Segregation by size in the mouthless crab *Cardisoma crassum* (Brachyura: Gecarcinidae) from Ponuga, Veraguas, Panama

Segregación por talla en el cangrejo sin boca, *Cardisoma crassum* (Brachyura: Gecarcinidae) en Ponuga, Veraguas, Panamá

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ABSTRACT

The mouthless crab *Cardisoma crassum* is an important socioeconomic fishery resource; thus, understanding its distribution pattern is key for its fishery management. The present study aimed to determine if mouthless crabs show segregation by size in contrasting habitat types. Three plots were sampled from February to June 2022 to collect data on biometric variables in Ponuga, Veraguas, Panama Pacific. A total of 151 crabs with average cephalothorax width of 56.24 ± 8.56 mm were captured; 97 were male and 54 were female. This proportion difference was significantly skewed towards males at 1.8:1. Subjects from plot 1 were larger and heavier than those from plots 2 and 3. Ovigerous females were found only in plots 1 and 2 during June (rainy season). The minimum cephalothorax width of functionally mature females was 47.11 mm. By this measure, mature females were present in higher proportions in all plots and were significantly more abundant in plot 1. Small crabs were segregated in plot 3; the plot of origin and size were significantly associated. This is the first report of segregation by size in *Cardisoma crassum*. The findings highlight the importance of habitat features and lead the way for further studies on the factors influencing this distribution pattern.

Keywords: Brachyuran, burrow, biometry, functional maturity, carapace

RESUMEN

El cangrejo sin boca, *Cardisoma crassum*, es un recurso pesquero de importancia socioeconómica, por lo que comprender su patrón de distribución es clave para su

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manejo. El propósito de esta investigación fue establecer si los cangrejos presentan segregación por talla en hábitats contrastantes. Se muestrearon tres parcelas de febrero a junio de 2022 para recolectar datos de variables biométricas en Ponuga, Veraguas, Panamá Pacífico. Se capturaron 151 cangrejos con ancho de cefalotórax promedio de 56.24 ± 8.56 mm; 97 machos y 54 hembras, con proporción sesgada hacia los machos (1.8:1). Los cangrejos en la parcela 1 alcanzaron mayor talla y peso que los de las parcelas 2 y 3. Se encontraron hembras ovígeras solo en las parcelas 1 y 2, durante junio (época de lluvias). El ancho mínimo del cefalotórax de las hembras, funcionalmente maduras, fue 47.11 mm. Según esta medida, las hembras maduras estuvieron presentes en proporciones más altas en todas las parcelas y fueron más abundantes en la parcela 1. Los cangrejos pequeños se segregaron en la parcela 3; la parcela de origen y talla estuvieron asociadas significativamente. Este es el primer reporte de segregación por tamaño y etapa de vida en *Cardisoma crassum*. Los hallazgos resaltan la importancia de las características del hábitat y abren el camino para más investigaciones sobre las causas de este patrón de distribución.

Palabras clave: Braquiuro, madriguera, biometría, madurez funcional, carapacho

INTRODUCTION

The mouthless crab (*Cardisoma crassum* Smith, 1870) is a common inhabitant of mangrove systems in the Panamanian Pacific, ranging from Espiritu Santo Island in Baja California (Mexico) to San Pedro de Vice in Piura, Peru (Hendrickx, 1995; Alemán & Ordinola, 2017; Lombardo & Rojas, 2022). Although *C. crassum* is an important fishery resource for coastal human settlements in Panama (Vega *et al.* 2018), little effort has been made to determine its distribution patterns and understand the factors affecting it. This is especially important because mouthless crabs can favor or restrict specific plant species recruitment through herbivory (Vargas-Téllez & Vázquez-López, 2020; Alemán & Ordinola, 2017), as well as play a critical role in the structure of mangrove forests (Smith, 1987; Smith *et al.* 1989; Wolcott & O'Connor, 1992; Lindquist *et al.* 2009).

Vegetative structure has repeatedly been associated to crab distribution and protection from predators in a variety of systems (Nomann & Pennings, 1998; Ngo-Massou *et al.* 2014). Furthermore, the distribution of the ocypodid and the grapsid crabs seems to be influenced by vegetation, substratum type, nutrients, salinity, tidal exposure, and the occurrence of other species (Nobbs, 2003; Arruda *et al.* 2006; Cannicci *et al.* 2018; Novais *et al.* 2021). These factors can produce segregation patterns of spatio-temporal nature, by sex and size, as in *Carcinus maenas* (Almeida *et al.* 2008),

Neohelice granulata (Casariego *et al.* 2011), *Ocypode gaudichaudii* (Yong & Lim, 2022) and *Cardisoma guanhumi* (Carmona-Suárez & Guerra-Castro, 2018).

Preliminary observations of a *C. crassum* population in Panama suggests that large and small individuals occupy different places in high mangrove areas. Large crabs were seen in open understory areas under shade from tall trees, while smaller crabs were observed under dense woody liana thickets without shade from trees (R. Lombardo, personal observation). We hypothesize that the distribution of crabs may be sufficiently segregated for size differences to be detected between discrete habitat types. Two studies have anecdotally reported the association between certain plant species and the concentrated presence of *C. crassum* burrows (Vera, 2012; Alemán *et al.* 2018); however, research confirming segregation by size and the factors influencing such patterns are lacking. Therefore, the goal of this study was to determine if such size differences between discrete habitat types exist in *C. crassum*.

MATERIALS AND METHODS

Study site: The present study was conducted between February and June 2022 at a site located along the Ponuga River in Veraguas, Panama (07° 51'

51.3756'' N, -081° 00' 52.6248'' W), where plants grow on sediment plains of alluvial origin and settled riverbeds (Intituto Geográfico Nacional Tommy Guardia, 1988; Lombardo & Rojas, 2022). February and March were dry months, with a monthly average of 14 days of precipitation, reaching 118.9 mm of rain. Heavy rains went from April to June, averaging 27.8 days of rain per month and 553.4 mm of precipitation, with a peak of 781.5 mm in June (ETESA, 2022).

Plot features: From February to June, crab biometrics was recorded for four days at the end of each month. Three plots were determined within the study site; the first plot (1.724 m²) was characterized by canopy-forming trees, composed of black mangrove (*Avicennia germinans*) and Cativo trees (*Prioria copaifera*), while ferns (*Acrostichum aureum*) and lilies (*Hymenocallis littoralis*) sparsely populated the undergrowth (Fig. 1A). The substrate in this plot consisted of a stable mix of mud and fine sand. The second plot (428 m²) was characterized by thorny undergrowth (Fig. 1B), dominated by Cañabrava (*Bactris major*), under the shade of Cativo trees and white mangrove (*Laguncularia racemosa*). This plot was located next to a natural shallow (~ 30 cm) drainage channel, and the substrate contained pebbles and gravel within the mud matrix. The third plot (591 m²) consisted

of exposed thicket-forming shrubs, 2 to 3 m tall with dense exposed roots of the woody liana *Dalbergia brownei* (Fig. 1C). The substrate in plot 3 was stable but consisted of a softer mix of clay, silt, and decaying leaf litter. Continuity of habitat characteristics in each plot ensured that all crabs were under the relative effect of the same ecological factors within their plots, regardless of plot area size. This is the case provided crabs are faithful to their burrows (Lombardo & Rojas, 2022) and, as generalists, they remain within small home ranges (Stachowicz & Hay, 1999). The plot and total study site area was calculated using ArcGIS 10.7.1. (ArcGIS, 2019).

Sampling procedure: Traps were deployed after visual confirmation of *C. crassum* presence or signs of burrow occupation within plots such as, fresh mud, droppings and/or plant remnants on the burrow opening. When a burrow matched these characteristics, the tunnel diameter beyond the opening (BD) was calculated as the distance between the needles of a compass. To collect crabs without injuring or damaging the burrow, a wooden handcrafted trap was set up. Bait type and trap success are not associated (Lombardo & Rojas, 2022); thus, each trap was baited with yuca (*Manihot esculenta*) throughout the study. Traps were placed at the entrance of a burrow for 24 hours and inspected hourly from 6:15 a.m. to 5:00 p.m.; they were left baited after 5:00 p.m. for the night. If unsuccessful, they were moved to another burrow the following morning. During field work, plots were visited multiple times; thus, in subsequent visits, previously inactive or blocked burrows found with activity signs were subject to trap deployment.

Crab data collection began *in situ* including the date and time of capture; crabs were then inspected to ascertain the sex by the abdomen shape (Hendrickx, 1995) and the reproductive status of females (ovigerous or not, Fig. 1D). Chi-square tests were used to compare the sex ratios for each plot. A digital Vernier caliper (0.1 mm) was used to measure the major chelae height (ChH), carapace length (CL), carapace width (CW), and third propodus length (P3). To avoid resampling, individuals received a number mark with fast drying white enamel paint and a coat of varnish. Individual weight (TW) was recorded using a scale once the paint dried (0.01 g). Processed crabs were then returned to their original burrow, which was likewise labeled with the matching ID number.

Biometry: Descriptive statistics were collected for all subjects, and differences in biometry between sexes were investigated using Student's t-test. A general lineal model was fitted using biometric variables as responses, and individual sex, plot of origin and their interaction as
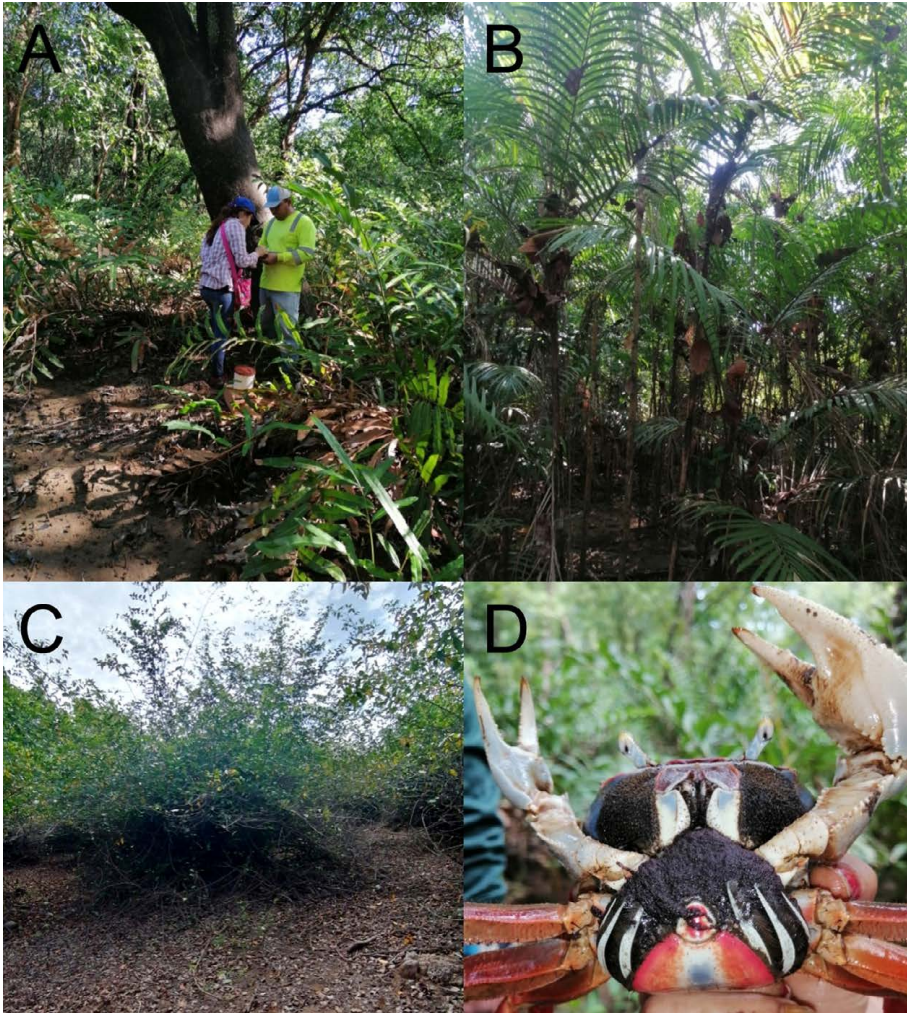
Fig. 1. Plot features and life history stage of *Cardisoma crassum* in Ponuga, Veraguas, Panama. A: plot 1 with canopy-forming trees and sparse undergrowth, B: plot 2 with thorny undergrowth under the shade of canopy-forming trees, C: low-level zone of plot 3 with exposed thicket-forming shrubs, D: ovate female captured in June (rainy season)

Fig. 1. Parcelas de muestreo y etapa de la historia de vida de *Cardisoma crassum* en Ponuga, Veraguas, Panamá. A: parcela 1 con dosel, formado por árboles y maleza escasa, B: parcela 2 con sotobosque espinoso, bajo la sombra de árboles formadores de dosel, C: zona de bajo nivel de la parcela 3, con arbustos formadores de matorrales expuestos, D: hembra ovada capturada en junio (temporada de lluvias)

factors to compare plots. Tukey pairwise comparisons were executed with 95% confidence level for all biometric variables. Plots were compared by sex using Welch's ANOVA provided variances of biometric variables (Bonett's method) between plots were different. In addition, pairs were contrasted using the Games-Howell simultaneous test to find differences between means (Games & Howell, 1976).

To compute the ratio of potentially mature females within plots, the size of the smallest egg-carrying female (functionally mature) was used as critical value to categorize them as mature or immature for plot comparison. The methods used in this study were meant to have the least negative impact possible; therefore, as there was no means to determine the gonad maturation stage in males without sacrificing them, the group was excluded from the analysis.

Burrow density by plot: Three 100 m^2-quadrants, one for each plot, were established to obtain indirect crab density estimates. As the rainy season is correlated with an increase in the *C. crassum* activity (Lombardo & Rojas, 2022), a monthly record of the number of active, inactive and blocked burrows was kept during heavy rain months (April to June). This allowed for the detection of changes in the activity pattern and comparison of burrow status between plots (Chi-square test).

RESULTS

A total of 151 mouthless crabs were captured, of which 97 were male and 54 were female. This proportion difference was significantly skewed towards males at 1.8:1 ($c^2 = 12.25$, *d.f.* = 1, $P < 0.001$). The CW of crabs averaged 56.24 ± 8.56 mm (22.74-74.95 mm); descriptive statistics of biometric variables are contained in Table 1. Male and female CW averaged 55.34 ± 9.38 mm and 57.84 ± 6.61 mm, respectively. Female CL was larger and significantly different than that of the males ($t = -2.14$, *d.f.* = 149, $P = 0.034$); no difference was detected in the rest of the variables between the sexes.

Plot biometry: In plot 1, a total of 74 (46 male and 28 female) mouthless crabs were captured, where male and female CW averaged 59.75 ± 8.69 mm and 60.79 ± 6.78 mm, respectively. The biometric variable comparison between sexes within plot 1 showed ChH to be the only variable with a difference: the male ChH was larger. The sex ratio was significantly skewed towards males at 1.6:1 ($c^2 = 4.38$, *d.f.* = 1, $P = 0.036$). In plot 2, a total of 36 (23 males and 13 females) crabs were captured; male and female CW averaged 51.72 ± 9.97 mm and 53.76 ± 3.56 mm, respectively. No significant differences were found between

Table 1. *Cardisoma crassum* biometric variable summary from the Ponuga River, Veraguas, Panama. CW: carapace width, CL: carapace length, ChH: chela height, P3: third propodal length, TW: total weight, BD: burrow diameter. Variables are in mm; weight (g)

Tabla 1. Variables biométricas de *Cardisoma crassum* del río Ponuga, Veraguas, Panamá. CW: ancho del carapacho, CL: longitud del carapacho, ChH: altura de la quela, P3: longitud del tercer propodio, PT: peso total, BD: diámetro de la madriguera. Las variables se presentan en mm, excepto el peso (g)

Variable	N	Mean	SD	Min.	Max.
CW	151	56.24	8.55	22.74	74.95
CL	151	45.96	7.13	19.09	60.28
ChH	151	32.53	14.69	9.54	79.82
P3	151	16.86	2.97	6.23	25.49
TW	151	95.70	43.47	22.86	212.83
BD	151	61.86	12.81	38.50	99.80

the sexes among biometric variables from plot 2. The sex ratio was not significantly different from 1:1. In contrast, plot 3 totaled 41 individuals (28 males and 13 females), where male and female CW averaged 51.07 ± 6.53 mm and 55.57 ± 5.70 mm, respectively. A significant biometric difference was found between the sexes in plot 3, where females were larger than males in CW, CL, ChH, TW, and BD; however, there was no difference in P3 between the sexes (Table 2). Plot 3 showed a heavily skewed male sex ratio of 2.2:1 ($c^2 = 4.38$, *d.f.* = 1, *P* = 0.036).

Through the general lineal model, a significant difference was detected between the three plots for CW, P3, TW, and BD, while ChH showed the same pattern but, in contrast, the interaction between plot and sex was also significant. Furthermore, crab CL was significantly different between the plots, and female's CL was significantly larger than males' (Table 3, Fig. 2). Males from plot 1 were larger than those in plot 2 and 3 for five and six of the biometric variables, respectively. No size difference was detected between males from plots 2 and 3. Females from plot 1 were larger in five out of six variables compared to females of plot 2. Plot 1 females were larger than those from plot 3 in CW, while CL from plot 3 female was larger compared to plot 2 (Table 4).

Table 2. Biometric variables within plots comparison between sexes in *Cardisoma crassum* from Ponuga, Veraguas, Panama. CW: carapace width, CL: carapace length, ChH: chela height, P3: third propodal length, TW: total weight, BD: burrow diameter

Tabla 2. Comparación de variables biométricas en parcelas entre sexos en Cardisoma crassum de Ponuga, Veraguas, Panamá. CW: ancho del carapacho, CL: longitud del carapacho, ChH: altura de la quela, P3: longitud del tercer propodio, PT: peso total, BD: diámetro de la madriguera

♂ vs. ♀	Plot 1			Plot 2			Plot 3		
Variable	*t*	*d.f.*	*P*	*t*	*d.f.*	*P*	*t*	*d.f.*	*P*
CW	0.54	72	0.591	0.71	34	0.485	2.13	39	0.039
CL	0.40	72	0.689	1.20	34	0.237	3.11	39	0.004
ChH	-2.84	71	0.006	1.52	34	0.137	2.64	39	0.012
P3	-0.13	72	0.898	-0.28	33	0.784	0.84	38	0.404
TW	-0.14	68	0.887	0.19	29	0.853	2.30	39	0.027
BD	-0.13	68	0.899	-0.03	31	0.978	2.80	37	0.008

Table 3. Biometrical contrast by plot for six variables in *Cardisoma crassum* from Ponuga, Veraguas, Panama. CW: carapace width, P3: third propodal length, TW: total weight, BD: burrow diameter, ChH: chela height, CL: carapace length

Tabla 3. Contraste biométrico por parcela para seis variables en *Cardisoma crassum* de Ponuga, Veraguas, Panamá. CW: ancho del carapacho, P3: longitud del tercer propodio, PT: peso total, BD: diámetro de la madriguera, ChH: altura de la quela, CL: longitud del carapacho

Variable	Factor	*d.f.*	F	P	Plot comparison	t	P
CW	Plot	2–145	15.44	< 0.001	2-1	-4.92	< 0.001
					3-1	-5.04	< 0.001
					3-2	0.08	0.997
P3	Plot	2–143	9.89	< 0.001	2-1	-4.38	< 0.001
					3-1	-3.09	0.007
					3-2	1.26	0.420
TW	Plot	2–136	13.33	< 0.001	2-1	-3.83	0.001
					3-1	-5.55	< 0.001
					3-2	-1.12	0.505
BD	Plot	2–136	6.62	0.002	2-1	-2.86	0.013
					3-1	-3.93	< 0.001
					3-2	-0.76	0.725

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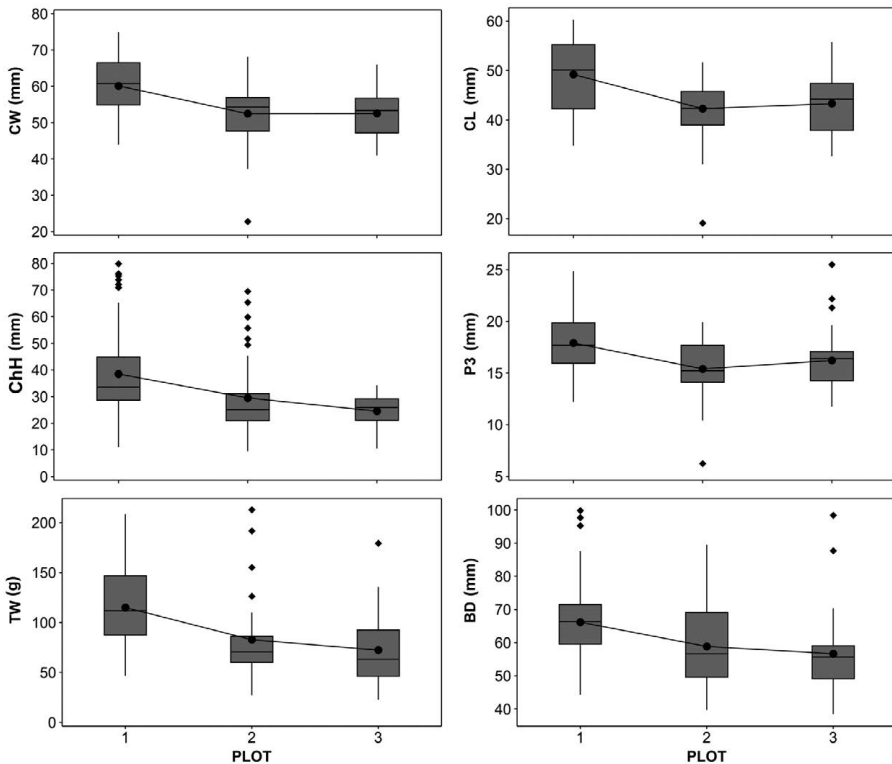| Variable	Factor	d.f.	F	P	Plot comparison	t	P
ChH	Plot	2–144	10.4	< 0.001	2-1	-3.28	0.004
					3-1	-5.32	< 0.001
					3-2	-1.62	0.240
	Plot*Sex	2–144	7.05	< 0.001			
CL	Plot	2–145	15.29	< 0.001	2-1	-5.35	< 0.001
					3-1	-4.68	< 0.001
					3-2	0.77	0.721
	Sex	1–145	6.30	0.013	♂ - ♀	-2.15	0.033

Fig. 2. *Cardisoma crassum* biometric variable between three contrasting plots from Ponuga, Veraguas, Panama. CW: carapace width, CL: carapace length, ChH: chela height, P3: third propodus length, TW: total weight, BD: burrow diameter
Fig. 2. Variables biométricas de *Cardisoma crassum* entre tres parcelas en Ponuga, Veraguas, Panamá. CW: ancho del carapacho, CL: longitud del carapacho, ChH: altura de la quela, P3: longitud del tercer propodio, TW: peso total, BD: diámetro de la madriguera

Table 4. Plot contrast by sex for six biometric variables in *Cardisoma crassum* from Ponuga, Veraguas, Panama. CW: carapace width, P3: third propodal length, TW: total weight, BD: burrow diameter, ChH: chela height, CL: carapace length. Means and their difference (DF) are given in mm; weight (g). Bold indicates significant difference at **α** = 0.05; (*d.f.* = 2)

Tabla 4. Contraste de parcelas por sexo para seis variables biométricas en *Cardisoma crassum* de Ponuga, Veraguas, Panamá. CW: ancho del caparazón, P3: longitud del tercer propodio, TW: peso total, BD: diámetro de la madriguera, ChH: altura de la chela, CL: longitud del caparazón. Las medias y su diferencia (DF) se dan en mm; peso (g). Negrita indica diferencia significativa, α = 0,05; (*d.f.* = 2)

Welch's ANOVA			Games–Howell pairwise comparison		
Variable	F	P	Plot 2 *vs.* Plot 1	Plot 3 *vs.* Plot 1	Plot 3 *vs.* Plot 2
♂CW	12.95	<0.001	$X2 = 51.72$; $X1 = 59.75$ $DM = -8.03$; $t = -3.29$; ***P* = 0.006**	$X3 = 51.07$; $X1 = 59.75$ $DM = -8.68$; $t = -4.88$; ***P* < 0.001**	$X3 = 51.07$; $X2 = 51.72$ $DM = -0.65$; $t = -0.27$; $P = 0.961$
♀CW	9.35	0.001	$X2 = 53.76$; $X1 = 60.80$ $DM = -7.04$; $t = -4.35$; ***P* < 0.001**	$X3 = 55.60$; $X1 = 60.80$ $DM = -5.22$; $t = -2.57$; ***P* = 0.041**	$X3 = 55.60$; $X2 = 53.76$ $DM = 1.82$; $t = 0.97$; $P = 0.601$
♂P3	6.01	0.005	$X2 = 15.50$; $X1 = 17.93$ $DM = -2.43$; $t = -2.99$; ***P* = 0.013**	$X3 = 15.95$; $X1 = 17.93$ $DM = -1.98$; $t = -2.67$; ***P* = 0.027**	$X3 = 15.95$; $X2 = 15.50$ $DM = 0.45$; $t = 0.49$; $P = 0.876$
♀P3	5.59	0.010	$X2 = 15.22$; $X1 = 17.85$ $DM = -2.63$; $t = -3.36$; ***P* = 0.007**	$X3 = 16.76$; $X1 = 17.85$ $DM = -1.09$; $t = -1.51$; $P = 0.303$	$X3 = 16.76$; $X2 = 15.22$ $DM = 1.54$; $t = 1.76$; $P = 0.206$
♂TW	17.28	<0.001	$X2 = 81.88$; $X1 = 115.68$ $DM = -33.8$; $t = -3.14$; ***P* = 0.008**	$X3 = 64.59$; $X1 = 115.68$ $DM = -51.09$; $t = -5.92$; ***P* < 0.001**	$X3 = 64.59$; $X2 = 81.88$ $DM = -17.29$; $t = -1.82$; $P = 0.176$
♀TW	18.06	<0.001	$X2 = 68.95$; $X1 = 114.22$ $DM = -45.27$; $t = -6.04$; ***P* < 0.001**	$X3 = 89.10$; $X1 = 114.22$ $DM = -25.10$; $t = -1.89$; $P = 0.168$	$X3 = 89.10$; $X2 = 68.95$ $DM = 20.15$; $t = 1.66$; $P = 0.254$
♂BD	11.23	<0.001	$X2 = 58.90$; $X1 = 66.33$ $DM = -7.43$; $t = -2.02$; $P = 0.121$	$X3 = 53.22$; $X1 = 66.33$ $DM = -13.11$; $t = -4.76$; ***P* < 0.001**	$X3 = 53.22$; $X2 = 58.90$ $DM = -5.68$; $t = -1.70$; $P = 0.221$
♀BD	10.16	0.001	$X2 = 56.21$; $X1 = 67.59$ $DM = -11.38$; $t = -4.25$; ***P* = 0.002**	$X3 = 60.62$; $X1 = 67.59$ $DM = -6.97$; $t = -2.10$; $P = 0.128$	$X3 = 60.62$; $X2 = 56.21$ $DM = 4.41$; $t = 1.08$; $P = 0.536$
♂ChH	24.56	<0.001	$X2 = 26.74$; $X1 = 42.39$ $DM = -15.65$; $t = -4.09$; ***P* < 0.001**	$X3 = 22.96$; $X1 = 42.39$ $DM = -19.43$; $t = -7.06$; ***P* < 0.001**	$X3 = 22.96$; $X2 = 26.74$ $DM = -3.78$; $t = -1.20$; $P = 0.464$

| Welch's ANOVA			Games-Howell pairwise comparison		
Variable	F	P	Plot 2 *vs.* Plot 1	Plot 3 *vs.* Plot 1	Plot 3 *vs.* Plot 2
♀ ChH	2.44	0.107	$X2 = 34.45; X1 = 32.25$; DM = 2.20; t = 0.45; P = 0.894	$X3 = 27.96; X1 = 32.25$; DM = -4.29; t = -1.83; P = 0.176	$X3 = 27.96; X2 = 34.45$; DM = -6.49; t = -1.45; P = 0.343
♂ CL	15.46	< 0.001	$X2 = 41.40; X1 = 48.96$; DM = -7.56; t = -4.24; **P < 0.001**	$X3 = 41.59; X1 = 48.96$; DM = -7.36; t = -5.11; **P < 0.001**	$X3 = 41.59; X2 = 41.40$; DM = 0.19; t = 0.11; P = 0.993
♀ CL	7.98	0.002	$X2 = 43.86; X1 = 49.63$; DM = -5.77; t = -3.66; **P = 0.002**	$X3 = 47.94; X1 = 49.63$; DM = -1.69; t = -1.00; P = 0.581	$X3 = 47.94; X2 = 43.86$; DM = 4.08; t = 2.91; **P = 0.021**
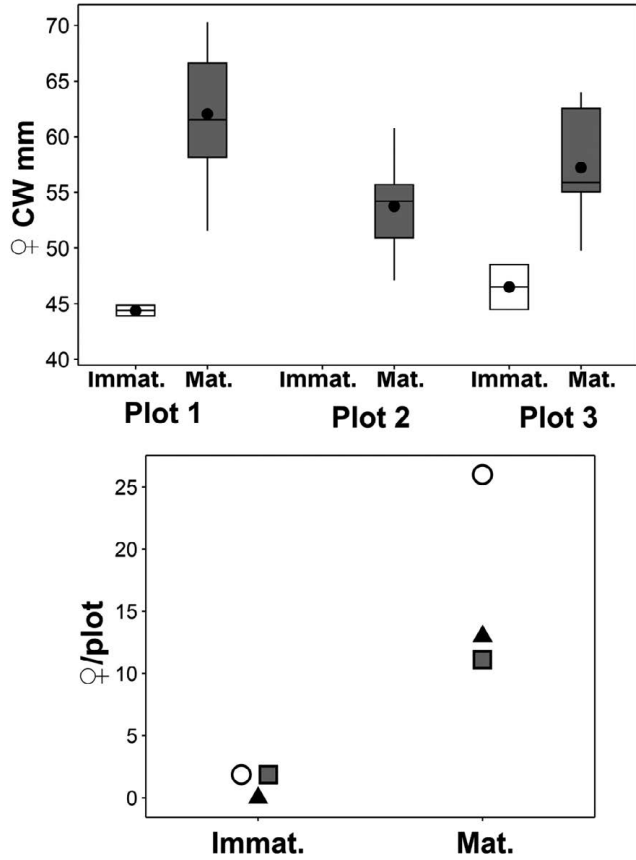
Fig. 3. Size (left) and number (right) of immature and mature *Cardisoma crassum* females within three plots from Ponuga, Veraguas, Panama. CW: carapace width, the gray boxes correspond to mature individuals, while the empty boxes represent immature crab. Circles, squares, and triangles represent counts in plots 1, 2 and 3, respectively

Fig. 3. Talla (izq.) y número (der.) de hembras inmaduras y maduras de *Cardisoma crassum* en tres parcelas en Ponuga, Veraguas, Panamá. CW: ancho de carapacho, cajas grises corresponden a individuos maduros, mientras que las vacías representan cangrejos inmaduros. Círculos, cuadrados y triángulos representan número de hembras en parcelas 1, 2 y 3, respectivamente

Table 5. *Cardisoma crassum* burrow counts comparison (Chi-square *d.f.* = 2) in three 100 m² plots with contrasting vegetation and habitat characteristics during rainy season in Ponuga, Veraguas, Panama

Tabla 5. Recuentos comparativos de madrigueras de *Cardisoma crassum* (Chi-cuadrado *g.l.* = 2) en tres parcelas de 100 m² con características contrastantes de vegetación y hábitat durante la temporada de lluvias en Ponuga, Veraguas, Panamá

Status	Month	Plot 1	Plot 2	Plot 3	Expected	*n*	c^2	*P*
Active	April	38	33	42	37.67	113	1.08	0.583
	May	41	40	58	46.33	139	4.42	0.110
	June	48	44	56	49.33	148	1.51	0.469
Inactive	April	7	9	6	7.33	22	0.64	0.727
	May	4	1	0	1.66	5	5.2	0.074
	June	0	1	2	1	3	2	0.368
Blocked	April	4	5	14	7.66	23	7.91	0.019
	May	5	6	3	4.66	14	1	0.607
	June	3	4	5	4	12	0.5	0.779

Ovigerous females were found only in plots 1 and 2 during June (rainy season); their average CW was 57.98 ± 10.17 (47.11-66.69 mm, N = 4). Using the CW of the smallest ovigerous female (47.11 mm) as a critical value to classify females into mature or immature, the proportion of functionally mature females in plots 1, 2, and 3 reached 93%, 100%, and 85%, respectively. There was a difference in the number of potentially mature females between plots, where plot 1 had more functionally mature females (c^2 = 7.96, *d.f.* = 2, *P* = 0.019; Fig. 3).

Burrow density by plot: Active burrow average density in plot 1 was 0.42 burrows/m², while plots 2 and 3 had 0.39 and 0.52 burrows/m²,

respectively. Comparison of monthly active burrow counts resulted in no differences between plots. This pattern was repeated for inactive burrows, while blocked burrow counts between plots showed a significant difference only in April; plot 3 had a higher blocked burrow count (Table 5).

DISCUSSION

Brachyuran male crabs tend to be larger and heavier than females (Hartnoll *et al.* 2009), as in *C. armatum* (Etchian *et al.* 2016), *C. guanhumi* (Hernández-Maldonado & Campos, 2015; Moraes-Costa & Schwamborn, 2018; Govender, 2019), *Gecarcinus ruricola* (Hartnoll *et al.* 2007) and

Johngarthia lagostoma (Hartnoll *et al.* 2009). This trend is consistent with *C. crassum* according to reports by Vega *et al.* (2018), Zambrano & Olivares (2020), and Lombardo & Rojas (2022). However, in this study, only males from plot 1 had larger ChH and females in plot 3 were overall larger than males, especially the CL. In brachyuran crabs, the egg mass is attached to the abdomen's pleopods; thus, protection and facilitation of egg hatching are among the key functions of the female abdomen. Consequently, with the start of sexual maturity, changes occur throughout the allometric development of this structure (Hartnoll, 1974). The sexual dimorphism of the abdomen is due to changes in the function of male and female pleopods; consequently, the CL is predicted to be larger in female crabs (Hartnoll, 1974; Mclay, 2015). This might be the reason behind significant biometric differences within plot 3, where 85% of the females were mature, and consequently, larger and heavier than males.

Furthermore, the sex and plot interaction term for ChH might have been significant due to asymmetry in male chela size (Zambrano & Olivares, 2020), especially as the contrast between individuals of plots 1 and 3 was high, suggesting segregation by size. Burrow diameter difference between plots also suggests segregation by size as there were no burrows corresponding to large males in this plot. Even if larger males moved, the long-standing nature of burrows (>40 days after vacancy) would have allowed their sampling, but this was not the case.

The distribution pattern observed might be influenced by the habitat features of plots; for instance, the shade-temperature relationship is important for crab survival (Nomann & Pennings, 1998; Nobbs, 2003), given that increased dehydration levels lead to reduced mobility and food intake in gecarcinid and fiddler crabs (McGaw *et al.* 2019; da Silva Vianna *et al.* 2020). However, shade alone might not account for the observed segregation pattern, as it was common to all plots. Moreover, burrowing activity patterns of *C. crassum* approximated by burrow counts did not vary between plots, except for blocked burrows in plot 3. This suggests that distribution and activity are relatively dependent on the same limiting factors across habitat types, but specific habitat features may also be important. For example, crabs in plot 3 were smaller and lived under the shade of woody liana thicket, among complex root systems, in a low-elevation area along the Ponuga river shore. Small crabs in this habitat may have access to softer substratum and shallow ground water, which is critical (Nobbs, 2003; Ngo-Massou *et al.* 2014; McGaw *et al.* 2019). In contrast, larger crabs, including mature females, were found in plot 1, where the ground is higher. Such physical factors

may limit the distribution of juveniles as shown in a closely related species, *C. guanhumi* (Novais *et al.* 2021).

Mortality by predation is another important factor shaping crab distribution (Koga *et al.* 2001; Christy, 2007; Casariego *et al.* 2011). Although it was not the focus of our study, differential mortality may be a contributing factor to the observed pattern in Ponuga, considering vegetation acts primarily as refugia from predators (Nomann & Pennings, 1998). Habitat complexity, conferred by vegetation cover in plots 2 and 3, may provide protection against predators due to reduced access (Almeida *et al.* 2008). Benefits from the protective role of vegetation cover in plot 1 are less obvious, provided that the undergrowth is sparse and may not present the same challenge for potential predators as the vegetation in plots 2 or 3; however, burrow fidelity in this species (Lombardo & Rojas, 2022) might offset potential costs (Moraes-Costa & Schwamborn, 2018; Nuñez *et al.* 2018).

Male biased sex ratios, as seen in the current study, appear to be the norm for crab species (Wenner, 1972); however, variation in size and sex ratios may be explained by extraction effects, unequal growth, variable maximum sizes, and lifespan (Wenner, 1972; Diele *et al.* 2005; Ewers-Saucedo, 2019). It is difficult to quantify the relative importance of each component in our scenario; nonetheless, sex ratio shifts are known to occur monthly in *C. guanhumi* (Shinozaki-Mendes *et al.* 2013), and seasonally in *Cardisoma armatum*, where the sex ratio during breeding season is affected by migratory movements (Etchian *et al.* 2016). Plot 2 in the present study showed no departure from the 1:1 sex ratio, while the remaining plots were male biased, suggesting small-scale sex ratio variation might be possible in this species.

CONCLUSION

Segregation by size in discrete habitat types was detected in *C. crassum*. Males showed strong segregation of large sizes towards plot 1, while female sizes were more evenly distributed among plots. Smaller crabs were segregated towards plot 3. Our contribution highlights the need for more studies about the factors driving distribution patterns and draw attention to the importance of habitat complexity and physical factors, especially early in crab life.

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