Population structure and fecundity of a Xanthid crab *Leptodius exaratus* (H. Milne Edwards, 1834) on the rocky shore of Gujarat state, India

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Background A Xanthid crab, *Leptodius exaratus* (H. Milne Edwards, 1834), was examined for its population structure and breeding biology on the rocky intertidal region of Shivrajpur beach in Saurashtra coast, Gujarat state.

Method Month wise sampling was conducted from March 2021 to February 2022 during low tide using catch per unit effort in the 500 m^2 area. The sampled specimens were categorised into male, non-ovigerous females or ovigerous females. In order to estimate fecundity, the morphology of the crab specimens (carapace width and body weight) as well as the size of egg, number of eggs and weight of egg mass were recorded.

Results A total 1215 individuals were sampled of which 558 individuals were males and 657 individuals were females. The size (carapace width) of males ranges from 5.15 mm to 29.98 mm, while females ranges from 5.26 mm to 28.63 mm which shows that the average size of male and female individuals did not differ significantly. The overall as well as monthly sex ratio was skewed towards males with a bimodal distribution while unimodal in females. The population breeds year round, which was indicated by the occurrence of ovigerous females throughout the year. However, the maximum percentage occurrence of ovigerous females was observed from December to April which indicates the peak breeding season. The size of egg, number of eggs and weight of egg mass were shown to positively correlate with the morphology of ovigerous females (carapace width and wet weight).

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Keywords: Breeding ecology, Population structure, Rocky intertidal, Saurashtra coast, Sex ratio, Xanthidae

Introduction

Investigation on the population structure of intertidal crabs started in early 1940s (Flores and Paula, 2002), which can reveal the patterns of species interactions and their roles within ecosystems. Accounts on population structure and breeding biology majorly try to understand the genetic diversity, age, spatial distribution, abundance, sex ratio, variation in year-round composition, , fecundity of the species, as well as juvenile recruitment (Litulo, 2005; Saher and Qureshi, 2010; Manzoor et al., 2016; Hu et al., 2015). A species' life history might differ by habitat or even by location. For example, a slight variation in the latitude leading to climatic variation can cause differences between the populations. Variations in the population trends are also due to the effects of several biotic and abiotic factors affecting populations differently (Lycett et al., 2020). Studies on the population structure and breeding biology of a species can help determine its ecological stability in a given habitat and also contribute to our understanding of the species' biology. (Santos et al., 1995; Takween and Qureshi, 2005). This knowledge helps ecologists understand how different species coexist, compete, and interact, influencing ecosystem dynamics. However, such studies have not been carried out so far on some of the commonly occurring brachyuran crabs on Gujarat state.

The Saurashtra coast of Gujarat state, India, is characterised by its rocky intertidal coasts, which support a great diversity of marine organisms, including intertidal crustaceans, especially crab population. With its major inhabiting marine intertidal species, majority of the crab studies have focused on the diversity (Trivedi and Vachhrajani, 2013a, b; 2015; 2016a; 2018; Trivedi et al., 2015a, b; 2016a, b; 2020a, b; 2021; Gosavi et al., 2017a, b; 2021; Patel et al., 2020; 2021a; Bhat and Trivedi, 2021; Padate et al., 2022). Very less is known about the population dynamics of these important intertidal organisms (Trivedi and Vachhrajani, 2016b; 2017; Patel et al., 2022).

Leptodius exaratus (H. Milne Edwards, 1834) is a Xanthid crab that is commonly found in the rocky shores of Saurashtra coast (Patel et al., 2021b). This crab species has been commonly reported from the rocky intertidal regions of Indo-Pacific region (Kneib and Weeks, 1990; Naderloo, 2017). It is an omnivorous species that prefers benthic fauna over algae to feed upon and is expected to have a considerable impact on how the benthic ecosystem is structured (Al-Wazzan et al., 2020).

In the Indian subcontinent *L. exaratus* is recorded from Andaman and Nicobar Islands, Maharashtra, Tamil Nadu, Lakshadweep Islands, Goa, Karnataka, and Gujarat (Trivedi et al., 2018a). Though the species is very commonly found on the Saurashtra coast of Gujarat, studies only on its taxonomy (Chopra and Das, 1937; Trivedi and Vachhrajani, 2015) and colour variation (Patel et al., 2021b) have been carried out so far. Hence the current investigation was aimed to 1) understand the population structure and 2) study the breeding biology of *L. exaratus* occurring on the rocky shore of Saurashtra coast Gujarat state, India in order to obtain knowledge about the ecology of rocky intertidal habitats. Studying the population structure and breeding biology of *L. exaratus* which is commonly found on the Saurashtra coast, would provide a baseline data that plays a pivotal role in understanding the effects of changing environment, habitat, or anthropogenic pressure. The present study will help in elucidating the coastal health of study area.

Materials & Methods

Study area

The investigation was conducted on the rocky shore of Shivrajpur beach (22°19'55" N 68°57'03" E) which is located on the Saurashtra coast of Gujarat state, India (Figure 1). *Leptodius exaratus* is abundantly occurring in the intertidal region having a very narrow range of exposure: 60 to 150 m.

Field methods

Monthly field work was conducted for 12 consecutive months from March 2021 to February 2022. The month wise data was compiled into winter season (including November to February months), summer season (including March to June months), and monsoon seasons (including July to October months), following Rao and Rama-Sharma (1990), to observe the seasonal variation. Catch-per-unit effort using the hand-picking method was used for the collection of specimens for a time period of 4 hours at the time of low tide. When the water receded, a 500 m^2 area in the intertidal region was marked off and thoroughly examined for the presence of *L. exaratus*. Small rocks were also upturned for the presence of *L. exaratus*, which they prefer to occupy. Whenever an individual was encountered, it was collected and kept in 10% formalin pending additional examination.

Laboratory analysis

The crabs were identified on the basis of their morphological characters as follows using standard identification key provided by Lee et al. (2013) and Trivedi and Vachhrajani (2015): Carapace: transversely sub ovate, somewhat convex dorsal surface, lightly granular. There are four large, triangular teeth on the anterolateral border, behind the exorbital angle. Male abdomen tapered, somites 3–5 fused, somite 6 elongated, 1.6 times longer than the telson. Subtriangular telson with a widely rounded tip. Chelipeds are unequal in size; merus bearing long setae on the anterior and posterior margins; carpus is finely granulated; fingers are stout with dark pigmentation excluding the tips, which are white in colour, irregular dentation on cutting margins; walking legs: anterior margins bear fine granules; merus with anterior and posterior margins bearing long setae. Further, the individuals were categorised as male, non-ovigerous female, or ovigerous female (Figure 2). For morphological character, carapace width (CW) was measured with the help of digital vernier callipers (Mitutoyo 500-197-20) (0.01 mm accuracy) and wet weight of crabs was measured using weighing balance (Sartorius–BSA224S–CW) (0.001 g accuracy).

The following method for fecundity study was adopted from Patel et al. (2023). Fecundity estimation conducted by cautiously taking out the mass of eggs present on the pleopods of ovigerous females (n=34) and measuring three parameters i.e., total number of eggs, weight of egg mass and size of eggs (diameter). For the total number of eggs, the egg mass was transferred into 20 ml of sea water and mixed gently so that the eggs got distributed evenly in the water. From this solution, three samples of 2 ml each were taken in a petri dish and observed under a stereo zoom microscope (Matlab–PST–901) to count the total number of eggs. The total number of eggs in each sample was divided by 3 and multiplied by the dilution factor (10) to obtain the total number of eggs (Litulo, 2004). Ovigerous females were weighed both with and without egg mass, and the difference in their weight was considered as the weight of egg mass. Eggs (n=10) from each ovigerous female were measured by means of an ocular micrometre under a microscope for the size range (Saher and Qureshi, 2010).

Data analysis

1. Population structure

The specimens were grouped in 2 mm size class intervals from 4 mm to 30 mm CW in order to get the overall size frequency distribution. Shapiro Wilk test was conducted to analyse the normality of the collected data, which suggests that the data distribution was not normal ($p<0.001$). Hence, non-parametric analysis was carried out. To investigate the difference in the variance of mean values of the carapace width of male, non-ovigerous, and ovigerous individuals Kruskal-Wallis (KW) test was conducted. On getting a significant difference ($p<0.05$) in the CW between the sexes, a multiple comparison analysis using Dunn's post hoc test was used to do a multiple comparison study.. Monthly variations in the size (CW) and sex composition of *L. exaratus* individuals were obtained by plotting the data on individuals' carapace width and sex.. The ratio of males and females (ovigerous and non-ovigerous females) was evaluated by the means of chi-square test (χ^2). The size at first maturity was determined by calculating the percentage of ovigerous females across various size classes from the total number of samples collected. Juveniles were defined as individuals that were smaller than the smallest ovigerous female (Baeza et al., 2013). The effect of temperature on *L. exaratus* breeding and juvenile settling was examined by plotting monthly data on the incidence of juvenile and ovigerous females against ambient temperature. The relationship between the mean ambient temperature and the relative juvenile frequency was examined using Pearson's correlation analysis.

2. Fecundity

To investigate the relationship between the morphological features of eggs (total number of eggs, egg mass weight and size of eggs) and crabs' morphology (CW and weight) regression analysis was performed. At $p<0.05$, the statistical significance was deemed significant. Microsoft Excel and PAST software, version 4.03 (Hammer et al., 2001), were used to carry out statistical analyses.

Results

During the course of the study, 1215 individuals were investigated in total; 558 of them were male (45.93%) and 657 of them were females (54.07%) (Table 1). The carapace width of *L. exaratus* males ranged from 5.15 mm to 29.98 mm, while in case of females it ranged from 5.26 mm to 28.63 mm. The size differences between the male and female individuals were not statistically significant (Kruskal-Wallis, H = 0.209, p = 0.646). (Table 1).

Table 2 shows that the year-round average total sex ratio (1:1.2) for L. exaratus was significantly distinct from the predicted 1:1 proportion ($\chi 2 = 4.1219$, p = 0.042) and biased towards females. Month wise, female biased sex ratio was observed in almost all the months except September (1:0.8), October (1:0.9), and November (1:0.7) (Table 2). November had the highest percentage of male occurrences (57.89%), while April had the lowest rate (37.41%). in terms of females, the highest percentages of non-ovigerous female occurrences were observed in June (50%) and August (50%), while the lowest percentages were observed in January (27.18%). Ovigerous females were collected all year, which shows the species is breeding year-round. However, from December to April, the greatest percentage of occurrence was recorded of ovigerous females, suggesting a peak in the breeding season.

The individuals of *Leptodius exaratus* occurred in all the size classes between 4 mm to 30 mm. it was observed that males exhibited bimodal pattern of distribution having maximum occurrence in 6–8 mm CW size class and 24–26 mm CW size class. On the other hand, females exhibited unimodal pattern of size frequency distribution, with maximum occurrence recorded in 14–16 mm CW size class (Figure 3).

Figure 4 shows that there was a considerable variation in the occurrence of adults, ovigerous females and juveniles (< 12 mm) during different months of the year. It was found that in April, May, June, and July (summer and early monsoon season) the population of juveniles was least as compared to the adult population. Moderately, less number of juveniles were also observed during the months of December to March (winter and early summer season) than August to November (Monsoon and early winter season) as compared to adult male and female (Figure 4).

Males had a bimodal distribution during most of the months, while non-ovigerous females showed a unimodal distribution pattern, as was also observed in ovigerous females. Furthermore, it was also observed that juveniles were present all year round (Figure 5–7). a Negative correlation (Pearson's correlation, r = -0.39) was observed between the mean ambient temperature and relative frequency of juveniles (Figure 8).

The results of fecundity revealed that the CW of ovigerous females was between 10.38 mm and 24.02 mm, with their average size being 17.95 ± 3.81 mm (n = 34). The wet body weight of the ovigerous females was recorded between 0.41 and 4.64 g, with the mean weight being 2.01 ± 1.1 g (n = 34). The average number of eggs observed was 4529 ± 2003 (n = 34), with the minimum and maximum reported being 920 and 8,730 eggs, respectively. The average egg size (n = 34) was 0.36 ± 0.07 mm, with the minimum and maximum observed sizes being 0.19 and 0.54 mm, respectively. The average egg mass weight (n = 34) was 0.29 ± 0.18 g, with the minimum and maximum observed egg mass weights being 0.04 and 0.88 mm, respectively (Table 3). The ovigerous females' carapace width and body weight were shown to be significantly correlated with both the egg weight and total number of eggs (Figure 9).

Discussion

A Significant variation was observed in the average CW of different sexes of *Dotilla blanfordi*, where it was found that male individuals were significantly larger than females. Studies conducted on the population structure of *Matuta planipes* and *Ashtoret lunaris* (Saher et al., 2017), *Uca bengali* (Tina et al., 2015), *Scylla olivacea*, *S. tranquebarica*, and *S. paramamosain* (Waiho et al., 2021), *Clibanarius ransoni* (Patel et al., 2020a; 2022), *C. rhabdodactylus* (Patel et al., 2023), and *Diogenes custos* (Patel et al., 2020b) also exhibited similar results. It has been observed that the growth rate of female individuals is generally reduced as a result of greater energy investment in gonadal development, which leads to decreased somatic growth in comparison to male individuals (Mantelatto et al., 2010). Another hypothesis suggests that the chances of attracting and obtaining females for the purpose of mating increases with increased size of male individuals (Wada et al., 2000), while the difference in size also reduces intraspecific competition among different sexes for available resources (Abram, 1988).

Overall sex ratio (1:1.2) was found to be female-biased, while month-wise also female biased sex ratio was observed except September, October and November months. In general, natural selection promotes a sex ratio of 1:1 parental expenditure on offspring (Taylor, 1996); however, deviation from the ideal sex ratios is common in marine Crustaceans, as observed in *Calcinus tibicen* (Fransozo and Mantelatto, 1998), *Limulus polyphemus* (Smith et al., 2002), *Crangon crangon* (Siegel et al., 2008), *Opusia indica* (Saher and Qureshi, 2011), and *Macrophthalmus* (*Venitus*) *dentipes* (Qureshi and Saher, 2012). The sex ratio also differed during different growth stages, with an ideal sex ratio (1:1) in smaller size classes (1–3 mm CW), female biased in intermediate size classes (3–6 mm CW) and exclusively male biased in larger individuals (6–8 mm CW). Certain other studies have found similar results (Gherardi and Nardone, 1997; Bezerra and Matthews-Cascon, 2007; Mishima and Henmi 2008; Manzoor et al., 2016). Numerous factors can be responsible for such deviation in the sex ratio including competition in local mate (Hamilton, 1967), differences in the efficiency of utilizing local resources that biases sex ratios (Silk, 1983), difference in the investment in male and female offspring (Kobayashi et al., 2018), and sexual selection (Swanson et al., 2013). Sexual dimorphism in size could be one of the reasons for the different sex ratio from the ideal 1:1 in different size classes. Higher male mortality in the intermediate-size classes often leads to a female biased sex ratio (Asakura, 1995). Moreover, males grow to bigger sizes quickly than females, leading to male biased sex ratio on the larger size classes (Wenner, 1972). Disparities in sexual mortality and dispersion may potentially contribute to unbalanced sex ratios in crab populations (Johnson, 2003).

Present investigation found that the size frequency distribution of *L. exaratus* males had a bimodal distribution, while the females had a unimodal distribution. Also, there was a considerable difference in the seasonal size frequency distribution. Similar results have been observed in *Paguristes tortugae* (Mantelatto and Sousa, 2000), *Chaceon affinis* (López Abellán et al., 2002), *Pilumnus vespertilio* (Litulo, 2005), *Dilocarcinus pagei* (Taddei et al., 2015) *Aegla georginae* (Copatti et al., 2016) and *Clibanarius rhabdodactylus* (Patel et al., 2023). Over time, the population size and frequency of dispersion may be significantly changed by the rapid recruitment of larvae and rate of reproductive rate (Thurman, 1985). Such distributions have been explained by a variety of theories, such as differential patterns of migration (Flores and Negreiros-Fransozo, 1999), rate of growth (Negreiros-Fransozo et al., 2003), and differential death rate (Diaz and Conde, 1989). It is commonly found in organisms that undergo several rounds of reproduction and generate a large number of clutches every season (Zimmerman and Felder, 1991). Unimodality is often seen in stable populations that have approximately equal numbers of new members and emigrants, consistent recruitment and mortality rates throughout the course of the life cycle, and steady demographics (Thurman, 1985; Diáz and Conde, 1989) whereas, bimodality could be an indication of the general tendencies in population increase.

The ambient temperature of the study site ranged from 22.1 to 32.5 °C, which is within the range of a tropical environment that may support continuous reproduction. Hence, there was year round occurrence of ovigerous females suggesting that *L. exaratus* is a continuously breeding species that has maximum recorded frequency from December to April. Similar studies carried out on *L. exaratus* (Al-Wazzan et al., 2020), *Scylla olivacea* (Ali et al., 2020), *Opusia indica* (Saher and Qureshi, 2011), *Emerita portoricensis* and *E. asiatica* (Goodbody, 1965), *Ilyoplax frater* (Saher and Qureshi, 2010), *Diogenes brevirostris* (Litulo, 2004) and *Petrochirus diogenes* (Bertini and Fransozo, 2002) did not find any association between the frequency occurrence of ovigerous females and ambient temperature. As *L. exaratus* is common inhabitant of upper intertidal region where higher temperature during summer season can greatly increase the desiccation risk, leading to migration of ovigerous females in deeper water (Allen, 1966; Asakura, 1987; Al-Wazzan et al., 2020) resulting in decreased abundance in the intertidal region. As a result, seasonal fluctuations in abundance reflect both migration and mortality, while summer abundance estimates may underestimate the size of the local population. However, it was found that juvenile percentage occurrence increased with a decline in ovigerous female percentage occurrence, whereas juvenile percentage occurrence declined when ovigerous female percentage occurrence increased. Such outcomes demonstrates that the species may recruit juveniles throughout the year as a result of rapid reproduction and a short incubation time. Similar outcomes have been reported in several other studies including *Deiratonotus japonicus* (Oh and Lee, 2020), *Scylla olivacea* (Rouf et al., 2021), *Clibanarius rhabdodactylus* (Patel et al., 2023), *Dardanus deformis* (Litulo, 2005), and *Menippe nodifrons* (Fransozo et al., 2000). There are a number of variables, including the availability of food for adults (Goodbody, 1965), the ecology of larvae (Reese, 1968), the amount of time to attain sexual maturity, the timing of mating and gonadal development, as well as the length of the incubation period (Sastry, 1983), which can lead to periodicity in the reproductive season. A variety of abiotic and biotic variables, including water temperature (Chou et al., 2019), salinity (Huang et al., 2022), the nutritional quality of the females (Matias et al., 2016), variations in photoperiod (Zhang et al., 2023), the amount and availability of nutrition (Viña-Trillos et al., 2023), and the threat of predation (Touchon et al., 2006), may affect the reproductive maxima among populations.

It was found that the CW and wet body weight of *L. exaratus* were having positive correlation with total number of eggs and egg mass weight. Several other studies have also found similar results (Patel et al., 2023; Crowley et al., 2019; Hamasaki et al., 2021; Aviz et al., 2022; Mustaquim et al., 2022). Additionally, it has been demonstrated that ovigerous females with the same CW had variations in the number of eggs, egg mass weight, and egg size resulting from variations in the food supply, variation in egg production, and egg loss (Hines, 1982).

Conclusions

The goal of the current study was to better understand the breeding biology and population structure of *L. exaratus*. Significant sexual dimorphism was found, with males being larger than females, most likely as a result of the size of gamete formation differing between the sexes and females investing more in egg production. Population skewed towards female in the overall (1:1.2) and monthly populations may be a result of differential biology and behaviour as well as the impact of biotic and abiotic variables on male and female individuals. The year-round occurrence of ovigerous females suggests continuous breeding of the population and an inverse relationship between the peak in juvenile recruitment and the occurrence of ovigerous females which is a common phenomenon of tropical brachyuran crabs. There was a positive correlation between the egg parameters (weight of egg mass and number of eggs) and the morphology of ovigerous females (carapace width and body weight). Fecundity may be impacted by a variety of internal and external variables, such as the amount of energy used for somatic development and egg production. The present study was conducted at Shivrajpur village, a renowned tourist site with a blue-flag beach where various water sports activities take place. These activities along with higher tourist rush at the study site, may impact the habitat composition of the beach, potentially influencing the ecology of *L. exaratus*. Furthermore, our findings will contribute to understanding the species' response to environmental changes, as both population structure and fecundity are closely tied to environmental variables.

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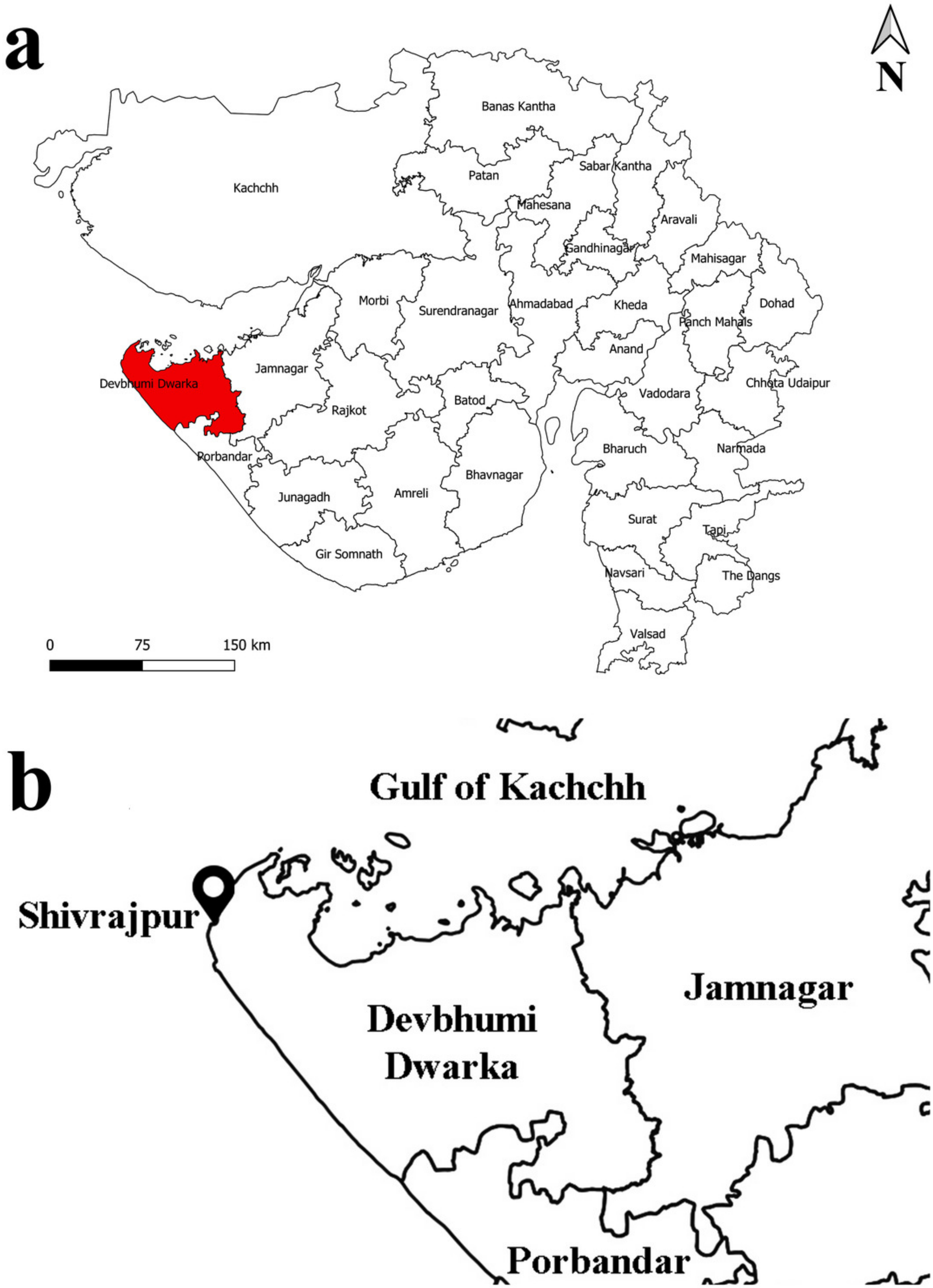
Figure 1

Map of study area: **a.** Gujarat state; **b.** Shivrajpur village, Gujarat state, India. (Prepared using QGIS version 3.14)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Rajkot
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Shivrajpur
Jamnagar
Devbhumi Dwarka
Porbandar

Figure 2

Leptodius exaratus **a.** dorsal view; **b.** ventral view male (CW–26.4 mm); **c.** ventral view ovigerous female (CW–18.4 mm), **d.** ventral view female (CW–18.2 mm). Scale bar 5 mm.

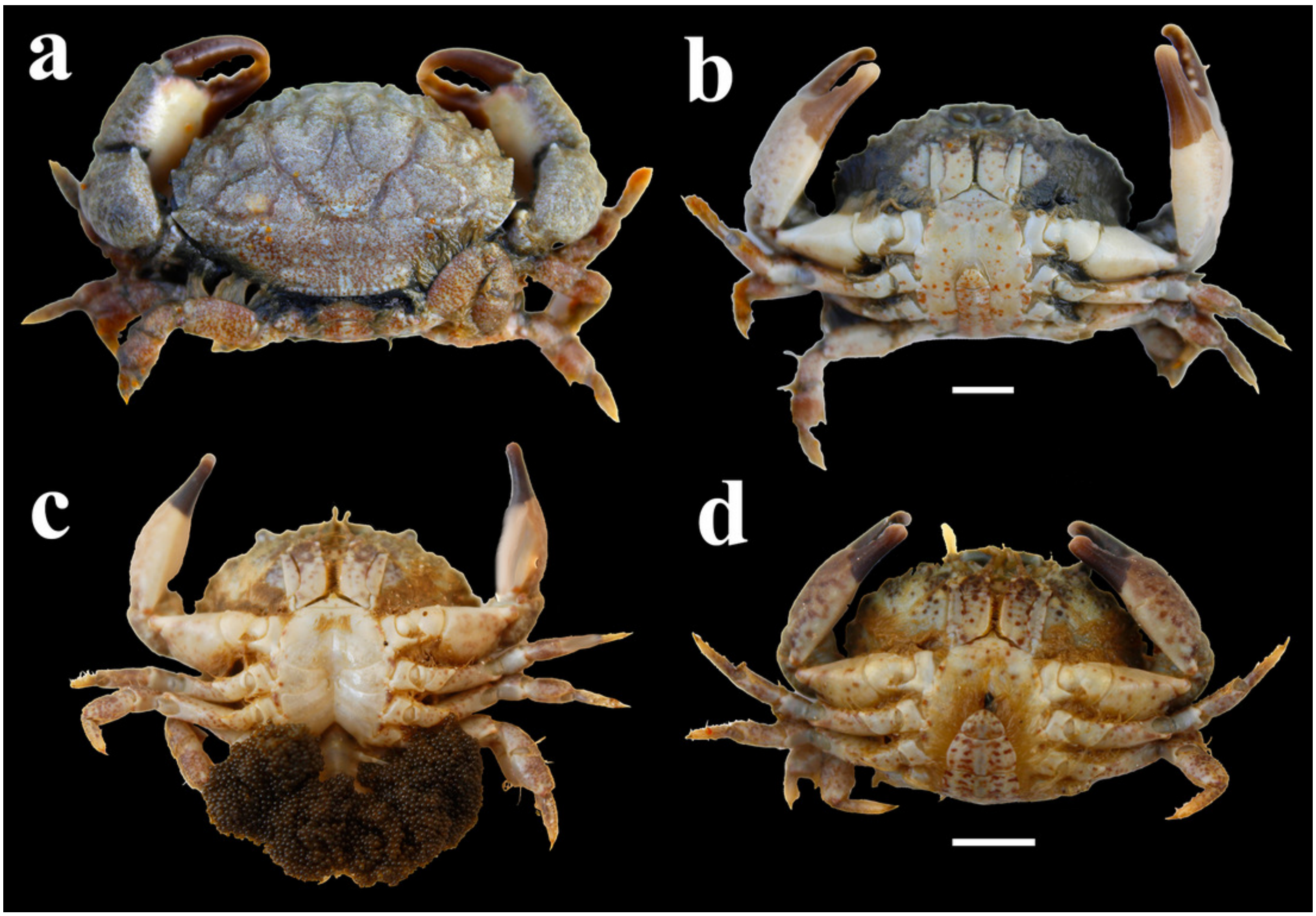

Figure 3

Overall size frequency distribution of *Leptodius exaratus* collected from Shivrajpur Beach, Gujarat state, India.

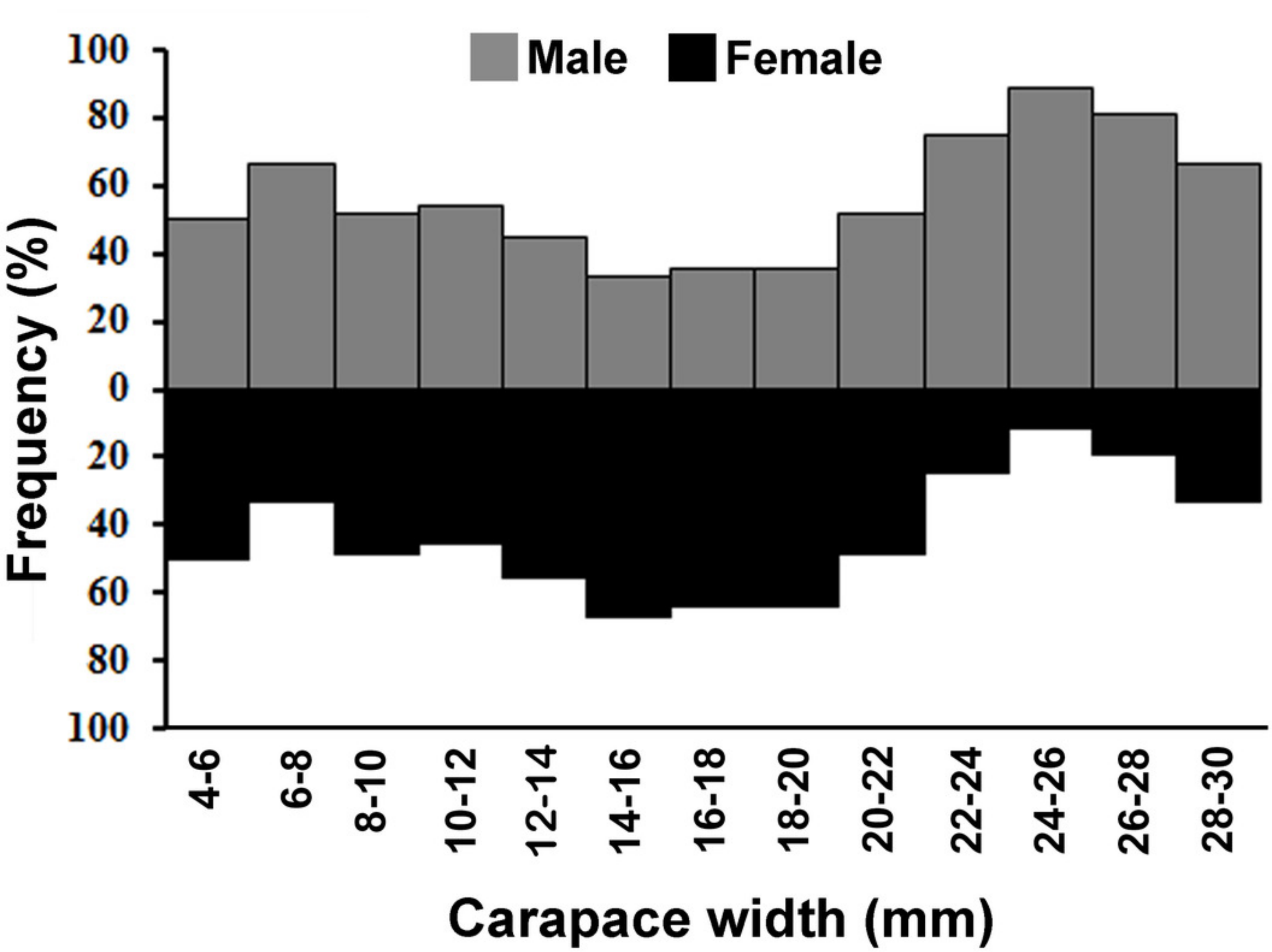

Figure 4

Percentage of deferent demographic categories of *Leptodius exaratus* at Shivrajpur Beach during the 12 months of study period.

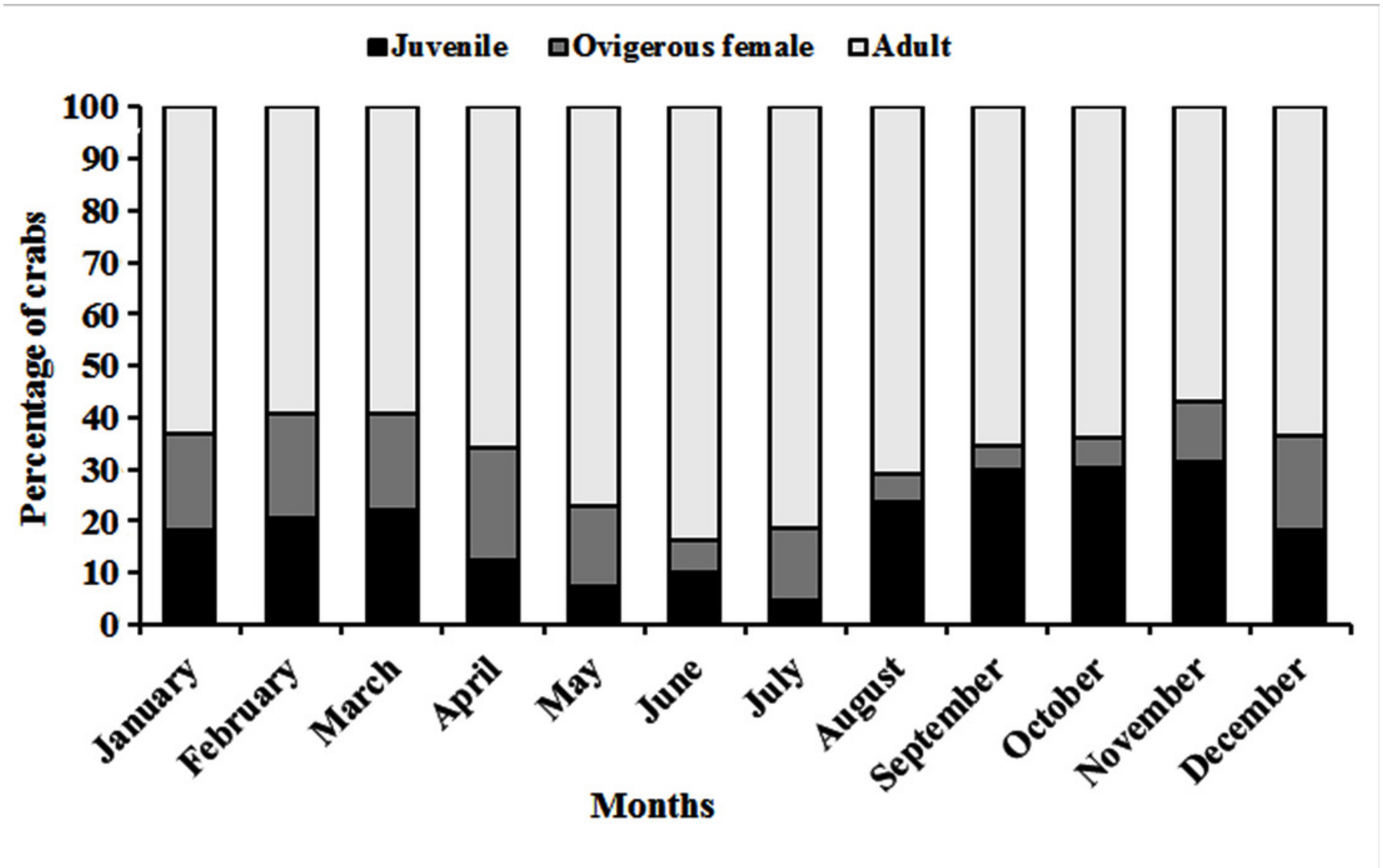

Figure 5

Size frequency distribution of *Leptodius exaratus* in **a.** January, **b.** February, **c.** March, **d.** April.

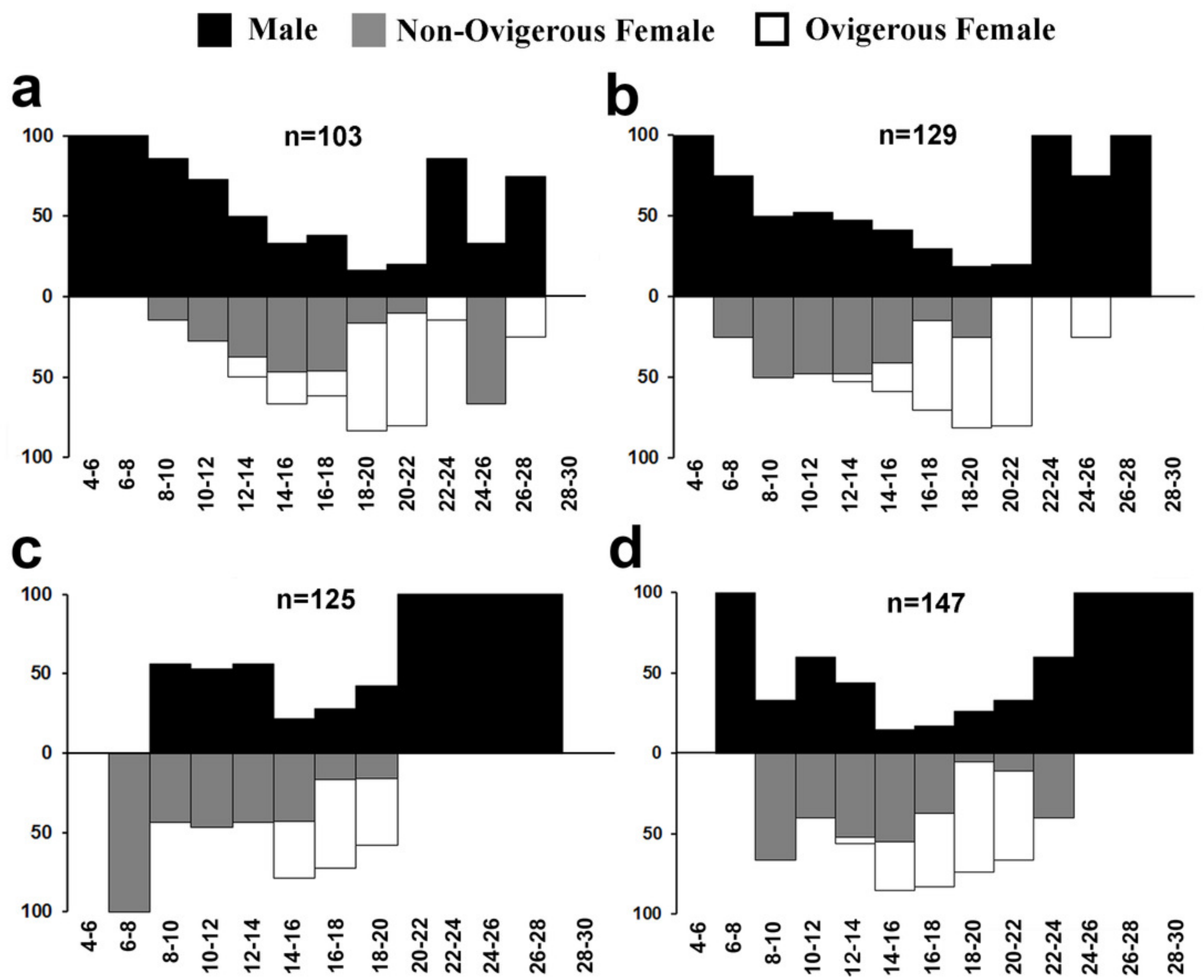

Figure 6

Size frequency distribution of *Leptodius exaratus* in **a.** May **b.** June **c.** July **d.** August.

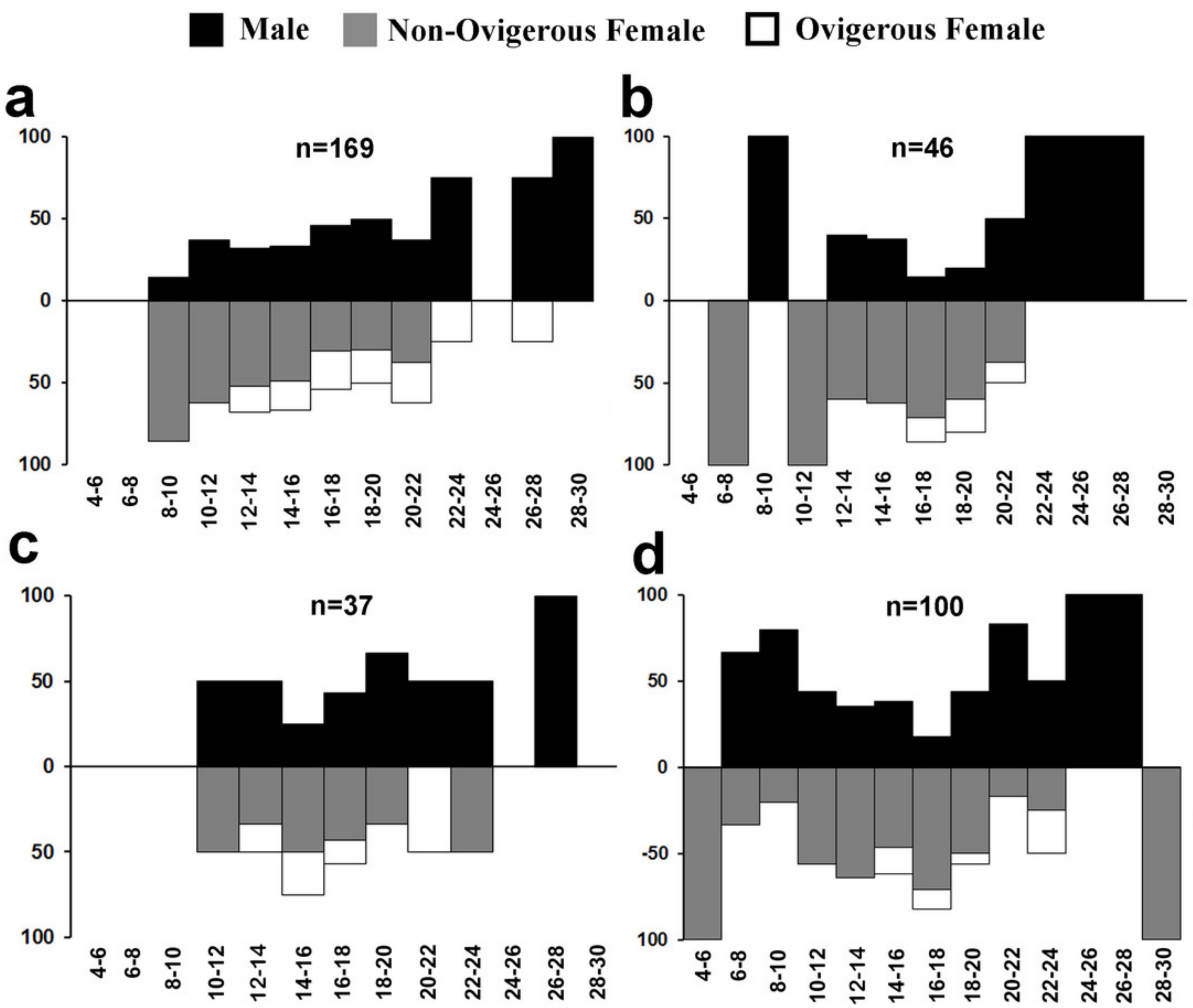

Figure 7

Size frequency distribution of *Leptodius* exaratus in **a.** September, **b.** October, **c.** November, **d.** December.

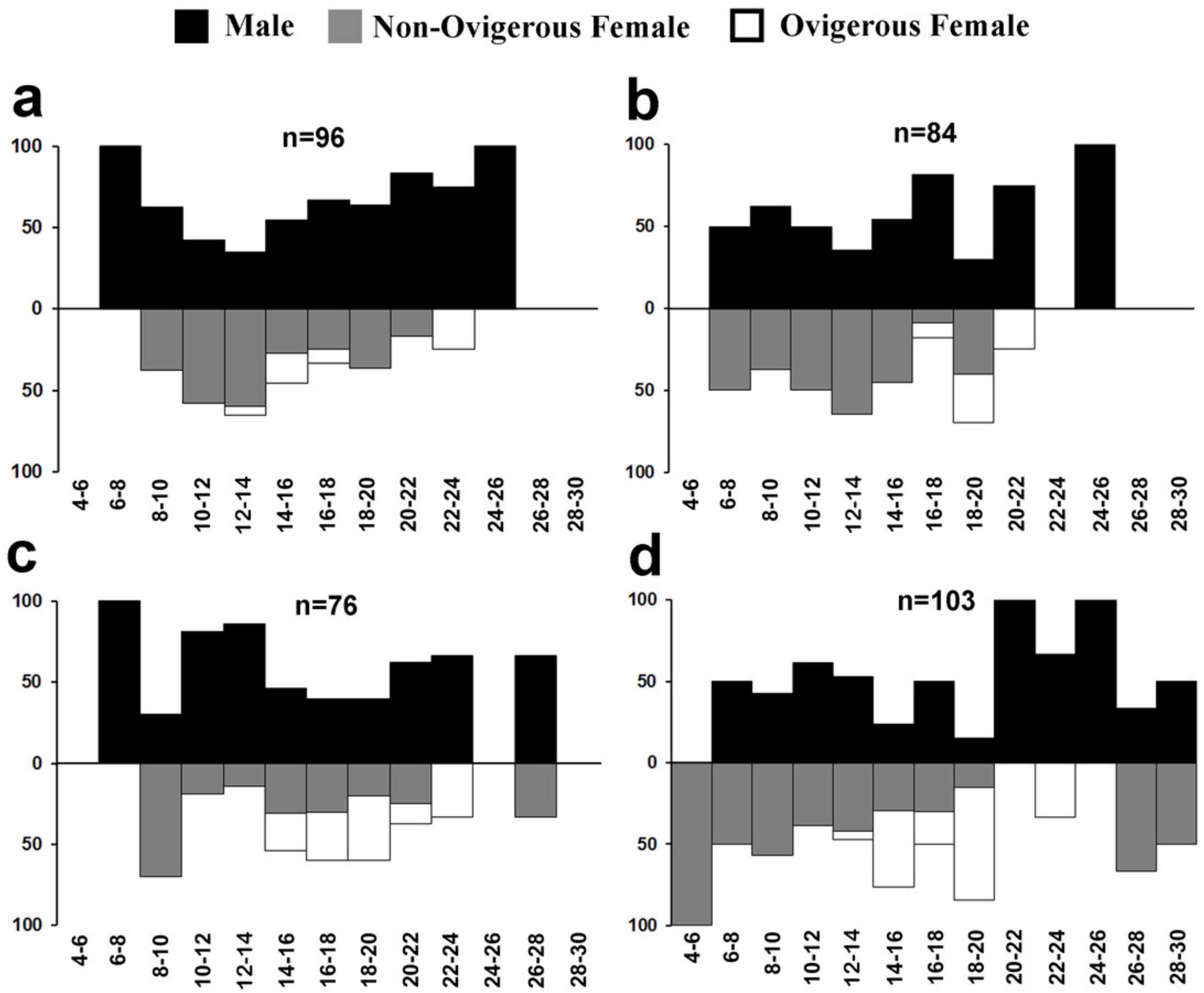

Figure 8

Association between the juveniles (of both sexes) and ovigerous female occurrence of *Leptodius exaratus* with monthly ambient and water temperatures at Shivrajpur Beach, Gujarat, India.

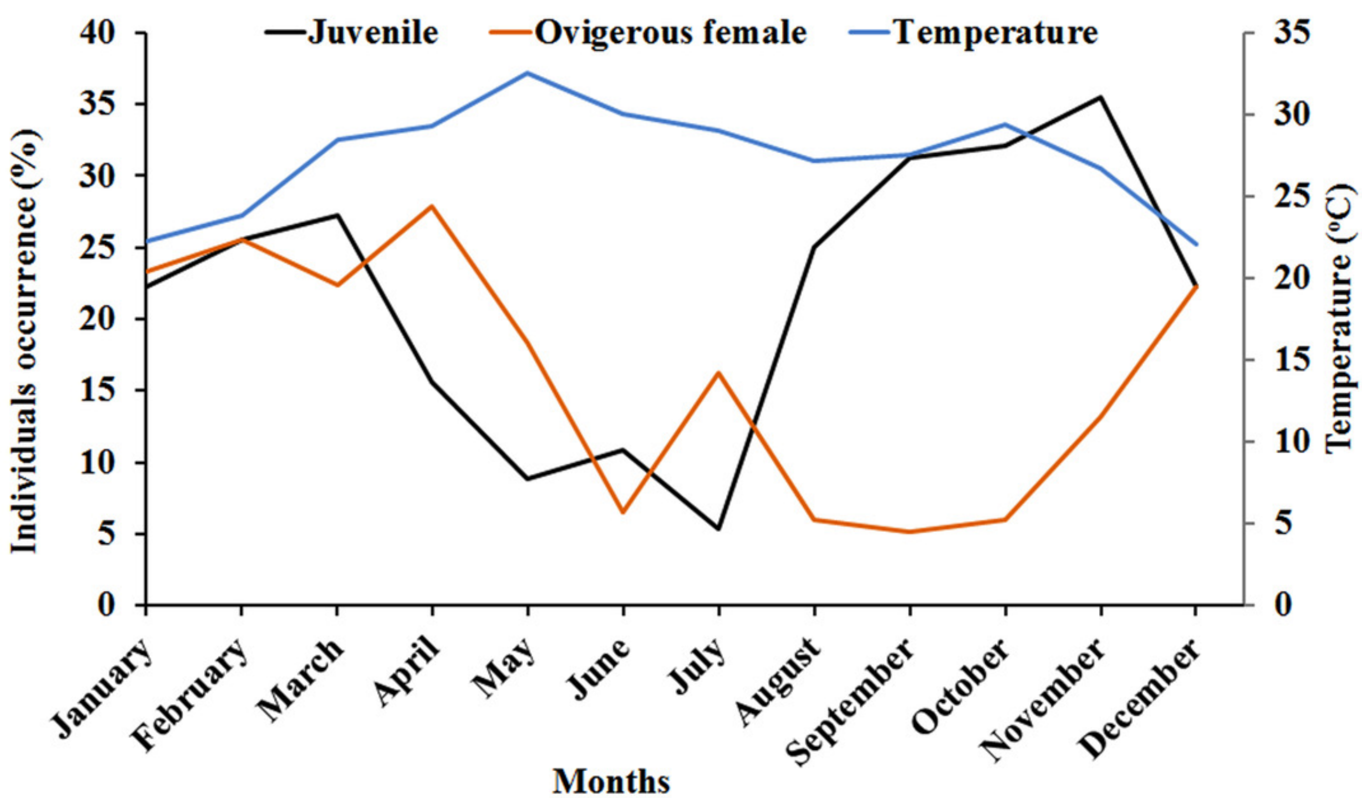

Figure 9

Relationship of *Leptodius exaratus* carapace width with **a.** total number of eggs; **b.** egg weight; and **c.** average egg size; and crab weight with **d.** total number of eggs; **e.** egg weight; and **f.** average egg size.

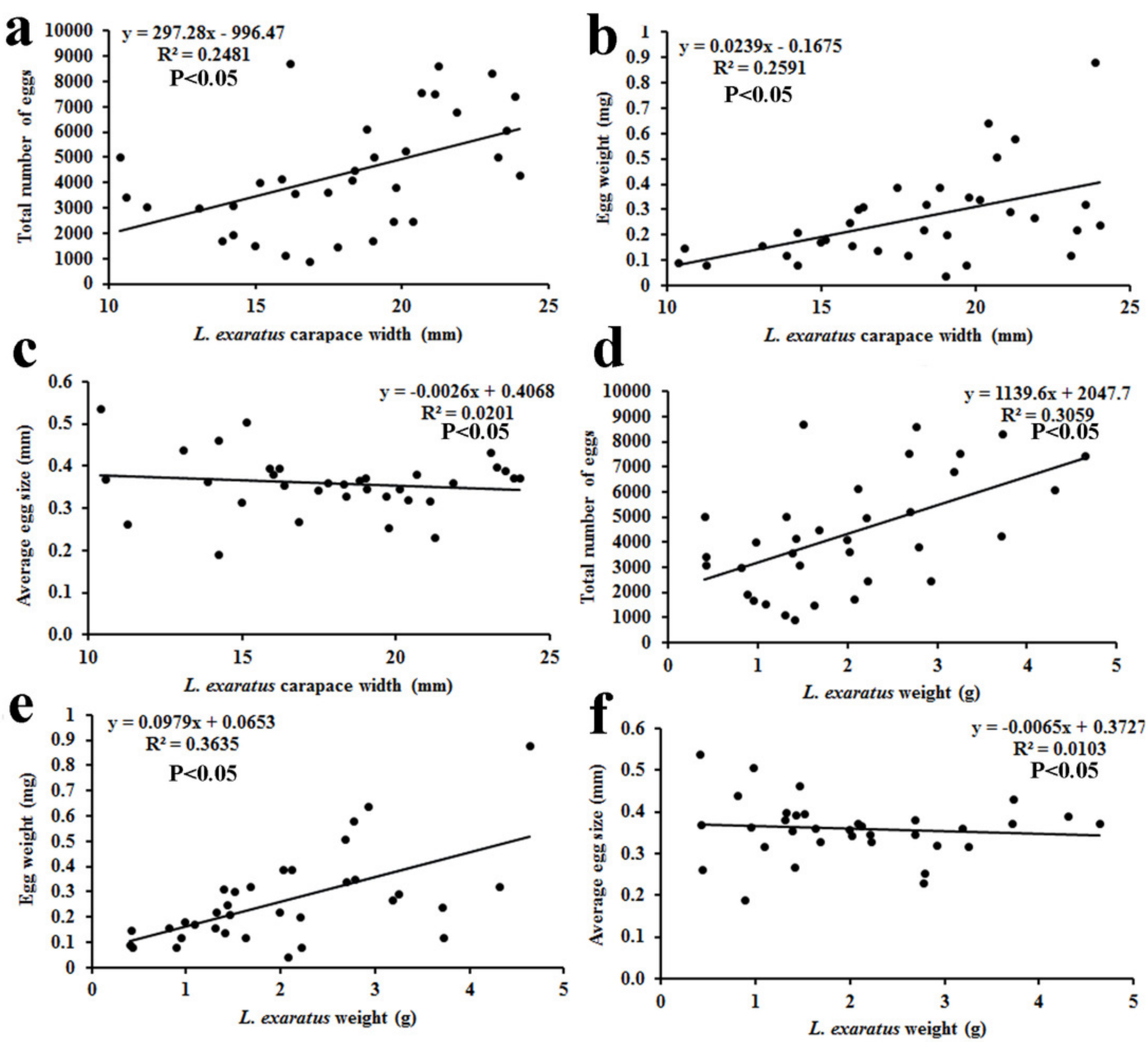

Table 1(on next page)

Carapace width values of male and female individuals of Leptodius exaratus. (n= total number of individuals, CW= carapace width). * Significant level if p<0.05 (*); p<0.01 (**); p<0.001 (***)

Sex	n	Min. CW (mm)	Max. CW (mm)	Mean ± SD
Male	558	5.15	29.98	15.967± 5.27*
Female	657	5.26	28.63	15.48 ± 3.77*

Table 2(on next page)

Total number of *Leptodius exaratus* specimens collected at rocky intertidal region of Veraval. (M: Male; NOF: Non-ovigerous female; OF: Ovigerous female) Chi-square test ($\chi 2$) = 4.1219, P=0.042, the result is significant at (*) $p < 0.05$.

Month	M	%	NOF	%	OF	%	NOF+ OF	%	Sex ratio
January	51	49.51	28	27.18	24	23.30	52	50.49	1:1.02
February	56	43.41	40	31.01	33	25.58	73	56.59	1:1.3
March	55	44.00	42	33.60	28	22.40	70	56.00	1:1.3
April	55	37.41	51	34.69	41	27.89	92	62.59	1:1.7
May	69	40.83	69	40.83	31	18.34	100	59.17	1:1.4
June	20	43.48	23	50.00	3	6.52	26	56.52	1:1.3
July	17	45.95	14	37.84	6	16.22	20	54.05	1:1.2
August	44	44.00	50	50.00	6	6.00	56	56.00	1:1.3
September	54	56.25	37	38.54	5	5.21	42	43.75	1:0.8
October	45	53.57	34	40.48	5	5.95	39	46.43	1:0.9
November	44	57.89	22	28.95	10	13.16	32	42.11	1:0.7
December	48	46.60	32	31.07	23	22.33	55	53.40	1:1.1
Total	558	45.93	442	36.38	215	17.70	657	54.07	1:1.2*

Table 3(on next page)

Summary of different morphological parameters of Leptodius exaratus ovigerous females and eggs. (n= total individuals; SD= standard deviation).

Variables	n	Mean ± SD	Min.	Max.
Crab weight (g)	34	2.04 ± 1.2	0.41	4.64
Weight of egg mass (g)	34	0.29 ± 0.18	0.04	0.88
Carapace length (mm)	34	12.14 ± 2.4	6.92	15.88
Carapace width (mm)	34	18.1 ± 3.8	10.38	24.02
Egg number	34	4529 ± 2003	920	8730
Egg size (mm)	34	0.36 ± 0.07	0.19	0.54