PUBLICATIONS AND PRESENTATIONS

Fellowships/Grants

- SHODH (ScHeme Of Developing High quality research) (Reference no. 201901720029) for doctoral research.
- Science and Engineering Research Board (**SERB**) International Travel scheme (**ITS**): International travel grant to attend 6th World Conference on Marine Biodiversity organized by Centre for Marine & Coastal Studies, Universiti Sains, Penang, Malaysia, 2nd – 5th July, 2023. (File Number: ITS/2023/002086)

Research Publications

List of papers published from Ph. D. Work

1. **Patel, K. J.,** Vachhrajani, K. and Trivedi, J. (2023). Seasonal variation in the intertidal distribution of the hermit crab *Clibanarius rhabdodactylus* Forest, 1953 on the rocky shores of Saurashtra coast, Gujarat, India. Munis Entomology & Zoology, 18(1): 580–589.
2. **Patel, K. J.,** Vachhrajani, K. D. and Trivedi, J. N. (2022). Study on Shell Utilization Pattern of Two Sympatric Hermit Crab Species on the Rocky Intertidal Region of Veraval, Gujarat, India. Thalassas: An International Journal of Marine Sciences, 1–13.
3. **Patel, K. J.,** Vachhrajani, K. D. and Trivedi, J. N. (2022). Population structure and reproductive biology of *Clibanarius rhabdodactylus* Forest, 1953 (Crustacea: Anomura: Diogenidae) in Gujarat state, India. Regional Studies in Marine Sciences, 63: 1–9.

List of papers published from other work carried out during Ph. D. Duration

1. Patel, D., **Patel, K. J.,** Patel, P. and Trivedi, J. (2020). Shell utilization pattern by the hermit crab *Diogenes custos* (Fabricius, 1798) along Gulf of Kachchh, Gujarat, India. Journal of Biological Studies, 3(2): 79–95.
2. Patel, P., **Patel, K. J.** and Trivedi, J. (2020). First record of Hermit crab *Clibanarius ransoni* Forest, 1953 (Crustacea: Anomura: Diogenidae) from India. Journal of Biological Studies, 3(1): 19–23.
3. Patel, P., **Patel, K. J.,** Vachhrajani, K. and Trivedi, J. (2020). Shell utilization pattern of the Hermit crab *Clibanarius rhabdodactylus* Forest, 1953 on rocky

shores of the Saurashtra coast, Gujarat State, India. Journal of Animal Diversity, 2(4): 33–43.

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5. **Patel, K. J.,** Patel, P. and Trivedi, J. (2021). First record of *Manningis arabicum* (Jones and Clayton, 1983) (Decapoda, Brachyura, Camptandriidae) from India. Nauplius, 29.
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7. **Patel, K. J.,** Patel, P., Trivedi, J., Kumar, A. and Prakash, S. (2021). On the diversity of some Brachyuran Crabs (Crustacea: Decapoda) from bycatch at the Gulf of Mannar, Tamil Nadu, India. Journal of Biological Studies, 4(2): 41–72.
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9. Trivedi, J., Mitra, S., Patel, P., Maheta, N., **Patel, K. J.** and Ng, P. K. L. (2021). On the Indian species of *Eurycarcinus* A. Milne-Edwards, 1867, *Heteropanope* Stimpson, 1858, and *Pilumnopeus* A. Milne-Edwards, 1867 (Decapoda: Brachyura: Pilumnidae). Nauplius, 29.
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16. Patel, H., **Patel, K. J.** and Trivedi, J. (2021). Study of colour variation in intertidal crab *Leptodius exaratus* (H. Milne Edwards, 1834) inhabiting rocky shores of Saurashtra coast, Gujarat, India. Proceedings of the "Marine Biology Research Symposium – MBRS 2021," 67–80.
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45. **Patel, K. J.**, Patel, H., Ali, D., Gosavi, S., Choudhary, N., Yadav, V. K., Vachhrajani, K., Patel, A., Sahoo, D. K., & Trivedi, J. (2024). On population structure and breeding biology of burrowing crab *Dotilla blanfordi* Alcock, 1900. *PeerJ*, *12*, e17065.

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Conference presentations

1. (2023) **Patel KJ**, Trivedi JN: On population structure and breeding biology of burrowing crab *Dotilla blanfordi* Alcock, 1900. 6th Bhartiya Vigyan Sammelan organized by Vijnana Bharti and Government of Gujarat at Ahmedabad, Gujarat, India, 21st – 24th December, 2023. (**POSTER PRESENTATION)**

2. (2023) **Patel KJ,** Vachhrajani KD and Trivedi JN: Population structure and breeding biology of *Clibanarius rhabdodactylus* Forest, 1953 (Crustacea: Anomura: Diogenidae) in Gujarat state, India. 6th World Conference on Marine Biodiversity organized by Centre for Marine & Coastal Studies, Universiti Sains, Penang, Malaysia, 2nd – 5th July, 2023. (**POSTER PRESENTATION) (Awarded: Best poster presentation)**

3. (2022) **Patel KJ**, Vachhrajani KD, and Trivedi JN: On seasonal variation in the intertidal distribution of the hermit crab *Clibanarius rhabdodactylus* Forest, 1953 on the rocky shores of Saurashtra coast, Gujarat, India. National Seminar & 33rd All India Congress Of Zoology (AICZ) On Emerging Trends In Biological Sciences In Light Of Environmental Degradation & Life Sustainability, Department of Zoology, Pandit S.N. Shukla University, Shahdol Madhya Pradesh, 10th – 12th August 2022. (**ORAL PRESENTATION).**

4. (2022) **Patel KJ**, Vachhrajani KD, and Trivedi JN: Study on shell utilization pattern of two sympatric hermit crab species on the rocky intertidal region of

Veraval, Gujarat, India. XI Brazilian Congress on Crustaceans (CBC) & The Crustacean Society Summer Meeting (TCS) Summer meeting, Brazil, 06th – 08th June 2022. **(Video Poster presentation).**

5. **Patel KJ**, Patel P and Trivedi JN: Gastropod Shell Utilization Pattern of *Clibanarius ransoni* Forest, 1953 in the Rocky Intertidal Zone of Saurashtra Coast, Gujarat state, India. National symposium on MARINE BIOLOGY RESEARCH SYMPOSIUM (MBRS–2021), Sathyabama Institute of Science and Technology, Chennai in association with ICAR – National Bureau of Fish Genetic Resources, Lucknow, 26th – 30th July 2021. (**ORAL PRESENTATION) (Awarded: Best Oral presentation).**

6. **Patel KJ**, Patel P, Maheta N and **Trivedi JN**: On Diversity of Hermit crabs (Crustacea: Decapoda: Anomura) of India. National Conference on Ocean-Atmosphere Science and Technology (COAST 2020), Berhampur University, Berhampur, Odisha, 28 February – 1 March, 2020 (**POSTER PRESENTATION)**

Training and Workshops

- Workshop on "Impact of Micro-plastic on Health and Environment" held at PDEU campus, Gandhinagar, Gujarat, sponsored by Gujarat Environment Management Institute (GEMI) on January 17, 2024, (Wednesday).

- Training on taxonomy and ecology of Crustaceans at Animal Taxonomy and Ecology Laboratory, Department of Life Sciences, Hemchandracharya North Gujarat University, Patan for the period of 5 months (August to December 2022).
- Online workshop on "Basics of Bioinformatics and Phylogenetics" by Biologia Life Science LLP on 2nd to 4th February 2021.
- Online workshop on "Data Analysis with SPSS" by Commacad from 10th – 11th July, 2021.

- Workshop on "Scientific Image and Graphic Editing" by Biologia Life Science LLP on 21 to 22 September 2020.

- Online course on "DNA Taxonomy and Phylogeny" by Sathyabama Institute of Science and Technology on 21st to 23rd May 2020.

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Study on Shell Utilization Pattern of Two Sympatric Hermit Crab Species on the Rocky Intertidal Region of Veraval, Gujarat, India

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Abstract

The present study illustrates the shell utilization and resource partitioning of two sympatric hermit crab species *Clibanarius rhabdodactylus* and *Clibanarius ransoni* with reference to gastropod shell species (shell shape), shell size and shell availability. Specimens were collected from January to March 2021 and hermit crab weight and shield length were measured. The gender of occupant hermit crab was identified and categorised into male, non-ovigerous female and ovigerous female. Gastropod shells were identified and different morphological parameters like shell length, shell aperture length and width, shell volume and dry weight were measured. The population of *C. rhabdodactylus* and *C. ransoni* was female biased with male: female ratio being 1:1.93 and 1:1.25 respectively. *Clibanarius rhabdodactylus* and *C. ransoni* were occupying 29 species and 28 species of gastropod shells respectively among which > 75% occupied shells were comprised of *Cerithium caeruleum, Lunella coronata*, *Turbo bruneus*, *Tenguella granulate* and *Pollia undosa*. Both the *Clibanarius* species were showing a high overlap in their intertidal distribution as well as gastropod shell use pattern. *Cerithium caeruleum* was found to occur in high abundance as compared to other gastropod species in the study area which may also influence the shell utilization of hermit crab species. Males and non-ovigerous females of the hermit crab species utilized almost all shell species, while ovigerous females used only a few shell species. Significant relationship was observed between different morphological parameters of the occupant crab species and occupied shells. Shell partitioning was evident between hermit crab sexes as well as reproductive stages on the basis of occupied shells of different species, shapes, and sizes. The present study revealed shell occupation pattern of *C. rhabdodactylus* and *C. ransoni* is highly influenced by the diversity, morphology and availability of gastropod shells in the study area.

Keywords Sympatric species · Resource partitioning · Shell availability · Shell occupation · Rocky shore · Gujarat

Introduction

Hermit crabs have evolved to occupy empty shells or pseudo shells for the protection of their non-calcified pleon (Schejter and Mantelatto 2011; Schejter et al. 2017). They occupy the shells of dead molluscs or by removing the live animal from the shell (Rutherford 1977; Elwood and Neil 1992). Furthermore, the occupied shell protects the crab from various biotic and abiotic factors including predation, competition, temperature, osmotic stress and wave action (Reese 1969; Bertness 1981a, 1982; Hahn 1998; Angel 2000). Studies have shown that shape, size, abundance and quality of gastropod shells affect the population size (Vance 1972), growth (Fotheringham 1976; Turra and Leite 2003), morphology (Blackstone 1985), fecundity (Childress 1972; Fotheringham 1976) and survivorship (Angel 2000; Lively 1988) of hermit crabs. Hermit crabs acquire empty shells from the 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

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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).

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 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, shows overlap in the 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 majorly occupied a few species only (Benvenuto and Gherardi 2001; Ismail 2010; Trivedi et al. 2013; Trivedi and Vachhrajani 2014; Patel et al. 2020a, b, 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 (Hazlett, 1966; Fotheringham, 1976; Gherardi and Nardone, 1977; Bertness 1981a, b; Busato et al. 1998; 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 shell is dependent on at least three major factors, shell species (shell shape), size, and availability (Teoh and Chong 2014); however, study evaluating all these factors in shell selection has not been carried out so far in India.

Gujarat is the westernmost state of India having ~ 1650 km long coastline which constitutes about 21% of the total coastline of the country (Trivedi et al. 2015). The coastline can be divided into three major coastal regions viz. Gulf of Kachchh, Gulf of Khambhat and Saurashtra coast (Trivedi et al. 2015). A total of 17 species (4 genera, 2 families) of hermit crabs are reported from the state (Trivedi and Vachhrajani 2017; Patel et al. 2020c), amongst which *Clibanarius rhabdodactylus* Forest, 1953 and *C. ransoni* Forest, 1953 are commonly found in the rocky intertidal region 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 2014; Patel et al. 2020a, b; 2021), but no study was focused on the shell use pattern of sympatric hermit crab species. Hence the present study was aimed to examine the difference in gastropod shell utilization and to assess the relationship between the morphology of the hermit crab species and different morphological parameters of gastropod shells utilized by these two hermit crab species.

Methodology

Study Area

The present study was conducted in the rocky intertidal zone of Veraval (20°54′37″N, 70°21′04″E) (Fig. 1) located on the Saurashtra coast. The width of the exposed rocky intertidal zone during low tide varies from 60 to 150 m. *Clibanarius rhabdodactylus* and *C. ransoni* occur in high abundance on the rocky shores of the study site where it occupies rock crevices and shallow tide pools found in the upper and middle intertidal zone (Patel et al. 2021).

Sampling Method

The specimens of *C. rhabdodactylus* and *C. ransoni* were randomly collected from January to March 2021 during low tide. Collected specimens were kept in an icebox and brought to the laboratory for the further analysis. In the laboratory, removal of hermit crabs from the shells was done by gently twisting them against the direction of the shell spiral. Only intact individuals were used for the study. Gender of each individual was identified using a stereomicroscope (Metlab PST 901) and categorized into male, non-ovigerous female and ovigerous female. Female individuals can be identified by the presence of gonopores on the ventral part of the first segment of the second pair of walking legs, while male individuals do not have such structure. Ovigerous females are the females carrying egg masses.

Two morphological characteristics, hermit crab weight (HW) (0.01 g) and shield length (0.01 mm) (from the midpoint of the rostrum to the midpoint of the posterior margin of the shield) were measured using a digital weighing scale and vernier callipers respectively for each individual of hermit crabs. Ovigerous females were weighed with the egg mass. Hermit crabs were sorted into different size classes based on their shield length (SL). The occupied gastropod shells were identified to species level using a monograph by Apte (2014). Five morphological parameters of gastropod shells were analysed viz. shell total length (SHL) shell aperture length (SHAL); shell aperture width (SHAW), shell dry weight (SHW) and shell volume (SHV). For SHW, the shells were dried at 60 °C in a laboratory oven for 24 h and weighed (Argüelles-Ticó et al. 2010). For SHV, the empty shells were filled with water using a syringe with needle drop by drop to avoid the formation of bubbles (0.1 ml) till the edge of the aperture and the total volume of water filled is considered as the shell volume (mm^3). The individuals smaller than the smallest ovigerous female were considered as juvenile (< 2.98 mm CW) (Baeza et al. 2013). The abundance of five highly occupied gastropod shells was quantified using line transects intercepted with $0.25 m^2$ quadrate

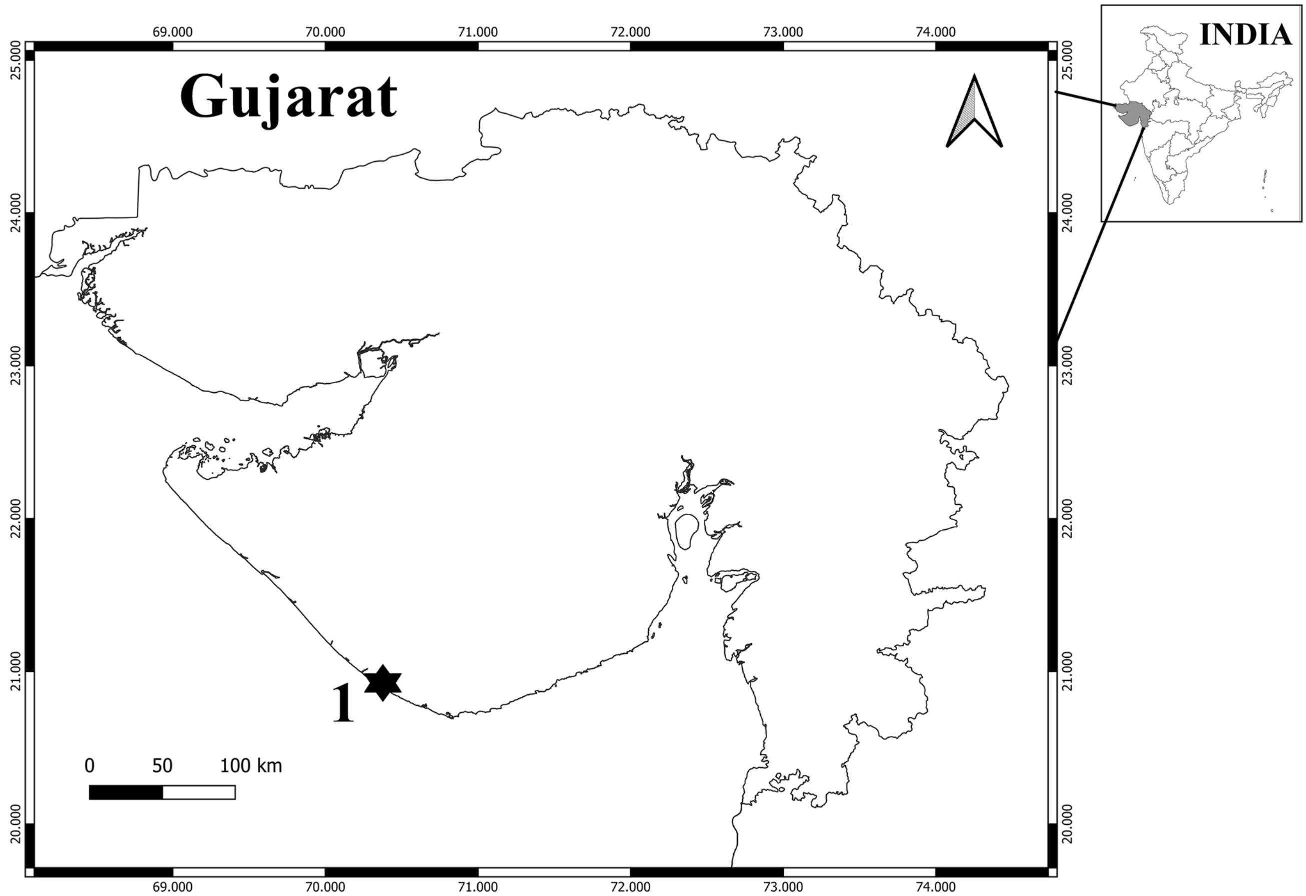

Fig. 1 Map of the study area. 1. Veraval, Saurashtra coast, Gujarat, India

every 5 m. A total of ten line transects were laid randomly, perpendicular to the shoreline from the high tide to the low tide mark to quantify the abundance of live and empty shells.

Data Analysis

The morphological parameters of gastropod shells and hermit crabs were correlated using Regression analysis to find out the relationship between them (Sant'Anna et al. 2006). Variation in mean values of shield length of different sexes of hermit crab was analysed using a one-way ANOVA at a 5% significance level. The shell species occupation rate was estimated as a percentage. Mean values of different morphological parameters of five highly occupied gastropod shells by different sexes as well as reproductive stages of *Clibanarius rhabdodactylus* and *Clibanarius ransoni* were calculated to understand the sexes or reproductive stage wise shell occupation pattern. Canonical Correspondence Analysis (CCA) was carried out to analyse the relationships between hermit crab morphometry (SL and HW) and shell parameters (SHL, SHAL, SHAW, SHW, SHV) and visualize the main features of crab (species, sex and size) distribution according to the gastropod shell species and characteristics. The sample data set comprised of the species of gastropod shells occupied by the hermit crab. The data set of the hermit crab species comprised by sex and size class (Table 4) was correlated, while the environmental data set comprised of the shell parameters (SHL, SHAL, SHAW, SHW, SHV). The data set for hermit crab species for different sex and size was given specific codes as: CRH = *C. rhabdodactylus*, CRS = *C. ransoni*, M = male, F = female, whereas the size classes are represented by numerals as shown in Table 4. All the statistical analysis were performed using PAST 4.03 software.

Results

A total of 1000 individuals each for both the species *C. rhabdodactylus* and *C. ransoni* were collected during the study period. Out of 1000 individuals of *C. rhabdodactylus* collected, 340 were males (34%), 305 were non-ovigerous females (30.5%) and 355 were ovigerous females (35.5%) which shows 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 1). The total collected specimens of *C. rhabdodactylus* and *C. ransoni* ranged from 1.01 mm to 8.0 mm SL with maximum number of individuals recorded from 3.01–4.0 mm SL size class and least from number of individuals recorded from 7.01–8.0 mm SL size class. 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 than females. Male individuals *C. rhabdodactylus* and *C. ransoni* were recorded in almost all size classes (Fig. 2B) with a maximum number of individuals recorded from 4.0 to 5.0 mm SL size class (Fig. 2). 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 (Fig. 2).

Individuals of *C. rhabdodactylus* were recorded occupying 29 gastropod shell species (males: 25 species, non-ovigerous females: 27 species, ovigerous females: 23 species) (Table 2) while *C. ransoni* were found occupying 28 gastropod shell species (males: 25 species, non-ovigerous females: 23 species, ovigerous females: 14 species) (Table 3). However, it was found that both the hermit crab species were frequently utilizing only five gastropod species viz. *Cerithium caeruleum* G. B. Sowerby II, 1855, *Lunella coronata* (Gmelin,1791), *Tenguella granulata* (Duclos, 1832), *Turbo bruneus* (Röding, 1798) and *Pollia undosa* (Linnaeus, 1758) (Tables 2 and 3). In terms of percentage of shell occupation, *C. caeruleum* was most frequently occupied by *C. rhabdodactylus* followed by *L. coronata*, *T. granulata*, *T. bruneus* and *P. undosa* (Table 2). 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 3). 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 (Fig. 3). The regression analysis showed a strong relationship between hermit crab morphology and gastropod shell morphological parameters (Table 4). It was observed that the SL and HW of both hermit crab species

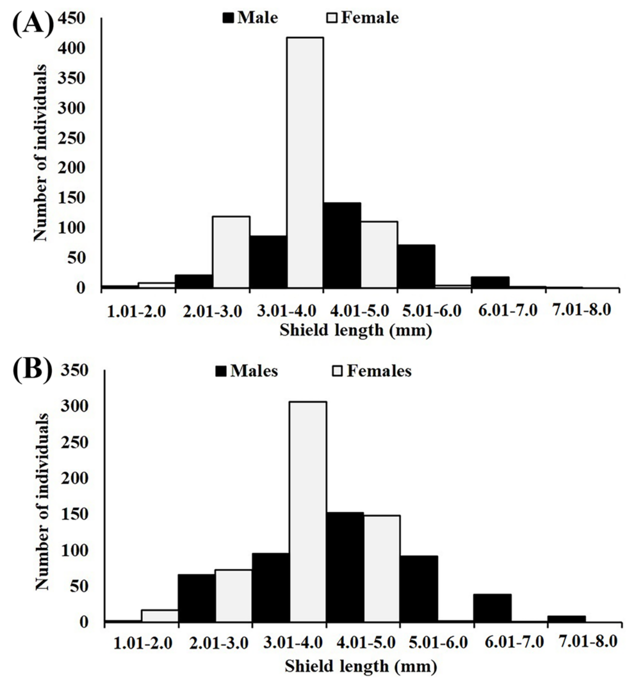

Fig. 2 Size frequency (SL) distribution of male and female individuals of **A** *Clibanarius rhabdodactylus* (n = 1000) and **B** *Clibanarius ransoni* (n = 1000)

showed a significant relationship with almost all the morphological parameters of gastropod shells (Table 4).

Table 5 shows evident shell occupation pattern between different sexes of *C. rhabdodactylus* and *C. ransoni*. Amongst the five highly occupied shells, males and ovigerous females occupy larger, heavier and voluminous shells while non-ovigerous females occupy comparatively smaller, lighter and less voluminous shells. Tables 6 and 7 shows evident shell occupation pattern between different reproductive stages of *C. rhabdodactylus* and *C. ransoni* respectively. Amongst the five highly occupied shells, juveniles (1–3 mm SL) were occupying the shells of *C. caeruleum* more which are comparatively smaller, lighter, elongated with smaller aperture. On the other hand, adults (3–7 mm SL) occupy comparatively larger, heavier and voluminous shells.

The five distinguishing morphological parameters (SHL, SHAL, SHAW, SHW, SHV) of five frequently occupied shells are represented in Fig. 4. The minimum (2.0 mm)

Table 1 Carapace shield length values of *Clibanarius rhabdodactylus and Clibanarius ransoni*

Species	Shield length	Male	Non-ovigerous female	Ovigerous female
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

ANOVA

****p* < 0.0001; n = total individuals; SL = Shield length

Table 2 Gastropod shell utilization by *Clibanarius rhabdodactylus*

Gastropod species	N	%	M	%	NOF	%	OF	%
Cerithium caeruleum G. B. Sowerby II, 1855	656	65.6	133	39.1	234	76.7	289	81.4
Lunella coronata (Gmalin, 1791)	78	7.8	67	19.7	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	11.2	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
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
Cerithium echinatum Lamarck, 1822	3	0.3	1	0.3	1	0.3	1	0.3
Chicoreus bruneus (Link, 1807)	12	1.2	11	3.2	1	0.3	0	0.0
Chicoreus maurus (Broderip, 1833)	9	0.9	7	2.1	1	0.3	1	0.3
Clypeomorus batillariaeformis Habe & Kosuge, 1966	3	0.3	1	0.3	1	0.3	1	0.3
Ergalatax contracta (Reeve, 1846)	7	0.7	1	0.3	5	1.6	1	0.3
Ergalatax heptagonalis (Reeve,1846)	3	0.3	0	0.0	2	0.7	1	0.3
Euchelus asper (Gmelin, 1791)	6	0.6	4	1.2	1	0.3	1	0.3
Gyrineum natator (Roding, 1798)	5	0.5	3	0.9	1	0.3	1	0.3
Indothais lacera (Born,1778)	3	0.3	2	0.6	0	0.0	1	0.3
Indothais sacellum (Gmelin, 1791)	12	1.2	10	2.9	1	0.3	1	0.3
Mitra scutulata (Gmelin, 1791)	2	0.2	1	0.3	1	0.3	0	0.0
Nerita oryzarum Recluz, 1841	3	0.3	2	0.6	1	0.3	0	0.0
Orania subnodulosa (Melvill,1893)	5	0.5	1	0.3	2	0.7	2	0.6
Paradrillia patruelis (E. A. Smith,1875)	3	0.3	0	0.0	1	0.3	2	0.6
Poliia rubiginosa (Reeve, 1846)	4	0.4	3	0.9	1	0.3	0	0.0
Purpura panama (Roding, 1798)	11	1.1	9	2.6	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
Vanikoro cuvieriana (Recluz, 1843)	1	0.1	1	0.3	0	0.0	0	0.0
Morula uva (Roding, 1798)	6	0.6	2	0.6	1	0.3	3	0.8
Nassarius marmoreus (A. Adams, 1852)	3	0.3	1	0.3	1	0.3	1	0.3
Monodata australis (Lamarck, 1822)	2	0.2	1	0.3	1	0.3	0	0.0
	1000		**341**		**304**		**355**	

N total individuals, M Male, NOF Non-ovigerous female, OF Ovigerous female

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, $p < 0.001$).

The CCA analysis between the hermit crab morphology and gastropod shell parameters is represented in Fig. 5 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*.

Table 3 Gastropod shell utilization by *Clibanarius ransoni*

Gastropod species	N	%	M	%	NOF	%	OF	%
Cerithium caeruleum G.B. Sowerby II, 1855	532	53.2	130	28.6	206	66.9	196	82.4
Lunella coronata (Gmalin, 1791)	91	9.1	84	18.5	7	2.3	0	0.0
Turbo bruneus (Röding, 1798)	73	7.3	59	13.0	11	3.6	3	1.3
Tenguella granulata (Duclos, 1832)	43	4.3	10	2.2	13	4.2	20	8.4
Pollia undosa (Linnaeus, 1758)	39	3.9	29	6.4	9	2.9	1	0.4
Cerithideopsilla cingulata (Gmelin,1971)	6	0.6	2	0.4	4	1.3	0	0.0
Euchelus asper (Gmelin, 1791)	18	1.8	12	2.6	6	1.9	0	0.0
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	1.5	1	0.3	0	0.0
Tibia insulaechorab Röding, 1798	2	0.2	2	0.4	0	0.0	0	0.0
Ergalatax contracta (Reeve, 1846)	4	0.4	0	0.0	1	0.3	3	1.3
Chicoreus bruneus (Link, 1807)	23	2.3	23	5.1	0	0.0	0	0.0
Chicoreus maurus (Broderip, 1833)	14	1.4	12	2.6	0	0.0	2	0.8
Indothais lacera (Born,1778)	5	0.5	3	0.7	1	0.3	1	0.4
Indothais sacellum (Gmelin, 1791)	18	1.8	10	2.2	3	1.0	5	2.1
Morula uva (Roding, 1798)	8	0.8	4	0.9	3	1.0	1	0.4
Orania subnodulosa (Melvill,1893)	7	0.7	4	0.9	2	0.6	3	1.3
Purpura panama (Röding, 1798)	13	1.3	10	2.2	3	1.0	0	0.0
Semiricinula tissoti (Petit de la Saussaye, 1852)	17	1.7	3	0.7	10	3.2	3	1.3
Chicoreus virgineus (Röding, 1798)	4	0.4	4	0.9	0	0.0	0	0.0
Nerita oryzarum Recluz, 1841	6	0.6	6	1.3	0	0.0	0	0.0
Nassarius pullus (Linneus 1758)	1	0.1	0	0.0	1	0.3	0	0.0
Nassarius reeveanus (Dunker, 1847)	2	0.2	1	0.2	1	0.3	0	0.0
Natica picta (Recluz,1844)	3	0.3	1	0.2	2	0.6	0	0.0
Cantharus spiralis (Gray, 1839)	8	0.8	6	1.3	1	0.3	1	0.4
Poliia rubiginosa (Reeve, 1846)	13	1.3	2	0.4	6	1.9	3	1.3
Astralium stellare (Gmelin, 1791)	28	2.8	16	3.5	11	3.6	2	0.8
Monodata australis (Lamarck, 1822)	6	0.6	5	1.1	1	0.3	0	0.0
	1000		**445**		**311**		**244**	

N total individuals, *M* Male, *NOF* Non-ovigerous female, *OF* Ovigerous female

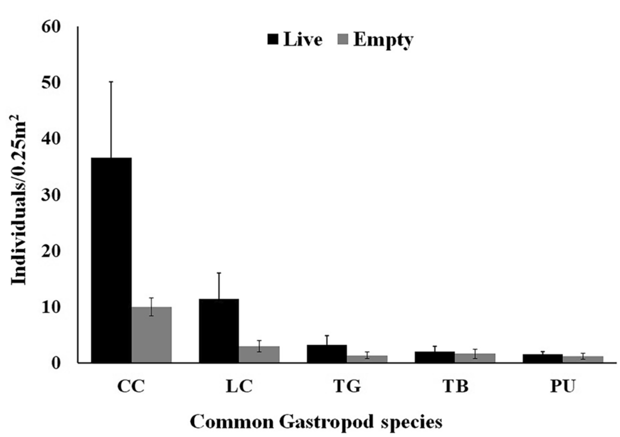

Fig. 3 Abundance of commonly occurring gastropod species in the intertidal zone of Veraval, Saurashtra coast, Gujarat, India. (CC: *C. caeruleum*, LC: *L. coronata*, TG: *T. granulata*, TB: *T. bruneus*, PU: *P. undosa*)

Discussion

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 environment (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 (Table 1 and Fig. 2). 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 2014). It was also found that the size of males and ovigerous females of both the

Table 4 Regression equation in relation to the morphological parameters of different sexes of *Clibanarius rhabdodactylus* and *Clibanarius ransoni* and that of gastropod shells measures

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***

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*

$^*P < 0.05$; $^{**}P < 0.01$; $^{***}P < 0.001$

species of hermit crab was larger than non-ovigerous females (Table 1). The ovigerous females of *C. rhabdodactylus* and *C. ransoni* occupied larger shells than non-ovigerous females (Table 5). Previous studies carried out on other hermit crab species like *Diogenes puligator* (Manjón-Cabeza and 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 utilise the majority of their energy in body growth while non-ovigerous females occupy smaller gastropod shells as they save energy for the purpose

Table 5 Mean values of different morphological parameters of five highly occupied gastropod shells by different sexes of *Clibanarius rhabdodactylus* and *Clibanarius ransoni*

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	0	17.00 ± 6.05
	SHAL (mm)	14.43 ± 2.77	12.42 ± 0.04	11.90 ± 3.26	11.36 ± 3.03	0	8.36 ± 2.71
	SHAW (mm)	12.91 ± 3.46	12.00 ± 0.03	9.55 ± 3.27	11.11 ± 2.92	0	7.52 ± 1.81
	SHW (g)	4.72 ± 1.52	4.96 ± 0.03	2.58 ± 0.72	4.86 ± 2.41	0	1.77 ± 1.32
	SHV (mm^3)	1.56 ± 0.42	1.99 ± 0.01	0.72 ± 0.38	1.58 ± 0.79	0	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

Male *M*, Ovigerous female O*F*, Non-ovigerous Female *F*, Shield length *SL*, Shell length *SHL*, Shell aperture length *SHAL*, Shell aperture width *SHAW*, Shell dry weight *SHW*, Shell volume *SHV*

of reproduction and egg development. Moreover, ovigerous females were observed occupying more voluminous and larger shells compared to non-ovigerous females since they need larger internal space for accommodation and protection of their eggs from predators and desiccation (Fotheringham 1976; 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 (Tables 2 and 3), which is higher as compared to the gastropod shells used by other hermit crab species like *C. vittatus* (13 species) (Sant'Anna et al. 2006), *C. antillensis* (25 species) (Argüelles-Ticó et al. 2010), *C. virescens* (17 species) (Wait and Schoeman 2012), *C. erythropus* (11 species) (Fatma El-Zahraa et al. 2015), *C. zebra* (23 species) (Trivedi and Vachhrajani 2014) and *Clibanarius albidigitus* (15 species) (Alcaraz and Kruesi, 2019). It was also observed that the ovigerous females of *C. rhabdodactylus* and *C. ransoni* were occupying 23 species and 14 species of gastropod shells respectively which is significantly less as compared to the shells occupied by males and non-ovigerous females. Similar results were observed for the ovigerous females of *D. puligator* (Manjón-Cabeza and Raso 1999), *C. vittatus* (Sant'Anna et al. 2006), *Isocheles sawayai* (Fantucci et al. 2008) and *C. zebra* (Trivedi and Vachhrajani 2014), which suggests that ovigerous females are choosy for appropriate shells having larger internal space suitable for accommodation and incubation of eggs (Abram 1978; Bertness 1981b; Sallam 2012).

It was found that both the *Clibanarius* species were showing a high overlap in their intertidal distribution as well as gastropod shell use pattern. Several other studies have also reported such coexisting pair of hermit crab species which share similarities in their microhabitat overlap and gastropod shell use (Abrams 1980; Bertness 1981a, b; Hazlett 1966, 1983; Bach et al. 1976; Fotheringham 1976; Floeter

Table 6 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*)

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

Shield length *SL*, Shell length *SHL*, Shell aperture length *SHAL*, Shell aperture width *SHAW*, Shell dry weight *SHW*, Shell volume *SHV*

et al. 2000; Turra and Leite 2000; Alcaraz and Kruesi 2019; Alcaraz et al. 2020a, b; Kruesi et al. 2022). It was also observed that *C. caeruleum* was the most preferred gastropod species by the individuals of *C. rhabdodactylus* and *C. ransoni* possibly due to the high abundance of *C. caeruleum* (31 individual /0.25m^2) in the intertidal region of the study area (Fig. 3). A similar pattern of shell utilization has been observed for *C. antillensis* utilizing *Tegula viridula* shells (Floeter et al. 2000), *Isocheles sawayai* utilizing *Stramonita haemastoma* shells (Fantucci et al. 2008), *Diogenes moosai* and *D. lopochir utilizing Cerithidea cingulata* shells (Teoh and Chong 2014), *C. zebra* utilizing *C. scabridum* shells (Trivedi

Table 7 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*

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	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

Shield length *SL*, Shell length *SHL*, Shell aperture length *SHAL*, Shell aperture width *SHAW*, Shell dry weight *SHW*, Shell volume *SHV*

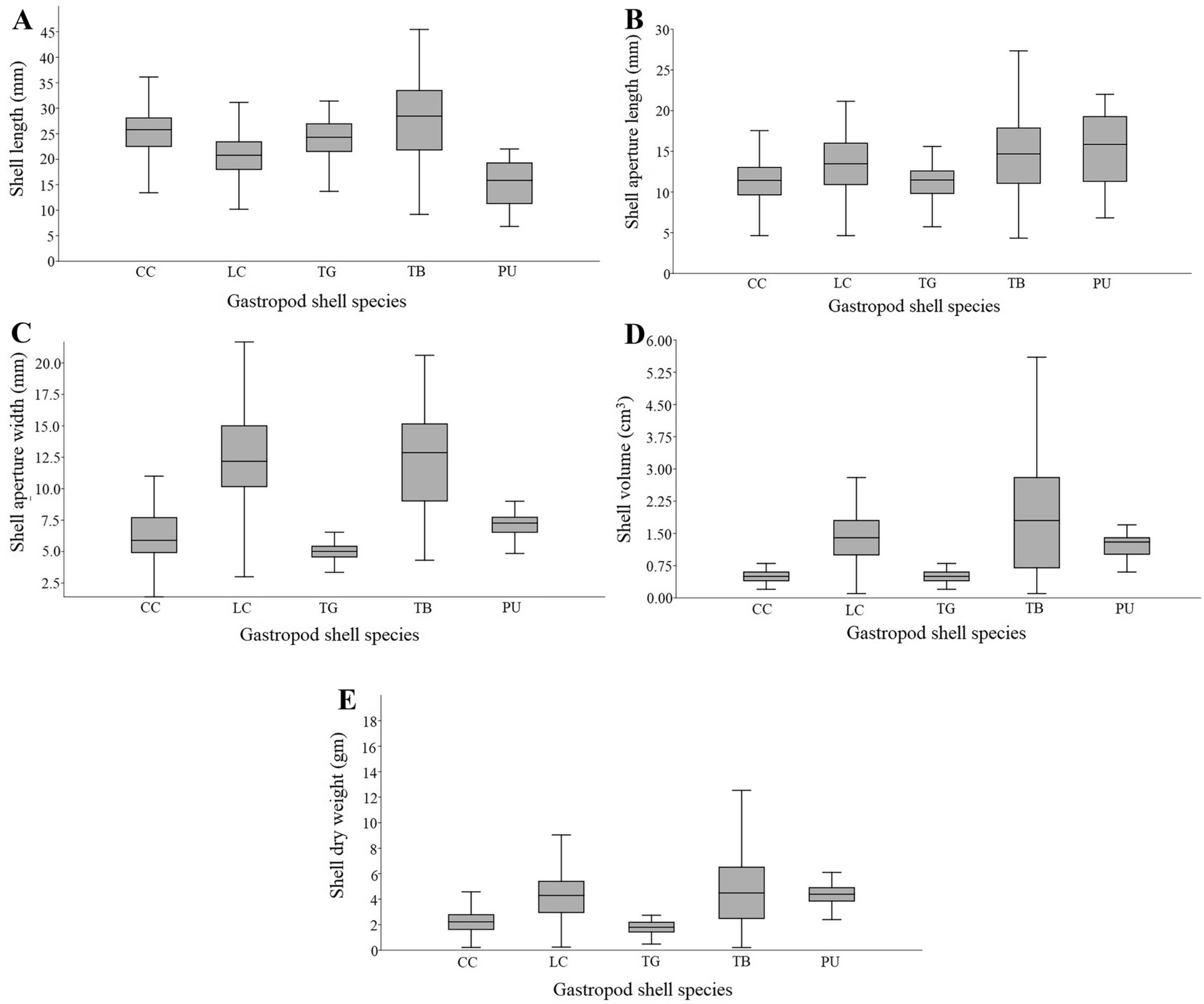

Fig. 4 Box and whisker plots of **A** shell length, **B** shell aperture length, **C** shell aperture width, **D** shell volume and **E** shell dry weight of five frequently occupied shells by *Clibanarius rhabdodactylus* and *Clibanarius ransoni*. CC: *C. caeruleum*, LC: *L. coronata*, TG: *T. granulata*, TB: *T. bruneus*, PU: *P. undosa*; Box = 25th and 75th percentiles, midline = mean, whiskers = minimum and maximum values

and Vachhrajani 2014) and *Diogenes custos* utilizing *Pollia undosa* shells (Patel et al. 2020a). It has been demonstrated that the availability and abundance of gastropod shells in the habitat play a major role in the shell utilization pattern of hermit crabs (Kellogg 1976; Scully 1979; Barnes 1999). The selection of gastropod shells by hermit crabs is not a random process even if the availability of shell resources is not a limiting factor (Grant and Ulmer 1974). The selection of gastropod shells is allied with the morphology of both, gastropod shell and hermit crabs that must be well-matched in a way to maximise shell utilization of available resources (Elwood et al. 1995; Caruso and Chemello 2009).

The variation in the shell utilization can occur due to differences in the hermit crab size varying between species, sexes as well as geographical habitat (Barnes 2005). In the present study, it was observed that all the gastropod shell parameters (SHL, SHAL, SHAW, SHW, SHV) showed a significant relationship with SL while the gastropod shell parameters (SHAL, SHAW, SHW, SHV) showed a significant relationship with HW (Table 4). Previous studies suggest that occupying larger and heavier shells by hermit crabs provide protection from the predators, desiccation and intense wave action (Reese 1969; Brown and McLachlan 2002). Moreover, shell aperture is an important factor as it is the only way to enter inside the shell. That is why it should be optimum enough to facilitate easy movement of the residential hermit crab to acquire food and to get protection from predators (Abd El-Aziz et al. 2015).

It has been observed that the behaviour of shell utilization by hermit crabs is not a random process even if plenty

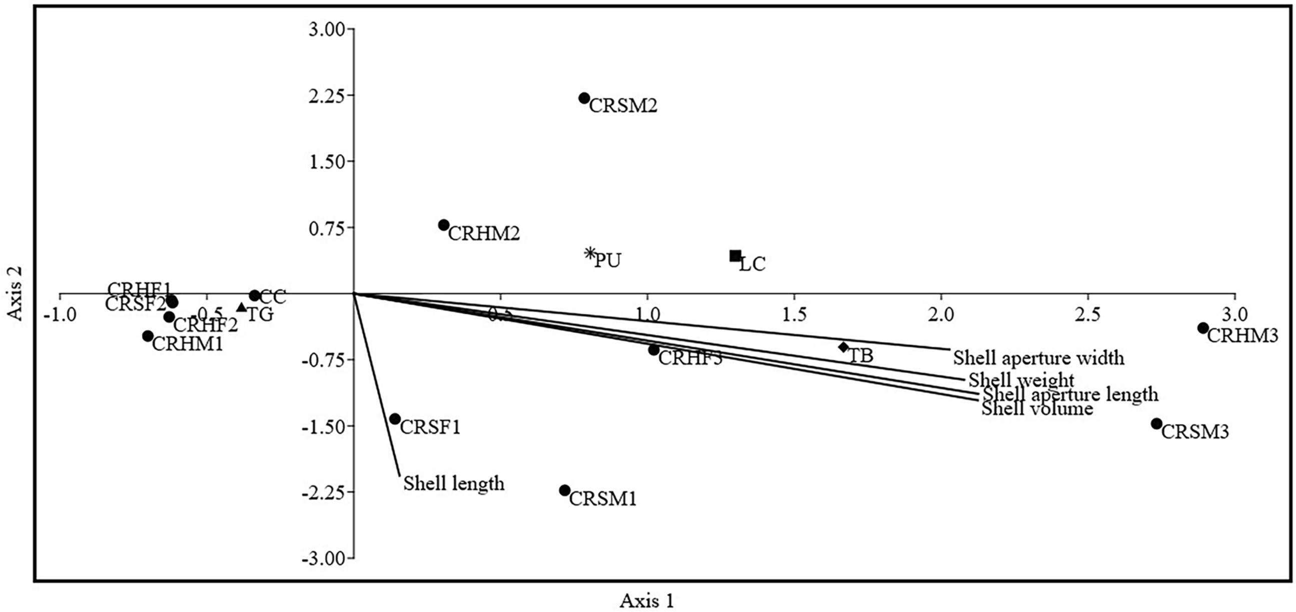

Fig. 5 Canonical correspondence analysis (CCA) of shell use by *Clibanarius rhabdodactylus* and *Clibanarius ransoni* of different size classes as influenced by shell parameters. CC: *C. caeruleum*, LC: *L. coronata*, TG: *T. granulata*, TB: *T. bruneus*, PU: *P. undosa*. Lines indicate shell attributes 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 (numeral, please refer to Table 8 for the explanation)

of empty shells are available (Grant and Ulmer, 1974). The selection of shells is allied with the morphological characters of both hermit crabs and gastropod shells which must be compatible in order to maximise the shell resource utilization (Caruso and Chemello 2009; Elwood et al. 1995). Similarly, in the present study, CCA analysis (Fig. 4) as well as Tables 6 and 7 showed that the smaller individuals of *C. rhabdodactylus* and *C. ransoni* profoundly utilised more spired and smaller aperture shells of *C. caeruleum* (Figs. 4B, C and 5) which protects the smaller individuals from the desiccation during low tide in the exposed rocky intertidal region of the study area. On the contrary, larger individuals of *C. rhabdodactylus* and *C. ransoni* utilised larger and voluminous shells of *L. coronata* and *T. bruneus* (Figs. 4D, E and 5; Tables 6 and 7) which can protect them from other predatory species. Different types of gastropod shells are beneficial to the occupant hermit crab in different ways. Highly spired or elongated shells can conserve more water which can prevent the resident hermit crab from desiccation during the exposure period whereas shells that are less spired but larger, heavier and voluminous shells are efficient to provide protection from predators (Bertness 1981a).

Table 8 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)

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

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Declarations

Competing Interests The authors have no conflict of interest.

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SEASONAL VARIATION IN THE INTERTIDAL DISTRIBUTION OF THE HERMIT CRAB *CLIBANARIUS RHABDODACTYLUS* FOREST, 1953 ON THE ROCKY SHORES OF SAURASHTRA COAST, GUJARAT, INDIA

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ABSTRACT: In the present study, the intertidal distribution of *Clibanarius rhabdodactylus* Forest, 1953 was studied in the rocky intertidal region of Veraval along the Saurashtra coast, Gujarat, India. Monthly sampling was carried out from September 2020 to August 2021 using line transect method intercepted with quadrates (0.25 m^2) from the upper intertidal mark to the lower intertidal mark for quantification of *C. rhabdodactylus*. Similar transect method intercepted with quadrates (1 m^2) was employed to quantify coverage of microhabitat. Individuals of *C. rhabdodactylus* from each quadrate were collected in zip-lock bags using hand-picking method. In the laboratory, shield length (SL) of each individual of *C. rhabdodactylus* was measured and classified as male, non-ovigerous female or ovigerous female. The monthly data of abundance was compiled for different seasons, viz., winter (November to February), summer (March to June) and monsoon (July to October). The abundance of *C. rhabdodactylus* varied significantly between seasons with maximum values recorded in winter followed by summer and monsoon. In case of microhabitat, upper intertidal zone was maximally composed of tide pools while middle and lower intertidal zone was maximally composed of open area. Tide pool water temperature and ambient temperature varied significantly between seasons. Overall abundance data showed that the species mostly preferred the upper intertidal region and the presence of higher number of tide pools in the upper intertidal zone might be the possible reason behind the confinement of *C. rhabdodactylus* in the upper intertidal region.

KEY WORDS: Anomuran crab, intertidal region, microhabitat preference, rocky coast, spatio-temporal variation, tidepool

Hermit crabs are unique in their reliance on empty gastropod shells to protect their non-calcified abdomen from different biotic and abiotic factors (Reese, 1969). For hermit crabs, intertidal habitats are favourable as there is continuous replenishment of detritus as a food source and refuge from specialised predators (Reese, 1969). The distribution of hermit crabs in intertidal zones is influenced by a variety of factors, including desiccation risk, the availability of empty gastropod shells in different zones (Kellogg, 1977), abiotic factors that move empty shells (Hazlett, 1981), and differences in larval settlement (Nyblade, 1974). Migration along the intertidal region has been observed in some hermit crab species, which can be attributed to various environmental or physiological factors. The tropical intertidal and shallow subtidal hermit crabs undergo seasonal vertical migration from shallow and colder to deep and warmer waters during the winter months (Fotheringham, 1975; Rebach, 1978, 1981). Migration into deeper water in the reproductive season has been reported in many species (Allen, 1966), including hermit crabs (Kikuchi, 1962; Asakura & Kikuchi, 1984; Asakura, 1987). Salinity is readily decreased by rainfall in the upper intertidal zones of rocky shores in the monsoon season (Lewis, 1964; Carefoot, 1977; Newell, 1979), thus the lower distribution of female hermit crabs can be an adaptation to avoid low salinity in the upper intertidal areas (Abram, 1988; Imazu & Asakura, 1994). Another factor influencing migration is the availability of gastropod shells in different zones (Fotheringham, 1975). The rocky intertidal region presents heterogeneous environment which support a huge variety of organisms that are distributed in a particular manner from the upper intertidal region to the lower intertidal region (Underwood, 1981; Ballesteros, 1995; Thompson et al., 2002; Araújo et al., 2005). Vertical zonation can be evidently observed in the rocky intertidal region where, from the upper to lower intertidal region, different zones possessing a different diversity of organisms can be observed (Stephenson & Stephenson, 1949; Bandel & Wedler, 1987).

The coastline of Gujarat is ~1650 km long and includes three important coastal regions: the Gulf of Kachchh, the Saurashtra coast and the Gulf of Khambhat (Trivedi et al., 2015a). Among these coastal regions, the Saurashtra coast is around 800 km long, having narrow, rocky intertidal habitats (Trivedi, 2015). A total of 18 species (4 genera, 2 families) of hermit crabs have been reported from Gujarat State (Trivedi et al., 2015a; Trivedi & Vachhrajani, 2016a, 2017; Kachhiya et al., 2017; Patel et al., 2020a). The brachyuran crab fauna of Saurashtra coast has been studied well for its diversity (Trivedi & Vachhrajani, 2012a, 2013a, 2014a, 2015, 2016b; Trivedi et al., 2015b,c,d, 2017, 2018; Ng et al., 2015; Gosavi et al., 2017) and ecological aspects (Trivedi & Vachhrajani, 2012b, 2013b, 2016c), however hermit crab fauna has not been studied well for its diversity (Trivedi et al., 2015d, 2016d; Kachhiya et al., 2017) and ecological aspects. Most of the studies are concentrated on their behavioural ecology like shell utilisation pattern (Trivedi et al., 2013; Trivedi & Vachhrajani, 2014b; Patel et al., 2020b,c, 2021a,b). Studies on the intertidal distribution of marine organisms of Saurashtra coast are carried out very rarely (Vaghela & Kundu, 2012; Trivedi & Vachhrajani, 2014c). *Clibanarius rhabdodactylus* is a hermit crab species found in the rocky intertidal region of the Saurashtra coast, Gujarat State, India (Kachiya et al., 2017). The ecological aspects of this species are not studied yet, and therefore, the present study was carried out to understand the seasonal variation in the intertidal distribution of hermit crab *C. rhabdodactylus* on the rocky shores of the Saurashtra coast, Gujarat State.

MATERIALS AND METHODS

Study area

The present study was conducted in the rocky intertidal region of Veraval (20°54'37''N, 70°21'04''E) situated on the Saurashtra coast, Gujarat (Fig. 1). The width of the rocky intertidal zone varies between 60 and 150 metres from high tide to low tide. *Clibanarius rhabdodactylus* occurs in high abundance on the rocky shores of the study site (Patel et al., 2020c).

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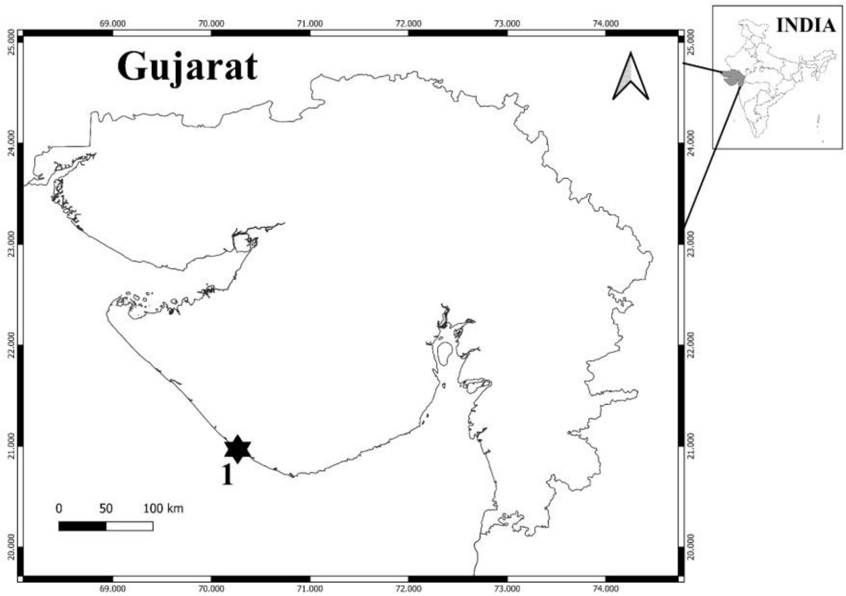

Figure 1. Map of study area. 1. Veraval, Saurashtra coast, Gujarat, India.

Sampling

The present study was conducted from September 2020 to August 2021 to carried out sampling in three seasons, *viz*. winter (November to February), summer (March to June), and monsoon (July to October). For sampling, the rocky intertidal region of the study site was divided into three different zones: the upper intertidal (0 to 20 meters), middle intertidal (20 to 40 meters) and lower intertidal zones (40 to 60 meters). The quantification of *C. rhabdodactylus* individuals was carried out using a line transect method, intercepted with quadrate. A total of 3 transects were laid 100 m apart, perpendicular to the shoreline. On each transect, quadrates (0.25 m^2) were laid at an interval of every 5 metre starting from the upper intertidal region to the lower intertidal region. All the *C. rhabdodactylus* individuals occurring in each quadrate were collected in tagged zip-lock bags and brought to the laboratory for further analysis. The temperature of tide pool water from upper, middle and lower intertidal regions was measured every hour during sampling. Moreover, ambient temperature was recorded every hour during the sampling period. The tide pool water temperature and ambient temperature were recorded using digital thermometer.

For microhabitat analysis, the rocky habitat was classified into tide pools, crevices and open area. In the intertidal region a total of 10 transect were laid 50 m apart, perpendicular to the shoreline. On each transect, quadrates (1 m^2) were laid at every 5 metre interval starting from the upper intertidal region to the lower intertidal region. Each quadrate was further divided into 100 sub-quadrates of 10×10 cm. Percentage microhabitat cover was assessed by counting the number of sub-quadrates occupied by each microhabitat type and giving 1% cover to each sub-quadrate. All sampling was carried out by a single person to avoid potential observer influence.

Data analysis

In the laboratory, for each quadrate sample, the hermit crabs were removed from the gastropod shell and their shield length (SL) was measured using vernier callipers (±0.01 mm accuracy). Furthermore, the hermit crabs were classified into male, non-ovigerous female or ovigerous female. Monthly data for each season was compiled, and quadrate-wise abundance was calculated. The abundance data was used to plot kite diagrams in order to know the variation in distribution of *C. rhabdodactylus* in different zones of intertidal area in different seasons. Variation in the mean values of shield length of different sexes as well as variation in the mean abundance of *C. rhabdodactylus* during different seasons was analysed using one-way ANOVA. Seasonal variation in the tide pool water and ambient temperature between different intertidal regions was calculated using two-way ANOVA.

RESULTS

A total of 3,423 individuals were collected during the study period. Out of 3,423 individuals collected, 1,019 individuals were males (29.77 %), 1,364 individuals were non-ovigerous females (39.85 %) and 1,040 individuals were ovigerous females (30.38 %) which shows that the population was female biased (1:2.36). The average size (SL) of males (4.58±0.98 mm) was significantly larger than non-ovigerous females (3.46±0.73 mm) and ovigerous females (3.74±0.51 mm) (ANOVA, $F = 218.47$, $df = 3,422$, $p<0.001$).

In case of temperature, the tide pool water temperature and ambient temperature varied significantly between all the three seasons (ANOVA: $F= 24.18$, $p<0.001$) (Fig. 2). The ambient temperature was recorded maximum during summer season followed by monsoon and winter. In case of the tide pool temperature of the upper intertidal region, the maximum temperature (38.27 ± 0.45˚C) was observed in the summer season, while the minimum temperature (30.63 ± 0.65˚C) was observed in the monsoon season. In the middle intertidal region, the maximum tide pool temperature (35.63 ± 0.37˚C) was observed in summer season while the minimum temperature (29.87 ± 0.88˚C) was observed in monsoon season. Similarly, in the lower intertidal region, the maximum tide pool temperature (31.09 ± 0.48˚C) was observed in the summer season while the minimum temperature (27.94 ± 0.65˚C) was observed in the winter season.

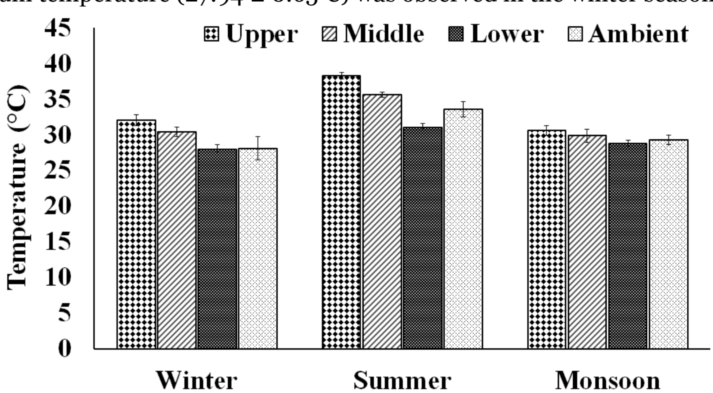

Figure 2. Seasonal variation in the mean values of temperature at different intertidal region.

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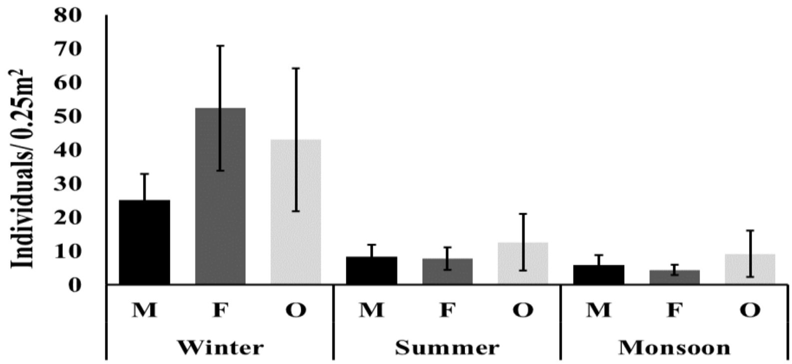

Figure 3. Seasonal variation in the mean values of abundance of different sexes of *Clibanarius rhabdodactylus*.

In the present study, the maximum abundance was observed in the winter season, followed by the summer and monsoon seasons. Gender wise, in the winter season, the maximum abundance of non-ovigerous females was observed, followed by ovigerous females and males. During the summer and monsoon season, the maximum abundance of ovigerous females was observed, followed by males and non-ovigerous females. The result of ANOVA ($F = 15.38$, $p < 0.01$) showed significant variation in the mean values of the seasonal abundance of the species.

Variation in the intertidal distribution was observed in the *C. rhabdodactylus* population. Fig. 4 represents the quadrate-wise mean abundance of *C. rhabdodactylus* individuals during different seasons. It was observed that in winter season, *C. rhabdodactylus* individuals were mostly distributed in the upper intertidal region where the mean water temperature was 32.05 ± 0.73°C. However, during the summer season, when the water temperature of the upper intertidal reaches 38.27 ± 0.45, *C. rhabdodactylus* population distributed in the middle and lower intertidal regions where the water temperature was 35.63 ± 0.37°C and 31.09 ± 0.48°C respectively. During the monsoon season, the water temperature did not vary from the upper to lower intertidal region, and the *C. rhabdodactylus* population was observed to be distributed from the upper to lower intertidal region with maximum abundance in the upper intertidal region.

The rocky intertidal region of Veraval is mostly composed of tidepools, crevices and open areas. The habitat analysis revealed that the maximum number of tidepools occurred in the upper intertidal region and gradually decreased towards the lower intertidal region. On the other hand, open areas occurred less in the upper intertidal region and gradually increased towards the lower intertidal region. The overall area covered by crevices was least and remained almost similar from the upper to lower intertidal region.

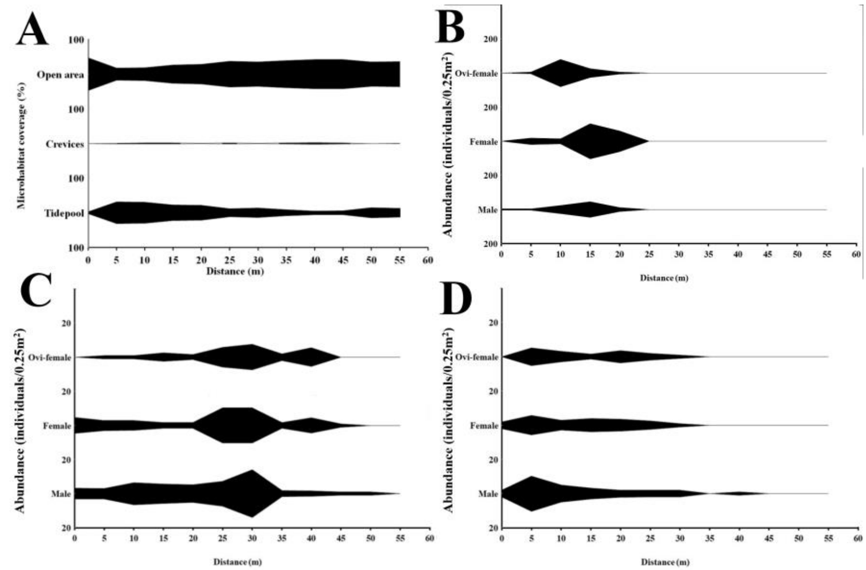

Figure 4. A. Microhabitat coverage of intertidal region in the study area; Intertidal distribution of *Clibanarius rhabdodactylus* at Veraval coast in B. winter season; C. Summer season and. Monsoon season.

DISCUSSION

In the present study, sexual dimorphism was evidently observed in the *C. rhabdodactylus* population where males were significantly larger as compared to non-ovigerous females and ovigerous females. Similar results were observed in previous studies for other species of *Clibanarius* like *C. laevimanus* (Gherardi et al., 1994), *C. erythropus* (Benvenuto & Gherardi, 2001), *C. vittatus* (Sampaio & Masunari, 2010), *C. zebra* (Trivedi et al., 2013, Trivedi & Vachhrajani, 2014b) and *C. ransoni* (Patel et al., 2021). It was also found that the size of males and ovigerous females of both the species of hermit crab was larger than non-ovigerous females. Generally, males attain larger size in a shorter period of time as they utilise most of their energy for physical growth, while females have to save their energy for the purpose of egg development and reproduction (Sant'Anna et al., 2006; Mantelatto et al., 2010).

The sex ratio of *C. rhabdodactylus* in the study area was female biased. The deviation from the ideal sex ratio 1:1 can be possibly due to several factors including sexual difference in spatio-temporal distribution and mortality rate, differential life span, activity and out migration of one sex, sex longevity, sampling methods, differential predation on crab and growth rates (Wenner, 1972; Montague, 1980; Conde & Diaz, 1989; Spivak et al., 2022). Such a deviation from the ideal sex ratio can regulate the population size by affecting its reproductive potential.

The upper intertidal region experiences the highest exposure to sunlight, leading to increased water temperature during low tide time, followed by middle and lower intertidal regions. Since the ambient temperature reaches its highest in the summer season, the water temperature was also recorded at its maximum in the upper and middle intertidal regions of the summer season. The temperature in the middle and lower intertidal region was recorded at its maximum in summer and least in the monsoon season. This could be due to two possible reasons: because of cloudy weather, the time of sunlight exposure decreases greatly, hence the water temperature does not rise. Moreover, the wave action increases during the monsoon season (Amrutha & Kumar, 2017), which leads to continuous water replenishment in the middle and lower intertidal regions even during low tide times.

The hermit crab species *C. rhabdodactylus* form aggregations during low tide time responsible for their patchy distribution in the study area. Similar results were obtained in studies carried out on the gastropod species *Cerithium scabridum* (Trivedi & Vachhrajani, 2013c) and *C. caeruleum* (Gohil & Kundu, 2013). It was suggested that the patchy distribution could be due to the specific microhabitat preference of the species. Moreover, abiotic factors like temperature and wave action can also be one of the factors affecting the distribution of the species. Another probable reason for such distribution is probably due to specific preference of *Cerithium caeruleum* shells (Patel et al., 2021) which are majorly found in the upper and middle intertidal region (Gohil & Kundu, 2013). Also, the species have a specific preference for microhabitat (crevices and tidepools) as it provides protection from wave action.

In the present study, the overall maximum abundance of the *C. rhabdodactylus* population was observed in the upper intertidal region. Variation in the abundance of *C. rhabdodactylus* was also observed between different genders during different seasons. The availability of gastropod shells in different zones can also be another aspect affecting the spatial distribution, like the fact that larger *Clibanarius vittatus* requires larger gastropod shells which are available in the sublittoral zone (Fotheringham, 1975). Similar results were observed in a study carried out on the gastropod species *Cerithium scabridum* (Trivedi & Vachhrajani, 2013).

In the present study, it was found that the species was occupying the intertidal region, having a water temperature between 30–35°C. Since the water temperature of the upper intertidal region in winter was within this range, the highest abundance was observed in this region as compared to the middle and lower intertidal regions with lower temperatures. Studies suggest that various factors are responsible for the distribution of hermit crabs in intertidal zones, like exposure to desiccation risk, availability of empty gastropod shells in different zones (Kellogg, 1977), abiotic factors that move empty shells (Hazlett, 1981) and differences in larval settlement (Nyblade, 1974). Migration into deeper water in the reproductive season has been reported in many hermit crab species (Kikuchi, 1962; Asakura & Kikuchi, 1984; Asakura, 1987) in order to avoid fluctuations in the abiotic factors for successful development.

During summer, it was observed that the *C. rhabdodactylus* population migrated to the middle and lower intertidal regions, which can be a behavioural adaptation to avoid desiccation and hyperthermia due to higher temperatures (Reese, 1969; Bertness, 1981; Taylor, 1981; Turra & Leite, 2000). Previous studies have also suggested that hermit crabs migrate into deeper subtidal water in the reproductive season to avoid extreme abiotic factors (Kikuchi, 1962; Asakura & Kikuchi, 1984; Asakura, 1987).

During the monsoon season, the *C. rhabdodactylus* population was observed to be distributed from the upper intertidal to the lower intertidal regions, with greater abundance in the upper intertidal region. However, studies suggest that salinity is readily decreased by rainfall in the upper intertidal zone of rocky shores during the monsoon season (Lewis, 1964; Carefoot, 1977; Newell, 1979). This leads to a lower distribution of female hermit crabs as an adaptation to avoid low salinity in the upper intertidal region (Abram, 1988; Imazu & Asakura, 1994). In the present study, the species was abundant in the upper intertidal region as the species prefers tidepools and crevices microhabitat which is higher in the upper intertidal region. As the wave action increases during the monsoon (Amrutha & Kumar, 2017), occupying tidepools in the upper intertidal region would protect the hermit crabs from crushing.

CONCLUSIONS

The present study was an attempt to understand the spatio-temporal distribution of a hermit crab species *C. rhabdodactylus* found on the rocky coasts of Gujarat, India. The distribution was governed by temperature fluctuation as well as microhabitat availability in the study site. Since the temperature of upper intertidal region was optimum in winter season, the species was distributed in the upper intertidal region. During summer, as the temperature exceed the optimum levels of temperature in the upper intertidal region, the species was distributed in the lower intertidal region. Overall, maximum abundance of the species was observed in the upper intertidal region as the species preferred tidepools and crevices microhabitat which was higher in the upper intertidal region which protects the hermit crabs from desiccation and wave action.

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Population structure and reproductive biology of *Clibanarius rhabdodactylus* Forest, 1953 (Crustacea: Anomura: Diogenidae) in Gujarat state, India

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ABSTRACT

The population structure of a hermit crab, *Clibanarius rhabdodactylus* Forest, 1953 (Diogenidae), was studied in the rocky intertidal region of Veraval, located on the Saurashtra coast, Gujarat state, India. Monthly sampling was carried out from March 2021 to February 2022 during low tide time using the handpicking technique, while the catch per unit effort method was employed by one person during the period of 4 h in an area of 500 m^2. The collected individuals were classified as male, non-ovigerous female, and ovigerous female. Size (mm) and weight (g), egg size, number, and egg mass weight were recorded and fecundity was calculated. A clear sexual dimorphism was observed, with males being significantly larger than females. The overall sex ratio was female biased. The overall size frequency distribution showed bimodal distribution in male while unimodal in females. Ovigerous females occurred throughout the year with peaks in January to June and September to October, showing a continuous reproductive pattern of the species. The total number of eggs, size of eggs, and total weight of egg mass showed a positive correlation with the shield length and body weight of the ovigerous females.

1. Introduction

Hermit-crab population is significantly impacted by shell supply, which is in turn controlled by the effective abundance of gastropods in the habitat, their death rate (Scully, 1979) and the inter- and intra-specific competition for the best fitting gastropod shells (Abrams, 1986). The structure of the gastropod shells has been proven to have an impact on the fecundity (Childress, 1972; Bach et al., 1976; Elwood et al., 1995) and mating activity (Bertness, 1981a; Hazlett, 1989; Carlon and Ebersole, 1995; Mantelatto et al., 2002).

The studies on population structure and reproductive biology mostly focus on the seasonal abundance, sex ratio, juvenile recruitment and fecundity of the individual (Garcia and Mantelatto, 2001; Costa and Negreiros-Fransozo, 2003; Litulo, 2005; Saher and Qureshi, 2010, 2011; De Lima et al., 2014). Each species has unique characteristics, such as fecundity and the pace at which broods are generated (Sastry, 1983). Fecundity is seen as an indicator of an individual's reproductive fitness (Childress, 1972), which can help in understanding the effect of environmental factors on their reproductive strategies (Cody, 1966; Alkhafaji et al., 2017). Most tropical and subtropical hermit species reproduce continuously (Turra and Leite, 2000; Litulo, 2004), whereas species of the temperate zone exhibit seasonality in their reproductive activity (Nyblade, 1987; Carlon and Ebersole, 1995; Mishima and Henmi, 2008; Terossi et al., 2010). The peak in reproductive activity may differ amongst populations in response to changes in temperature, salinity, oxygen, food availability, photoperiod, rainfall and response of the hermit crab population towards environmental conditions of the habitat (Meusy and Payen, 1988; Negreiros-Fransozo et al., 2003; Litulo, 2004).

There are very few studies in India that described the population structure and reproductive biology of some hermit crab species, including *Clibanarius olivaceus* (Kamalaveni, 1947), *C. clibanarius* (Varadarajan and Subramoniam, 1982) and *Diogenes miles* (Sankolli and Shenoy, 1993). Such studies of the population provide understanding about the ecological stability of the species in its habitat along with the information about the biology of the species (Pillay and Nair, 1971; Jones and Simons, 1981; Santos et al., 1995; Takween and Qureshi, 2005). However, no such studies have been carried out on any hermit crab species occurring on the Gujarat coast.

Veraval city is located on the west coast of Gujarat, which is very important from a commercial fisheries point of view as

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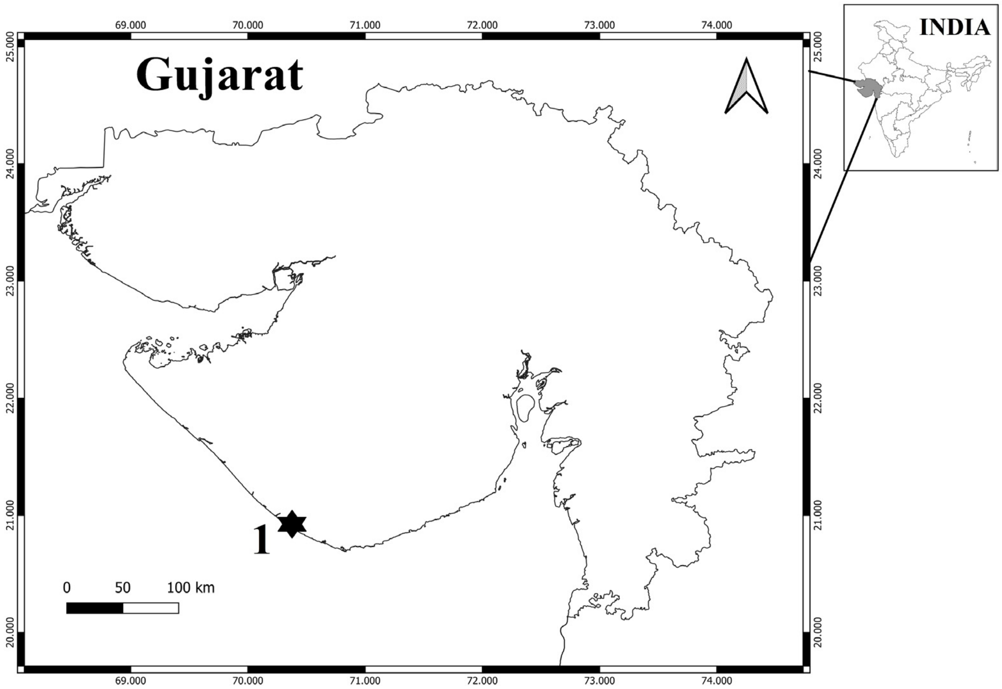

Fig. 1. Map of the study area. 1. Veraval, Saurashtra coast, Gujarat, India.

it is one of the largest fish landing centres in India. The exposure area of the intertidal zone varies between 60 and 150 metres during low tide. The intertidal area is flat in nature, with the lower intertidal zone ending with a steep vertical slope towards the subtidal zone. *Clibanarius rhabdodactylus* Forest, 1953 (Diogenidae) is found in the intertidal region of Gujarat coast with greater abundance at Veraval. Its distribution extends from Philippines (Malay et al., 2018), South Japan (Osawa and Yoshida, 2009), to India (Kachhiya et al., 2017). Ecological aspects of the species are studied in terms of shell utilisation pattern and intertidal distribution only (Patel et al., 2020a, 2022, 2023; Thacker et al., 2021). However, no studies have been carried out on the population structure of *C. rhabdodactylus*. The aim of this work was to describe the population structure and reproductive biology (size dimorphism, sex ratio) of *Clibanarius rhabdodactylus* in the rocky intertidal zone of the Saurashtra coast, Gujarat state, India.

Fig. 2. *Clibanarius rhabdodactylus* Forest, 1953 (SL: 10.54 mm) dorsal view.

2. Materials and methods

2.1. Study area

The rocky intertidal zone at Veraval city (20°54'37''N, 70°21'04''E) of Saurashtra coast, Gujarat (Fig. 1) varies between 60 and 150 m from high tide to low tide where *Clibanarius rhabdodactylus* (Fig. 2) occurs in high abundance (Patel et al., 2020a).

2.2. Field methods

Sampling was carried out for 12 months (March 2021 to February 2022). Specimens were collected randomly using hand-picking technique from the intertidal region during low tide time by employing the catch per unit effort method by one person during a period of 4 h. In this method, first the intertidal area of 500 m^2 was marked during low tide, and thoroughly scanned for the presence of *C. rhabdodactylus* individuals by one person. Whenever an individual was encountered, it was handpicked and collected in a zip-lock bag. The collected specimens were transferred to 10% formalin until further analysis.

2.3. Laboratory analysis

In the laboratory, the crabs were first identified and classified as male, non-ovigerous female, or ovigerous female. Individuals having gonopores on the ventral side of the first segment of their second pair of walking legs (third periopod) were considered females, while males do not have such a structure. If there were egg masses on the pleopods, the individuals were considered ovigerous females. As a morphological characteristic of the hermit crabs, the shield length and wet weight of each individual was measured using vernier callipers (±0.01 mm accuracy) and weighing balance (0.001 g accuracy) respectively.

Fecundity estimation was carried out by carefully removing the egg mass from the pleopods of ovigerous hermit crabs (n=50). The egg mass was then transferred into 20 ml of sea water and gently mixed to evenly distribute the eggs in water. Three samples of 2 ml each were taken in a petri dish and observed under a stereomicroscope to count the total number of eggs. Average of the three samples was multiplied by the dilution factor (10) to obtain the total number of eggs (Llodra, 2002; Litulo, 2004). For the weight of egg mass, the wet ovigerous females were weighed with and without egg mass and the difference in the weight was considered as the weight of egg mass. The size range (diameter) of eggs (n=10) from each crab was measured by means of an ocular micrometre under a microscope (Saher and Qureshi, 2010).

2.4. Data analysis

The population size structure was analysed as a function of the size frequency distribution of the individuals. Specimens were grouped in 1 mm size-class intervals, from 1 to 8 mm SL. Normality test of the collected data was tested using Shapiro Wilk test suggesting that the data was not normally distributed ($p<0.001$), hence non-parametric methods were used. Variation in mean values of shield length of different sexes (males, non-ovigerous females and ovigerous females) of *C. rhabdodactylus* was evaluated using Kruskal–Wallis (KW) test to assess the sexual dimorphism. On finding a significant difference ($p<0.001$) in the KW test, Dunn's post hoc test was carried out for multiple comparison tests. For month-wise variation in the size and sex composition (modal distribution), the monthly data of hermit crab size (shield length) and sex were plotted. Occurrence of more ovigerous females in the monthly samples indicates the breeding season of the species. Chi-square test (χ^2) was calculated to evaluate the sex ratio between male and female (non-ovigerous females and ovigerous females) individuals. To determine the size at first maturity of females, the percentage of ovigerous females in different size classes was calculated for all 12 months (March 2021 to February 2022) since ovigerous females occurred throughout the year. The size at which the frequency of ovigerous females was estimated to be over 50% (SM50) as the maturity size (Goshima et al., 1996; Wada et al., 2000; Mishima and Henmi, 2008). The monthly data of juvenile and ovigerous female occurrence was plotted against the ambient and water temperature to understand the effect of temperature on the breeding and juvenile settlement of *C. rhabdodactylus*. Pearson's correlation analysis was carried out between the relative frequency of juveniles and mean ambient temperature. Monthly data of relative frequency of juveniles was plotted against ambient temperature to understand the relation between temperature and juvenile settlement. Regression analysis was performed to find out the relationship between the morphological parameters of eggs and hermit crabs' morphology (shield length and weight). The statistical significance was accepted if $p<0.05$. All the statistical analyses were performed using PAST software, version 4.03 (Hammer et al., 2001) and Microsoft Excel.

3. Results

A total of 1640 individuals of *Clibanarius rhabdodactylus* were collected out of which 604 were male (36.83%), while 1036 were female (63.17%) including 615 non-ovigerous females (37.50%) and 421 ovigerous females (25.67%). (Table 1). The shield length of *C. rhabdodactylus* males ranged from 1.96 mm to 7.71 mm SL, non-ovigerous females ranged from 1.66 mm to 5.06 mm SL and ovigerous females ranged from 3.02 mm to 4.98 mm SL. The size of male, non-ovigerous female, and ovigerous female individuals varied significantly (Kruskal–Wallis, H=653.3, $p<0.001$). Dunn's multiple comparison tests showed that the males were significantly larger than females (Dunn's test - Bonferroni corrected, $p<0.001$), while among female individuals, ovigerous females were significantly larger than non-ovigerous females (Dunn's test - Bonferroni corrected, $p<0.001$) (Table 1).

Table 1
Carapace shield length values of different sexes of *Clibanarius rhabdodactylus*.

Sex	n	Min. SL (mm)	Max. SL (mm)	Mean ±SD
Male	604	1.96	7.71	5.05 ± 0.99***
Non-ovigerous female	615	1.66	5.06	3.80 ± 0.52***
Ovigerous female	421	3.02	4.98	3.95 ± 0.41***

(Kruskal–Wallis; n = total individuals; SL = shield length).
***$p < 0.001$.

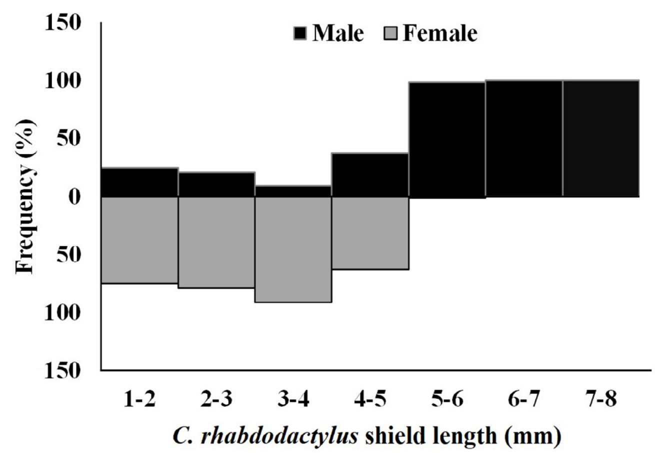

Fig. 3. Overall size-frequency distributions of *Clibanarius rhabdodactylus* collected at Veraval coast.

The overall sex ratio of *C. rhabdodactylus* significantly differed from the expected 1:1 proportion ($\chi 2 = 8.27$, $P<0.01$) and was female biased (1:1.72) (Table 2). Female biased sex ratio was observed throughout the year except in August and December. Ovigerous females were recorded throughout the year, which shows that the species has a continuous pattern of reproduction with high percentages of occurrence from January to June and September to October.

Clibanarius rhabdodactylus individuals were recorded from all the size classes of shield length, ranging from 1 mm to 8 mm. The size frequency distribution of male individuals showed bimodal distribution, with the maximum peak observed in the 1–2 mm SL size class and the 6–8 mm SL size class. On the other hand, the size frequency distribution of female individuals showed a unimodal distribution, with the maximum peak observed in the 3–4 mm SL size class (Fig. 3). The size classes at which the frequency of ovigerous females reached over 50% (SM50) was 3–4 mm size class. The frequency of spawning in females was 50.67% at 3–4 mm size class which increased to 66.55% in 4–5 mm size class (Fig. 4).

During majority of the months, male individuals had bimodal distribution whereas non-ovigerous females had unimodal distribution. Ovigerous females showed only unimodal distribution throughout the year. Moreover, it was also observed that juvenile individuals occurred throughout the year (Fig. 5). Pearson's correlation analyses suggested a negative correlation between the relative frequency of juveniles and mean ambient temperature (r=−0.12, $p>0.05$). There was no trend observed between monthly ambient and water temperature and the percentage of

Table 2
Total number of *Clibanarius rhabdodactylus* specimens collected at rocky intertidal region of Veraval.

Month	M	%	NOF	%	OF	%	NOF+OF	%	Male: Female
January	90	40.00	61	27.11	74	32.89	135	60.00	1:1.5
February	68	43.04	40	25.32	50	31.65	90	56.96	1:1.32
March	55	28.65	63	32.81	74	38.54	137	71.35	1:2.49
April	42	31.11	49	36.30	44	32.59	93	68.89	1:2.21
May	57	32.76	83	47.70	34	19.54	117	67.24	1:2.05
June	93	28.88	173	53.73	56	17.39	229	71.12	1:2.46
July	30	31.25	64	66.67	2	2.08	66	68.75	1:2.20
August	15	75.00	3	15.00	2	10.00	5	25.00	1:0.33
September	52	48.15	14	12.96	42	38.89	56	51.85	1:1.08
October	28	48.28	8	13.79	22	37.93	30	51.72	1:1.07
November	24	39.34	30	49.18	7	11.48	37	60.66	1:1.54
December	50	54.95	27	29.67	14	15.38	41	45.05	1:0.82
Total	604	36.83	615	37.50	421	25.67	1036	63.17	1:1.72

M = male; NOF = non-ovigerous female; OF= ovigerous female.

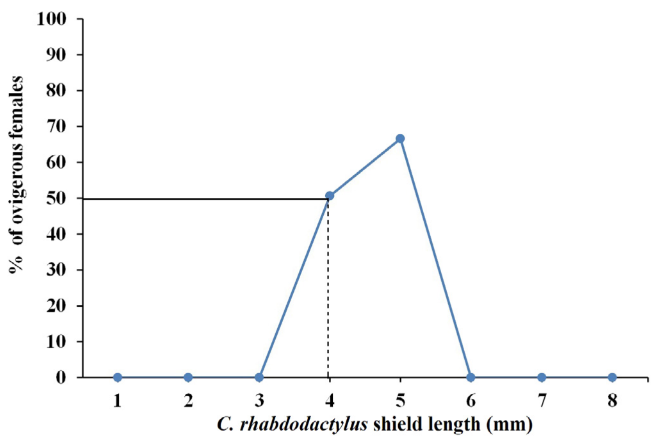

Fig. 4. Percentage of ovigerous female *Clibanarius rhabdodactylus* as a function of shield length from (n = 421) form March 2021 to February 2022. Dashed lines indicate the shield length corresponding to the 50% maturity level (SM50).

Table 3
Summary of hermit crab weight, shield length, shield width, weight of egg mass, egg number and egg size in ovigerous females of *Clibanarius rhabdodactylus* collected from Veraval coast.

Variables	N	Mean ±SD	Min.	Max.
Crab weight (gm)	50	0.34 ± 0.18	0.05	1.28
Shield length (mm)	50	4.06 ± 0.57	2.34	5.39
Shield width (mm)	50	3.1 ± 0.70	1.4	4.22
Weight of egg mass (gm)	50	0.13 ± 0.08	0.01	0.37
Egg number	50	1322.08 ± 838.36	246	3460
Egg size	50	0.47 ± 0.07	0.31	0.61

N = total individuals.

ovigerous female and juvenile occurrence (of both sexes) (Fig. 6). The percentage occurrence of juveniles decreases with the increase in ovigerous female occurrence while the percentage occurrence of juveniles increased with decrease in ovigerous female occurrence.

The fecundity data revealed that the maximum and minimum number of eggs recorded were 3460 and 246 eggs respectively with average number of eggs being 1322.08 ± 838.36 (n=50). The maximum and minimum size of eggs recorded were 0.60 and 0.31 mm respectively with average size of eggs being 0.47 ± 0.07 mm (n=50). The maximum and minimum egg mass weight recorded were 0.37 and 0.01 mm respectively with average egg mass weight being 0.13 ± 0.08 gm (n=50) (Table 3). It was observed that the total number of eggs, size of eggs, and total weight of egg mass showed significant relation with the shield length and body weight of the ovigerous females (Fig. 7).

4. Discussion

Clibanarius rhabdodactylus males were significantly larger as compared to the non-ovigerous and ovigerous females. Similar results have been observed for other hermit crab species like *Clibanarius virescens* (Imazu and Asakura, 1994), *C. zebra* (Trivedi and Vachhrajani, 2014), *C. symmetricus* (Rodrigues and Martinelli-Lemos, 2016), *C. rhabdodactylus* (Patel et al., 2020a, 2022), *Diogenes custos* (Patel et al., 2020b), and *C. ransoni* (Patel et al., 2021). Generally, three hypotheses have been postulated that explain the sexual size dimorphism in hermit crabs which are as follows: (1) competitive displacement hypothesis, which states that a size difference reduces intraspecific competition for the available shells (Abrams, 1988); (2) energy hypothesis, which states that since the female ovary uses more energy than the male testes, it leads to reduced growth in females (López Greco et al., 2000; Mantelatto et al., 2010); (3) sexual selection hypothesis, which states that a large-sized male will have greater chances of success in a male–male competition for acquiring a mature female which results in males attaining larger size (Asakura, 1987; Hazlett, 1988; Abrams, 1988; Wada et al., 2000).

Growth of crustaceans in general is limited to the oxygen availability. The gill-oxygen limitation theory (GOLT) suggests that the surface area of gills or other respiratory surfaces of water-breathing ectotherms (WBE) as two-dimensional structures are not efficient enough to provide enough oxygen required for further growth of their three-dimensional bodies. Therefore, decreased relative supply of oxygen can restrict overall body growth and leads to sexual maturation (Pauly, 2021). Moreover, male hermit crabs are more aggressive and dominant as compared to females (Absher et al., 2001; Yoshino and Goshima, 2002; Briffa and Dallaway, 2007). As a result of aggressive or dominant behaviour, male hermit crabs' chances of acquiring larger shells increase, allowing them to grow larger as compared to females. Further, the requirements of shell are different in different sexes like, the ovigerous females need voluminous shell for accommodation and incubation of eggs (Abrams, 1978; Bertness, 1981b; Sallam, 2012) and hence can restrain growth for more internal shell space which aids in higher fecundity. Previous study conducted at Veraval suggests that *Cerithium caeruleum* is the most abundantly occurring shell in the intertidal region which is a long, more spired and less voluminous (internal space) shell (Patel et al., 2022) which could be another reason for smaller sized female for the purpose of eggs accommodation.

Overall and monthly sex ratios of male and female individuals were skewed towards females. The sex ratio was female-biased in the smaller and intermediate size classes (1 to 5 mm SL), whereas in the largest size classes it was male-biased (5 to

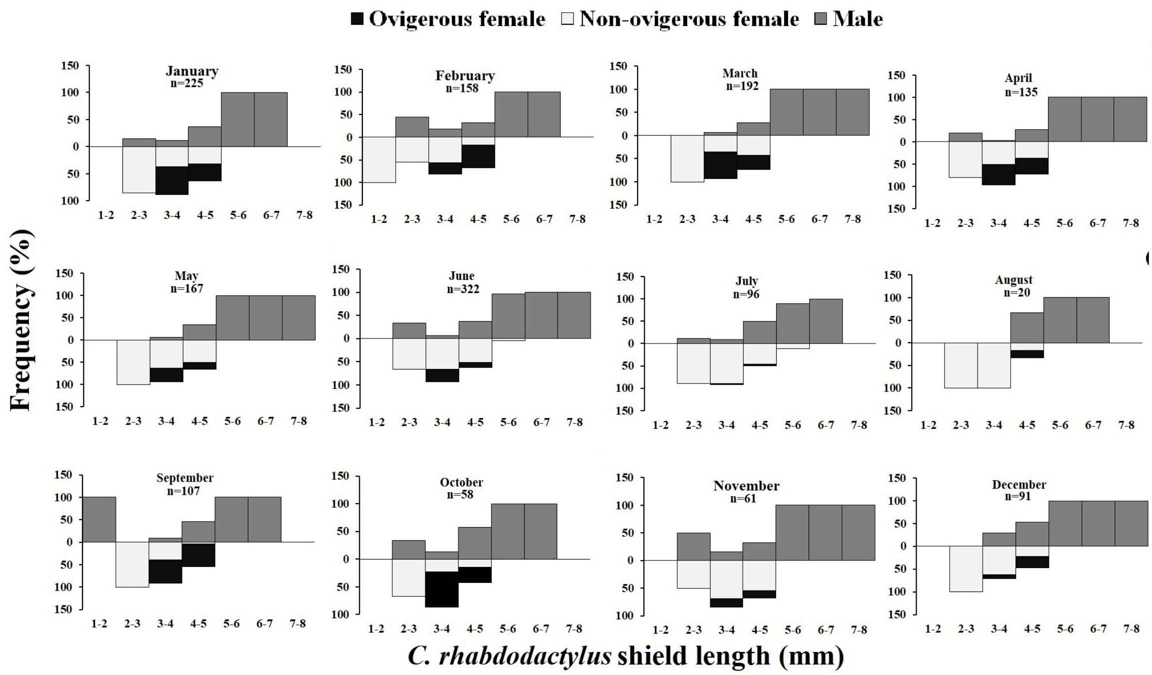

Fig. 5. Monthly size–frequency distributions of *Clibanarius rhabdodactylus* from January to December.

8 mm SL). Similar results have been obtained in several other studies (Wenner, 1972; Manjón-Cabeza and García Raso, 1995; Nardone and Gherardi, 1997; Fransozo and Mantelatto, 1998). Several factors like differences between sexes in their pattern of habitat utilisation and partition, spatio-temporal distribution, life span, migration, feeding restriction, growth rates, as well as sex reversal and sex longevity, are responsible reasons for the deviation from the ideal 1:1 sex ratio (Darnell, 1962; Wenner, 1972; Lardies et al., 1998; Wada et al., 2000). Sexual size dimorphism can be one of the possible reasons for the deviation from the ideal sex ratio in different size classes. It was observed that the sex ratio of intermediate size class was female biased which could be due to increased male mortality leading to a sex ratio skewed towards females (Asakura, 1992). In the larger size classes, the population was male biased as males generally attain a larger size compared to females in less time, and as a result the sex ratio in the larger size classes is mostly skewed towards males (Wenner, 1972). Markham (1968) hypothesised in his study that females have slower rates of growth as compared to their conspecific males since they get to utilise inadequate gastropod shells and have to spend more energy on reproduction. However, previous study has found that the availability of shell is not a limiting factor in the study site (Patel et al., 2022).

Overall size frequency distribution of *C. rhabdodactylus* showed unimodal distribution frequency in females, whereas bimodal in the case of males. Significant seasonal differences were observed in the size frequency distribution of *C. rhabdodactylus*. Such pattern of frequency distribution has been reported previously in *Aratus pisonii* (Díaz and Conde, 1989), *Leptuca uruguayensis* (Spivak et al., 1991), *Clibanarius antillensis* (Turra and Leite, 1999), *Lophozozymus incisus* and *Pachygrapsus marmoratus* (Flores and Paula, 2002), *Aegla franciscana* (Gonçalves et al., 2006) and *A. georginae* (Copatti et al., 2016). Various factors like differential mortality (Díaz and Conde, 1989), growth rates (Negreiros-Fransozo et al., 2003), and differing migratory patterns (De Arruda Leme and Negreiros-Fransozo, 1998; Flores and Negreiros-Fransozo, 1999) have been proposed as possible explanations for such distributions. Zimmerman and Felder (1991) suggested that it is a common phenomenon in organisms that reproduce several

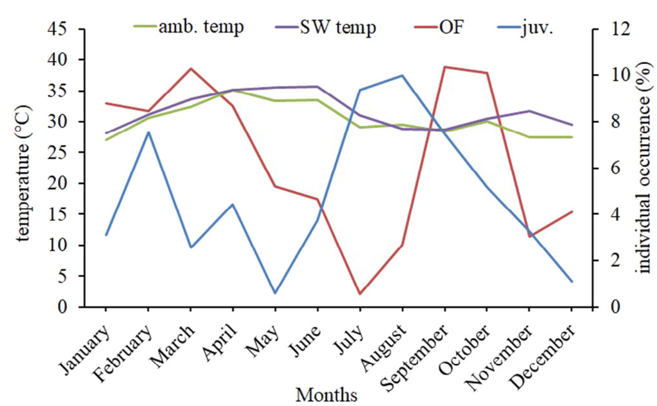

Fig. 6. Association between the juveniles (of both the sexes) and ovigerous female occurrence of *Clibanarius rhabdodactylus* with monthly ambient and water temperature at Veraval coast. (amb. Temp.: ambient temperature, SW temp: sea water temperature, OF: ovigerous females, juv: juveniles).

times and have numerous clutches each season. Unimodality is often seen in stable populations that have steady recruitment and death rates throughout the life cycle and the proportion of individuals joining the population and those leaving it is about equal (Thurman, 1985; Díaz and Conde, 1989). On the other hand, bimodality might reflect the population's overall growth trends. In the present study, the smaller size classes had both male and female individuals whereas in the intermediate size classes the frequency of males decreases and female population remains almost stable probably due to higher mortality rate of males. Since males reach larger size in short period of time, the larger size classes were dominated by male individuals only, and hence unimodal frequency distribution in females and bimodal frequency distribution in males are observed. For a deeper understanding of size frequency distribution, detailed knowledge on the growth and moulting rate of hermit crabs should be acquired and analysed, as proposed by Turra and Leite (1999).

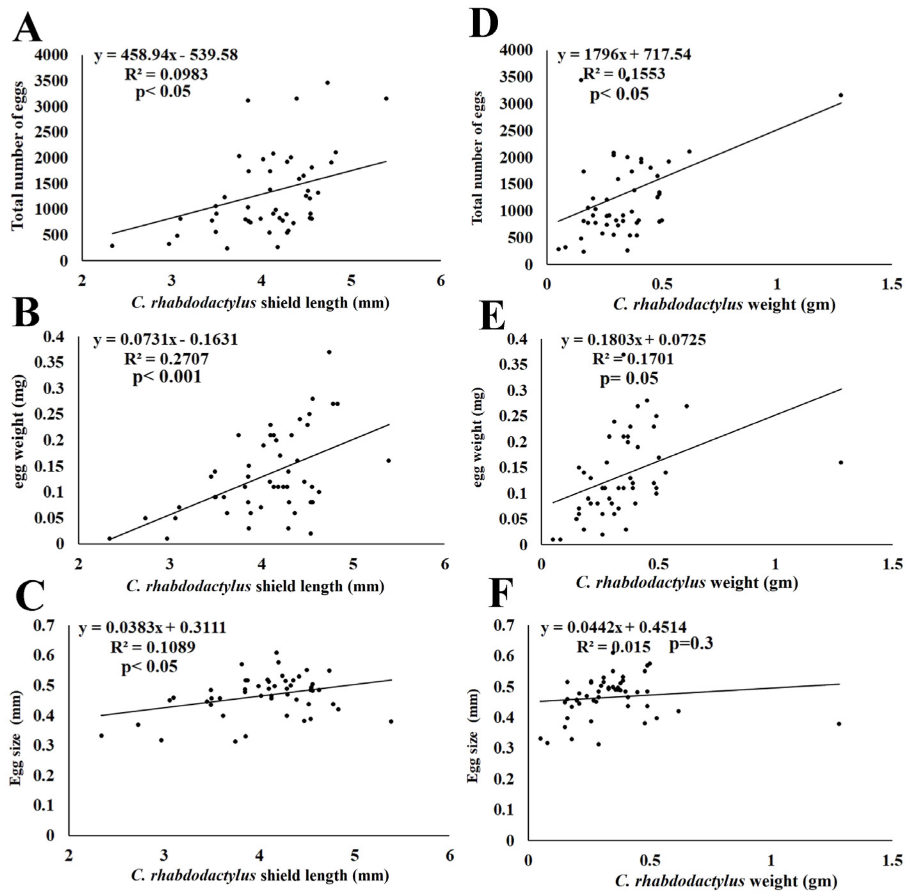

Fig. 7. Relationship of *Clibanarius rhabdodactylus* shield length with A. total number of eggs; B. Egg size and C. weight of egg mass; and wet weight with D. total number of eggs; E. Egg size and F. weight of egg mass.

The temperature range was recorded between 27 °C and 35 °C falling in tropical climatic conditions which supports continuous reproduction. Hence, ovigerous females occurred throughout the year with two peaks: January to June and September to October, showing that *C. rhabdodactylus* is a continuously reproducing species. The ovigerous females belonging to the size class of 3–4 mm SL exceed 50% (SM50) frequency in the peak reproductive months (January, March, April, September and October). Several tropical hermit crab species such as *Clibanarius chapini* and *C. senegalensis* (Ameyaw-Akumfi, 1974), *C. clibanarius* (Varadarajan and Subramoniam, 1982), *C. antillensis* (Turra and Leite, 1999, 2000), *Petrochirus diogenes* (Bertini and Fransozo, 2002), *Paguristes tortugae* (Mantelatto et al., 2002), and *Diogenes brevirostris* (Litulo, 2004) have also displayed the well-known pattern of continuous reproduction with reproduction peaks. There was no trend observed between monthly temperature and the percentage of ovigerous female occurrence. However, it was observed that the percentage occurrence of juveniles decreased during the two peaks in ovigerous female occurrence while the percentage occurrence of juveniles increased with decrease in ovigerous female occurrence. It suggests that *C. rhabdodactylus* has a rapid reproductive cycle and incubation period while juvenile recruitment also occurs year-round. Reproductive season is immediately followed by juvenile recruitment season with peaks occurring during decreased reproductive period. Similar results have been reported in some other studies as well (Fransozo et al., 2000; Litulo, 2005). Periodicity in the reproductive season could be due to various factors like food availability for adults (Goodbody, 1965), the ecology of larvae (Reese, 1968), the availability of shells (Bertness, 1981b), the frequency of sexual maturity, mating, gonad growth, and incubation time (Sastry, 1983), and the temperature of the sea water (Lancaster, 1990). It is believed that increased reproductive activity and longer reproductive phases are adaptations to gastropod shell restriction (Bertness, 1981b; Carlon and Ebersole, 1995). Reproductive peaks may differ across populations in response to interspecies antagonism and shell availability (Reese, 1968; Ameyaw-Akumfi, 1974; Fotheringham, 1976b). Fecundity and reproductive activity might also change from region to region since shell supply and availability vary across various regions (Bach et al., 1976; Bertness, 1981d).

The number of eggs, weight of egg mass, and size of eggs were positively correlated with the size and weight of the ovigerous female. Similar results have been recorded in several other studies (Fotheringham, 1976a; Bertness, 1981c; Wilber, 1989). Hermit crab fertility and body size are known to be constrained by shell size restrictions (Markham, 1968; Fotheringham, 1976a,b; Bertness, 1981c) and increase with increasing body size (Vance, 1972; Bertness, 1980). Turra and Leite (1999) observed that regardless of differences in brood size amongst females with various types of shells, the relationship between female size and egg production remains constant. However, gastropod shells may also affect fecundity as the female cannot grow further in a small shell and hence, the female diverts her energy to immediate reproduction which results in developing smaller broods (Turra and Leite, 1999).

5. Conclusion

The present study was carried out to understand the population structure and reproductive biology of *Clibanarius rhabdodactylus*. Prominent sexual dimorphism was observed with males being significantly larger than females possibly because male individuals are more aggressive or due to the different requirements of both sexes. The overall and monthly sex ratio was female biased. Moreover, the size frequency distribution was unimodal in females, whereas it was bimodal in males. Since the male and female growth rate and mortality rate are different at different life stages it leads to differential sex ratio and size frequency distribution. Detail studies conducted on the growth and moulting rate of *C. rhabdodactylus* can provide deeper knowledge of the size frequency distribution. Ovigerous females occurred throughout the year with two peaks followed by the peak in juvenile settlement which is a common phenomenon in tropical hermit crab species. The number of eggs, weight of egg mass, and size of eggs were positively correlated with the size and weight of the ovigerous female which can be affected by the size and availability of gastropod shells. Detailed studies on egg development and hatching, role of biotic and abiotic factors on the growth and development of *C. rhabdodactylus* can be studied to understand the population dynamics of the species in more detail.

CRediT authorship contribution statement

Krupal J. Patel: Conception, Design, Material preparation, Data collection, Analysis, Writing – first draft, Commented on previous versions of the manuscript. **Kauresh D. Vachhrajani:** Conception, Design, Analysis, Writing – first draft, Commented on previous versions of the manuscript. **Jigneshkumar N. Trivedi:** Conception, Design, Analysis, Writing – first draft, Commented on previous versions of the manuscript.

Declaration of competing interest

The authors declare that they have no known competing financial interests or personal relationships that could have appeared to influence the work reported in this paper.

Data availability

Data will be made available on request.

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