
- Ross DM, 1974a. Evolutionary aspects of associations between crabs and sea anemones. In: Vernberg WB (ed) *Symbiosis in the sea*. University of South Carolina Press, Columbia, pp.111-125.
- Ross DM, 1974b. Behavior patterns in associations and interactions with other animals. In: Muscatine L, Lenhoff HM (eds) *Coelenterate Biology: Reviews and New Perspectives*. Academic Press, New York, pp. 281-312.
- Ross DM, 1979. "Stealing" of the symbiotic anemone, *Calliactis parasitica*, in interspecific and intraspecific encounters of three species of Mediterranean pagurids. *Canadian Journal of Zoology* 57: 1181-1189.
- Ross DM, 1983. Symbiotic relations. In: Bliss D (ed) *The Biology of the Crustacea*, vol. 7. Academic Press, New York, pp. 163-212.
- Ross DM, 1984. The symbiosis between the "cloak anemone" *Adamsia carciniopados* (Otto) (Anthozoa-Actinaria) and *Pagurus prideauxi* Leach (Decapoda-Anomura). *Bolletino di Zoologia* 51: 413-421.
- Ross DM, Sutton L, 1961. The association between the hermit crab *Dardanus arrosor* (Herbst) and the sea anemone *Calliactis parasitica* (Couch). *Proceedings of the Royal Society B: Biological Sciences* 155: 282-291.
- Ross DM, Sutton L, 1963. A sea anemone, a hermit crab and a shell. – An ecological triangle. *Proceedings of the International Congress of Zoology* 1,62 pp.
- Ross DM, Boletzky S, 1979. The association between the pagurid *Dardanus arrosor* and the actinian *Calliactis parasitica*. Recovery of activity in "inactive" *D. arrosor* in the presence of cephalopods. *Marine Behaviour and Physiology* 6: 175-184.
- Ross DM, Zamponi MO, 1982. A symbiosis between *Paracalliactis mediterranea* n. sp. (Anthozoa-Actiniaria) and *Pagurus variabilis* A. Milne-Edwards and Bouvier. *Vie et Milieu* 32: 175-181.
- Roughgarden J, 1975. Evolution of Marine Symbiosis - A Simple Cost-Benefit Model. *Ecology* 56: 1201-1208.
- Smith D.C., 2001. Symbiosis research at the end of the millennium. *Hydrobiologia* 461: 49-54.
- Stachowicz JJ, 2001. Mutualism, facilitation, and the structure of ecological communities. *Bio. Science* 51: 235-246.
- Stachowitsch M, 1979. Movement, activity pattern, and role of a hermit crab population in a sublittoral epifaunal community. *Journal of Experimental Marine Biology and Ecology* 39: 135-150.
- Stachowitsch M, 1980. The epibiotic and endolithic species associated with the gastropod shells inhabited by the hermit crabs *Paguristes oculatus* and *Pagurus cuanensis*. *Marine Ecology* 1: 73-101.
- Styron CE, 1977. An Ecological Triangle. *The American Biology Teacher* 39: 102-104.
- Trivers RL, 1971. The evolution of reciprocal altruism. *The Quarterly Review of Biology* 46: 35-57.
- Turra A, 2003. Shell condition and adequacy of three sympatric intertidal hermit crab populations. *Journal of Natural History* 37: 1781-1795.

- Vafeiadou AM, Antoniadou C, Chintiroglou C, 2011. Symbiosis of sea anemones and hermit crabs: different resource utilization patterns in the Aegean Sea. *Helgoland Marine Research*, in press.
- Vance RR, 1972. Competition and mechanism of co-existence in three sympatric species of intertidal hermit crabs. *Ecology* 53: 1062-1074.
- Wada S, Ohmori H, Goshima S, Nakao S, 1997. Shell-size preference of hermit crabs depends on their growth rate. *Animal Behaviour* 54: 1-8.
- Walker SE, 1992. Criteria for recognizing marine hermit crabs in the fossil record using gastropod shells. *Journal of Paleontology* 66: 535-558.
- Williams JD, McDermott JJ, 2004. Hermit crab biocoenoses: a worldwide review of the diversity and natural history of hermit crab associates. *Journal of Experimental Marine Biology and Ecology* 305: 1-128.
- Wortley S, 1863. On the habits of *Pagurus prideauxii* and *Adamsia palliata*. *Annals and Magazine of Natural History* 12: 388-390.
- Xu FL, Zhao SS, Dawson RW, Hao JY, Zhang Y, Tao S, 2006. A triangle model for evaluating the sustainability status and trends of economic development. *Ecological Model* 195: 327-337.
- Yasuda C, Suzuki Y, Wada S, 2011. Function of the major cheliped in male-male competition in the hermit crab *Pagurus nigrofascia*. *Marine Biology* 158: 2327-2334.
- Yoshino K, Koga T, Oki S, 2011. Chelipeds are the real weapon: Cheliped size is a more effective determinant than body size in male-male competition for mates in a hermit crab. *Behavioral Ecology and Sociobiology* 65: 1825-1832.

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