

Rediscovery of *Mesotheres unguifalcula* (Glassell, 1936) (Crustacea: Brachyura: Pinnotheridae) with Remarks on the Symbiotic Relationship with its New Host, the Spindle Sea Snail *Leucozonia cerata* (W. Wood, 1828) (Mollusa: Gastropoda: Fasciolaridae)

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The symbiotic pinnotherid crab *Mesotheres unguifalcula* was rediscovered in Acapulco Guerrero, Mexico, and was found infesting the spindle sea snail *Leucozonia cerata* (Fasciolaridae), a new host record for this crab. A total of 432 snails were collected in 2020, with a prevalence of 77%, well explained by the host width frequency. Monthly prevalence varied from 54% to 90%, and the mean intensity was 1.4 +/- 0.5 crabs per host. The sex ratio of snails was 1:1, and the crab did not prefer to infest males or females. The sex ratio of the crabs was positively skewed towards females. Crabs may infest small to large snails; however, most infested snails range between 20 and 40 mm in width. Prevalence increases with the host size, smaller than 30 mm, averaging 53% infestation, while those from 30 mm to 52 mm represented 82 to 100% infestation. The number of crabs by host varied from 1 to 3; solitary females and males were dominant (51%), followed by heterosexual couples (24%) and other combinations that included homosexual couples and triads, which barely represented 2%. Although there are many heterosexual couples, monogamy is ruled out due to the higher number of solitary males and females and the lower number of heterosexual couples compared to those statistically expected. The available evidence about the life history of *Mesotheres unguifalcula*, like for another studied species of the subfamily Pinnotherinae sensu stricto, suggests a pure-search

polygynandry of sedentary females as its mating system (*i.e.*, larger, solitary, and sedentary females, and smaller males who, in reproductive season, are roaming from one host to another in search of females receptive to copulation).

Key words: Symbiosis, prevalence, host use pattern, Pinnotheridae, Crustacean

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BACKGROUND

The Pinnotheridae constitute a heterogeneous group of symbiotic crabs of invertebrates and chordate inhabiting the mantle cavity of Mollusca (Bivalvia and Gastropoda) and Brachiopoda, test, cloaca and respiratory trees of Echinodermata (Echinoidea and Holothurioidea), burrows of decapod Crustacea (Thalassinidea), Echiura and Sipuncula, tubes of Polychaeta and atria of Ascidiacea (Castro 2015; Campos 2016). Currently, 56 species have been recorded for the Mexican Pacific (Campos 2016) in two large groups, one with transversely elongated carapace symbionts of organisms that build burrows, *e.g.*, pinnixids in Thalassinidea burrows and another with subquadrate, suborbicular or subrectangular carapace, associated with organisms that do not build burrows, *e.g.*, pinnotherine symbionts of mollusks, echinoderms, and related (Hultgren et al. 2022). The subfamily Pinnotherinae *sensu lato* belongs to the latter group (Palacios-Theil et al. 2009, 2016; but see discussion in Campos 2009) with 26 species in 16 genera on the Mexican coasts (11 monotypic) (Campos 2016). Steve A. Glassell (1936) described one of these species, the enigmatic and poorly known *Fabia unguifalcula*, which ranges from the upper Gulf of California to Acapulco, Guerrero, Mexico (Ng et al. 2019). Campos (1989) studied the taxonomy of *F. unguifalcula* Glassell, 1936 and assigned it to the Asian genus *Orthotheres* Sakai, 1969. More recently, Ng and Ho (2016) restricted the distribution of *Orthotheres* *sensu stricto* to the Western Pacific (Japan, Taiwan, and Australia), and all the American species previously assigned to *Orthotheres* were transferred to a new genus, *Mesotheres* Ng, Ah Yong and Campos, 2019 (type species *P. strombi* Rathbun, 1905).

Ongoing studies on pinnotherid crabs from the Mexican tropical Pacific resulted in the discovery of a small pinnotherid crab living in a commercially exploited marine snail. Comparison of this crab species with all the species assigned to this subfamily in the American Pacific resulted in the rediscovery of pea crab *Mesotheres unguifalcula* (Glassell, 1936) on the coast of Acapulco, Guerrero, México. This species was collected 73 years ago by E.C. Huffman in this locality and deposited in the Smithsonian Institution without information about its host (Ng et al. 2019). *Mesotheres unguifalcula* is symbiotic with *Leucozonia cerata* (W. Wood, 1828) (Fasciolariidae), representing the second pinnotherids crab species recorded in a marine snail along America's Pacific coast. The first one was *Opisthopus transversus* Rathbun, 1918, a generalist symbiont crab of the Californian province, which may occasionally occur in symbiosis with *Bulla gouldiana* Pilsbry, 1895 (Bullidae), *Megastraea undosa* (W. Wood, 1828) (Turbinidae) and *Neverita lewisii* (Gould, 1847) (Naticidae) (Schmitt et al. 1973; Campos 2016). In addition to recording *L. cerata* as a confirmed host for the first time, we provide some ecological data for this symbiotic crab, including prevalence, sex ratio, host use pattern, preference of the crab by infesting a particular sex or size of this snail, and a discussion on its mating system.

MATERIALS AND METHODS

Sample processing

Samples of *Leucozonia cerata* were acquired from January to December 2020 from commercial catches in La Angosta and Caleta beaches, Acapulco, Mexico. A fisherman collected 30 to 78 monthly snails in multiple free dives between 10 and 15 meters deep. The specimens were stored in individual plastic bags, chilled, and analyzed in the Ecología Costera y Sustentabilidad laboratory, Facultad de Ecología Marina, Universidad Autónoma de Guerrero, Mexico. In the laboratory, the snails were cleaned of epizootic organisms, and the maximum width of the shell of each snail was measured with a Vernier caliper to 0.01 mm precision. The snails were broken with a hammer and sexed; when present, the pea crabs were extracted from the mantle cavity and individually placed in a plastic vial of 4 ml, fixed in formaldehyde 4% for 12 hours, and preserved in 70% ethanol. The sex of each snail was determined by the presence of a muscular penis behind the cephalic tentacle in males and the absence of such an appendage in females. The snails collected in January 2020 resulted from a feasibility study on symbiotic crabs. The specimens were dissected entirely in search of crabs, but their sexes were

unrecorded. Each crab was photographed from a dorsal view using a stereomicroscope Leica EZ4HD. The maximum width and length of the carapace were measured using ImageJ software. The sex of the crab was determined by the shape of the abdomen in adults, narrow in males and broad in females, and confirmed by the presence and absence of gonopods (Ng et al. 2019).

Data analysis

We provide the total prevalence and intensity, *i.e.*, the percentage of infested snails and the number of crabs per infested snail, respectively (Reiczigel et al. 2019). Snail width was used to generate width-frequency distributions of both infested and non-infested snails (Mena et al. 2014). The number of classes was determined by the Sturges (1926) formula: $k = 1 + \log_2 n$; “k” is the number of classes, and “n” is the size of the sample. Values are expressed as means \pm standard deviation (SD) for prevalence, intensity, and snail width.

To determine if the frequency of the snail explains the pea crab prevalence observed by class size, we calculated the coefficient of determination for the linear relation between pea crab prevalence and the frequency of snails for each size. The same method assessed the relationship between the shell's width and the prevalence's variability.

Statistical analyses were performed using PAST program, version 4.11 (Hammer et al. 2022), and Microsoft Excel 16.66.1. Statistical symbols follow Sokal and Rohlf (1981).

Host use pattern of *Mesotheres unguifalcula* in *Leucozonia cerata*

We studied the host-use pattern of *M. unguifalcula* in *L. cerata* with a description of its population, sexual association, and preference by sex and size of the host. First, we examined whether *M. unguifalcula* in *L. cerata* differed from a random distribution. The observed distribution (*i.e.*, frequency of occurrence of hosts with one, two, or three crabs) was compared with the Poisson distribution (Elliott 1983). Significant differences between distributions were examined using a Chi-square test of goodness-of-fit (Sokal and Rohlf 1981). If significant differences were observed, specific frequencies between the observed and expected distributions were compared by subdivision of the Chi-square test and using the sequential Bonferroni correction to control the Type-I error rate (Rice 1989, Boustani 2022). If the empirical variance/mean quotient was less than 1, the same procedure would be performed but comparing the frequency of occurrence with a positive Binomial distribution.

We analyze if the frequency of the solitary (male or female), pairs (heterosexual or

homosexual), and multiple crabs (male-male-female, male-female-female) in the same host was random. The observed distribution was compared with a Binomial random distribution. For crabs in pairs (male-female, male-male, female-female) on a single host, we evaluated whether its observed distribution differed significantly from an expected random binomial distribution. A Chi-square goodness of fit test was used to inspect for significant differences between the distributions as indicated above (Sokal and Rohlf 1981). In addition, we tested whether the body size of solitary males and females differed significantly from that of paired males and females, respectively. For this purpose, two different Student t-tests were conducted (Sokal and Rohlf 1981). Before the Student's *t*-tests, the data were analyzed for normality (Shapiro-Wilk's test) and homogeneity of variances (Leneve's test) and, if necessary, were transformed to meet statistical assumptions (Underwood 1997).

We calculated the sex ratio as the number of males divided by the total number of crabs. The observed proportion of males to females was tested to determine differences from a 1:1 sex ratio with a binomial test (Wilson and Hardy 2002). To examine whether crabs choose one host sex over another, we compared the observed distribution of the crabs on male and female hosts with the binomial random distribution, which, in the case of no difference, indicated no preference by any sex (Sokal and Rohlf 1981). The significance level was established with a two-tailed binomial test (Zar 1999).

Lastly, to assess whether crabs choose a particular snail size range, we analyze the presence and absence of crabs in all snail sizes. The data were divided into three groups using the K-medoids algorithm (Hammer et al. 2022), and the snails with and without crabs were compared between the clustered groups. A Chi-square test was used to inspect for significant differences between the distributions as indicated above (Sokal and Rohlf 1981).

RESULTS

Prevalence, intensity, and frequency distribution of snail and crab

A total of 432 specimens of *L. cerata* were collected in Acapulco Bay, Guerrero, Mexico, in 2020, of which 332 (77%) were infested by *M. unguifalcula*. Crabs are sexually dimorphic; males have a carapace width of 1.2 to 6.5 mm (3.9 +/- 1.2), whereas females vary from 2.0 to 11.8 (7.0 +/- 1.5). The crabs positioned themselves along the mantle cavity of the snail. Monthly prevalence ranged from 54% to 90% (79.4 +/- 10.9, Fig. 1). The mean intensity was 1.4 +/- 0.5, crabs by the host. The width of the shell of *L. cerata* varied between 12.1 to 51.9 mm (30.2 +/- 5.8). Most of the infested snails (303;

91.3%) ranged between 20 and 40 mm, and the infestation was associated with the abundance of the different width sizes (Table 1; Fig. 2); snails below 15 mm width were uninfested. The host width frequency explained the prevalence well ($r^2 = 0.97$). The host width, however, did not explain the variability of the prevalence by size class ($r^2 = 0.00031$). Furthermore, a low-moderate positive correlation was observed, in decrease order, between the carapace width of females ($r = 0.462, p < 0.001$), males ($r = 0.412, p < 0.01$), and sexes combined ($r = 0.39, p < 0.001$) with the shell of *L. cerata*. Nevertheless, small crabs (< 4 mm), males alone, and combined males and females, did not correlate with their hosts ($r = -0.21611, p > 0.05$; $r = -0.072, p > 0.05$ respectively), while the combined non-gravid and gravid females (> 4 mm) showed the best, although only statistically moderate, correlation ($r = 0.57, p < 0.001$). Oviporous females were recorded year-round, with a monthly frequency of 38-67% (53 +/- 10).

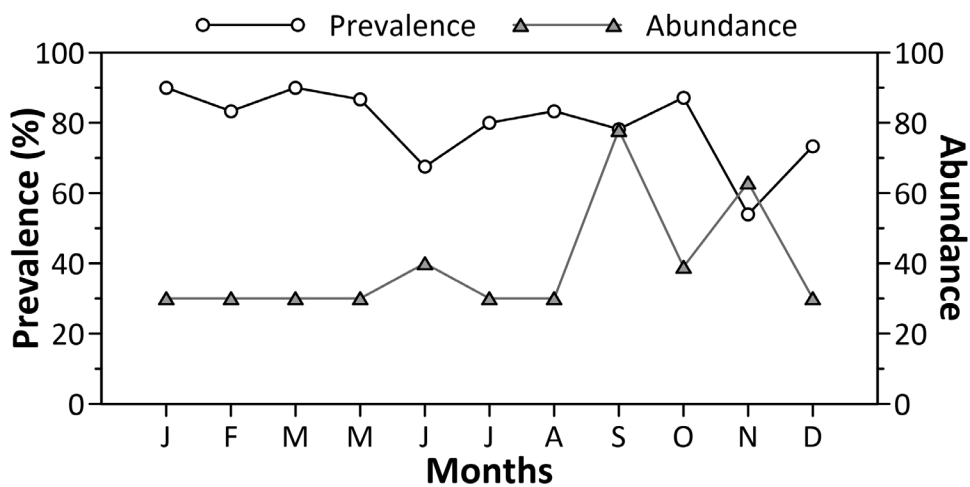


Fig. 1. The monthly abundance of *Leucozonia cerata* and prevalence of its symbiont *Mesotheres unguifalcula* at La Angosta and Caleta beaches, Acapulco, Mexico, 2020.

Table 1. Variation of the sea snail frequency *Leucozonia cerata* by size class, and its infestation by and prevalence of *Mesotheres unguifalcula* at La Angosta and Caleta beaches, Acapulco, Mexico, 2020

Wide (mm)	Frequency	Snail relative frequency	Infested snails	Peacrab prevalence	Class prevalence
12-16	5	1.2	2	0.5	40.0
16-20	8	1.9	5	1.2	62.5
20-24	42	9.7	20	4.6	47.6
24-28	88	20.4	56	13.0	63.6
28-32	143	33.1	117	27.1	81.8
32-36	91	21.1	81	18.8	89.0
36-40	33	7.6	29	6.7	87.9
40-44	13	3.0	13	3.0	100.0
44-48	5	1.2	5	1.2	100.0
48-52	4	0.9	4	0.9	100.0

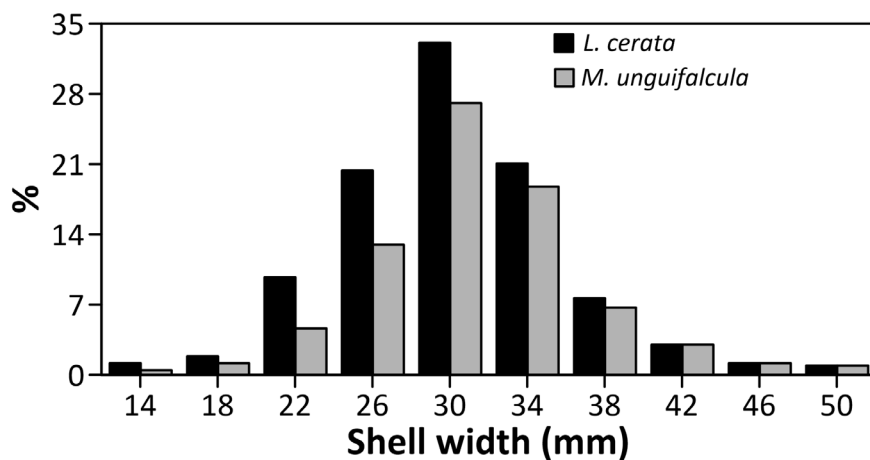


Fig. 2. Relative frequency of *Leucozonia cerata* and prevalence of its symbiont *Mesotheres unguifalcula* at La Angosta and Caleta beaches, Acapulco, Mexico, monthly pooled data for 2020.

Host use pattern of *Mesotheres unguifalcula* in *Leucozonia cerata*.

The population distribution of *M. unguifalcula* differed significantly from a random distribution (observed versus expected Poisson distribution, Chi-square test of goodness of fit, $X^2 = 74.404$, $d.f. = 4$, $p < 0.000001$, Fig. 3a), with a high frequency of snails inhabited by solitary male and female crabs, (52%, Fig. 4), ($X^2 = 34.27$, $p < 0.00001$, sequential Bonferroni $\alpha = 0.001$). The number of crabs by host varied from 0 to 3. The empirical variance/mean ratio ($0.53/ 1.04 = 0.51 < 1$) suggests a

regular distribution; however, the distribution was not perfectly uniform (observed versus expected, Positive Binomial, Chi-square test of goodness of fit, $X^2 = 29.16$, $d.f. = 3$, $p < 0.0001$, Fig. 3b), (Elliot 1983).

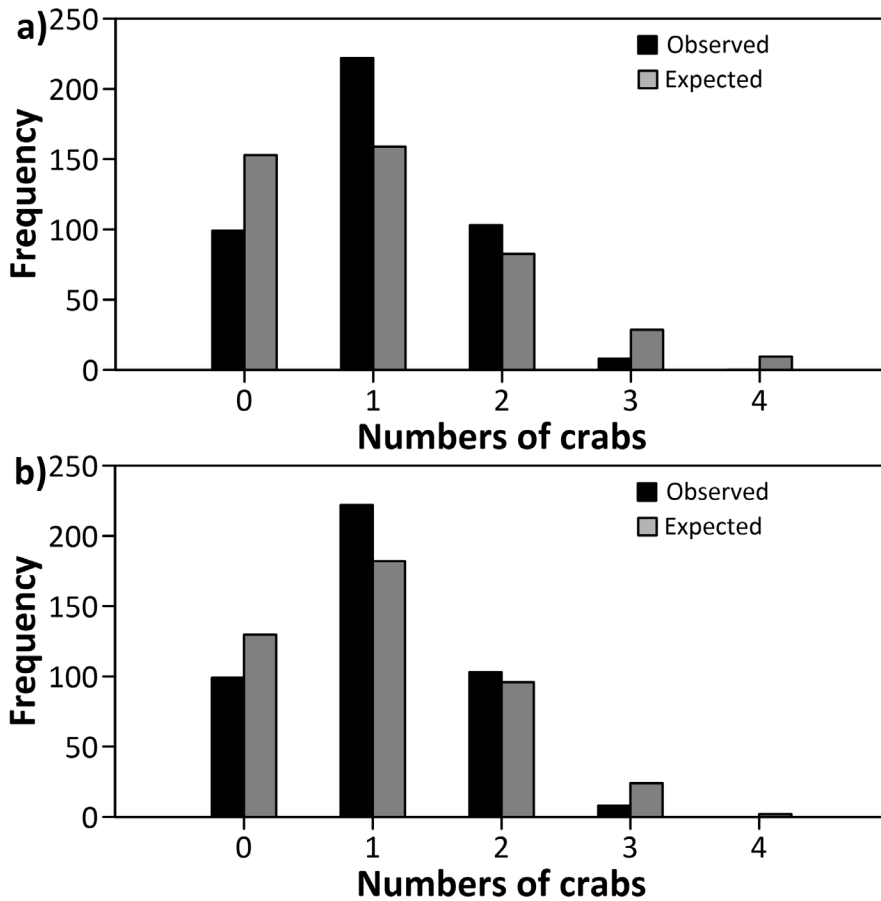


Fig. 3. Population distribution of the pea crab *Mesotheres unguifalcula*, symbiotic with *Leucozonia cerata* at La Angosta and Caleta beaches, Acapulco, Mexico. a) The observed population distribution of all crabs found on hosts differs significantly from the expected Poisson random distribution ($X^2 = 74.404$, $d.f. = 4$, $p < 0.000001$). b) The observed population distribution of all crabs found on hosts differs significantly from the expected Binomial random distribution ($X^2 = 29.16$, $d.f. = 3$, $p < 0.0001$).

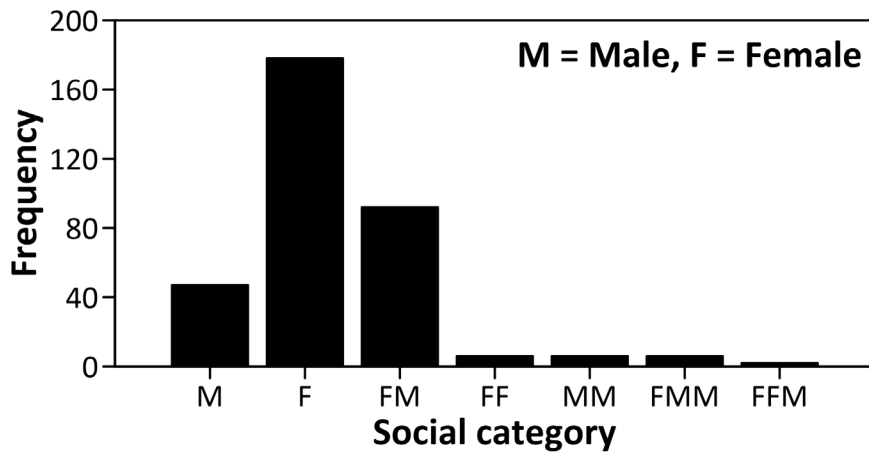


Fig. 4. Frequency and social organization of the pea crab *Mesotheres unguifalcula*, symbiotic with *Leucozonia cerata* at La Angosta and Caleta beaches, Acapulco, Mexico.

As noted above, 432 specimens of *L. cerata* were collected. However, because the prospective sample of January 2020 was thoroughly dissected and discarded, only 374 were sexed, 186 males and 188 females (sex ratio = 0.497, Binomial test = 0.96), and the sex ratio was close to 1:1. The abundance of the different male and female associations of *M. unguifalcula* was composed as follows (Fig. 4): 222 snails harbored solitary crabs, 47 males, and 178 females; 104 hosted pairs, 92 heterosexuals, and 12 homosexuals, six were male-male, and six female-female. The remainder were triads, heterosexual couples plus one male (6) and homosexual females plus one male (2). The frequency of pooled solitary male and female crabs was higher than expected at random, contrarily to heterosexual pair that was lower than expected ($X^2 = 94.3$, $p < 0.00001$, sequential Bonferroni $\alpha = 0.003$; Fig. 5). The same occurred with triads, which observed frequencies were less than that expected ($X^2 = 113.5$, $p < 0.00001$, sequential Bonferroni $\alpha = 0.005$; Fig. 5). A specific analysis on the sexual couples indicates that the frequency of heterosexual pairs was higher than expected at random, contrarily to homosexual couples ($X^2 = 99.9$, $p < 0.000001$, sequential Bonferroni $\alpha = 0.0033$, Fig. 6). The population sex ratio after pooling the monthly collected specimens, differs significantly from a 1:1 ratio (sex ratio = 0.37, males = 165, females = 286, Binomial test, $p < 0.000001$), and categorically was positively skewed towards females. Further, solitary ovigerous females (N = 148, = 71%) were more frequent than those inhabiting with males (N = 61, = 29%) (Chi-square test of independence, $X^2 = 6.9$, $d.f. = 1$, $p < 0.01$). In contrast, the frequency of solitary non-ovigerous females (N = 31, 52%) was slightly higher than those inhabiting in pairs (N = 28, 48%).

We found a significant difference between the carapace width of solitary females (6.9 +/- 1.49), most of them ovigerous (N = 148 from 209, 7.09 +/- 1.12) and females inhabiting with a male (7.39 +/- 1.33)) (*t*-test, *t* = 2.6684, *d.f.* = 253, *p* < 0.01, Bayes factor = 4.046). Contrarily, no significant differences were detected between the carapace width of solitary males and males paired with females (*t*-test, *t* = 0.675, *d.f.* = 130, *p* > 0.05, Bayes factor = 0.24). Heterosexual couples showed a low correlation (*r* = 0.44, *p* < 0.01).

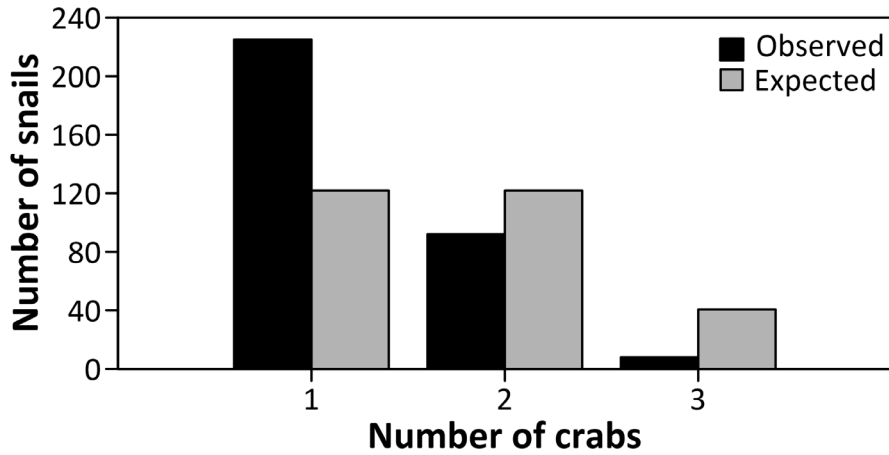


Fig. 5. Population distribution of the pea crab *Mesotheres unguifalcula*, symbiotic with *Leucozonia cerata* at La Angosta and Caleta beaches, Acapulco, Mexico. The observed frequencies of crabs (N = 325) found

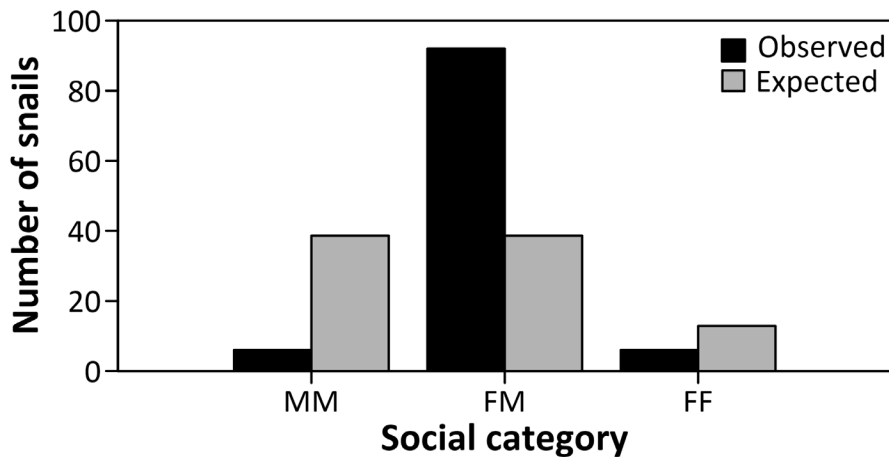


Fig. 6. Population distribution of the pea crab *Mesotheres unguifalcula*, symbiotic with *Leucozonia cerata* at La Angosta and Caleta beaches, Acapulco, Mexico. The observed frequencies of crab pairs (N = 104) found on *L. cerata* differ from the expected binomial frequencies; additional explanation in the text.

To test if crabs choose a particular sex of snail with a sex ratio of 1:1, the number of crabs of each sex was counted. The frequency of crabs inhabiting male or female snails was almost identical (145 and 142, respectively), and non-indication of preference by any sex was found (Binomial test, $p > 0.90$). Lastly, we analyzed the presence/absence of crabs in three different size groups of snails classified using the k-medoids algorithm (small 12.1–27.4 mm, medium, 27.5–33 mm, and large 33.1–51.9 mm). The selection of different sizes of snails by crabs seems to be not an independent event (Chi-square test of independence, $X^2 = 45.6$, $d.f. = 2$, $p < 0.000001$). Although crabs infested all sizes of snails, those of medium and large size were relatively more infested than small ones; the infestation rate between medium and large sizes ($n = 182$, 83% and 115, 91.3%, respectively) was not different (Chi-square test of independence, $X^2 = 4.1$, $d.f. = 1$, $p > 0.01$, sequential Bonferroni $\alpha = 0.05$, Fig. 7); however, the infestation in medium and large sizes markedly exceeds that of small ones ($n = 132$, 57.6%), (Chi-square test of independence: small-medium, $X^2 = 24.6$, $d.f. = 1$, $p < 0.000001$, sequential Bonferroni $\alpha = 0.003$; small-large, $X^2 = 35.7$, $d.f. = 1$, $p < 0.000001$, sequential Bonferroni $\alpha = 0.005$, Fig. 7).

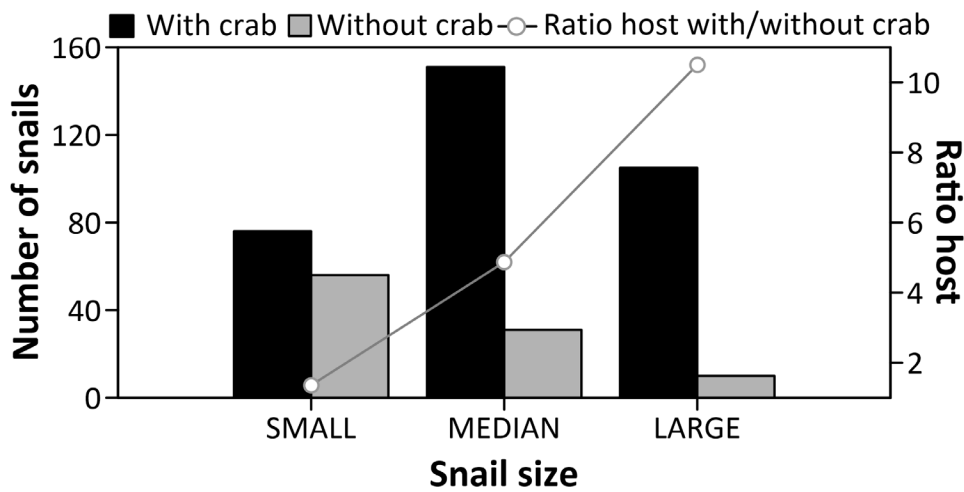


Fig. 7. Population distribution of the pea crab *Mesotheres unguifalcula*, symbiotic with *Leucozonia cerata* at La Angosta and Caleta beaches, Acapulco, Mexico, sorted into three groups by k-medoids algorithm. Bars indicate the number of hosts with and without crabs. The line shows the ratio of hosts with/without crabs. The selection of different sizes of snails by crabs seems to be not an independent event (Chi-square test of independence, $X^2 = 45.6$, $d.f. = 2$, $p < 0.000001$).

DISCUSSION

Currently, two genera of pinnotherid crabs from the Mexican Pacific are known as obligate symbionts of gastropod mollusks: *Calyptraeotheres* Campos, 1990, with five species all symbionts of limpets of the family Calyptraeidae (Campos, 1990, 1996, 2018) and *Mesotheres*, with four species symbiont of marine snails of the families Fasciolaridae, Strombidae, and Tegulidae (Schmitt et al. 1973; Ng et al. 2019). A third genus, *Opisthopus* Rathbun, 1894, appears to be a generalist symbiont that sometimes inhabits this group of mollusks (Campos 2016). The only known species of *Mesotheres* for the Mexican Pacific is *M. unguifalcula*, which has been recorded for two distant localities, its type locality, Puerto Peñasco, Sonora, in the upper Gulf of California, and more than 2000 km south in Acapulco, Guerrero, without any record of its host (Ng et al. 2019). The first and new host record for this crab is *Leucozonia cerata*, the second species of the family Fasciolariidae hosting a species of *Mesotheres*, previously *Triplofusus giganteus* (Kiener, 1840) was recorded as a host of the Atlantic species *M. strombi* (Ng et al. 2019).

Host use pattern of *Mesotheres unguifalcula* in *Leucozonia cerata*.

The number of *M. unguifalcula* specimens per host ranged from 0 to 3; solitary females and males were dominant (51%), followed by heterosexual couples (24%) and other combinations that included homosexual couples and triads, which barely represented 2%. At first, 24% of heterosexual couples suggested a monogamous social system; however, a higher number of solitary males and females and a lower number of heterosexual couples, compared to those statistically expected, appear to rule out monogamy for these crabs. Pinnotherid species with a solitary lifestyle include *Arcotheres sinensis* (Shen, 1932), *Calyptraeotheres garthi* (Fenucci, 1975), *Pinnotheres pisum* (Linnaeus, 1767), *Tumidotheres maculatus* (Say, 1818), and *Zaops ostreum* (Say, 1817), (Christensen and McDermott 1958; Tablado and López Gappa 1995; Pearce 1964; Seed 1969; Asama and Yamaoka 2002; Ocampo et al. 2012). Monogamy has also been recorded for *Pinnixa (Tubicolixa) chaetoptera* Stimpson, 1860 and *Pinnixa transversalis* (H. Milne Edwards and Lucas, 1842), both living permanently in tubes of Chaetopteridae worms (Grove and Woodin 1996; Baeza 1999) and *Holotheres halingi* (Hamel, Ng and Mercier, 1999) and *H. semperi* (Burger, 1895) symbionts in the right respiratory tree of *Holothuria (Metriatyla) scabra* Jaeger, 1833 (Holothuriidea), (Hamel et al. 1999, 2019). The striking morphological difference and host between *Pinnixa* and *Holotheres* species support the hypothesis that both genera evolved independently and that monogamy was a convergent event. This could also be the

case for other species of symbiotic crabs of holothurians from the Indo-West Pacific, collected frequently in heterosexual couples from their host (see Ng and Manning 2003).

The prevalence and host's preference of *M unguifalcula* markedly increased with the host size; those snails smaller than 30 mm averaged 53% infestation. In comparison, those from 30 mm to 52 mm represented 82% to 100% infestation (mean = 93%). Seed (1969) recorded something similar for *P. pisum*, who presented a direct relationship between its prevalence and the size of *Mytilus edulis* in the southwest of England. Still, it differed from what was recorded for *Austinotheres angelicus* (Lockington, 1877) inhabiting *Saccostrea palmula* (P. P. Carpenter, 1857) in Costa Rica (Mena et al. 2014). In our case, we agree with Seed (1969) that the time the host has been exposed to infestation by crabs could explain the increase in prevalence in larger sizes. But also, the greater abundance of medium and large snail size groups is directly related to the prevalence. This suggests that more than one factor could be involved in controlling the spatio-temporal variations of the prevalence of *M. unguifalcula* and probably in another species of pinnotherids. The spatio-temporal changes have also been observed for *Zoaps ostreum*, *Austinotheres angelicus*, *Afropinnotheres monodi* Manning, 1993 and *Arcotheres placunicola* Ng, 2018 (see Byers et al. 2014; Mena et al. 2014; Drake et al. 2014 and Ng and Ahyong 2022 respectively), and the mechanisms that control prevalence in this group of crabs continue to be a challenge to investigate.

The monthly infestation of *Mesotheres unguifalcula* on *L. cerata* during the year in Acapulco, Guerrero, Mexico, varied from 54% to 90%. This level of infestation is much higher than that recorded for its Atlantic congener *M. strombi* hosted in *Strombus pugilis* Linnaeus 1758, off the coast of La Parguera, Puerto Rico, with a prevalence of 7.2% or less, which agrees with the observations of Hernandez et al. (2017) in Venezuela, who recorded a prevalence around 1% in the same host. Some authors have documented changes in prevalence when comparing different areas, tidal levels, cultivated and wild hosts, or by host preference (Houghton 1963; Seed, 1969; Kruczyzinski 1974; Pregonzer 1978; Tablado and López Gappa 1995; O'Beirn and Walker 1999; Sun et al. 2006; Asama and Yamaoka 2009; Saeedi and Aradalan 2010; Ocampo et al. 2012, 2014; Drake et al. 2014, Perez Madrigal et al. 2018; Cuesta et al. 2020). In our case, gravid females recorded throughout the year support a continuous reproduction and infestation, like other marine tropical crustaceans, including the pinnotherid *Holotheres halingi* (see Sastry 1983; Bauer 1989; Hamel et al. 1999). This would explain a consistently high monthly prevalence and a relatively stable average monthly size in both sexes.

Seed (1969) found that *Pinnotheres pisum* larger than 5.5 mm of carapace width did not inhabit small sizes of the mussel *Mytilus edulis* Linnaeus, 1758. On the contrary, small-sized male and female crabs of *M. unguifalcula* can inhabit small (15 mm) to large (52 mm) snails without any preference by

male or female. Additionally, combining all sizes, the carapace width of males and females correlated moderately well with host size. However, males and combined male and female crabs less than 4 mm did not correlate, contrary to the combined non-gravid and gravid females greater than 4 mm, which showed the best, although moderate, correlation with their host. We consider the low correlation between solitary males and their host size because they select a wider range of host sizes at the invasive phase. In addition, the high frequency of solitary ovigerous females, the low size correlation between male-female pairs, and the female-biased sexual relationship suggest that a male can move from one host to another during mating without respect to the female size. The stimulus to leave their solitary life could involve the detection of sedentary females receptive to copulation during the mating period. The low correlation between male-female pairs suggests that after copulation, the male abandons the host and its temporary heterosexual relationship to continue searching for another receptive female or uninfested host. In contrast, ovigerous females are not receptive to copulation, which may explain why they are frequently solitary, although 30% (N = 209) of the ovigerous females were paired with a male. This contradicts the male behavior described above and is not easy to explain. Experiments under controlled conditions should be designed to study which stimulus or stimuli would regulate the mating system and the time and purpose that males guard females after copulation (Alves et al. 2017). Even so, the cost to the male in going in and out of one host to another would be that some of them must die, but some will probably remain alive outside the reservoir waiting for a new infestation. That would explain the low number in their hosts compared to sedentary females (Haines et al. 1994; Sun et al. 2006; Baeza and Thiel 2007).

Additionally, sedentary females remain in their respective host after infestation, and their growth rate would be restricted to the space available within the snail's mantle cavity. This would explain the positive and significant, although moderate, correlation between adult females and their host, similar to that recorded for other pinnotherids (Seed 1969; Haines et al. 1994; Tablado and López Gappa 1995; Cruz-Kaled 2006; Miller et al. 2008; Saeedi et al. 2010; Ocampo et al. 2012). Despite observations of heterosexual couples, the available evidence about the life history of *M. unguifalcula* and other studied species of the subfamily Pinnotherinae sensu stricto (see Baeza and Thiel 2007; Campos 2009; Palacios Thiel 2016, Fig 1, clade 1) suggests a pure-search polygynandry mating system model characterized by solitary and sedentary females and smaller males who, in reproductive season, are roaming from one host to another in search of females receptive to copulation, only high-quality males would be chosen to mate with (Baeza and Thiel, 2007).

CONCLUSIONS

This study rediscovers the sexually dimorphic symbiotic pinnotherid *Mesotheres unguifalcula* infesting the spindle sea snail *Leucozonia cerata* in Acapulco, Guerrero, México. The average monthly prevalence of 79% is one of the highest recorded for an American pinnotherid crab, with a trend of a regular distribution in its host. The crab did not show a preference for any sex of the host, with a major prevalence and preference by medium and large host sizes (20 and 40 mm). The presence of gravid females throughout the year supports the hypothesis that there is continuous reproduction for this species. Despite the finding of heterosexual couples in the same host, the dominance of solitary males and females of *M. unguifalcula* in *L. cerata* allowed us to rule out monogamy as a mating strategy. The evidence available, including a low correlation between the male size and its host and between heterosexual pairs, the high frequency of solitary ovigerous females, and the female-biased ratio, suggests a pure-search polygynandry of sedentary females as its mating system (see Baeza and Thiel 2007).

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in *L. cerata* differ from the expected binomial frequencies; additional explanation in the text.