Chapter 3:

Shell utilization pattern of

Clibanarius rhabdodactylus

Hermit crabs are the unique members of the infraorder Anomura that have evolved to occupy empty shells or pseudoshells for the protection of their non-calcified pleon (Schejter and Mantelatto, 2011; Schejter et al., 2017). Hermit crabs occupy empty gastropod shells (Reese, 1969) that are available in their habitat and remain dependent on the shells for the majority of their life time (Turra and Leite, 2000). The occupied gastropod shell provides "portable refugia" for the inhabiting hermit crab, which can retract its body inside the shell when threatened (Bertness, 1982).

They occupy the shells of dead molluscs or remove the live animal from the shell (Rutherford, 1977; Elwood and Neil, 1992). Selection of the gastropod shell does not occur by chance; in fact, the hermit crab conducts a complex process of evaluation that is based on several factors, like predation risk, abundance of hermit crab species, availability of gastropod shells (Reese, 1969; Conover, 1978), environmental factors including wave action, tidal height, and temperature (Vermeij, 1976; Bertness, 1982), as well as the behaviour of the coexisting hermit crab species (Sant'Anna et al., 2012). Some of the evidence suggests that the conditions of the local habitat may also affect the selection of gastropod shells by the hermit crab; for example, hermit crabs residing in habitats with high water turbulence and wave action will select heavy shells (Partridge, 1980). However, such a heavy shell can reduce its reproductive success and increase its energy expenditure for the purpose of locomotion (Argüelles et al., 2009). The occupied gastropod shell plays a vital role for hermit crabs, as it protects the hermit crab from various biotic and abiotic factors, including predation, competition, temperature, osmotic stress, and wave action (Reese, 1969; Bertness, 1981a; Hahn, 1998; Angel, 2000).

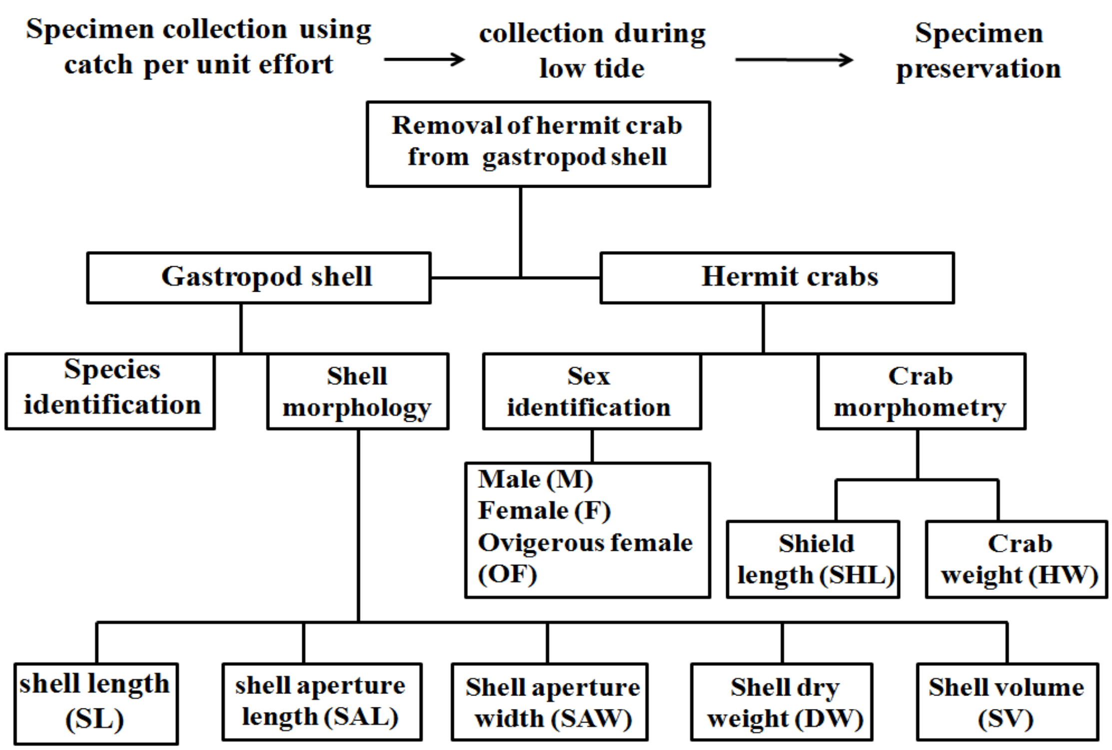
Studies have shown that shape, size, abundance, and quality of gastropod shells affect the population size (Vance, 1972), growth (Fotheringham, 1976c; Turra and Leite, 2003), morphology (Blackstone, 1985), fecundity (Childress, 1972; Fotheringham, 1976a), and survivorship (Lively, 1988; Angel, 2000) of hermit crabs. Hermit crabs acquire empty shells from their habitat and require increasingly larger shells throughout their lifespan to maintain shelter and protection from predators, keeping them in constant search of a suitable shell

(Childress, 1972; Bertness, 1981a, b). As the hermit crabs constantly need new and favourable shells, the availability of the shells becomes a limiting factor for their distribution (Shih and Mok, 2000). Before acquiring a new shell, the hermit crab performs an evaluation process to assess the fitness of the shell, which includes assessing the condition, shape, size, aperture width, and internal volume of the shell (Elwood and Neil, 1992; Biagi et al., 2006). As suggested by Abrams (1978), the occupant hermit crab considers mainly three factors of the gastropod shells, which are: shell condition, shell size, and shell species. It has been observed that the abundance and mortality of gastropod species greatly affect the shell preference of hermit crabs, whereas the architecture of the shell is mostly determined by the aperture width and length, total shell length, shell volume, and shell weight which are important factors governing the shell utilisation pattern as well (Bertness, 1980).

In the coastal region, the coexistence of multiple hermit crab species is common (Barnes, 2002). In sympatric hermit crab species, coexistence is possible due to the differential use of gastropod shells of various shapes and sizes, resulting in inter-specific resource partitioning (Bach et al., 1976; Teoh and Chong, 2014). On the other hand, it has also been observed that several coexisting *Clibanarius* species worldwide show overlap in shell occupancy and share the same gastropod shell species on rocky shores (Kruesi et al., 2022). Previous studies have shown that despite the high diversity of available gastropod shells, hermit crabs mostly occupy a few species (Trivedi et al., 2013; Trivedi and Vachhrajani, 2014a; Patel et al., 2020b, c; 2021; Thacker et al., 2021). Hence, the shell used by the hermit crab appears to be selective and not random; however, the preference and availability of shells also play a key role (Bertness, 1981a; Turra and Leite, 2000; Alcaraz and Kruesi, 2019; Kruesi et al., 2022). Apart from the preferences for shells with and without epibionts (Gherardi, 1990), the selection of shells is dependent on at least three major factors: shell species (shell shape), size, and availability (Teoh and Chong, 2014); however, a study evaluating all these factors in shell selection has not been carried out so far in India.

A total of 18 species (4 genera, 2 families) of hermit crabs are reported from the state (Trivedi and Vachhrajani, 2017; Patel et al., 2020a), among which *Clibanarius rhabdodactylus* and *C. ransoni* are commonly found in the rocky intertidal region of the Saurashtra coast. In the state, several studies have been carried out on the ecology of hermit crabs (Desai and Mansuri, 1989; Vaghela and Kundu, 2012; Trivedi et al., 2013; Trivedi and Vachhrajani, 2014a; Patel et al., 2020b, c, 2021), but no study has focused on the shell use pattern of sympatric hermit crab species. Hence, the present study was aimed at examining the difference in gastropod shell utilisation and assessing the relationship between the morphology of the hermit crab species and the different morphological parameters of gastropod shells utilised by these two hermit crab species.

The detailed methodology for data collection has been described in Materials and Methods chapter (page 55). The following flow chart shows a summary of the methodology used in the present chapter.



Results

In the present study, a total of 1000 individuals for each of the species, viz., *C. rhabdodactylus* and *C. ransoni*, were collected during the study period. Out of these 1000 individuals of *C. rhabdodactylus* collected, 340 individuals were males (34%), 305 individuals were non-ovigerous females (30.5%) and 355 individuals were ovigerous females (35.5%). The result suggests that the population was female biased (1:1.93). In the case of *C. ransoni*, 455 were males (45.5%), 308 were non-ovigerous females (30.8%) and 237 were ovigerous females (23.7%) having a female biased population (1:1.25) (Table 4). Among the total collected specimens of *C. rhabdodactylus,* their size ranged in the 1.01 mm to 8.0 mm SL, with the maximum number of individuals recorded from 3.01–4.0 mm SL size class and the least number of individuals recorded in the 7.01–8.0 mm SL size class (Figure 25A). Similarly, the size of the collected specimens of *C. ransoni* ranged from 1.01 mm to 8.0 mm SL, with the maximum number of individuals recorded in the 3.01–4.0 mm SL size class and the least number of individuals recorded in the 7.01–8.0 mm SL size class (Figure 25B).

Table 4. Carapace shield length values of *Clibanarius rhabdodactylus and Clibanarius ransoni*. (ANOVA; ***p <0.001; N = total individuals; SL = Shield length; M = Male; NOF = Non-ovigerous female; OF = Ovigerous female).

Species	**SL (mm)**	**M**	**NOF**	**OF**
C. rhabdodactylus	mean ± SD	4.58±0.98***	3.46±0.73***	3.74±0.51***
	N	340	305	355
C. ransoni	mean ± SD	4.38±1.27***	3.44±0.78***	3.74±0.5***
	N	455	308	237

The male individuals of *C. rhabdodactylus* (ANOVA F = 218.47, df = 999, p <0.001) and *C. ransoni* (ANOVA F = 87, df = 999, p <0.001) were significantly larger as compared to the female individuals. Male individuals of *C. rhabdodactylus* and *C. ransoni* were recorded in almost all the size classes, with a maximum number of individuals recorded from 4.0 to 5.0 mm SL size class. The female individuals of *C. rhabdodactylus* and *C. ransoni* were recorded from 1.0 to 7.0 mm SL size class, with a maximum number of individuals recorded from 3.0 to 4.0 mm SL size class (Figure 25).

It was observed that the individuals of *C. rhabdodactylus* were occupying a total of 29 gastropod shell species, out of which male individuals occupied 25 species, non-ovigerous female individuals occupied 27 species, and ovigerous female individuals occupied 23 species of gastropod shells (Table 5). On the other hand, the individuals of *C. ransoni* were found occupying 28 gastropod shell species, out of which male individuals occupied 25 species, non-ovigerous female individuals occupied 23 species, and ovigerous female individuals occupied 14 species (Table 6). However, it was found that both the hermit crab species were frequently utilising only five gastropod species: *Cerithium caeruleum* G. B. Sowerby II, 1855; *Lunella coronata* (Gmelin, 1791); *Tenguella granulata* (Duclos, 1832); *Turbo bruneus* (Röding, 1798) and *Pollia undosa* (Linnaeus, 1758) (Figure 26, Tables 5 and 6).

In terms of percentage of shell occupation, *C. caeruleum* was the most frequently occupied by *C. rhabdodactylus,* followed by *L. coronata*, *T. granulata*, *T. bruneus* and *P. undosa* (Table 5). In the case of *C. ransoni* also, *C. caeruleum* shells were most frequently occupied, followed by *L. coronata*, *T. bruneus*, *T. granulata* and *P. undosa* (Table 6). It was observed that *C. rhabdodactylus* occupied 87.3% of the five gastropod species, while *C. ransoni* occupied 77.8% of the five gastropod species. Among the most frequently occupied gastropod species, the abundance of *C. caeruleum* was highest recorded, followed by *L. coronata, T. granulata, T. bruneus,* and *P. undosa* in the rocky intertidal region of Veraval (Figure 27). The regression analysis showed a strong relationship between hermit crab morphology and gastropod shell morphological parameters. It was observed that the SL and HW of both hermit crab species showed a significant relationship with almost all the morphological parameters of gastropod shells (Table 7).

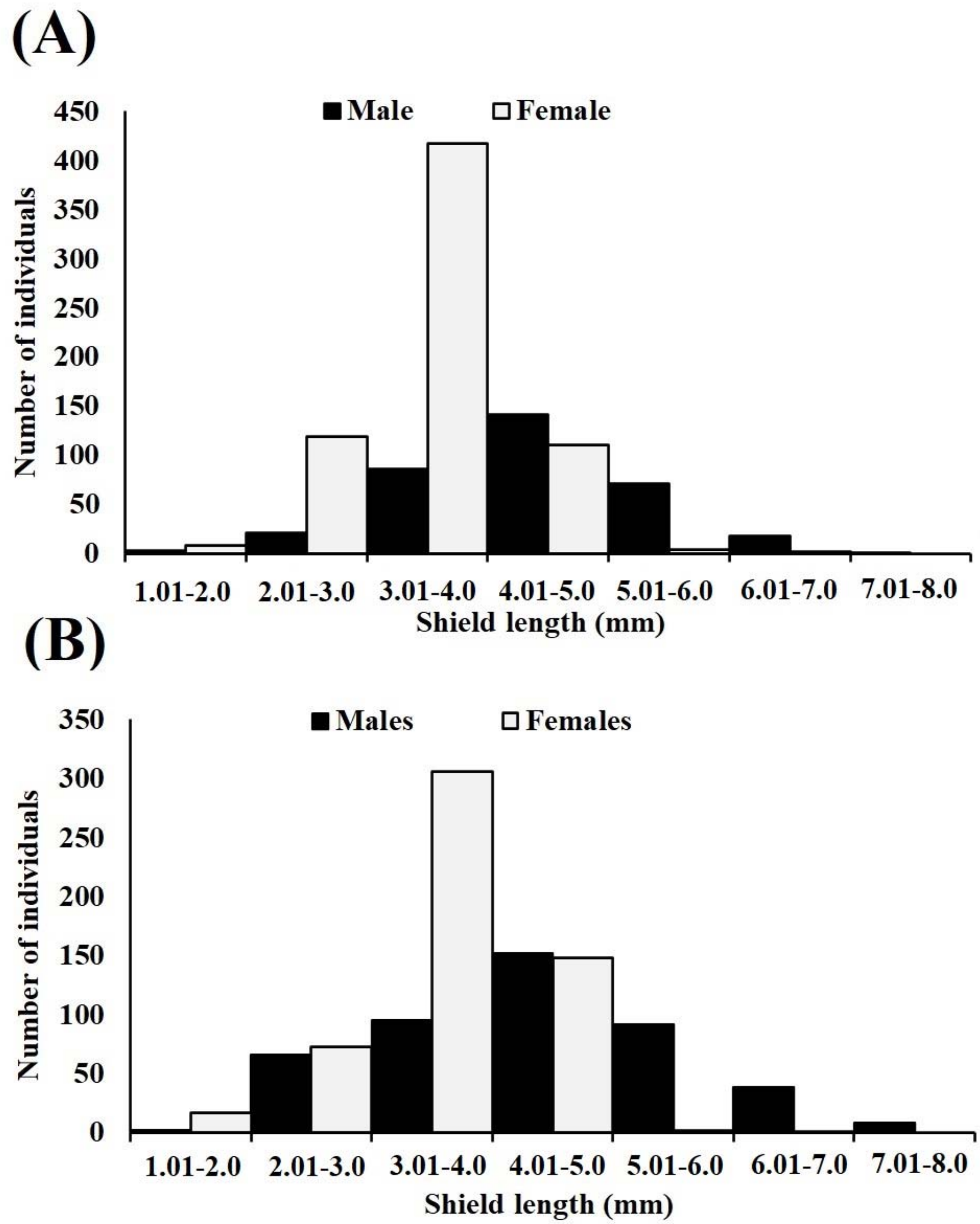


Figure 25. Size frequency (SL) distribution of male and female individuals of (A) *Clibanarius rhabdodactylus* (n= 1000 individuals) and (B) *Clibanarius ransoni* (n=1000 individuals).

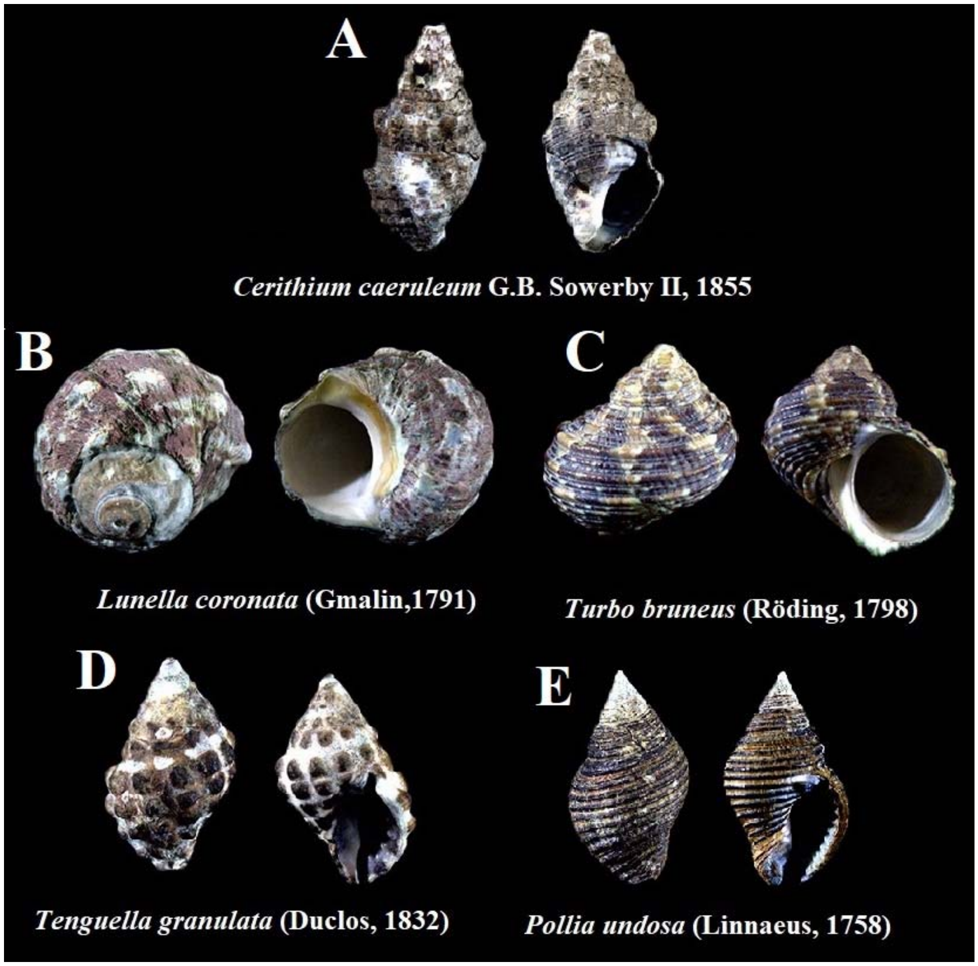


Figure 26. Five most frequently occupied gastropod shells by the hermit crab species *Clibanarius rhabdodactylus* and *Clibanarius ransoni*.

Table 8 shows an evident shell occupation pattern among different sexes of *C. rhabdodactylus* and *C. ransoni*. It was observed that among the five highly occupied gastropod shells, the male and ovigerous female individuals occupied comparatively larger, heavier, and more voluminous shells, while non-ovigerous female individuals occupied comparatively smaller, lighter, and less voluminous gastropod shells. Table 9 shows an evident shell occupation pattern among different reproductive stages of *C. rhabdodactylus,* while Table 10 shows an evident shell occupation pattern among different reproductive stages of *C. ransoni*. It was observed that amongst the five highly occupied shells, juvenile individuals (1–3 mm SL) were occupying the shells of *C. caeruleum* more, which are comparatively smaller, lighter, elongated and have a smaller aperture. On the other hand, the adult individuals (3–7 mm SL) occupied comparatively larger, heavier, and voluminous shells.

The five distinguishing morphological parameters (SHL, SHAL, SHAW, SHW, and SHV) of five frequently occupied gastropod shells are represented in Figure 28. The minimum (2.0 mm) and maximum (48.76 mm) SHL were observed in *L. coronata* and *C. caeruleum* respectively, while the mean SHL varied significantly among the five gastropod shell species ($F = 86.20$, $df = 1999$, $p<0.001$). The minimum (3.44 mm) and maximum (40.0 mm) SHAL were observed in *C. caeruleum* and *T. bruneus,* respectively, while the mean SHAL varied significantly among the five gastropod shell species ($F = 79.48$, $df = 1999$, $p<0.001$). The minimum (1.4 mm) and maximum (21.67 mm) SHAW were observed in *C. caeruleum* and *L. coronata,* respectively, while the mean SHAW varied significantly among the five gastropod shell species ($F = 535.40$, $df = 1999$, $p<0.001$). The minimum (0.21 g) and maximum (16.00 g) SHW were observed in *T. bruneus,* while the mean SHW varied significantly among the five gastropod shell species ($F = 312.65$, $df = 1999$, $p<0.001$). The minimum (0.05 mm^3) and maximum (6.0 mm^3) SHV were observed in *C. caeruleum* and *T. bruneus,* respectively, while the mean SHV varied significantly among the five gastropod shell species ($F = 618.62$, $df = 1999$, $p<0.001$).

Table 5. Gastropod shell utilisation by *Clibanarius rhabdodactylus*. (N = total individuals; M = Male; NOF = Non-ovigerous female; OF = Ovigerous female).

Gastropod species	**N**	**%**	**M**	**%**	**NOF**	**%**	**OF**	**%**
Cerithium caeruleum G. B. Sowerby II, 1855	654	65.4	133	39.0	233	76.6	288	81.1
Lunella coronata (Gmalin,1791)	78	7.8	67	19.6	9	3.0	2	0.6
Tenguella granulata (Duclos, 1832)	57	5.7	3	0.9	21	6.9	33	9.3
Turbo bruneus (Roding, 1798)	44	4.4	38	11.1	4	1.3	2	0.6
Pollia undosa (Linnaeus, 1758)	38	3.8	29	8.5	5	1.6	4	1.1
Astralium stellare (Gmelin, 1791)	13	1.3	9	2.6	3	1.0	1	0.3
Chicoreus bruneus (Link, 1807)	12	1.2	11	3.2	1	0.3	0	0.0
Indothais sacellum (Gmelin, 1791)	12	1.2	10	2.9	1	0.3	1	0.3
Purpura panama (Roding, 1798)	11	1.1	9	2.6	1	0.3	1	0.3
Chicoreus maurus (Broderip, 1833)	9	0.9	7	2.1	1	0.3	1	0.3
Semiricinula tissoti (Petit de la Saussaye, 1852)	9	0.9	1	0.3	4	1.3	4	1.1
Ergalatax contracta (Reeve, 1846)	7	0.7	1	0.3	5	1.6	1	0.3

Euchelus asper (Gmelin, 1791)	6	0.6	4	1.2	1	0.3	1	0.3
Morula uva (Roding, 1798*)*	6	0.6	2	0.6	1	0.3	3	0.8
Gyrineum natator (Roding, 1798)	5	0.5	3	0.9	1	0.3	1	0.3
Orania subnodulosa (Melvill,1893)	5	0.5	1	0.3	2	0.7	2	0.6
Poliia rubiginosa (Reeve, 1846)	4	0.4	3	0.9	1	0.3	0	0.0
Cerithium echinatum Lamarck, 1822	3	0.3	1	0.3	1	0.3	1	0.3
Clypeomorus batillariaeformis Habe & Kosuge, 1966	3	0.3	1	0.3	1	0.3	1	0.3
Ergalatax heptagonalis (Reeve,1846)	3	0.3	0	0.0	2	0.7	1	0.3
Indothais lacera (Born,1778)	3	0.3	2	0.6	0	0.0	1	0.3
Nerita oryzarum Recluz, 1841	3	0.3	2	0.6	1	0.3	0	0.0
Paradrillia patruelis (E. A. Smith,1875)	3	0.3	0	0.0	1	0.3	2	0.6
Nassarius marmoreus (A. Adams, 1852)	3	0.3	1	0.3	1	0.3	1	0.3
Cerithium columna Sowerby I, 1834	2	0.2	0	0.0	1	0.3	1	0.3
Cerithium coralium kiener, 1841	2	0.2	0	0.0	1	0.3	1	0.3
Mitra scutulata (Gmelin, 1791)	2	0.2	1	0.3	1	0.3	0	0.0

Monodata australis (Lamarck, 1822)	2	0.2	1	0.3	1	0.3	0	0.0
Vanikoro cuvieriana (Recluz, 1843)	1	0.1	1	0.3	0	0.0	0	0.0
	1000		**341**		**304**		**355**	

Table 6. Gastropod shell utilisation by *Clibanarius ransoni*. (N = total individuals; M = Male; NOF = Non-ovigerous female; OF = Ovigerous female).

Gastropod species	**N**	**%**	**M**	**%**	**NOF**	**%**	**OF**	**%**
Cerithium caeruleum G.B. Sowerby II, 1855	532	53.2	130	29.2	206	66.2	196	80.3
Lunella coronata (Gmalin,1791)	91	9.1	84	18.9	7	2.3	0	0.0
Turbo bruneus (Röding, 1798)	73	7.3	59	13.3	11	3.5	3	1.2
Tenguella granulata (Duclos, 1832)	43	4.3	10	2.2	13	4.2	20	8.2
Pollia undosa (Linnaeus, 1758)	39	3.9	29	6.5	9	2.9	1	0.4
Astralium stellare (Gmelin, 1791)	28	2.8	16	3.6	11	3.5	2	0.8
Chicoreus bruneus (Link, 1807)	23	2.3	23	5.2	0	0.0	0	0.0
Euchelus asper (Gmelin, 1791)	18	1.8	12	2.7	6	1.9	0	0.0
Indothais sacellum (Gmelin, 1791)	18	1.8	10	2.2	3	1.0	5	2.0

Semiricinula tissoti (Petit de la Saussaye, 1852)	17	1.7	3	0.7	10	3.2	3	1.2
Chicoreus maurus (Broderip, 1833)	14	1.4	12	2.7	0	0.0	2	0.8
Purpura panama (Röding, 1798)	13	1.3	10	2.2	3	1.0	0	0.0
Poliia rubiginosa (Reeve, 1846)	13	1.3	2	0.4	6	1.9	3	1.2
Anachis terpsichore (G. B. Sowerby ll, 1822)	8	0.8	0	0.0	8	2.6	0	0.0
Gyrineum natator (Röding, 1798)	8	0.8	7	1.6	1	0.3	0	0.0
Morula uva (Roding, 1798)	8	0.8	4	0.9	3	1.0	1	0.4
Cantharus spiralis (Gray, 1839)	8	0.8	6	1.3	1	0.3	1	0.4
Orania subnodulosa (Melvill,1893)	7	0.7	4	0.9	2	0.6	3	1.2
Cerithideopsilla cingulata (Gmelin,1971)	6	0.6	2	0.4	4	1.3	0	0.0
Nerita oryzarum Recluz, 1841	6	0.6	6	1.3	0	0.0	0	0.0
Monodata australis (Lamarck, 1822)	6	0.6	5	1.1	1	0.3	0	0.0
Indothais lacera (Born,1778)	5	0.5	3	0.7	1	0.3	1	0.4
Ergalatax contracta (Reeve, 1846)	4	0.4	0	0.0	1	0.3	3	1.2
Chicoreus virgineus (Röding, 1798)	4	0.4	4	0.9	0	0.0	0	0.0

Natica picta (Recluz,1844)	3	0.3	1	0.2	2	0.6	0	0.0
Tibia insulaechorab Röding, 1798	2	0.2	2	0.4	0	0.0	0	0.0
Nassarius reeveanus (Dunker, 1847)	2	0.2	1	0.2	1	0.3	0	0.0
Nassarius pullus (Linneus 1758)	1	0.1	0	0.0	1	0.3	0	0.0
	1000		**445**		**311**		**244**	

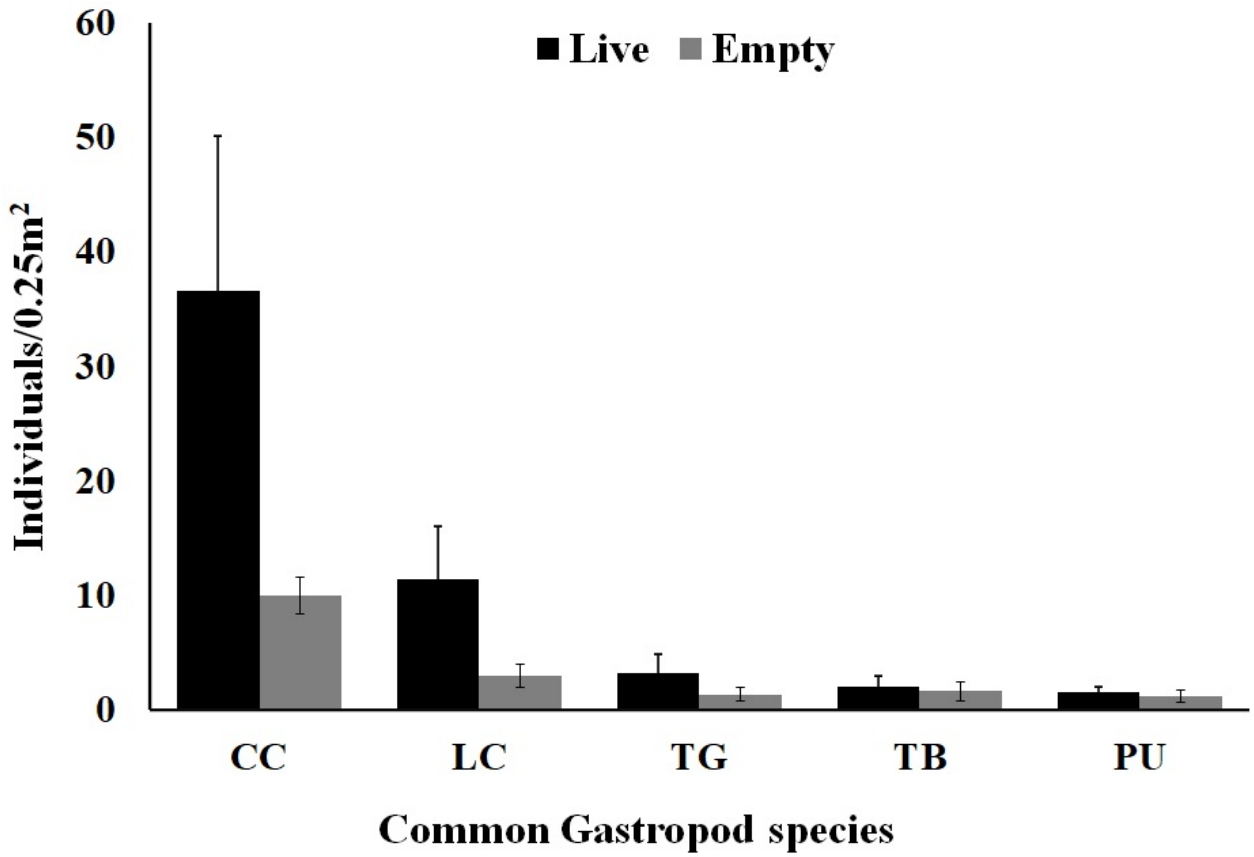


Figure 27. Abundance of commonly occurring gastropod species in the intertidal zone of Veraval, Saurashtra coast, Gujarat, India. (CC: *C. caeruleum*, LC: *L. coronata*, TG: *T. granulata*, TB: *T. bruneus*, PU: *P. undosa*).

Table 7. Regression equation in relation to the morphological parameters of different sexes of *Clibanarius rhabdodactylus* and *Clibanarius ransoni* and that of gastropod shells measures (*P < 0.05; **P<0.01; ***P<0.001; Shield length= SL; Hermit crab wet weight= HW; Shell length= SHL; Shell aperture length= SHAL; Shell aperture width= SHAW; Shell dry weight= SHW; Shell volume= SHV).

Species	Sex	N	Relationship	Y= axb	R^2
C. rhabdodactylus	Male	340	SLxSHL	y = 4.4527x + 8.5038	0.37***
			SLxSHAL	y = 2.0576x + 4.659	0.24***
			SLxSHAW	y = 1.625x + 0.6086	0.22***
			SLxSHW	y = 0.9784x - 1.3981	0.46***
			SLxSHV	y = 0.2469x - 0.3021	0.23***
			HWxSHL	y = 16.423x + 19.097	0.31***
			HWxSHAL	y = 7.3461x + 9.634	0.19***
			HWxSHAW	y = 6.6233x + 4.2675	0.23***
			HWxSHW	y = 4.0698x + 0.7782	0.49***
			HWxSHV	y = 1.0657x + 0.2342	0.27***
	Female	660	SLxSHL	y = 4.3381x + 8.1011	0.27***
			SLxSHAL	y = 2.5232x + 2.9572	0.30***
			SLxSHAW	y = 2.1274x - 0.4627	0.39***
			SLxSHW	y = 1.8132x - 4.1818	0.52***
			SLxSHV	y = 0.5261x - 1.2514	0.56***

			HWxSHL	y = 12.438x + 19.828	0.30
			HWxSHAL	y = 6.0764x + 10.535	0.23*
			HWxSHAW	y = 5.2355x + 5.8532	0.32*
			HWxSHW	y = 5.2152x + 0.709	0.58***
			HWxSHV	y = 1.495x + 0.1796	0.60***
C. ransoni	Male	455	SLxSHL	y = 6.2441x + 0.4477	0.57***
			SLxSHAL	y = 2.8026x - 0.3961	0.53***
			SLxSHAW	y = 2.1214x - 0.4868	0.58***
			SLxSHW	y = 2.551x - 6.4568	0.59***
			SLxSHV	y = 0.7986x - 2.113	0.60***
			HWxSHL	y = 12.685x + 18.877	0.56***
			HWxSHAL	y = 4.8788x + 8.4501	0.38***
			HWxSHAW	y = 3.6365x + 6.249	0.40***
			HWxSHW	y = 5.7064x + 0.7034	0.70***
			HWxSHV	y = 1.7751x + 0.1365	0.71***
	Female	545	SLxSHL	y = 5.7577x + 4.3753	0.54***
			SLxSHAL	y = 2.3247x + 1.2253	0.39***
			SLxSHAW	y = 1.5436x + 0.5425	0.39***
			SLxSHW	y = 1.2133x - 1.9048	0.55**

					*
			SLxSHV	y = 0.2463x - 0.3144	0.35***
			HWxSHL	y = 21.305x + 17.211	0.53***
			HWxSHAL	y = 7.0202x + 6.9784	0.25
			HWxSHAW	y = 5.3969x + 4.0972	0.34
			HWxSHW	y = 4.743x + 0.7088	0.59***
			HWxSHV	y = 0.915x + 0.2333	0.34***

Table 8. Mean values of different morphological parameters of five highly occupied gastropod shells by different sexes of *Clibanarius rhabdodactylus* and *Clibanarius ransoni* (Male= M; Ovigerous female= OF; Female= F; Shield length= SL; Shell length= SHL; Shell aperture length= SHAL; Shell aperture width= SHAW; Shell dry weight= SHW; Shell volume= SHV; NO= Not occupied).

Shell species	**Parameters**	***C. rhabdodactylus***			***C. ransoni***		
		Mean (mm)			**Mean (mm)**		
		M	**OF**	**F**	**M**	**OF**	**F**
Cerithium caeruleum	SHL (mm)	26.46±5.10	25.29±3.82	24.06±4.70	25.73±6.50	26.51±3.70	25.56±4.85
	SHAL (mm)	13.18±2.82	12.47±2.46	11.68±2.48	9.70±3.16	9.89±2.12	9.32±2.05
	SHAW (mm)	7.11±2.20	6.58±2.36	6.27±1.84	6.48±1.97	6.21±1.58	6.06±1.60
	SHW (g)	2.56±1.10	2.22±0.65	1.96±0.85	2.63±1.50	2.55±0.80	2.51±1.02
	SHV (mm^3)	0.69±0.29	0.59±0.19	0.53±0.21	0.57±0.34	0.56±0.22	0.53±0.20
Lunella coronata	SHL (mm)	21.38±4.39	22.28±0.04	18.40±6.98	21.82±5.04	NO	17.00±6.05
	SHAL (mm)	14.43±2.77	12.42±0.04	11.90±3.26	11.36±3.03	NO	8.36±2.71
	SHAW (mm)	12.91±3.46	12.00±0.03	9.55±3.27	11.11±2.92	NO	7.52±1.81
	SHW (g)	4.72±1.52	4.96±0.03	2.58±0.72	4.86±2.41	NO	1.77±1.32
	SHV (mm^3)	1.56±0.42	1.99±0.01	0.72±0.38	1.58±0.79	NO	0.62±0.50

Polia undosa	SHL (mm)	32.16±2.05	30.53±0.86	30.89±2.79	30.81±4.81	30.48±0.00	26.63±9.27
	SHAL (mm)	19.06±1.69	18.37±1.17	17.91±3.25	13.95±4.37	11.30±0.00	10.66±1.62
	SHAW (mm)	7.67±0.74	7.42±0.73	6.90±0.88	7.03±1.03	6.49±0.00	6.39±0.83
	SHW (g)	4.44±0.65	3.42±0.98	3.00±2.28	4.14±1.43	4.23±0.00	3.75±1.15
	SHV (mm^3)	1.28±0.25	1.30±0.14	1.25±0.21	1.24±0.44	1.00±0.00	1.02±0.34
Tenguella granulata	SHL (mm)	29.06±2.05	24.72±2.80	22.90±3.14	20.39±4.30	24.78±3.21	22.72±2.91
	SHAL (mm)	13.38±1.91	11.66±2.00	10.84±1.90	7.61±2.71	11.10±2.33	10.46±1.80
	SHAW (mm)	5.20±0.63	5.16±0.88	4.81±1.34	3.72±0.80	5.26±1.14	5.18±1.72
	SHW (g)	2.14±0.24	1.84±0.48	1.48±0.47	1.38±0.48	1.96±0.57	1.66±0.39
	SHV (mm^3)	0.57±0.12	0.57±0.19	0.47±0.16	0.45±0.20	0.55±0.17	0.41±0.11
Turbo bruneus	SHL (mm)	29.48±6.05	29.035±0.21	21.35±4.43	29.09±11.36	31.71±0.00	12.31±1.22
	SHAL (mm)	16.35±5.68	14.85±0.03	9.92±2.00	13.94±6.01	11.67±0.00	5.59±0.66
	SHAW (g)	12.93±2.86	10.71±0.06	9.45±1.95	12.56±4.91	7.75±0.00	5.60±0.72
	SHW (mm)	5.71±2.60	3.72±0.06	2.63±1.22	6.15±4.74	3.59±0.00	0.56±0.20
	SHV (mm^3)	2.18±0.99	1.30±0.14	1.04±0.47	2.48±1.85	0.70±0.00	0.32±0.11

Table 9. Mean values of different morphological parameters of five highly occupied gastropod shells by different reproductive stages (juveniles=1–3 mm; adults= 3–7 mm) of *Clibanarius rhabdodactylus* Male= M; Ovigerous female= OF; Female= F; Shield length= SL; Shell length= SHL; Shell aperture length= SHAL; Shell aperture width= SHAW; Shell dry weight= SHW; Shell volume= SHV; NO= Not occupied).

Occupied shell species	Hermit crab size class (SL)	(n)	SHL (mm)	SHAL (mm)	SHAW (mm)	SHW (gm)	SHV (mm^3)
Cerithium caeruleum	1-3 mm	124	19.88 ± 4.89	9.85 ± 3.22	4.76 ± 1.61	1.25 ± 0.74	0.37 ± 0.15
	3-5 mm	527	26.17 ± 3.42	12.83 ± 2.06	6.92 ± 2.02	2.37 ± 0.67	0.63 ± 0.2
	5-7 mm	5	27.1 ± 5.5	13.93 ± 2.46	10.03 ± 4.73	4.17 ± 1.91	1.08 ± 0.44
Lunella coronata	1-3 mm		*NO*	*NO*	*NO*	*NO*	*NO*
	3-5 mm	41	19.51 ± 3.58	13.53 ± 2.41	12.31 ± 3.07	3.72 ± 1	1.28 ± 0.42
	5-7 mm	37	23.03 ± 4.86	14.9 ± 3.12	12.99 ± 3.9	5.51 ± 1.53	1.77 ± 0.4
Polia undosa	1-3 mm		*NO*	*NO*	*NO*	*NO*	*NO*
	3-5 mm	29	31.9 ± 2.24	18.94 ± 1.87	7.62 ± 0.81	4.21 ± 1	1.27 ± 0.25
	5-7 mm	9	31.97 ± 0.58	18.68 ± 1.03	7.42 ± 0.21	4.34 ± 0.54	1.33 ± 0.1
Tenguella granulata	1-3 mm	9	20.84 ± 3.09	9.83 ± 1.44	4.2 ± 0.52	1.24 ± 0.49	0.37 ± 0.11

	3-5 mm	48	25.1 ± 2.7	11.83 ± 1.96	5.22 ± 1.06	1.84 ± 0.44	0.57 ± 0.17
	5-7 mm		*NO*	*NO*	*NO*	*NO*	*NO*
Turbo bruneus	1-3 mm		*NO*	*NO*	*NO*	*NO*	*NO*
	3-5 mm	16	23.43 ± 3.92	13.28 ± 3.45	10.68 ± 2.69	3.19 ± 1.21	1.36 ± 0.62
	5-7 mm	28	32 ± 4.79	17.11 ± 6.17	13.62 ± 2.43	6.61 ± 2.36	2.43 ± 0.96

Table 10. Mean values of different morphological parameters of five highly occupied gastropod shells by different reproductive stages (juveniles=1–3 mm; adults= 3–7 mm) of *Clibanarius ransoni* (N = total individuals; M = Male; OF = Ovigerous female; F = Female; SL = Shield length; SHL = Shell length; SHAL = Shell aperture length; SHAW = Shell aperture width; SHW = Shell dry weight; SHV = Shell volume; NO = Not occupied).

Occupied shell species	Hermit crab size class	N	SHL (mm)	SHAL (mm)	SHAW (mm)	SHW (gm)	SHV (mm^3)
Cerithium caeruleum	1-3 mm	84	18.13 ± 4.59	6.82 ± 2.67	4.24 ± 1.06	1.12 ± 0.87	0.28 ± 0.2
	3-5 mm	444	27.16 ± 3.46	10.06 ± 1.98	6.52 ± 1.53	2.76 ± 0.85	0.59 ± 0.2
	5-7 mm	4	37.94 ± 7.59	13.43 ± 1.81	9.31 ± 0.98	6.33 ± 2.48	1.55 ± 0.87

Lunella coronata	1-3 mm	7	12.25 ± 1.75	6 ± 0.81	5.93 ± 0.85	0.98 ± 0.44	0.38 ± 0.12
	3-5 mm	57	20.55 ± 3.89	10.51 ± 2.21	10.38 ± 2.44	3.83 ± 1.44	1.34 ± 0.62
	5-7 mm	27	25.82 ± 3.96	13.79 ± 2.56	13.07 ± 2.32	7.19 ± 2.14	2.14 ± 0.76
Polia undosa	1-3 mm	4	21.1 ± 6.62	8.28 ± 2.04	5.73 ± 1.66	1.69 ± 1.7	0.48 ± 0.36
	3-5 mm	27	29.42 ± 6.04	13.03 ± 3.95	6.72 ± 0.81	3.9 ± 0.95	1.15 ± 0.32
	5-7 mm	8	34.12 ± 1.51	15.27 ± 3.67	7.74 ± 0.53	5.32 ± 0.62	1.54 ± 0.33
Tenguella granulata	1-3 mm	12	19.11 ± 2.55	7.29 ± 2.03	3.85 ± 0.77	1.44 ± 0.58	0.38 ± 0.18
	3-5 mm	31	23.89 ± 3.45	10.52 ± 2.46	5.03 ± 1.45	1.78 ± 0.5	0.5 ± 0.16
	5-7 mm		*NO*	*NO*	*NO*	*NO*	*NO*
Turbo bruneus	1-3 mm	4	6.14 ± 1.01	5.96 ± 0.86	0.75 ± 0.37	0.38 ± 0.12	0 ± 0
	3-5 mm	27	19.99 ± 6.27	9.44 ± 2.76	8.63 ± 2.26	2.34 ± 1.54	0.92 ± 0.77
	5-7 mm	42	37.39 ± 5.8	18.09 ± 4.01	16.16 ± 2.66	9.34 ± 3.59	3.77 ± 1.28

The CCA analysis between the hermit crab morphology and gastropod shell parameters is represented in Figure 29, which revealed that the smaller size males (CRHM1, CRHM2, CRSM1 and CRSM2) and females (CRHF1, CRHF2, CRSF1 and CRSF2) of *C. rhabdodactylus* and *C. ransoni* occupied the shells with smaller SHAL and lesser SHW and SHV, such as C. *caeruleum*, *T. granulata* and *P. undosa.* The larger males (CRHM3 and CRSM3) and females (CRHF3) of *C. rhabdodactylus* and *C. ransoni* occupied more globular shells with higher SHAW and SHV, like *L. coronata* and *T. bruneus*.

Discussion

The intertidal region represents a unique type of habitat that shows a transition between terrestrial and aquatic habitats. During high tide, the intertidal region is converted into an aquatic habitat, while it becomes semi-terrestrial during low tide when the water recedes to its lower level (Trivedi and Vachhrajani, 2014a). Animals residing in this habitat need to develop special adaptations that enable them to survive in an environment where environmental conditions fluctuate continuously. Hermit crabs are among such marine organisms that have adapted to successfully thrive in the ever-fluctuating intertidal and subtidal habitats (Schembri, 1982), and hence they are the most common group of decapod crustaceans that can be found in the intertidal region (Trivedi and Vachhrajani, 2014a). Occupying empty shells protects the hermit crab from various predators (Elwood et al., 1995), mechanical damage caused by the wave action mostly at the lower intertidal region (Reese, 1962, 1969), as well as desiccation due to higher temperature, which is a major abiotic factor affecting the upper intertidal zone (Bertness and Cunnigham, 1981).

The behaviour of hermit crabs associated with the use of shells is their major behavioural adaptation, enabling them to survive successfully in the intertidal and sub-tidal environments (Reese, 1969; Elwood et al., 1995). In the present study, it was found that the males, non-ovigerous females, and ovigerous females of both the hermit crab species were almost similar in size. Sexual dimorphism was observed in both the populations of *C. rhabdodactylus* and *C. ransoni*, where males were significantly larger compared to non-ovigerous females and ovigerous females. Previous studies have also found similar results for other species of *Clibanarius*, like *C. laevimanus* (Gherardi et al., 1994), *C. erythropus* (Benvenuto and Gherardi, 2001), *C. vittatus* (Sampaio and Masunari, 2010) and *C. zebra* (Trivedi et al., 2013, Trivedi and Vachhrajani, 2014a).

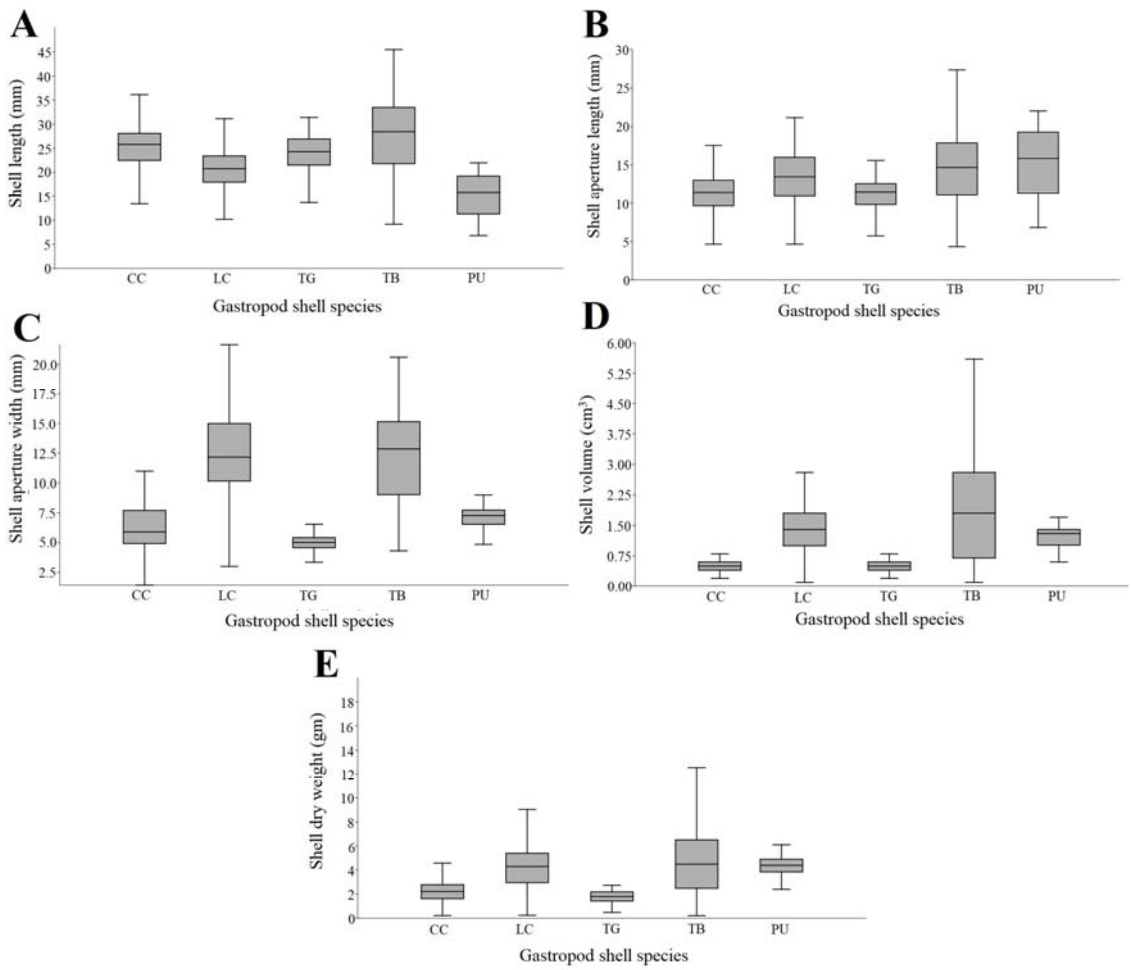


Figure 28. Box and whisker plots of (A) shell length, (B) shell aperture length, (C) shell aperture width, (D) shell volume and (E) shell dry weight of five frequently occupied shells by *Clibanarius rhabdodactylus* and *Clibanarius ransoni*. CC: *C. caeruleum*, LC: *L. coronata*, TG: *T. granulata*, TB: *T. bruneus*, PU: *P. undosa*; Box = 25th and 75th percentiles, midline = mean, whiskers = minimum and maximum values.

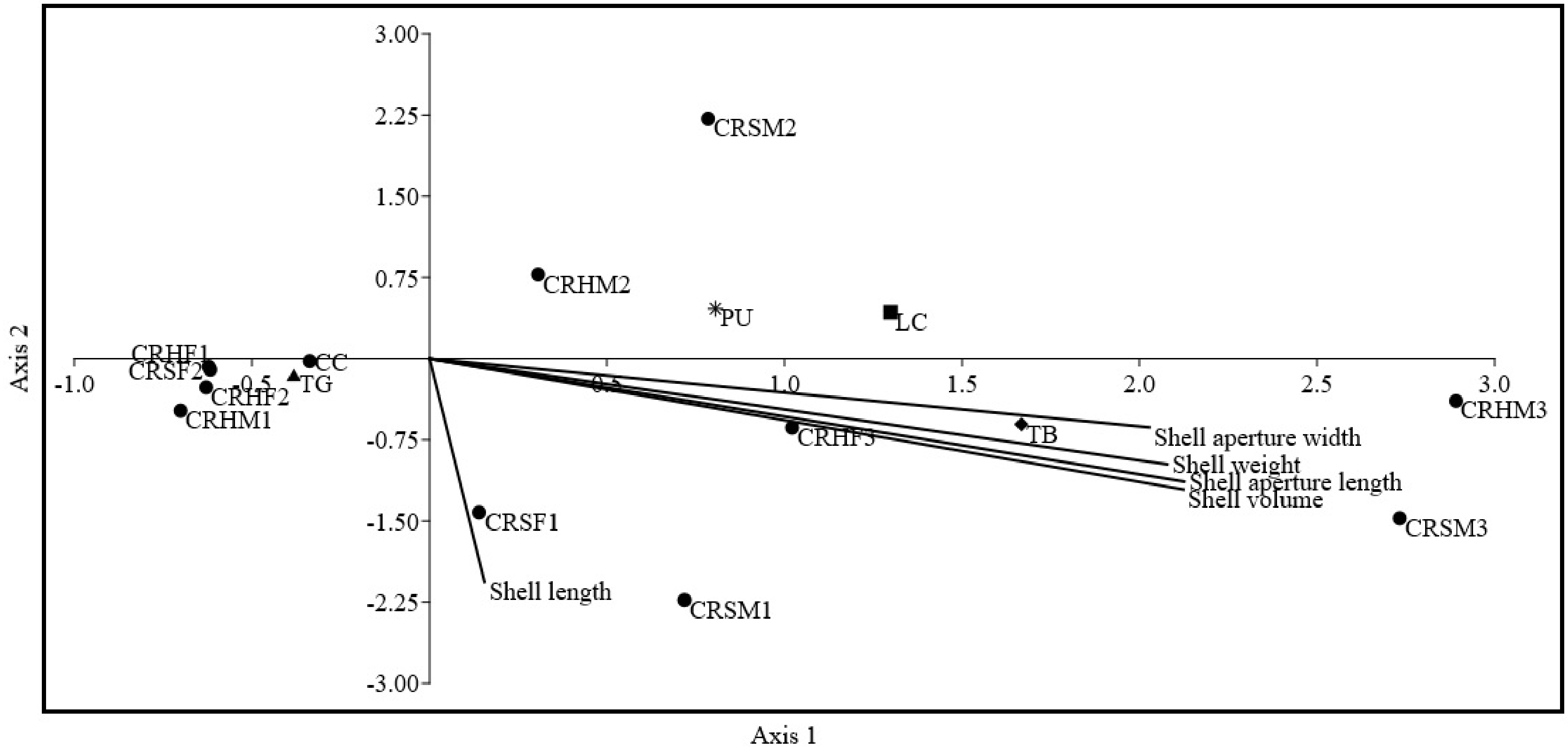


Figure 29. Canonical correspondence analysis (CCA) of shell use by *Clibanarius rhabdodactylus* and *Clibanarius ransoni* of different size classes as influenced by shell parameters. CC: *C. caeruleum*, LC: *L. coronata*, TG: *T. granulata*, TB: *T. bruneus*, PU: *P. undosa*. Lines indicate shell attributes in a direction of increasing magnitude. Filled circles indicate hermit crab species (CRH = *C. rhabdodactylus*, CRS=*C. ransoni*) by sex (M = male, F = female) and size class (please refer to Table 11 for the explanation).

Table 11. Groupings of hermit crab individuals on the basis of species, sex and size classes (shield length) with their annotated codes for canonical correspondence analysis (CCA). (N = total individuals).

Species	Sex	Size class (mm)	Code	N
C. rhabdodactylus	Female	1.0–3.0	CRHF1	114
		3.0–5.0	CRHF2	478
		5.0–7.0	CRHF3	5
	Male	1.0–3.0	CRHM1	18
		3.0–5.0	CRHM2	172
		5.0–7.0	CRHM3	62
C. ransoni	Female	1.0–3.0	CRSF1	59
		3.0–5.0	CRSF2	392
	Male	1.0–3.0	CRSM1	59
		3.0–5.0	CRSM2	180
		5.0–7.0	CRSM3	72

It was also found that the size of males and ovigerous females of both species of hermit crab was larger than that of non-ovigerous females. It was observed that the male individuals were occupying larger shells as compared to non-ovigerous females and ovigerous females in both species. The ovigerous females of *C. rhabdodactylus* and *C. ransoni* occupied larger shells than non-ovigerous females. Previous studies carried out on other hermit crab species, like *Diogenes puligator* (Manjón-Cabeza and Garcia-Raso, 1999), *D. nitidimanus* (Asakura, 1995), *Calcinus laevimanus*, *C. latens* and *Clibanarius humilis* (Nardone and Gherardi, 1997) have also found similar results. Generally, it has been observed that males occupy larger and more robust gastropod shells since they can use the majority of their energy for body growth, while non-ovigerous females occupy smaller gastropod shells as they save energy for the purpose of reproduction and egg development. Moreover, ovigerous females are observed to occupy more voluminous and larger shells compared to non-ovigerous females since they need more internal space for accommodation and protection of their eggs from predators and desiccation (Fotheringham, 1976a, b; Abrams, 1978; Wilber, 1989; Mantelatto and Garcia, 2000).

In the present study, it was observed that *C. rhabdodactylus* and *C. ransoni* utilised 29 species and 28 species of gastropod shells, respectively, which is higher as compared to the gastropod shells used by other hermit crab species. Sant'Anna et al. (2006), investigated the shell utilisation pattern of *C. vittatus* at the estuary of Sao Vicente, State of Sao Paulo, Brazil, and found that the hermit crab species was occupying only 13 gastropod shell species. Argüelles-Ticó et al. (2010) studied the shell utilisation pattern of *C. antillensis* at the rocky intertidal coast of Montepio, Veracruz, Mexico, and found that the hermit crab species was occupying only 25 gastropod shell species. Wait and Schoeman (2012), studied the shell utilisation pattern of *C. virescens* and discovered that the hermit crab species occupied only 17 gastropod shell species. Trivedi and Vachhrajani (2014a) studied the shell utilisation pattern of *C. zebra* and found that the hermit crab species occupied 23 gastropod shell species. Abd et al. (2015) studied the shell utilisation pattern of *C. erythropus* and found that the hermit crab species occupied only 11 gastropod shell species. Recently, in a study, Alcaraz and Kruesi (2019) investigated the shell utilisation pattern of *C. albidigitus* and found that the hermit crab species was occupying only 15 gastropod shell species.

It was also observed that the ovigerous female individuals of *C. rhabdodactylus* were occupying 23 species of gastropod shells, while the ovigerous female individuals of *C. ransoni* were occupying 14 species of gastropod shells. The gastropod shells occupied by the ovigerous female individuals of both species were significantly less as compared to the male and non-ovigerous female individuals of the same species. Similar types of results have been obtained for the ovigerous females of several other hermit crabs. For example, in a study carried out on *Diogenes puligator*, it was observed that out of 42 occupied gastropod shell species, the male and non-ovigerous female individuals occupied 31 and 29 species of gastropod shells, respectively, while the ovigerous female individuals occupied only 17 species of gastropod shells (Manjón-Cabeza and Garcia-Raso, 1999). Sant'Anna et al. (2006) studied the shell utilisation pattern of *C. vittatus* and found that out of 13 occupied gastropod shell species, the male and non-ovigerous female individuals occupied 10 and eight species of gastropod shells respectively, while the ovigerous female individuals occupied only two species of gastropod shells. In another study carried out on the shell utilisation pattern of *Isocheles sawayai* it was observed that out of 17 occupied gastropod shell species, the male and non-ovigerous female individuals occupied 14 and 10 species of gastropod shells respectively, while the ovigerous female individuals occupied only nine species of gastropod shells (Fantucci et al., 2008). In a similar study carried out in Gujarat state, it was observed that out of 23 gastropod shell species occupied by *C. zebra* individuals, the male and non-ovigerous female individuals occupied 22 and 21 species of gastropod shells, respectively, while the ovigerous female individuals occupied only 14 species of gastropod shells (Trivedi and Vachhrajani, 2014a). Studies suggest that ovigerous females have to accommodate and also incubate their egg mass in the gastropod shell, and therefore the ovigerous females are selective for the gastropod shells that have a larger internal space (Abram, 1978; Bertness, 1981c; Sallam, 2012).

In the present study, it was observed that *C. rhabdodactylus* and *C. ransoni* both had a great overlap in the pattern of distribution in the intertidal region of the study site. It was also observed that both the hermit crab species were using almost similar species of major occupied gastropod shells. Such a coexisting pair of hermit crabs sharing similar microhabitat and gastropod shell utilisation has also been documented in numerous other studies (Turra and Leite, 2000; Alcaraz and Kruesi, 2019; Alcaraz et al., 2020a, b; Kruesi et al., 2022). Additionally, it was found that individuals of *C. rhabdodactylus* and *C. ransoni* maximally utilised *C. caeruleum* over other gastropod species, probably as a result of the higher abundance of *C. caeruleum* species at the study site (31 individuals/0.25 m^2) (Figure 27). Previous studies carried out in different parts of the world have also reported similar types of results for the species, which are as follows: *C. antillensis* utilising *Tegula viridula* shells (Floeter et al., 2000); *Isocheles sawayai* utilising *Stramonita haemastoma* shells (Fantucci et al., 2008); *Diogenes moosai* and *D. lopochir* utilising *Cerithidea cingulata* shells (Teoh and Chong, 2014); *C. zebra* utilising *C. scabridum* shells (Trivedi and Vachhrajani, 2014a) and *Diogenes* *custos* utilising *Pollia undosa* shells (Patel et al., 2020b). Studies suggest that the availability as well as the abundance of gastropod shells in local habitat greatly affect the shell utilisation pattern of the hermit crab species (Kellogg, 1976; Scully, 1979; Barnes, 1999). Before occupying a gastropod shell, the hermit crab carries out a complex evaluation process of the shell and does not occupy the shell randomly, even if the gastropod shells are abundantly available in the habitat (Grant and Ulmer, 1974). The decision of shell selection is generally dependent on the morphology of the gastropod as well as the hermit crab itself, and accordingly, the best-fitting shell in terms of size, aperture, weight, and volume will be occupied by the hermit crab (Elwood et al., 1995; Caruso and Chemello, 2009).

Several other factors are also involved that determine the variation in the shell occupation by the hermit crab, including differences in the geographic habitat, differences in the size of hermit crabs of two species, and sexual differences (Barnes 2005). The analysis of the present study revealed that there was a significant relationship between the size (SL) of both the hermit crabs and all the morphological parameters of gastropod shells (SHL, SHAL, SHAW, SHW and SHV). Moreover, the hermit crab weight of both species of hermit crab also showed a significant relationship with the majority of the morphological parameters of gastropod shells (SHAL, SHAW, SHW and SHV).

Studies report that the larger and more robust shells occupied by the hermit crab provide them protection from predators and strong wave action, whereas the more spired shell protects the resident hermit crab from desiccation (Reese, 1969; Brown and McLachlan, 2002). Furthermore, the shell aperture is also a crucial morphological factor of the shell, as it is the only opening through which the resident crab can enter inside the shell. Hence, it should be optimally large enough to provide effortless mobility for the resident hermit crab to acquire food and at the same time, it should be narrow enough to provide protection from the predators (Abd El-Aziz et al., 2015).

It has been observed that hermit crabs do not occupy shells randomly, even if they are present abundantly (Grant and Ulmer, 1974). Only the best-fitting shell that fulfils almost all the requirements of the hermit crab is selected, which supports the better survival, mate choice, and resource utilisation of the resident. A similar pattern was observed, which was revealed by the CCA analysis as well as by the comparison between occupied shell morphology and different life stages (juveniles and adults). The analysis revealed that the smaller individuals of both hermit crab species frequently occupy *C. caeruleum* shells that are more spired and have a smaller aperture. Such greatly spired shells provide protection to the resident hermit crab from desiccation when it is exposed on the open surface at the time of low tide. Contrastingly, individuals larger in size occupied shells of *L. coronata* and *T. bruneus*, which were larger in size, voluminous, and more robust and could provide protection to the resident crab from predatory species as well as crushing action by strong waves in the lower intertidal region. The resident hermit crab benefits in various ways on the basis of the type of gastropod shell it occupies. For instance, the highly spired and elongated shells are best at providing protection from desiccation when exposed at the time of low tide, as they retain more amount of water. On the other hand, less spired but larger, voluminous and robust shells are effective for providing protection from predators and crushing by waves in the low tide zone (Bertness, 1981a).