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Ecological Interactions Based on Shell Selection in Hermit Crabs (Decapoda: Anomura): A Case Study from Kerala Coast

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Abstract

Hermit crab extensively distributed along tropics and subtropics, forms a perfect example for ecological interaction. Mobile habitat selection by hermit crabs is very complex phenomenon extremely important for their survival. Hermit crabsare engaged in shell fights for choosing suitable shells andexhibit mutualism with sea anemone. Sea anemone attached to shell provides additional protection to the hermit crab, while both are mutually benefited by their food gathering activity.Inorder to understand the shell selection behaviour of hermit crabs in natural conditions 35 species of hermit crabs along with their shells were collected from the Kerala coast, and regression analysis of seven species was done to understand the shell selection pattern. In nature, hermit crab exhibits a greater plasticity in shell selection and it varies with species.

Keywords: Crustacea, Ecology, Gastropoda, Paguroidea

Introduction

The superfamily Paguroidea of the infraorder Anomura comprises hermit crabs and their relatives in the families Coenobitidae (17 species in 2 genera), Diogenidae (428 species in 20 genera), Paguridae (542 species in 75 genera), Parapaguridae (76 species in 10 genera), Pylochelidae (52 species in 10 genera), and Pylojacquesidae (2 species in 2 genera)(McLaughlin, 2003).Hermit crabs represent an important portion of the intertidal, sublittoral and moderately deep benthic marine communities worldwide (McDermott, 1999; Shives and Dunbar, 2010),although some species have physiological and behavioural adaptations for living in almost all habitats such as estuarine, semi-terrestrial and terrestrial (Mantelatto and Sousa, 2000).They have high diversity in tropical and subtropical regions (McLaughlin *et al*., 2007), where they play an important role in food web (Balkıs and Kurun, 2008). They are ecologically important scavengers, feeding on organic deposits and are also good predators (Whitman *et al*., 2001).

Hermit crabs have a soft abdomen, and they keep the abdomen tucked away in a discarded gastropod shell or cavities of appropriate size for safety from predation, desiccation and mechanical damage (Khan, 1992;Gherardi, 1996; Balkıs and Kurun, 2008).Few hermit crabs are found inhabiting shelters other than shells, which includesbivalve and scaphopod shells, hollowed cylinders of wood (McLaughlin and Lemaitre, 1997);stones, calcareous tubes of polychaetes, or vermetid gastropods which are immobile (Gherardi and Cassidy, 1994; Rodrigues *et al*., 2000);corals (McLaughlin and Lemaitre, 1993);and sponges (Sandford, 2003). Terrestrial hermit crab, popularly known as "coconut crab" [*Birguslatro* (Linnaeus, 1767)], is fully calcified andexist without a shell, although megalopae and young crabs of this species require shells (Greenaway, 2003).

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Survival and reproductive fitness of hermit crab critically depend on the gastropod shellsmaking it alimiting factor(Mantelatto and Meireles, 2004;Laidre, 2011). Hermit crabsselect the most suitable shell, perfect for their size and shapeby exchanging or sharing shells among individuals of same or different species (Gherardi and Nardone, 1997), seeking empty shells or migrating to areas where gastropod shells are abundant (Mantelatto and Garcia, 2000; Halpern, 2004; Mantelatto*et al*., 2004). Shell abundance may regulate their fecundity (Bertness, 1981a), growth rate (Fotheringham, 1976; Bertness, 1981b; Blackstone, 1985), survival (Vance, 1972; Bertness, 1981c), copulatory success (Hazlett andBaron, 1989), intra- and interspecific interactions among them (Bach *et al*., 1976),and the resource partitioning (Mantelatto*et al*.,2010).Gastropod shells thus form an indispensable resource for hermit crabs.

Shell exchanges take place by agonistic interactions called 'shell fights' between intraspecific and interspecific populations (Barron and Hazlett, 1989) in order to obtain better-quality shell. Those hermit crabs are aware of the information about the shells, opponent and their own physiological condition (Briffa and Elwood, 2004). Hermit crabs choose suitable shells after a lengthy process of shell investigation (Elwood and Stewart, 1985).Hermit crabs are ideal model organisms showing vacancy chain process (Mclean, 1974).

Relationship between hermit crabs and gastropod shells is an excellent example of decision-making during habitat selection (Hazlett, 1981), which requires good cognitive abilities (Elwood and Appel, 2009). The intrinsic relationship between crab and shell, their shell use pattern, shell preferences, etc., can be understood only by experimental analysis (Dominciano *et al*., 2009). Hermit crabs are good example of 'ecosystem engineers' as they influence the abundance and distribution of diverse variety of invertebrates through use of gastropod shells (Jones *et al*., 1994, 1997). As such they bring dead gastropod shells back to life (Gutiérrez *et al*., 2003) that would have been otherwise degraded.

The previous studies on the shell selection and utilization by hermit crabs in context to the Indian subcontinent were mainly those of Trivedi and Vachhrajani (2014), Reshmi *et al*.(2018), Sardar *et al.* (2019), Nirmal *et al.* (2020), and Patel *et al.* (2020).The present study explains the shell selection done by 35 species of hermit crabs from the southwest coast of India in their natural environment.

Material and Methods

Study sites

Hermit crabs were collected during November 2021 to October 2022 from major fishing harbours, landing centers, intertidal areas, mangrove swamps and sandy beaches along seven coastal districts of Kerala coast (Figure1).

Collection and Preservation

The collected animals were transported to the laboratory in plastic containers. The date, time andlocality of collection and the live colourationof the specimens were recorded. The specimens collected were cleaned, washed and photographed in the field. The dead specimens with shells were preserved in 10% formaldehyde after noting necessary morphometric measurements of the host and shell. The shells of each species of hermit crabs were dried and identified for studying the shell selection in hermit crabs.

Identification and Morphometry

Each hermit crab and its shell were identified up to species level using standard literature and online databases. The identification keys of McLaughlin *et al.* (2007) were the primary source for identification. Shells were identified followingApte (1998), Subba Rao (2003), Robin (2008) and other molluscan databases.Shell morphometric characters like Shell Length (SHL), Shell Width (SW), Aperture Length (AL), Aperture Width (AW), Shell Weight (W), Internal Volume (IV), External Volume (EV) and Aperture Perimeter (AP) were recorded. Hermit crab measurements like Shield Length (SL), Carapace Length (CL), Thoracic Length (TL), Abdominal Length (AL), Carapace Width (W) and Wet weight were also taken(Figure2).

Statistical Analysis

Regression analysis (Zar, 1996) of seven species of hermit crabs wasdone. Shell-size preference was analyzed using multiple linear regression $\log Y = a + b \log X$,where Y = shell measurements and X = hermit crab measurements. The level of significance was 5%.

Results and Discussion

Thirty-five species of hermit crabs were chosen, and they showed different patterns of shell selection.Hermit crabs and their preferred shell in nature are shown inTable 1. Diogenidae was the most diverse family obtained throughout the study, and the shell selection was most abundantly found among the species in this family (Figure3). The species of *Diogenes* Dana, 1851 occupied the most diverse variety of shells; among them, *Diogenes alias*, *Diogenes canaliculatus* and *Diogenes mannarensis* occupied the most diverse varieties of shells. Great diversity of shell occupied by a hermit crab species in nature depends on the availability of different shell species, the relative abundance of the gastropods, and their mortality rate in an area (Meireles *et al*., 2008). *Coenobita rugosus*, the semi-terrestrial species, was found occupying a great variety of shells; they, however, preferred shells lacking columella. Kinosita and Okeyima (1968) studied *Coenobita rugosus* occupying shells of *Nerita striata* from Japan and found that the shells occupied by this species had missing columella. Majority of shells occupied by *Coenobita* lack columella (Ball, 1972), and this may be due to the reason that land hermit crab tend to inhabit shells that are modified by previous hermit crab use (Wolcott, 1988). A well-fitting shell is essential for semiterrestrial hermit crab for preventing evaporation and to carry ample water (Sallam*et al*., 2008).

From the study, it is clear that morphometry of shells plays a significant role in its selection by the host hermit crabs. According to Sallam *et al*. (2008), shell dimensions are the main determinant of shell utilization in hermit crabs. *Ciliopagurus grandis* and *Clibanarius longitarsus* were found occupying certain shells with larger aperture length. This was due to the shape and size of the hermit crab carapace which allows it to completely fit into the preferred shell. In the case of *Diogenes miles* and *Ciliopagurus krempfi*, the carapace was much flattened so they choose shells which had large shell length and aperture length. *Clibanarius longitarsus* has a rounded carapace and was collected mainly from the mangrove ecosystems, and the species preferred the shells of *Telescopium telescopium* that has a rounded aperture. Hermit crabs in nature have a greater choice of shell selection, and the selection depends upon certain shell characters, which vary among one another and is not based on previous experiences (Conover, 1978). The morphometric characters of hermit crabs and the shells associated with it have morphometric relation and were independent of shell species (Mantellato *et al*., 2010). According to Meireles *et al.* (2008), the morphometric relationships between shell aperture length and hermit crab shield length best describes the selected shells. Single shell species preference showed by certain hermit crab indicates active selection behaviour. There is a close relationship between the shell use and availability of resources (Volker, 1967).

The results of the regression analysis showing morphometric relationships of seven species of hermit crabs collected from sea and their host gastropod shells are given in Table 2. The study showed positive correlations between morphometry of hermit crab and shell morphometry. *Coenobita rugosus* showed a positive correlation to all shell parameters of *Euchelus asper.* Shield length of *Diogenes alias* showed a positive correlation to shell parameters of*Babylonia spirata* and *Babylonia zeylanica* ($p<0.01$). With shells of *Cantharus tranquebaricus, Diogenes alias* showed a positive correlation to all shell parameters except AW×SL. Parameters of *Bufonaria crumena* and *Diogenes alias* showed significant value, $p<0.05$. *Murex ternispina* showed a high significant relation with parameters like shield length and shield width of *D. alias* ($p<0.01$).*Diogenes dubius* mainly occupied three species of shells, viz., *Babylonia spirata*, *Babylonia zeylanica* and *Bufonaria crumena*. High significance of 'p' value ($p<0.01$) was shown by shell length, shell width and aperture length versus shield width in the case of *Bufonaria crumena* and shell width versus shield length with shells of *Babylonia spirata. Clibanarius longitarsus* occupied the shell of *Telescopium telescopium* and showed a positive correlation between all morphometric parameters except aperture width versus shield length and shield width. *Ciliopagurus grandis* was most abundantly found hermit crab, occupying the shells of *Conus inscriptus*. Significant correlations were observed for the parameters like shell length × shield length, shell width × shield length and aperture length × shield length. *Ciliopagurus krempfi* possesses much flattened carapace than rest of the species and were found occupying the shells of *Conus inscriptus* that has a narrow shell aperture. Significant relationships were recorded for parameters such as shell length × shield length, aperture length × shield width and aperture width × shield width. *Diogenes miles* were found occupying shells of *Agaronia gibbosa* and showed correlation for all morphometric shell and hermit crab parameters. High significance was obtained for parameters like shell length, shell width and aperture length verses shield width ($p<0.01$).

Shell utilization pattern varies between hermit crab and are greatly influenced by the available shell's size and type, hermit crabs shell preferences and by area of occurrence of hermit crab (Mantelatto and Garcia, 2000;Meireles*et al*., 2003; Mantelatto and Meireles, 2004). A great variety of shells werefound occupiedby the hermit crabs, and this indicates resource partitioning between hermit crabs.In general, hermit crabs always select optimal shells based on shell characters like shell length, shell width, aperture length, aperture width and aperture perimeter in addition to certain other characters like shell type, weight, internal volume, shell availability, current shell quality and shell experience (Figure4). Hermit crab are good 'ecosystem engineers' as they help in distribution of diverse variety of invertebrates through use of gastropod shells and are the key species because the degree of healthiness of a shore is determined by the rarity or abundance of hermit crabs.

Table 1. Systematic list of hermit crabs and their preferred shell species along the Kerala coast.

Sl.No.	Hermit crab species	Preferred shell species
1.	**Class: Malacostraca** **Order: Decapoda** **Family: Coenobitidae** Genus: *Coenobita* Latreille, 1829 *Coenobita brevimanus* Dana, 1852	*Turbo intercostalis, Nerita albicilla* and *Nerita polita*
2.	*Coenobita rugosus*H. Milne Edwards, 1837	*Purpura panama, Turbo brunneus, Purpura bufo, Neritapolita, Euchelus asper, Babylonia zeylanica*and *Babylonia spirata.*
3.	**Family: Diogenidae** Genus: *Paguristes*Dana, 1851 *Paguristesmiyakei* Forest & McLaughlin, 1998	*Xenophora pollidula, Biplexperca*and *Polinices mamilla.*
4.	*Paguristesluculentus*Komai, Reshmi and Bijukumar, 2015	*Fusinuscolus*
5.	Genus: *Ciliopagurus*Forest, 1995 *Ciliopagurusgrandis*Komai, Reshmi and Bijukumar, 2012	*Ficusgracilis*, *Conus textile,Fusinuscolus*and *Turris javana*.
6.	*Ciliopaguruskrempfi*Forest, 1995	*Conus inscriptus*.
7.	*Ciliopagurusliui* Forest, 1995	*Conus inscriptus*.
8.	Genus: *Dardanus*Paul'son, 1875 *Dardanus pedunculatus* (Herbst, 1804)	*Chicoreus chicoreusramosus*and*Phaliumglaucum*.
9.	*Dardanus hessi* (Miers, 1884)	*Phaliumglaucum,Bufonariacrumena, Bufonaria echinata, Natica vitellus* and *Vokesimurexmalabaricus.*
10.	*Dardanus megistos* (Herbst, 1804)	*Lambis lambis*and *Tibia curta.*
11.	*Dardanus setifer*(H. Milne Edwards, 1836)	*Rapanarapiformis, Bufonaria echinata, Tibia curta, Tutufa bufo, Harpulina loroisi*and *Phaliumglaucum.*
12.	Genus: *Clibanarius* Dana, 1852 *Clibanarius Clibanarius*	*Rapanarapiformis*and*Phaliumglaucum*
13.	*Clibanarius longitarsus* (De Haan, 1849)	*Bufonaria echinata*, *Telescopium telescopium, Tibia curta*, *Phaliumglaucum, Pugilina cochlidium* and *Murex trapa*
14.	*Clibanarius merguiensis* De Man, 1888	*Turbo intercoastalis*

Sl.No.	Hermit crab species	Preferred shell species
15.	*Clibanarius arethusa* De Man, 1888	*Purpura bufo, Indothais lecera,Thiasmancinella*and *Tibia curta*
16.	*Clibanarius padavensis* de Man 1888	*Babylonia zeylanica, Bufonaria echinata, Bufonaria crumena, Babylonia spirata* and *Tibia curta.*
17.	Genus: *Diogenes*Dana, 1851 *Diogenes alias* McLaughlin & Holthuis 2001	*Babylonia zeylanica, Babylonia spirata, Phaliumglaucum, Phaliumbandatum, Natica vitellus, Natica lineata, Polinix*sp., *Purpura bufo, Harpa major, Rapanarapiformis, Bufonaria echinata, Bufonaria crumena, Turbinella pyrum, Ficusvariegata, Chicoreus ramosus, Murex trapa, Vokesimurexmalabaricus, Pugilina cochlidium, Tibia curta, Indothais lecera, Conus inscriptus, Cantharus melanostomus, Cantharus tranquebaricus, Euchelus asper, Gyrinium natator, Colus*sp., *Turrisamicta, Fusinuscolus, Fusinuslaticostatus, Turritella duplicate* and *Turritella banksi.*
18.	*Diogenes avarus* Heller 1865	*Clypeomorus batillariaeformis,Turricula javana* and *Euchelus asper.*
19.	*Diogenes canaliculatus* Komai, Reshmi and Bijukumar, 2013	*Distorsio reticularis*, *Nassarius distortus*, *Agaronia gibbosa*, *Margistrombusmarginatus*, *Euchelus asper*, *Gyrinium natator*, *Polinices mammilla*, *Natica vitellus*, *Umbonium vestiarium*, *Thias*sp., *Cantharus tranquibaricus*, *Dolomena sibbaldi*,*Turrisamicta*, *Turris tornata*, *Turrisamicta*, *Turritella duplicata*, *Ranularia obesa* and *Dentalium* sp.
20.	*Diogenes custos* (Fabricius, 1798)	*Tonna dolium,Pugilina cochlidium, Bufonaria echinata, Purpura bufo, Turritella duplicata, Babylonia zeylanica,Babylonia spirata, Natica vitellus* and *Natica lineate*
21.	*Diogenes dubius* (Herbst 1804)	*Turbo intercoastalis, Purpura bufo, Babylonia zyelanica, Babylonia spirata* and *Natica vitellus.*
22.	*Diogenes klaasi* Rahayu and Forest, 1995	*Bufonaria crumena* and*Cerithiacea cingulata.*
23.	*Diogenes mannarensis* Henderson, 1893	*Fusinuslaticostatus, Tibia curta, Murex trapa, Bufonaria echinata, Tonna dolium, Turricula javana, Turritella vittata, Natica vitellus, Purpura bufo, Babylonia spirata* and *Babylonia zeylanica.*
24.	*Diogenes merguiensis* de man 1888	*Babylonia zeylanica,Babylonia spirata* and *Bufonaria crumena*
25.	*Diogenes miles* Herbst, 1791	*Agaronia gibbosa*
26.	*Diogenes planimanus* Henderson, 1893	*Fusinuslaticostatus, Purpura bufo* and *Indothais lecera.*
27.	*Diogenes violaceus* Henderson, 1893	*Turris tornata, Natica pulcaria, Bullia vitellus, Indothais lacera* and *Euchelus asper.*

Sl.No.	Hermit crab species	Preferred shell species
28.	Genus: *Calcinus*Dana, 1851 *Calcinus morgani*Rahayu and Forest, 1999	*Turbo intercoastalis*and *Trochus radiatus*
29.	*1.* *Calcinus laevimanus* (Randall, 1840)	*Thiasmoncinella*and *Turbo intercostalis*
30.	**Family: Paguridae** Genus: *Nematopagurus* A. Milne-Edwards and Bouvier, 1892 *Nematopagurus squamichelis* Alcock, 1905	*Cantharus* sp., *Indothais lacera* and *Natica* sp.
31.	Genus: *Pagurus*Fabricius, 1775 *Pagurus carpoforaminatus* (Alcock, 1905)	*Nassariacrematus* and*Distorsio reticularis*
32.	*2.* *Pagurus kulkarni*Sankoli, 1962	*Indothais lacera*
33.	*Pagurus pitagsaleei* McLaughlin, 2002	*Indothais lacera*
34.	*Pagurus spinossior*Komai, Reshmi and Bijukumar, 2013	*Ficusinvestigatoris*
35	Genus: *Phylopaguropsis*Alcock, 1905 *Pylopaguropsis magnimanus (*Henderson, 1896)	*Biplexperca* and *Gemmula*sp

Table 2. Regression equation showing morphometric relationship between hermit crabs and their host gastropod shells collected from natural condition.

Hermit crab species	Shell species	Relation	Linear equation	r value
Coenobita rugosus	*Euchelus asper* (n=26)	Sh.L x SL	ln Sh.L= -1.84+ 0.32 lnSL	0.838**
		Sh.L x SW	ln Sh.L= -1.50 + 0.38 lnSW	0.881**
		Sh.W x SL	ln Sh.W= -0.30 + 0.32 lnSL	0.849**
		Sh.W x SW	ln Sh.W= 1.24 + 0.36 ln SW	0.826**
		AL x SL	lnAL= -0.43 + 0.48 ln SL	0.776**
		AL x SW	lnAL=1.55+ 0.68 ln SW	0.767**
		AW x SL	lnAW= -1.04 + 0.66 ln SL	0.840**
		AW x SW	lnAW=1.55 + 0.68 ln SW	0.767**

Hermit crab species	Shell species	Relation	Linear equation	r value
Diogenes alias	*Babylonia spirata* (n=9)	Sh.L x SL	ln Sh.L= -12.48+ 0.479lnSL	0.892**
		Sh.L x SW	ln Sh.L= 20.00- 0.052 lnSW	0.159
		Sh.W x SL	ln Sh.W= -4.15+0.469lnSL	0.818**
		Sh.W x SW	ln Sh.W=16.13+0.052 lnSW	0.149
		AL x SL	lnAL= -3.79+0.491 ln SL	0.897**
		AL x SW	lnAL=21.431-0.143 ln SW	0.427
		AW x SL	lnAW= 1.170+0.459 ln SL	0.783**
		AWxW	lnAW=20.99-0.191 ln SW	0.532
	Cantharus tranquebaricus (n=16)	Sh.L x SL	ln Sh.L= 6.96+0.081 lnSL	0.538*
		Sh.L x SW	ln Sh.L= 8.94+0.151 lnSW	0.671**
		Sh.W x SL	ln Sh.W= 7.44+ 0.098 lnSL	0.497*
		Sh.W x SW	ln Sh.W= 9.35+0.20 ln SW	0.678**
		AL x SL	lnAL= 7.190+0.117 ln SL	0.585**
		AL x SW	lnAL=9.72+0.206 ln SW	0.687**
		AW x SL	lnAW= 8.127+0.145 ln SL	0.401
		AWxSW	lnAW=11.06+0.275 ln SW	0.509*
	Babylonia zeylanica (n=15)	Sh.L x SL	ln Sh.L= 1.05+0.18 lnSL	0.780**
		Sh.L x SW	ln Sh.L= 7.38+0.17 lnSW	0.504*
		Sh.W x SL	ln Sh.W= -1.37+0.37 lnSL	0.830**
		Sh.W x SW	ln Sh.W= 0.56+0.50 ln SW	0.766**
		AL x SL	lnAL= 1.40+0.31ln SL	0.730**
		AL x SW	lnAL=9.84+0.21 ln SW	0.336
		AW x SL	lnAW= 0.66+0.49 ln SL	0.734**
		AWxSW	lnAW=8.52+0.37 ln SW	0.384
	Bursa crumenacrumena (n=14)	Sh.L x SL	ln Sh.L= 5.85+0.09 lnSL	0.508*
		Sh.L x SW	ln Sh.L= 9.15+0.13 lnSW	0.543*
		Sh.W x SL	ln Sh.W= 4.95+0.15 lnSL	0.640**
		Sh.W x SW	ln Sh.W= 9.03+0.18 ln SW	0.578*
		AL x SL	lnAL= 6.42+0.12 ln SL	0.578*
		AL x SW	lnAL=10.23+0.17 ln SW	0.587*
		AW x SL	lnAW= 7.19+0.17 ln SL	0.575*
		AWxSW	lnAW=10.90+0.25 ln SW	0.630**
	Murex ternispina (n=11)	Sh.L x SL	ln Sh.L= 0.761+0.16 lnSL	0.880**
		Sh.L x SW	ln Sh.L= 3.027+0.19lnSW	0.988**
		Sh.W x SL	ln Sh.W= 4.94+0.21 lnSL	0.873**
		Sh.W x SW	ln Sh.W= 8.524+0.22 ln SW	0.886**
		AL x SL	lnAL= 2.56+0.21ln SL	0.826**
		AL x SW	lnAL=5.84+0.22 ln SW	0.860**
		AW x SL	lnAW= 5.04+0.34 ln SL	0.774**
		AWxSW	lnAW=8.14+0.37 ln SW	0.841**

Hermit crab species	Shell species	Relation	Linear equation	r value
Diogenes dubius	*Bursa crumenacrumena* (n=15)	Sh.L x SL	ln Sh.L= 6.74+0.07 lnSL	0.441
		Sh.L x SW	ln Sh.L= 7.18+0.13 lnSW	0.844**
		Sh.W x SL	ln Sh.W= 4.85+0.14 lnSL	0.545*
		Sh.W x SW	ln Sh.W= 4.81+0.23 ln SW	0.797 **
		AL x SL	lnAL= 6.43+0.11 ln SL	0.418
		AL x SW	lnAL=6.37+0.23 ln SW	0.714**
		AW x SL	lnAW= 8.86+0.05 ln SL	0.154
		AWxSW	lnAW=9.11+0.19 ln SW	0.456
	Babylonia spirata (n=15)	Sh.L x SL	ln Sh.L= -10.13+3E-15lnSL	0
		Sh.L x SW	ln Sh.L= 18.25-0.07 lnSW	0.146
		Sh.W x SL	ln Sh.W= 6.04+0.129 lnSL	0.600*
		Sh.W x SW	ln Sh.W= 9.81+ 0.16 ln SW	0.350
		AL x SL	lnAL= 10.04+0.002ln SL	0.017
		AL x SW	lnAL=16.90- 0.05 ln SW	0.141
		AW x SL	lnAW= 8.95+0.06 ln SL	0.311
		AWxSW	lnAW=15.15-0.004 ln SW	0.009
	Babylonia zeylanica (n=15)	Sh.L x SL	ln Sh.L= 8.77+0.06 lnSL	0.290
		Sh.L x SW	ln Sh.L= 4.15+0.23 lnSW	0.581*
		Sh.W x SL	ln Sh.W= 12.22-0.01 lnSL	0.031
		Sh.W x SW	ln Sh.W= 4.23+0.39 ln SW	0.560*
		AL x SL	lnAL= 11.87+0.02 ln SL	0.051
		AL x SW	lnAL=7.11+0.28 ln SW	0.340
		AW x SL	lnAW= 16.27-0.23 ln SL	0.500*
		AWxSW	lnAW=21.32-0.30ln SW	0.321
Diogenes miles	*Oliva gibbosa* (n=30)	Sh.L x SL	ln Sh.L= 9.131– 0.001lnSL	0.006
		Sh.L x SW	ln Sh.L= 7.707+0.264 lnSW	0.682**
		Sh.W x SL	ln Sh.W= 11.03-0.088 lnSL	0.224
		Sh.W x SW	ln Sh.W= 8.99+0.441 ln SW	0.725**
		AL x SL	lnAL= 9.4299-0.0116 ln SL	0.036
		AL x SW	lnAL=10.296+0.267 ln SW	0.541**
		AW x SL	lnAW= 10.077-0.086 ln SL	0.229
		AW x SW	lnAW=16.789+0.172 ln SW	0.295
Clibanarius longitarsus	*Telescopium telescopium* (n=15)	Sh.L x SL	ln Sh.L= 4.32+0.066 lnSL	0.602**
		Sh.L x SW	ln Sh.L= 4.71+0.10 lnSW	0.641**
		Sh.W x SL	ln Sh.W= 3.52+0.13 lnSL	0.812**
		Sh.W x SW	ln Sh.W= 3.73+0.20 ln SW	0.832**
		AL x SL	lnAL= 7.44+0.05 ln SL	0.603**
		AL x SW	lnAL=9.84+0.08 ln SW	0.640**
		AW x SL	lnAW= 6.15+0.14 ln SL	0.422
		AWxSW	lnAW=7.89+0.23 ln SW	0.442

Hermit crab species	Shell species	Relation	Linear equation	r value
Ciliopaguruskrempfi	*Conus inscriptus* (n=17)	Sh.L x SL	ln Sh.L= -7.08+0.25 lnSL	0.79**
		Sh.L x SW	ln Sh.L= -0.34+0.30 lnSW	0.40
		Sh.W x SL	ln Sh.W= 3.07+0.12 lnSL	0.28
		Sh.W x SW	ln Sh.W= 6.57+0.32 ln SW	0.31
		AL x SL	lnAL= -8.99+0.34 ln SL	0.58**
		AL x SW	lnAL= -0.33+0.35 ln SW	0.25
		AW x SL	lnAW= -1.55+0.91 ln SL	0.60**
		AWxSW	lnAW=3.92+1.33ln SW	0.37
Ciliopagurusgrandis	*Conus inscriptus* (n=15)	Sh.L x SL	ln Sh.L= -5.41+0.35 lnSL	0.864**
		Sh.L x SW	ln Sh.L= 16.82+0.26 lnSW	0.490*
		Sh.W x SL	ln Sh.W= -1.47+0.54 lnSL	0.732**
		Sh.W x SW	ln Sh.W= 21.15+0.35 ln SW	0.364
		AL x SL	lnAL= -4.39+0.40 ln SL	0.844**
		AL x SW	lnAL=17.63+0.29 ln SW	0.498*
		AW x SL	lnAW= 6.72+0.79 ln SL	0.280
		AWxSW	lnAW=23.92+0.78 ln SW	0.216

(**= significant correlation, P<0.01; *= significant correlation, P<0.05)

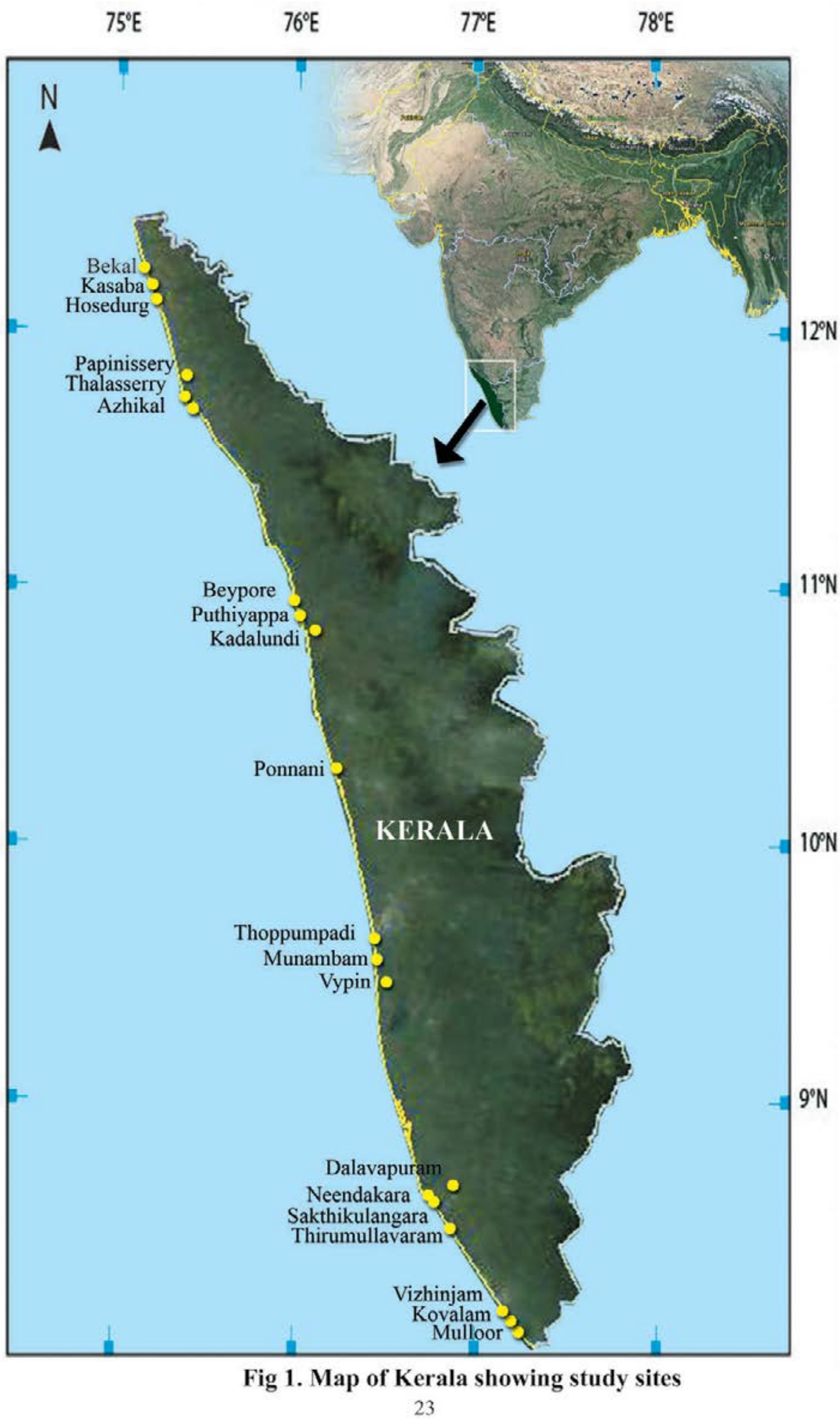


Figure 1. Map showing the study sites along the Kerala coast.

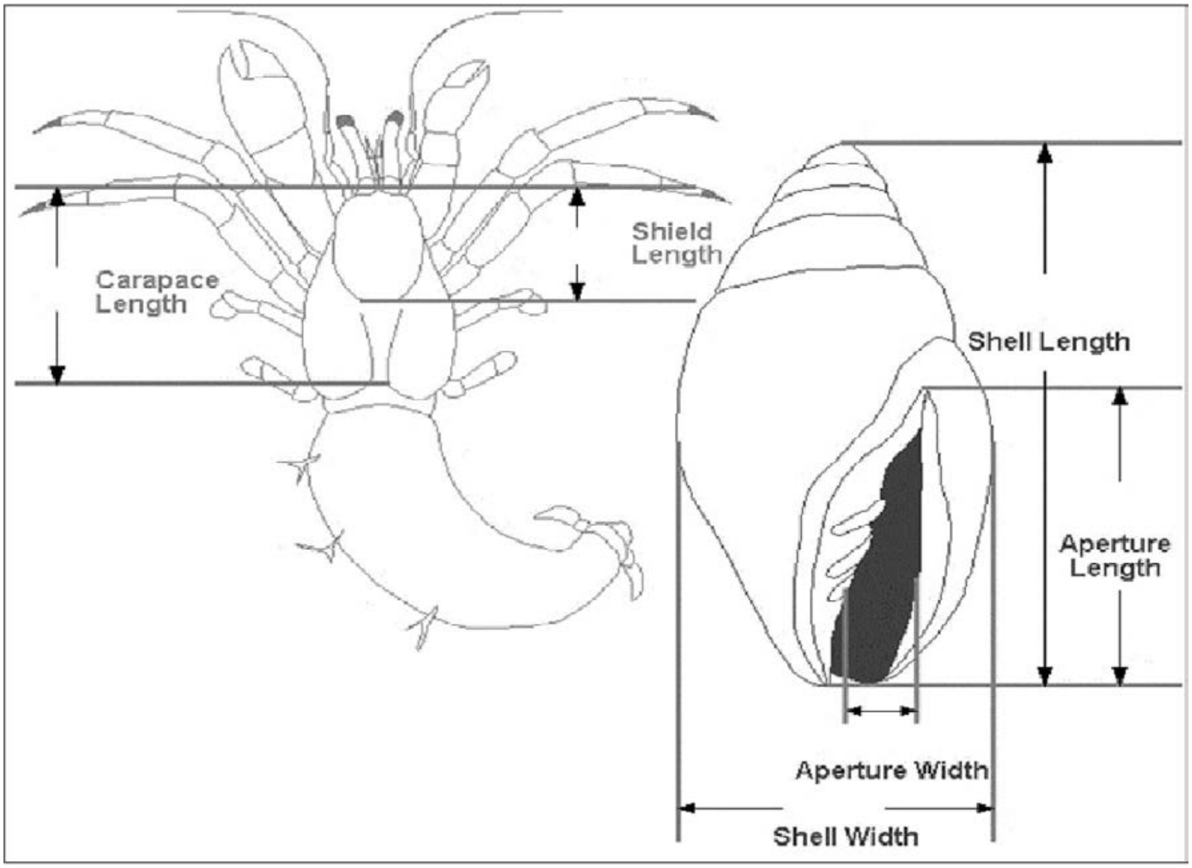


Figure2. Diagrammatic representation of hermit crab and shell showing key measurements. Modified after Sardar *et al*. (2019).

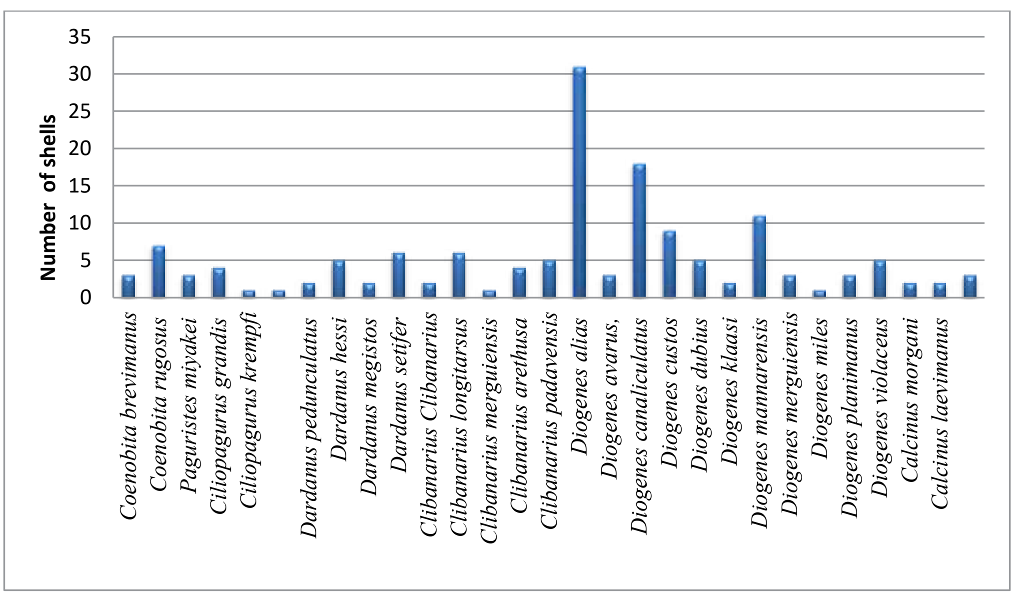
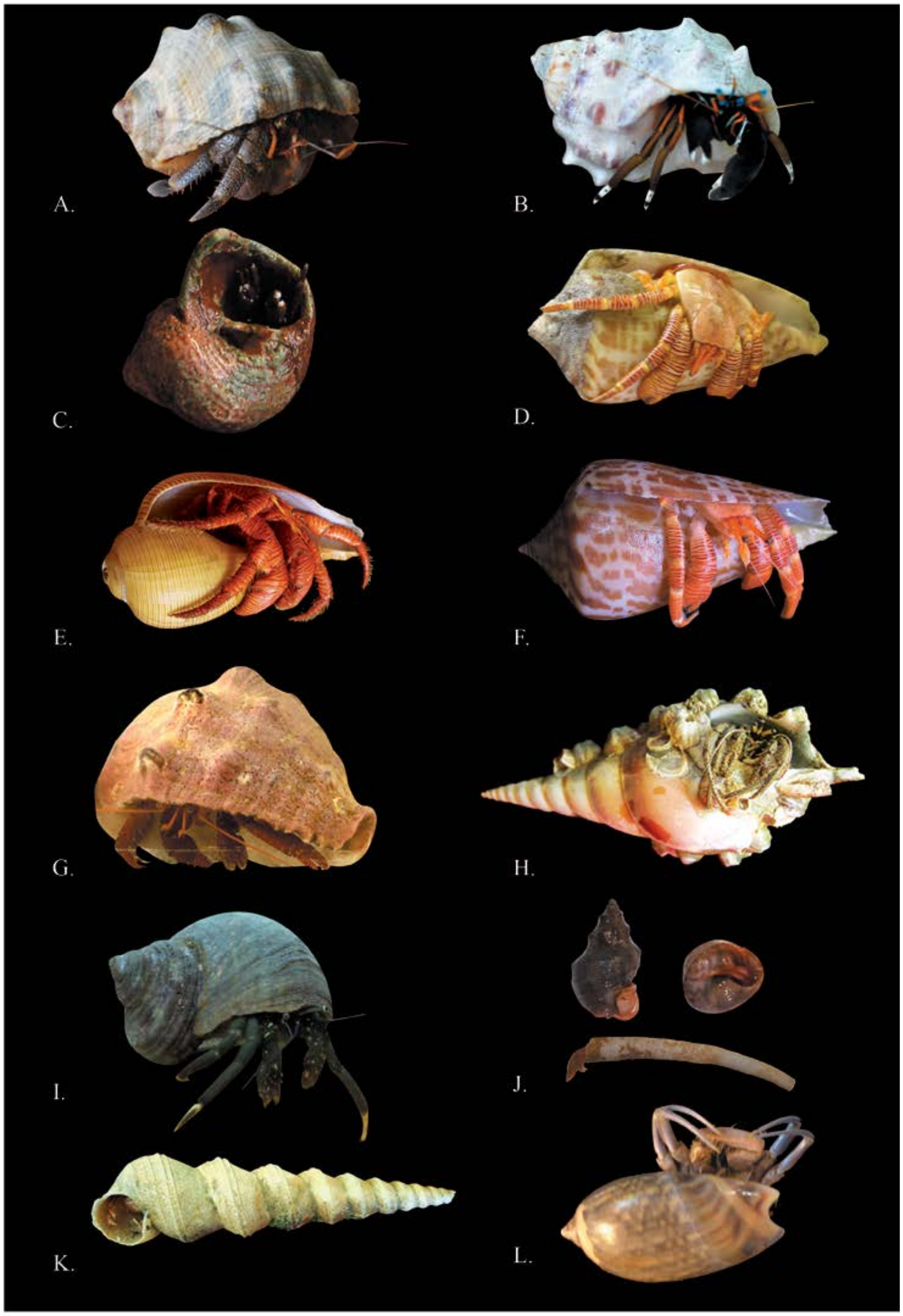


Figure3. Number of shells selected by each species of the family Diogenidae.

Figure 4. Some species of hermit crabs with their shells.



FigureA. *Coenobita rugosus;* FigureB. *Calcinus laevimanus*; FigureC. *Calcinus morgani*; FigureD. *Ciliopagurus liui*; FigureE. *Ciliopagurus grandis*; FigureF. *Ciliopagurus krempfi*; FigureG. *Clibanarius arethusa*; FigureH. *Clibanarius longitarsus*; FigureI. *Clibanarius merguiensis*; FigureJ. *Diogenes cannaliculatus*; FigureK. *Diogenes custos*; FigureL. *Diogenes miles*; Figure

FigureM. *Diogenes alias*; FigureN. *Diogenes planimanus*; FigureO. *Diogenes violaceus*; FigureP. *Dardanus pedunculatus*; FigureQ. *Dardanus hessi*; FigureR. *Dardanus megistos*; FigureS. *Dardanus setifer*; FigureT. *Nematopagurus squamichelis*; FigureU. *Oncopagurus monstrosus*; FigureV. *Phylopaguropsis magnimanus*; FigureW. *Paguristes miyakei*; FigureX. *Pagurus spinossor*; FigureY. *Pagurus kulkarnii.*

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