RESULTS
AND
DISCUSSION

Chapter 1:

Population structure of *Clibanarius rhabdodactylus*

Hermit crabs are a substantial element of the many tropical intertidal and relatively deep benthic habitats, where they play a significant role in the marine food chain (Fransozo and Mantelatto, 1998). Hermit crabs are the only species of crustacea that have evolved to acquire empty shells or pseudoshells over time to safeguard their non-calcified pleon from biotic and abiotic stresses (Schejter and Mantelatto, 2011; Schejter et al., 2017). In their environment, empty snail shells are accessible for hermit crabs to inhabit, and they are reliant on these shells for the remainder of their lives (Reese, 1969; Turra and Leite, 2000). According to Childress (1972), Spight (1977), and Bertness (1981b), these shells are often scarce, especially for the population's largest members (Vance, 1972; Kellogg, 1976; Conover, 1978). They might alter the size and development of the occupant hermit crabs (Fotheringham, 1976b; Blackstone, 1985) and restrict the size of the population (Fotheringham, 1976a; Kellogg, 1976). Hermit crabs are one of the best organisms for research on population management and competition due to their discrete way of utilising resources. Numerous instances of competition between and among species of hermit species for empty gastropod shells have been recorded (Kellogg, 1977; Hazlett, 1981; Abrams, 1980; 1981a, b).

There has been a few research conducted on the population structure of hermit crabs in South American, temperate, and European species (Garcia and Mantelatto, 2001; Martinelli et al., 2002; Macpherson and Raventos, 2004). According to these studies, the hermit-crab community 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), along with the inter- and intra-specific competition for the best-fitting gastropod shells (Abrams, 1986). In such competition between sympatric hermit crab species, they compete for the best suitable shells, where the dominant species acquires the best gastropod shells while the recessive species have to utilise the discarded, unsuitable gastropod shell (Abrams et al., 1986). Occupation of such an unsuitable shell is least beneficial and highly stressful for the occupant crabs (Chase et al., 1988; Turra and Leite, 2001, 2004). Previous research on the intraspecific competition of hermit crabs has mainly sought to ascertain if the availability of empty snail shells affected the size of the hermit crab population

(Vance, 1972; Spight, 1977). It has been observed that the hermit crabs are unable to utilise shells that have been highly damaged by predators, buried in the sand, or washed away by currents (Vance, 1972; Kellogg, 1976).

Most tropical and subtropical decapod species reproduce continuously, which is often correlated with warm waters and the availability of food supplies for planktonic larvae. In contrast, temperate zone species typically exhibit seasonality in their reproductive activity due to the cooler climate (Orton, 1920; Thorson, 1950; Mantelatto and Garcia, 2000; Mantelatto and Martinelli, 2001). Similarly, hermit crabs also display seasonal rather than continuous reproduction (Turra and Leite, 2000; Litulo, 2004). According to the studies carried out on the reproductive biology of hermit crabs, year-round reproductive seasons have been reported in the tropical hermit crab species, *Clibanarius zebra, C. chapini, C. senegalensis* (Ameyaw-Akumfi, 1975), *C. clibanarius* (Varadarajan and Subramoniam, 1982), *Calcinus laevimanus* and *C. latens* (Reese, 1968). Among temperate species on the Pacific coast of Northern America, very long reproductive seasons are also known, such as 11 months in *Pagurus armatus* and *P. granosimanus* and 10 months in *P. beringanus* and *P. hirsutiusculus* (Nyblade, 1987). However, both continuous and seasonal reproductive patterns are common in tropical and subtropical environments. This is explained by the narrow variations in temperature, rainfall, photoperiod and nutrient input that influence reproduction and larval growth. Turra and Leite (2000) hypothesised that the occurrence of seasonal breeding patterns in tropical habitats and continuous reproduction in temperate waters may be based on the population's evolutionary life histories. However, some factors, such as competition, shell use and abiotic factors should be considered when assessing the reproductive traits of a species or population.

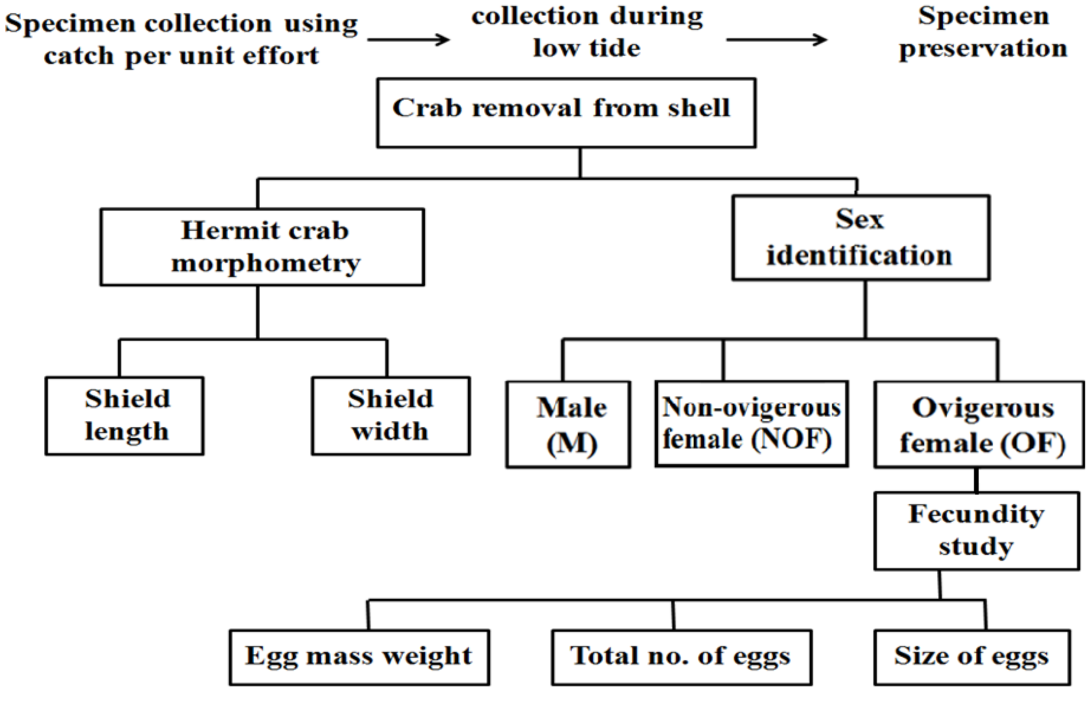
Reproduction is the primary mechanism for maintaining species proliferation and continuity (Hartnoll and Gould, 1988). In crustaceans, reproduction is highly varied and eventually oriented to optimise egg output and offspring survivability. A complex combination of endogenous and external variables determines breeding seasons, enabling intra- and inter-specific differences in the length of the reproductive season (Sastry, 1983). According to some studies (Meusy and Payen, 1988; Costa and Negreiros-Fransozo, 2003; Litulo, 2004), reproductive peaks may differ amongst populations in response to interspecies competition, shell availability, changes in temperature, salinity, oxygen, food availability, photoperiod, rainfall and the response of the hermit crab population towards environmental conditions of the habitat.

As a result of intraspecies competition, Bertness (1981e) hypothesised that the reproductive behaviour of a population of hermit crabs is strongly connected to shell availability. The structure of the gastropod shells has been proven to have an impact on the reproductive behaviour of occupant crabs (Mantelatto et al., 2002). These shells also have an impact on their fecundity (Childress, 1972; Bach et al., 1976; Elwood et al., 1995) and mating activity (Bertness, 1981a; Hazlett, 1989; Carlon and Ebersole, 1995). Fecundity is seen as an indicator of an individual's reproductive fitness (Childress, 1972) and is susceptible to a variety of environmental factors (Cody, 1966). Each species has unique characteristics, such as fecundity and the pace at which broods are generated (Sastry, 1983), which may be influenced by the environment, such as gastropod shells in the particular instance of hermit crabs. Crustaceans in general (Jensen, 1958), and hermit crabs in particular, have a strong correlation between the quantity of eggs and female size (Fotheringham, 1976a; Bertness, 1981b; Wilber, 1989; Negreiros-Fransozo and Fransozo, 1992).

The global sex ratio of hermit crabs did not differ from the 1:1 ratio, but significant deviations were recorded monthly, with females appearing in larger numbers in relation to males, which is a frequent phenomenon in hermit crabs. Moreover, it has also been observed that in a population, males mostly attain larger sizes as compared to females, as a result of which the sex ratio in smaller and intermediate sizes is generally skewed for females whereas it is skewed for males in larger sizes (Bertini and Fransozo, 2000; Garcia and Mantellato, 2001). Several causes have been postulated for this unequal sex ratio, with the most reported being differences between sexes in longevity and maturation time, differential migration, feeding restriction and spatial dispersion between sexes, mortality rates, which are prominent factors for males, habitat partitioning, and sex reversal (Turra and Leite, 2000; Macpherson and Raventos, 2004; Litulo, 2005a).

Numerous studies have been conducted on various biological characteristics of hermit crab species, mainly in relation to relative development and behaviour, such as the utilisation of gastropod shells in their habitat (Bertness, 1981a, b, c; Gherardi, 1991; Hazlett, 1992; Pessani et al., 2000). However, there are very few studies describing the population structure and breeding biology of hermit crabs in India. There are no such data for the hermit crab *C. rhabdodactylus* in particular. Therefore, the present study has been designed to better understand the population structure and breeding biology of *C. rhabdodactylus,* which is commonly found in the rocky intertidal zone of the Saurashtra coast of Gujarat state, India.

The detailed methodology for data collection has been described in Materials and Methods chapter (page 49). The following flow chart shows a summary of the methodology used in the present chapter.



Results

There were a total of 1640 individuals of *C. rhabdodactylus* collected for the study of their population structure and reproductive biology. Out of these 1640 individuals, 604 individuals were male (36.83%), while 1036 individuals were female (63.17%), (615 were non-ovigerous female individuals (37.50%) and 421 were ovigerous female individuals (25.67%)) (Table 1). The shield length of the male individuals of *C. rhabdodactylus* ranged from 1.96 mm to 7.71 mm SL, whereas the shield length of the non-ovigerous female individuals ranged from 1.66 mm to 5.06 mm SL. The shield length of the ovigerous female individuals of *C. rhabdodactylus* ranged from 3.02 mm to 4.98 mm SL. The size of male, non-ovigerous female, and ovigerous female individuals was significantly different, with males being larger than the female individuals (ANOVA, F = 543.6, df = 1639, $p < 0.001$) (Table 1).

Table 1. Carapace shield length values of different sexes of *Clibanarius rhabdodactylus* (ANOVA; ***p<0.001; N = total individuals; SL= Shield length).

Sex	N	Min. SL (mm)	Max. SL (mm)	Mean ± SD (mm)
Male	604	1.96	7.71	5.05±0.99***
Non-ovigerous female	615	1.66	5.06	3.80±0.52***
Ovigerous female	412	3.02	4.98	3.95±0.41***

In the present study, it was observed that the overall sex ratio of *C. rhabdodactylus* was significantly different from the expected 1:1 proportion ($\chi2$= 8.27, P<0.01) and was female biased during most parts of the study. Although the months of August and December represented a male-biased ratio, a female-biased ratio was observed in the remaining months of the year. Furthermore, the overall sex ratio was skewed towards females (1:1.72) for the majority of the study (Table 2). It was also observed that the ovigerous females were recorded during all months of 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. The size of the smallest ovigerous female collected was 2.98 mm, and all individuals of a smaller size than this were considered to be juveniles. Juveniles were found year-round, with the highest incidence of occurrence in February, April, and July to October (Figure 14). Pearson's correlation analyses indicate that the relative frequency of juveniles was negatively correlated with mean ambient temperature (r = -0.12, p > 0.05).

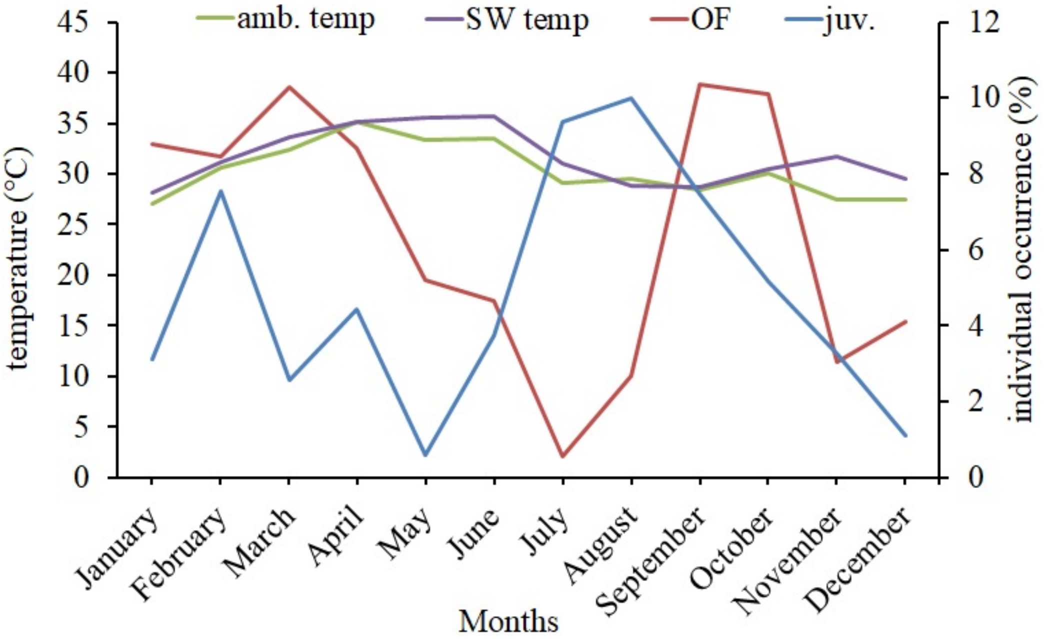


Figure 14. Association between monthly temperature and *Clibanarius rhabdodactylus* juveniles (of both the sexes) occurrence at Veraval coast.

Figure 15 shows the size frequency distributions for all the individuals of *C. rhabdodactylus* during the study period. During the study period of 12 months, *C. rhabdodactylus* individuals were recorded from all the size classes of shield length, ranging from 1 mm to 8 mm. It was observed that the size frequency distribution of male individuals was showing a 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. In the case of male individuals, minimum prevalence was observed in the 3–4 mm SL size class, while in the case of female individuals, minimum prevalence was observed in the 4–5 mm SL size class.

The size class 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% in 3–4 mm size class, which increased to 66.55% in the 4–5 mm size class.

The month-wise frequency distribution of the male, non-ovigerous female and ovigerous female individuals on the basis of their shield length is represented in Figures 16–18. It was observed that the male individuals had bimodal distribution in the majority of the months, whereas unimodal distribution was observed in a few. In the case of non-ovigerous females, unimodal distribution was observed in the majority of the months, while a bimodal distribution pattern was observed in only one month. The ovigerous females showed only a unimodal type of distribution throughout the year.

In the month of November, individuals of *C. rhabdodactylus* were recorded from 2–8 mm SL size classes. It was observed that the male individuals were occurring in 2–8 mm SL size classes. The maximum number of male individuals were recorded in 5–8 mm SL size classes, while the minimum number of individuals were recorded in 3–4 mm SL size classes. The non-ovigerous female individuals were recorded in the 2–5 mm SL size classes. The maximum number of non-ovigerous female individuals were recorded in the 3–4 mm SL size class, while the minimum number of individuals were recorded in the 2–3 mm size class. The ovigerous female individuals were recorded only in the 3–5 mm SL size classes. The maximum number of ovigerous female individuals were recorded in the 3–4 mm SL size class, while the minimum number of individuals were recorded in the 4–5 mm SL size class (Figure 16A).

Table 2. Total number of *Clibanarius rhabdodactylus* specimens collected at rocky intertidal region of Veraval. (M = Male; NOF = Non-ovigerous female; OF= Ovigerous female).

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**

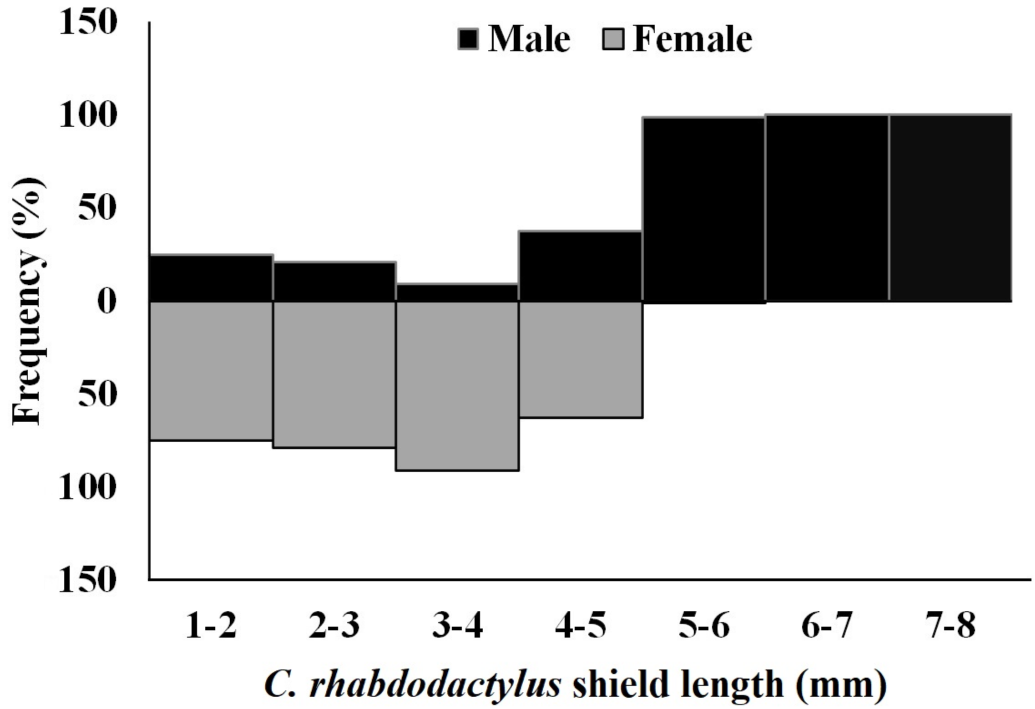


Figure 15. Overall size–frequency distributions of all individuals of *Clibanarius rhabdodactylus* collected at Veraval coast.

In the month of December, individuals of *C. rhabdodactylus* were recorded from 2–8 mm SL size classes. It was observed that the male individuals were occurring in 3–8 mm SL size classes. The maximum number of male individuals were recorded in 5–8 mm SL size classes, while the minimum number of individuals were recorded in 3–4 mm SL size classes. The non-ovigerous female individuals were recorded in the 2–5 mm SL size classes. The maximum number of non-ovigerous female individuals was recorded in the 4–5 mm SL size class, while the minimum number of individuals was recorded in the 3–4 mm SL size class. The ovigerous female individuals were recorded only in the 3–5 mm SL size classes. The maximum number of ovigerous female individuals were recorded in the 4–5 mm size class, while the minimum number of individuals were recorded in the 3–4 mm SL size class (Figure 16B).

In the month of January, individuals of *C. rhabdodactylus* were recorded from 2–7 mm SL size classes. It was observed that male individuals were occurring in all the size classes. The maximum number of male individuals were recorded in 5–7 mm SL size classes, while the minimum number of individuals were recorded in 3–4 mm SL size classes. The non-ovigerous female individuals were recorded in the 2–5 mm SL size classes. The maximum number of non-ovigerous female individuals was recorded in the 2–3 mm size class, while the minimum number of individuals was recorded in the 4–5 mm SL size class. The ovigerous female individuals were recorded only in the 3–5 mm SL size classes. The maximum number of ovigerous female individuals were recorded in the 3–4 mm SL size class, while the minimum number of individuals were recorded in the 4–5 mm SL size class (Figure 16C).

In the month of February, individuals of *C. rhabdodactylus* were recorded from 1–7 mm SL size classes. It was observed that the male individuals were occurring in 2–7 mm SL size classes. The maximum number of male individuals were recorded in 5–7 mm SL size classes, while the minimum number of individuals were recorded in 3–4 mm SL size classes. The non-ovigerous female individuals were recorded in the 1–5 mm SL size classes. The maximum number of non-ovigerous female individuals were recorded in the 1–2 mm SL size class, while the minimum number of individuals was recorded in the 4–5 mm SL size class. The ovigerous female individuals were recorded only in the 3–5 mm SL size classes. The maximum number of ovigerous female individuals were recorded in the 4–5 mm size class, while the minimum number of individuals were recorded in the 3–4 mm SL size class (Figure 16D).

In the month of March, individuals of *C. rhabdodactylus* were recorded from 2-8 mm SL size classes. It was observed that the male individuals were occurring in 3–8 mm SL size classes. The maximum number of male individuals were recorded in 5–8 mm SL size classes, while the minimum number of individuals were recorded in 3–4 mm SL size classes. The non-ovigerous female individuals were recorded in the 2–5 mm SL size classes. The maximum number of non-ovigerous female individuals were recorded in the 2–3 mm SL size class, while the minimum number of individuals were recorded in the 3–4 mm SL size class. The ovigerous female individuals were recorded only in the 3–5 mm SL size classes. The maximum number of ovigerous female individuals were recorded in the 3–4 mm SL size class, while the minimum number of individuals were recorded in the 4–5 mm SL size class (Figure 17A).

In the month of April, individuals of *C. rhabdodactylus* were recorded from 2–8 mm SL size classes. It was observed that the male individuals were occurring in 2–8 mm SL size classes. The maximum number of male individuals were recorded in 5–8 mm SL size classes, while the minimum number of individuals were recorded in 3–4 mm SL size classes. The non-ovigerous female individuals were recorded in the 2–5 mm SL size classes. The maximum number of non-ovigerous female individuals were recorded in the 2–3 mm SL size class, while the minimum number of individuals was recorded in the 4–5 mm SL size class. The ovigerous female individuals were recorded only in the 3–5 mm SL size classes. The maximum number of ovigerous female individuals were recorded in the 3–4 mm SL size class, while the minimum number of individuals were recorded in the 4–5 mm SL size class (Figure 17B).

In the month of May, individuals of *C. rhabdodactylus* were recorded from 2–8 mm SL size classes. It was observed that the male individuals were occurring in 3–8 mm SL size classes. The maximum number of male individuals were recorded in 5–8 mm SL size classes, while the minimum number of individuals were recorded in 3–4 mm SL size classes. The non-ovigerous female individuals were recorded in the 2–5 mm SL size classes. The maximum number of non-ovigerous female individuals were recorded in the 2–3 mm SL size class, while the minimum number of individuals were recorded in the 3–4 mm SL size class. The ovigerous female individuals were recorded only in the 3–5 mm SL size classes. The maximum number of ovigerous female individuals were recorded in the 3–4 mm SL size class, while the minimum number of individuals were recorded in the 4–5 mm SL size class (Figure 17C).

In the month of June, individuals of *C. rhabdodactylus* were recorded from 2–8 mm SL size classes. It was observed that the male individuals were occurring in 3–8 mm SL size classes. The maximum number of male individuals were recorded in 6–8 mm SL size classes, while the minimum number of individuals were recorded in 3–4 mm SL size classes. The non-ovigerous female individuals were recorded in the 2–6 mm SL size classes. The maximum number of non-ovigerous female individuals were recorded in the 3–4 mm SL size class, while the minimum number of individuals were recorded in the 5–6 mm SL size class. The ovigerous female individuals were recorded only in the 3 to 5 mm SL size classes. The maximum number of ovigerous female individuals were recorded in the 3–4 mm SL size class, while the minimum number of individuals were recorded in the 4–5 mm SL size class (Figure 17D).

In the month of July, individuals of *C. rhabdodactylus* were recorded from 2–7 mm SL size classes. It was observed that the male individuals were occurring in 2–7 mm SL size classes. The maximum number of male individuals were recorded in 6–7 mm SL size classes, while the minimum number of individuals were recorded in 3–4 mm SL size classes. The non-ovigerous female individuals were recorded in the 2–6 mm SL size classes. The maximum number of non-ovigerous female individuals were recorded in the 3–4 mm SL size class, while the minimum number of individuals were recorded in the 5–6 mm SL size class. The ovigerous female individuals were recorded only in the 3–5 mm SL size classes. The maximum number of ovigerous female individuals was recorded in the 4–5 mm SL size class, while the minimum number of individuals was recorded in the 3–4 mm SL size class (Figure 18A).

In the month of August, individuals of *C. rhabdodactylus* were recorded from 2–7 mm SL size classes. It was observed that the male individuals were occurring in 4–7 mm SL size classes. The maximum numbers of male individuals were recorded in 5–7 mm SL size classes, while the minimum numbers of individuals were recorded in 4–5 mm SL size classes. The non-ovigerous female individuals were recorded in the 2–5 mm SL size classes. The maximum numbers of non-ovigerous female individuals were recorded in the 2–4 mm SL size class, while the minimum numbers of individuals were recorded in the 4–5 mm SL size class. The ovigerous female individuals were recorded only in the 4–5 mm SL size classes (Figure 18B).

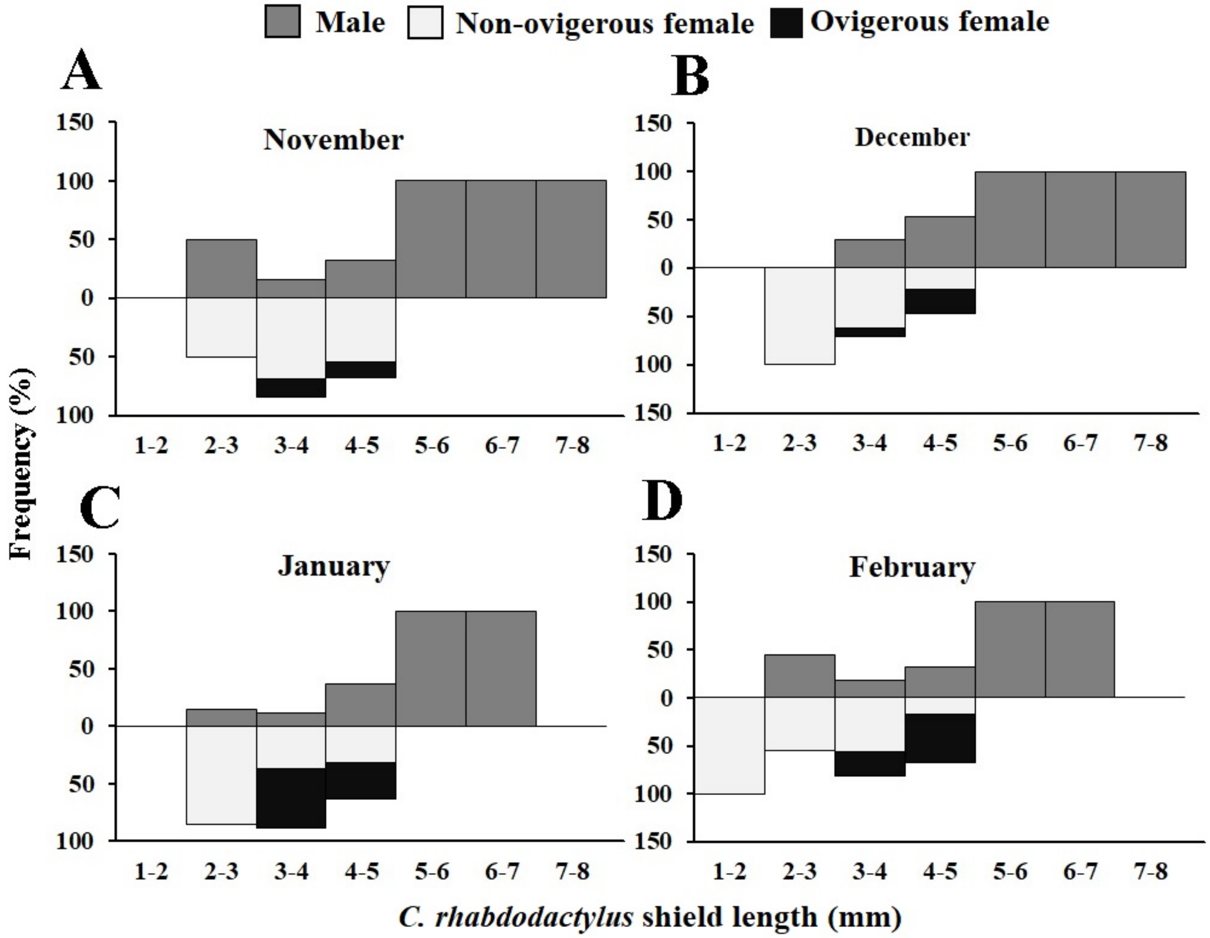


Figure 16. Size frequency distribution of *Clibanarius rhabdodactylus* in the months of winter season.

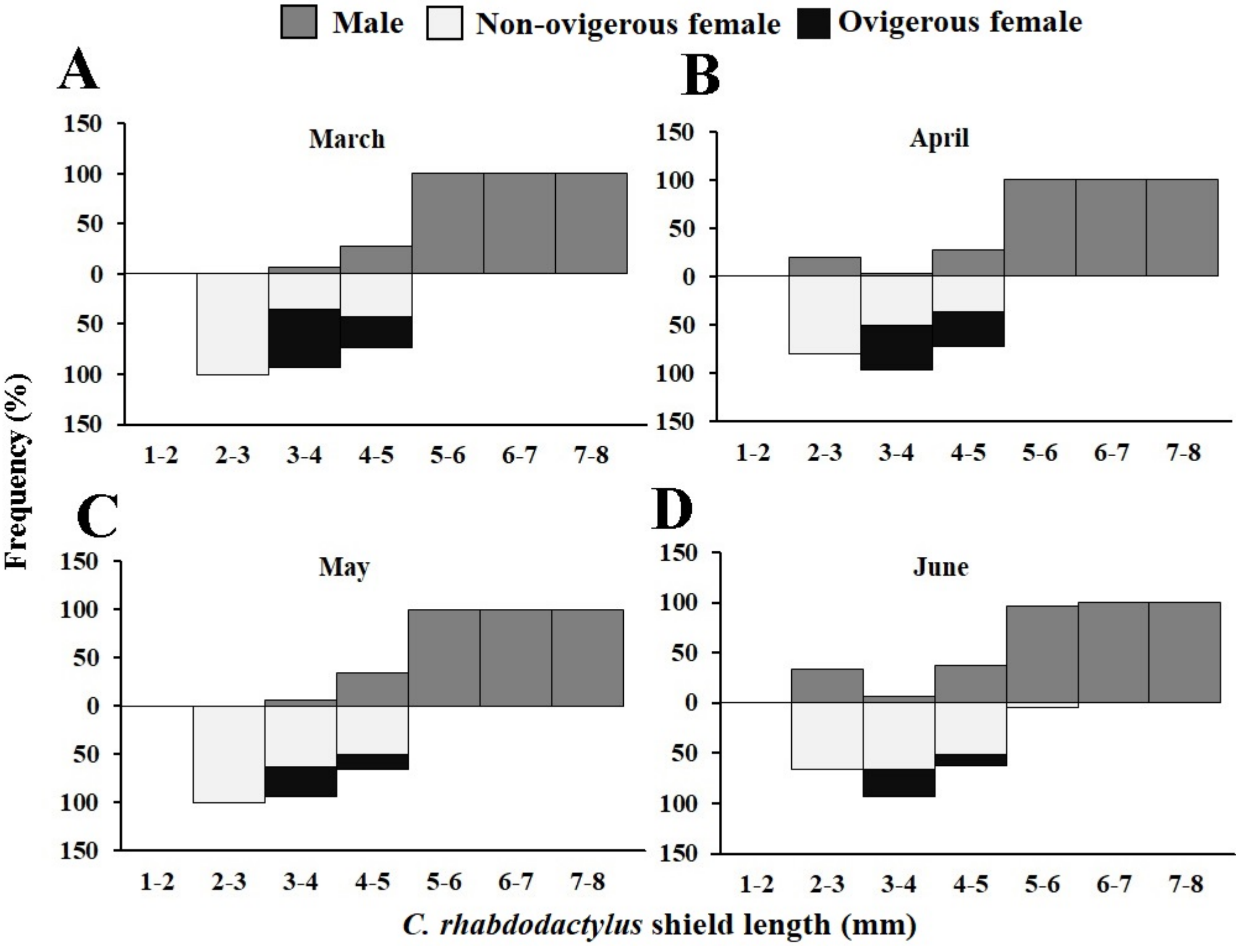


Figure 17. Size frequency distribution of *Clibanarius rhabdodactylus* in the months of summer season.

In the month of September, individuals of *C. rhabdodactylus* were recorded from 1–7 mm SL size classes. It was observed that the male individuals were occurring in 1–2 mm SL and 3–7 mm SL size classes. The maximum number of male individuals were recorded in the 1–2 mm SL and 5–7 mm SL size classes, while no individuals were recorded in the 3–7 mm SL size class, and the minimum number of individuals were recorded in the 3–4 mm SL size classes. The non-ovigerous female individuals were recorded in the 2–5 mm SL size classes. The maximum number of non-ovigerous female individuals were recorded in the 2–3 mm SL size class, while the minimum number of individuals was recorded in the 4–5 mm SL size class. The ovigerous female individuals were recorded only in the 3–5 mm SL size classes. The maximum number of ovigerous female individuals were recorded in the 3–4 mm SL size class, while the minimum number of individuals were recorded in the 4–5 mm SL size class (Figure 18C).

In the month of October, individuals of *C. rhabdodactylus* were recorded from 2–7 mm SL size classes. It was observed that the male individuals were occurring in 2–7 mm SL size classes. The maximum number of male individuals were recorded in 5–7 mm SL size classes, while the minimum number of individuals were recorded in 3–4 mm SL size classes. The non-ovigerous female individuals were recorded in the 2–5 mm SL size classes. The maximum number of non-ovigerous female individuals was recorded in the 2–3 mm SL size class, while the minimum number of individuals was recorded in the 4–5 mm SL size class. The ovigerous female individuals were recorded only in the 3–5 mm SL size classes. The maximum number of ovigerous female individuals were recorded in the 3–4 mm SL size class, while the minimum number of individuals were recorded in the 4–5 mm SL size class (Figure 18D).

In the present study, the fecundity data revealed that the estimated average number of eggs was 1322 ± 838 (n = 50), with the minimum number of eggs observed in the ovigerous female being 246 eggs and the maximum number of eggs recorded in the ovigerous female being 3460 eggs. The average egg size recorded was 0.47 ± 0.07 mm (n = 50), with the minimum egg size recorded being 0.31 mm and the maximum egg size recorded being 0.61 mm. The average egg mass weight was recorded at 0.13 ± 0.08 gm (n = 50), with the minimum egg mass weight recorded at 0.01 gm and the maximum egg mass weight recorded at 0.37 gm (Table 3). It was observed that the total number of eggs, size of eggs, and total weight of egg mass show no correlation with the shield length and body weight of the ovigerous females (Figures 19 and 20).

Discussion

In general, populations are exposed to distinct environmental stresses that drive them to develop separately from one another and to express specific gene frequencies preserved by geographic isolation. Hence, populations function as a reflection of the limitations imposed by the environments to which they are exposed. A thorough examination of the crustaceans' wide array of reproductive patterns has been conducted via several studies (Hartnoll and Gould, 1988; Reid and Corey, 1991; Giangrande et al., 1994). It is widely accepted that their life history patterns are adaptable and that selected forces to increase offspring survival for the following generation have formed them (Stearns, 1992; Wootton, 1993). According to several studies (Fransozo and Mantelatto, 1998; Manjón-Cabeza and García-Raso, 1998), changes in temperature, photoperiod, and availability of food have all been linked to temporal variations of sex ratio, reproduction activities, mature size, and size-frequency distributions seen in natural populations.

Hermits need a source of protective structures, ‘the gastropod mollusc shells’, which they do not produce themselves, for continuous development and, subsequently, reproduction. As a result, the number of available shells may limit crab population sizes (as shell "enrichment" experiments easily demonstrated by Vance, 1972). Whereas the parameters of the native gastropods may determine the final sizes reached by individual crabs (Drapkin, 1963), the sizes of different body parts (Blackstone, 1985, 1986, 1987), their life expectancy (Lancaster, 1988b), or their capacity to reach sexual maturity (Markham, 1968; Fotheringham, 1976a). This essential resource shortage is referred to as "shell-limitation."

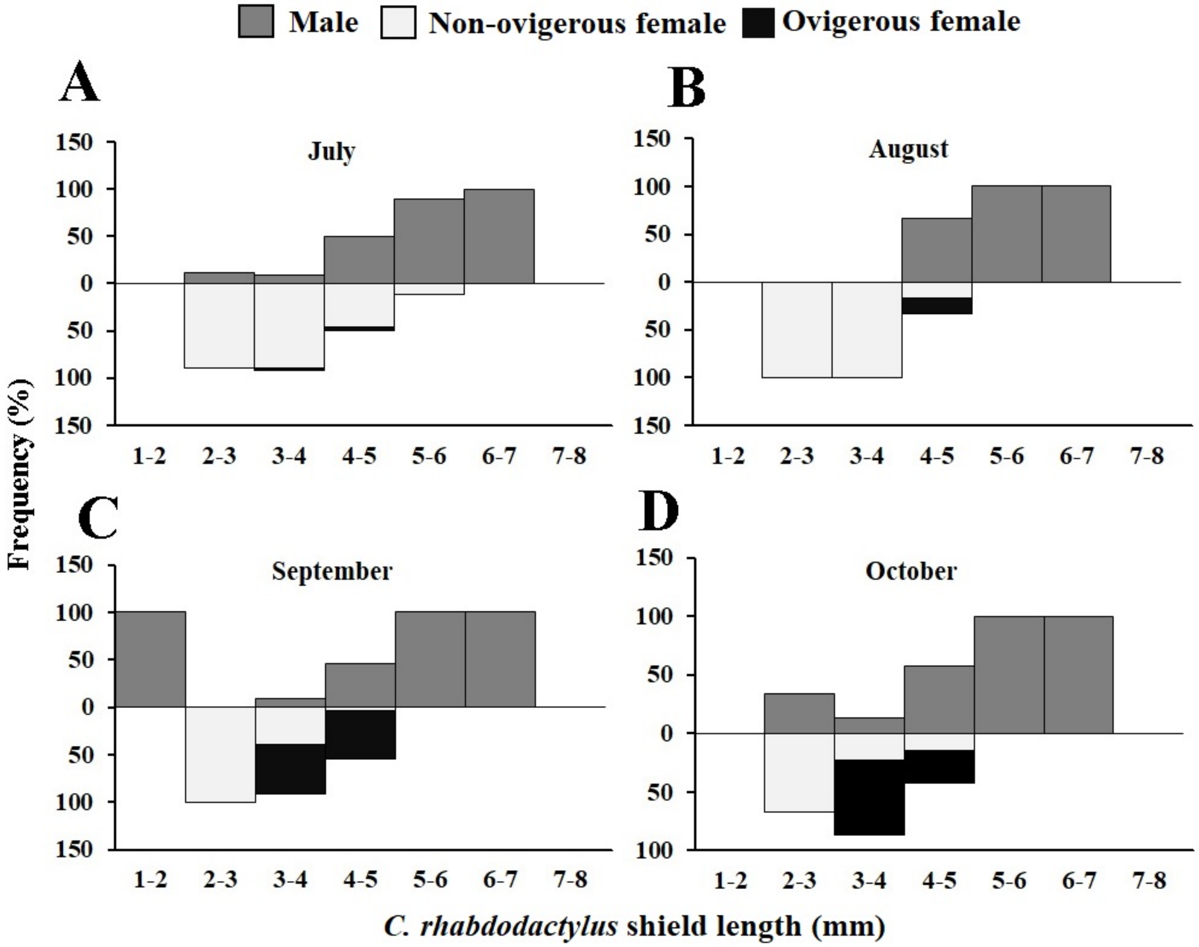


Figure 18. Size frequency distribution of *Clibanarius rhabdodactylus* in the months of monsoon season.

Table 3. Summary statistics 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. (N = total individuals).

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 (mm)	50	0.47±0.07	0.31	0.61

Breakage, erosion, burial, or removal by currents can quickly make the empty shells worthless, leaving the shell supply the most potent factor affecting hermit crab population dynamics (Vance, 1972; Kellogg, 1976). This describes why the hermit crab niche is made up of two essentially different components: the littoral part, which supplies the variety of tiny shells required by the post-larval phase, whereas the sublittoral part supplies the bigger shells required for the hermit crabs to grow to their maximum possible size (Lancaster, 1990).

Animal species that exhibit sexual size dimorphism vary from those in which females are several times larger than males to those in which males are several times bigger than females (for example, "parasitic males" in angler fish and sand crabs) (Harvey, 1990). There are many explanations for sexual dimorphism in size, each based on a particular selected system or set of limitations that applies to each of the sexes. The common reason why females develop larger as compared to males is that larger females can generate larger clutches, while male gamete production is unlikely to be hindered by size (Trivers, 1972; Shine, 1988; Wiklund and Karlsson, 1988). Alternatively, the most often cited mechanism by which males may become bigger than females is sexual selection, defined as variance in male mating success (Alexander et al., 1979; Shine, 1979; Carothers, 1984).

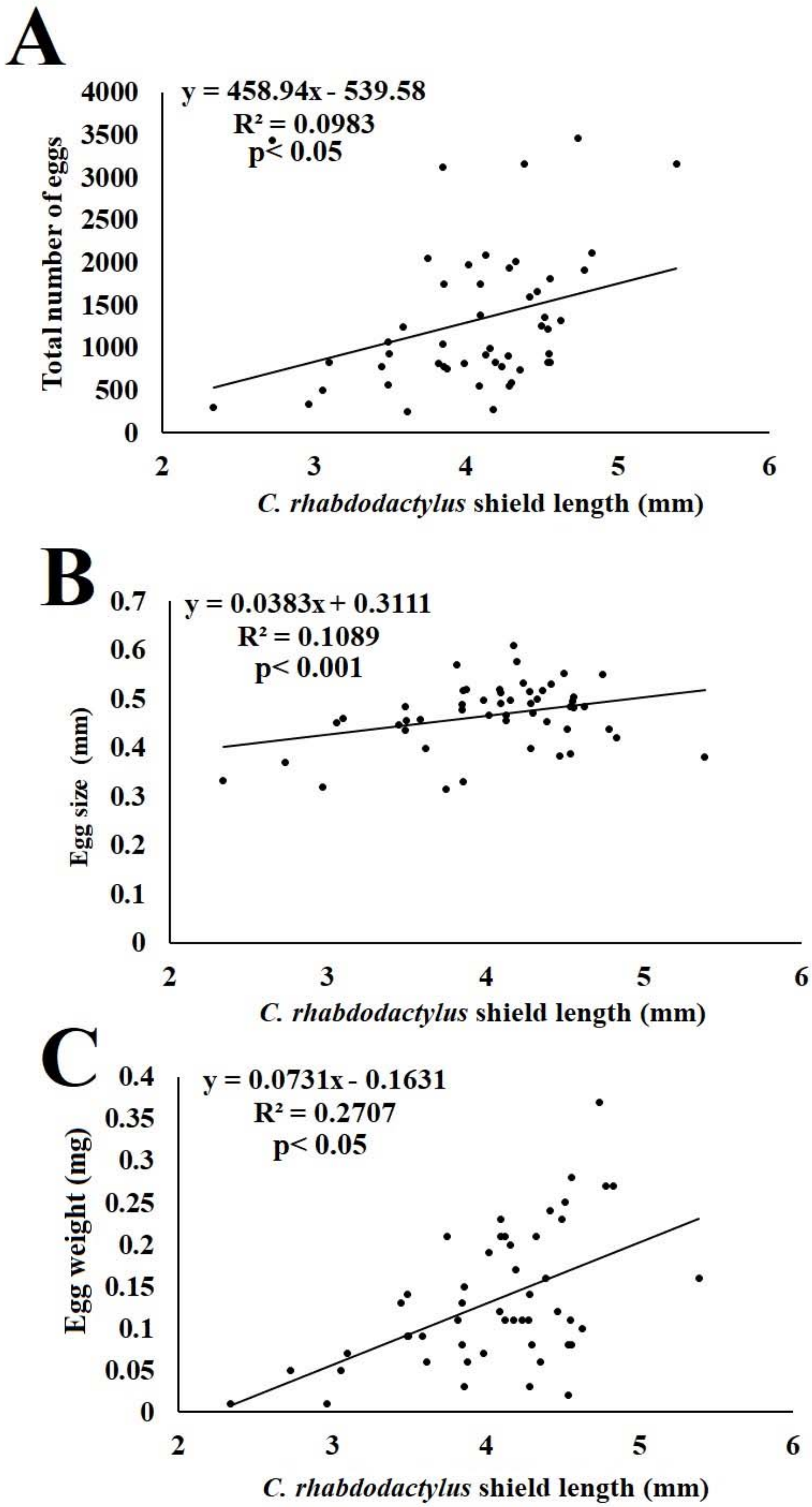


Figure 19. Relationship between *Clibanarius rhabdodactylus* shield length and A. total number of eggs; B. Egg size and C. weight of egg mass.

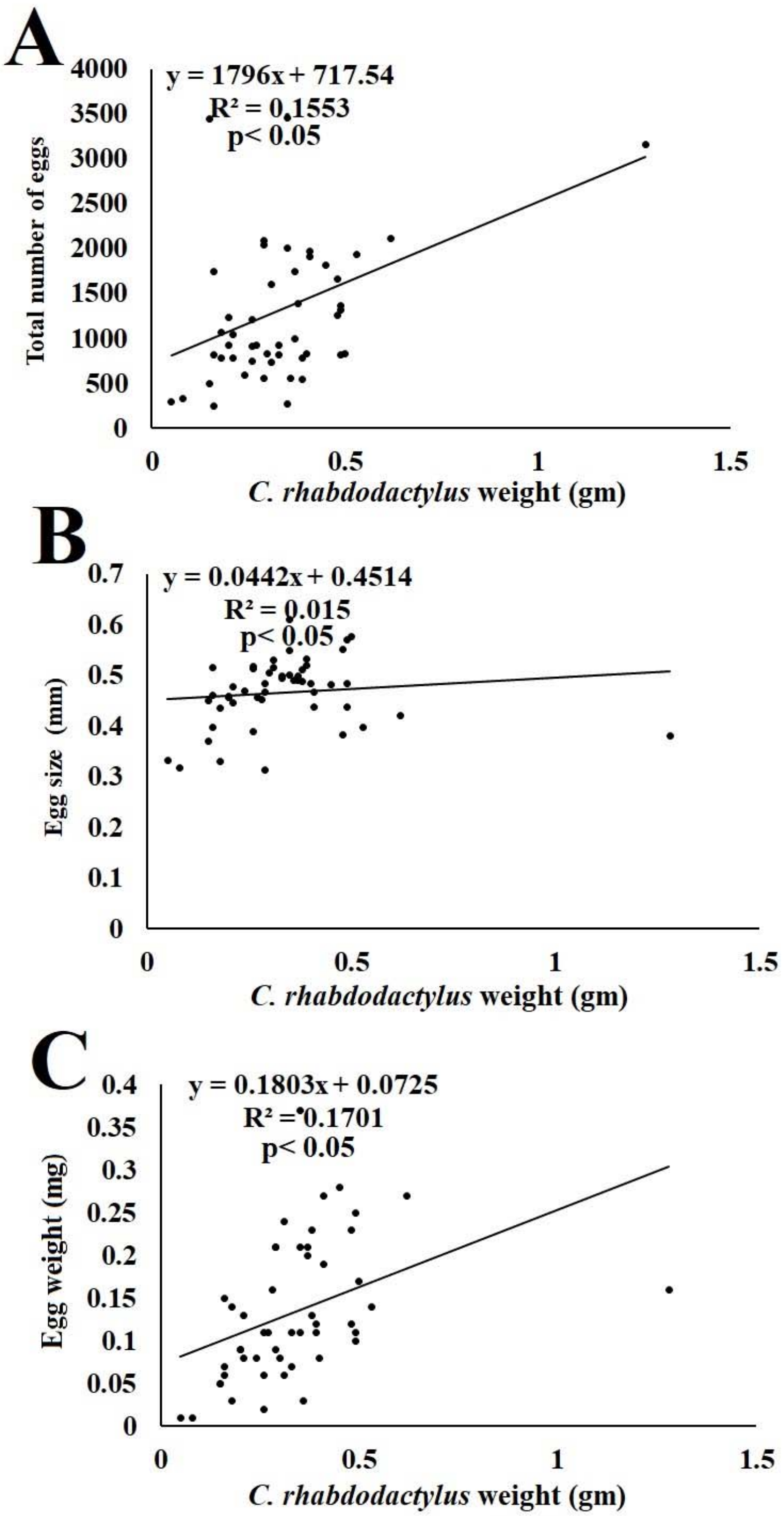


Figure 20. Relationship between *Clibanarius rhabdodactylus* wet weight and A. total number of eggs; B. Egg size and C. weight of egg mass.

A more realistic perspective emphasises sexual variations in overall selection intensity on size as the cause of sexual size dimorphism. The expression of body size for each sex can be thought of as a compromise or balance between a set of selective pressures that endorse large size and another set of selective forces that admonish large size (or benefit small size), all while operating within the limitations (such as genetic or energetic) placed on the specific system. When the strengths of the selected pressures encouraging or discouraging great size fluctuate between the sexes, creating a distinct equilibrium, or when there are sexual variations in the restrictions to responding to selection, sexual size dimorphism may arise (Badyaev, 2002; Janicke and Fromonteil, 2021).

In crustaceans, growth and reproduction are opposing activities that compete with one another for resources of energy that are essential to all of these organisms' life cycle processes (Adiyodi and Adiyodi, 1970; Hartnoll, 2006). As it was already stated, a number of variables, including the amount of nutrition available and the temperature, photoperiod, and rainfall, can alter the development rate and size of crustaceans when they reach maturity (Teissier, 1960; Campbell and Eagles, 1983; von Hagen, 1987). Numerous species of hermit crabs have been observed to exhibit strong sexual dimorphism (Barnes, 1997; Trivedi and Vachhrajani, 2014a; Patel et al., 2020b, 2021a, 2022b). The three hypotheses that explain the sexual size dimorphism in hermit crabs 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 (Abrams, 1988); (3) sexual selection hypothesis, a large sized male will have greater chances of success in a male-male competition for acquiring a mature female result in males attaining larger size (Asakura, 1987; Hazlett, 1988; Abrams, 1988). In these organisms, sexual selection may have a significant impact on the development of sexual size differences.

In the present study, it was found that the males were significantly larger in body size as compared to the females (non-ovigerous females and ovigerous females). Similar results were observed for other hermit crab species like *Clibanarius virescens* (Imazu and Asakura, 1994) and *C. symmetricus* (Rodrigues and Martinelli-Lemos, 2016), where males were significantly larger as compared to females and ovigerous female individuals. Generally, it has been observed that male individuals use most of their energy in physical growth, and as a result, they can attain larger sizes, which require larger shells. Bigger males are more fit as compared to the smaller males, which is attributed to their greater success in copulating with females (Harvey, 1990), except when there is a shortage of shells (Hazlett and Baron, 1989).

Harvey (1990), in his study on *Clibanarius digueti*, clearly showed that males are subject to higher selection for the massive size of gastropod shells as compared to females. This is an essential (but not sufficient) requirement for the development of sexual size dimorphism due to sexual differences in selection. As a result of the significantly higher rates of mating success experienced by large males, there is a significant sexual selection based on male size. In other hermit crab species, such as *Pagurus hirsutiusculus* (Abrams, 1988), *Diogenes nitidimanus* (Asakura, 1987), and an undescribed species of *Paguristes*, larger males usually prevail in competitions for mates (Harvey, 1990). When a female reaches sexual maturity, her growth rate significantly decreases. Passano (1960) discussed how carrying eggs prevents females from moulting. It is likely that there could be a direct selection, irrespective of any nutritional depletion, for a reduction in growth rate (Ameyaw-Akumfi, 1975). Contrary to males, females are supposed to accommodate their bodies as well as the egg mass they carry within the gastropod shell. As a result of that, if a female continues to grow even after attaining sexual maturity, there are possibilities that she may not be able to find a suitable shell to accommodate herself as well as her egg mass.

According to Ameyaw-Akumfi (1975), adults grow to their maximum extent until they can obtain such a large shell to occupy (Markham, 1968). As a result, it is reasonable to anticipate that females will be smaller than males in these circumstances. According to Asakura (1992), the use of relatively tiny shells and the increased energy expenditure for reproduction in comparison to males would lead to slower development rates in females. In this manner, as also presented by Wada (1999), shell partitioning between sexes may result in size variations between males and females and, as a result, a reduction in intraspecific antagonism.

Other factors that could affect size differences between male and female crabs include different rates of mortality, migration, a relatively high resistance of one gender to unfavourable environmental conditions, differential spatial and temporal resource utilisation, differences in foraging efficiency, acquisition or assimilation of food, and variation in behavioural patterns between sexes (Giesel, 1972; Crane, 1975; Wolf et al., 1975; Montague, 1980; Johnson, 2003). As compared to non-ovigerous females, ovigerous females inhabit bigger, more voluminous shells as they need more room to accommodate and incubate their eggs (Sant'Anna et al., 2006; Mantelatto et al., 2010).

Wenner (1972) asserted that sex ratios differing from 1:1 are common in crustaceans. By influencing a population's reproductive capacity, the sex ratio divergence from 1:1 can internally govern the growth of a population. The fluctuation in sex ratio of brachyuran crabs may also be predicted by lunar cycles and intertidal zones (Emmerson, 1994). Hermit crabs, for example, show varying patterns for the correlation between the sex ratio and crab size (Wenner, 1972). In a population, hermit crab females are probably more numerous than males (Asakura, 1992; Imazu and Asakura, 1994; Gandolfi, 1996; Trivedi and Vachhrajani, 2014a). In the present study, the overall and monthly sex ratios of male and female individuals were skewed towards females. Moreover, it was also observed that 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 8 mm SL). Similar results have been obtained in several other studies (Wenner, 1972; Manjón-Cabeza and García Raso, 1995; Gherardi and Nardone, 1997; Fransozo and Mantelatto, 1998) for hermit crab populations inhabiting both the intertidal and infralittoral areas. However, this skewness is generally related to the size of individuals.

According to Asakura (1992), initially the rate of growth of male and female individuals is equivalent in the lowest size class; however, male mortality increases in the intermediate individuals, leading to a sex ratio skewed towards females. Males generally attain a larger size compared to their conspecific female counterparts, and as a result, the sex ratio in the larger size classes is mostly skewed towards males. The largest size classes with male-biased sex ratios demonstrate that men tend to grow to larger sizes than females. Wenner (1972) proposed that this asymmetrical sex ratio may also be explained by the fact that males develop to bigger sizes in less time as compared to females however, they are still constrained by shell availability. Natural selection, however, may favour larger male individuals if they have an advantage over smaller male individuals in the quest for fertile females and/or if they engage in successful mating more frequently (Abrams, 1988). According to Mantelatto and Garcia (2000), hermit crabs frequently exhibit larger males, indicating sexual dimorphism, which may provide them an edge in the struggle for resources. Moreover, 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.

The male individual's involvement in certain behaviours, such as defending territory or engaging in conflict with other males, might be seen as another explanation for the deviations in the overall sex ratio towards females. As a result of such behaviour, male individuals become more vulnerable to predation, which is observed by several authors (Valiela et al., 1974; Montague, 1980; Emmerson, 1994). As a result, the lower proportion of males seen in the study might be attributed to either differing mortality rates (Wolf et al., 1975; Genoni, 1985) or to differential male and female migratory patterns (Montague, 1980). Therefore, several factors like differences between sexes in their patterns 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).

The size frequency distribution is a dynamic feature of a population that varies across the year as a result of reproduction and rapid larval settling (Thurman, 1985). In the present study, the overall size frequency distribution of *C. rhabdodactylus* showed a unimodal distribution frequency in female individuals, whereas the size frequency distribution was bimodal in the case of male individuals. There were significant seasonal differences observed in the size frequency distribution of *C. rhabdodactylus*. Monthly size–frequency distributions in the male population of *C. rhabdodactylus* showed a bimodal pattern of distribution during the majority of the months of the year (January, February, April, June, July, September, October, and November); however, a unimodal pattern of distribution was observed in a few months (March, May, August, and December). On the other hand, the monthly size-frequency distributions in the female population of *C. rhabdodactylus* showed a unimodal pattern of distribution during the majority of the months of the year (January, March, April, May, June, July, August, September, October, November, and December); however, a bimodal pattern of distribution was observed only in February.

Such a pattern of frequency distribution has also been reported previously in several other studies carried out on some other species of crustaceans, including *Aratus pisonii* (H. Milne Edwards, 1837) (Diaz and Conde, 1989), *Uca uruguayensis* Nobili, 1901 (Spivak et al., 1991), *Clibanarius antillensis* Stimpson, 1862 (Turra and Leite, 1999), *Xantho incisus* H. Milne Edwards, 1834, *Pachygrapsus marmoratus* (Fabricius, 1787) (Flores and Paula, 2002), *A. franciscana* Buckup & Rossi, 1977 (Gonçalves et al., 2006) and *Aegla georginae Santos* and *Jara,* 2013 (Copatti et al., 2016). Various factors have been proposed as possible explanations for these types of distributions, which include differential mortality (Diaz and Conde, 1989), growth rates (Costa and Negreiros-Fransozo, 2003), and differing migratory patterns (De Arruda Leme and Negreiros-Fransozo, 1998; Flores and Negreiros-Fransozo, 1999). Studies show that in organisms that reproduce several times and have numerous clutches each season, there is a common phenomenon that is shown by the variation in month-wise size frequency distribution (Zimmerman and Felder, 1991). Unimodality is often seen in stable populations that have steady recruitment and death rates throughout the life cycle and where the proportion of individuals joining the population and those leaving it is about equal (Thurman, 1985; Dáz and Conde, 1989). On the other hand, bimodality might reflect the population's overall growth trends. The smaller crabs emerging in late spring and summer may be the cause of the larger crabs in autumn and spring (Turra and Leite, 1999). 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).

The tropical crustacean species exhibit a continuous reproduction pattern, with a persistent occurrence of individuals in the reproductive phase throughout the year and/or peaks during specific months (Pinheiro and Fransozo, 2002; Colpo and Negreiros-Fransozo, 2004; Castiglioni and Negreiros-Fransozo, 2005; Castiglioni et al., 2006; Hirose and Negreiros-Fransozo, 2008; Costa and Soares-Gomes, 2009). However, crabs often reproduce seasonally in temperate climates (Flores and Negreiros-Fransozo, 1999; Costa and Negreiros-Fransozo, 2003; Costa et al., 2006; Castiglioni, 2013). Reproductive activity that is intensified during a certain season, often spring and summer, may be correlated with temperature, sunlight, and increased food sources for larvae during the warmer seasons (Pillay and Ono, 1978; Sastry, 1983; Costa and Negreiros-Fransozo, 2003). Rainfall is another element that could affect the periodicity of reproduction, and in certain subtropical species, reproduction is regulated more by the amount of rainfall than by temperature (Crane, 1975; Litulo, 2004; Litulo, 2006). Spawning during rainy seasons may provide selection benefits to intertidal crabs, as heavier precipitation can alter the salinity of sea water and facilitate an increased nutrient content, both of which are necessary for the growth of larvae (Conde and Dáz, 1989; Litulo, 2004).

Seasonal reproduction is often linked to environmental conditions where there are a lot of temperature variations or the availability of food (Giese, 1959). In temperate waters, seasonal patterns of reproduction are more common (87%) as compared to continuous reproduction (13%), whereas in the tropical region, both seasonal and continuous patterns are observed commonly (55% and 45%, respectively) (Turra and Leite, 2000). In the present study, ovigerous females occurred throughout the year with two peaks: January to June and September-October, which shows that *C. rhabdodactylus* is a continuously breeding species. Numerous authors have studied the life cycle of anomuran crabs that inhabit tropical and subtropical regions (Williams, 1984; Scelzo, 1985; Reid and Corey, 1991; Oliveira and Masunari, 1995; Pinheiro and Franzoso, 1995; Negreiros-Fransozo et al., 1999). Several tropical marine crustaceans display the well-known pattern of continuous reproduction with breeding peaks (Goodbody, 1965; Reese, 1968; Nyblade, 1987; Tunbergetal., 1994), including several hermit crab species such as *Clibanarius chapini* and *C. senegalensis* (Ameway-Akumfi, 1975), *Clibanarius clibanarius* (Varadarajan and Subramoniam, 1982), *Clibanarius antillensis* (Turra and Leite, 1999, 2000), *Petrochirus diogenes* (Bertini and Fransozo, 2002), *Paguristes tortugae* (Mantelatto et al., 2002), and *Diogenes brevirostris* (Litulo, 2004).

In the present study, the temperature range was recorded between 27°C and 35°C, falling under tropical climatic conditions that support 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. It was also observed that juveniles were found year-round, with the highest incidence of occurrence in February, April, and July to October, which shows that the breeding season is immediately followed by the juvenile recruitment season. Some previous studies have also observed a similar pattern with the continuous occurrence of juveniles throughout the year with peaks in the *Uca urvillei* (Litulo, 2005c), *U. rapax* (Castiglioni and Negreiros-Fransozo, 2005), *U. chlorophthalmus* (Litulo, 2006), *U. burgersi* (Benetti et al., 2007) and *U. thayeri* (Farias et al., 2014), *Clibanarius chapini* and *C. senegalensis* (Ameyaw-Akumfi, 1975), *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). It has been proposed that the increased reproductive activity in the summer accounts for the greater occurrence of juveniles during the winter, whereas another peak of ovigerous females during the winter and spring leads to increased juvenile occurrence during the summer (Farias et al., 2014).

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 a 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 the decreased reproductive period. Similar results have been reported in some other studies as well (Negreiros-Fransozo et al., 1999; Litulo, 2005a). 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).

Monthly sampling throughout the year has been employed to study the reproductive periodicity of anomuran species. Hermit crab reproductive cycles have been extensively studied and demonstrate a continuous or seasonal pattern of reproduction (Ameway-Akumfi, 1975; Asakura and Kikuchi, 1984; Negreiros-Fransozo and Fransozo, 1992; Bertini and Fransozo, 2000). However, there is no direct connection between the reproductive cycles and taxa, as also indicated by Asakura and Kikuchi (1984). It is believed that increased reproductive activity and longer reproductive phases are adaptations to gastropod shell restriction (Bertness, 1981b; Carlon and Ebersole, 1995). Additionally, reproductive peaks may differ across populations in response to interspecies antagonism and shell availability (Reese, 1968; Ameyaw-Akumfi, 1975; Fotheringham, 1976b). Such variation in the reproductive peak among different populations has been recorded for different species of hermit crabs, viz., *Pagurus geminus*, *P. lanuginosus*, *Clibanarius virescens*, *C. antillensis*, and *C. vittatus* (Turra and Leite, 2000). These minor variations among these groups may be influenced by regional and local factors. Fecundity and reproductive activity might also change from region to region since shell supply and availability vary across regions (Bach et al., 1976; Bertness, 1981d).

The ecology as well as the life history of hermit crabs are greatly governed by the number of eggs as well as the rate at which they are produced (Sastry, 1983). Fecundity among hermit crabs may vary inter- and intra-specifically, and various environmental factors can have distinct effects (Fotheringham, 1980; Turra and Leite, 1999, 2001). It is seen as an indicator of an individual's reproductive fitness (Childress, 1972) and is susceptible to a variety of environmental factors (Cody, 1966). Each species has unique characteristics, such as fecundity and the pace at which broods are generated (Sastry, 1983), which may be influenced by the environment, such as gastropod shells in the case of hermit crabs.

In the present study, it was observed that the number of eggs, weight of egg mass, and size of eggs were positively correlated with the size and weight of the ovigerous female. In the majority of crustaceans, the egg numbers produced by a female are strongly correlated with its size (Jensen, 1958), and similar scenarios have been reported in hermit crabs as well (Fotheringham, 1976a; Bertness, 1981c; Wilber, 1989; Negreiros-Fransozo et al., 1999). 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). In their study, 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. The study revealed that fecundity is greatly influenced by the size of the ovigerous female. However, several times gastropod shells may also affect the fecundity as the female cannot grow further in a small shell and hence, the female diverts her energy into immediate reproduction, which results in developing smaller broods (Turra and Leite, 1999).

Hermit crabs have remarkable levels of flexibility in their reproductive activities, as shown by the various reproductive strategies used among conspecifics in various locations as well as by distinct species coexisting within the same habitat. The reproductive variances are the consequence of regional ecological adaptations, and when only one environmental element is taken into account, it is possible that the temporal emergence pattern cannot be generalised (Reese, 1968). Hence, research on fecundity, gonadal development, and interaction with other hermit crab species is a must in order to better understand its reproductive biology.