Monogamy does not last long in *Pontonia mexicana*, a symbiotic shrimp of the amber pen-shell *Pinna carnea* from the southeastern Caribbean Sea

J. Antonio Baeza a,b,c,*, Juan A. Bolaños d, Jesús E. Hernandez d, Carlos Lira d, Régulo López d

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1. **Introduction**

The adoption of a symbiotic lifestyle (symbiosis here defined sensu de Bary [1865] quoted by Vermeij (1983) as dissimilar organisms living together) is one of the most important adaptations among vertebrate and invertebrate organisms from terrestrial and marine environments (Currie et al., 2003; Margulis and Fester, 1991; Ross, 1983). Some degree of dependence between pairs (the spider crab *Inachus phalangium* and the snakelock anemone *Anemonia sulcata–Diesel*, 1986) or among assemblages of species (e.g., fungus growing ants – fungal cultivars – *Escovopsis* microbial pathogens – Currie et al., 2003) has evolved multiple times independently. Most commonly, symbiotic associations comprise small organisms (hereafter symbionts) and large partners that serve as hosts. Symbiotic relationships can be characterized in terms of the costs and benefits experienced by partners (i.e., parasitism, commensalism, mutualism), the degree of interdependency between associates (i.e., facultative versus obligate symbiosis), and the number of species used by one or both entities involved in the relationship (i.e., generalists versus specialists). Usually, hosts vary considerably in their biology and ecology (body plan, abundance, distribution and habitat) and a wide diversity of host-use patterns has been described for symbionts (Baeza and Thiel, 2007; Margulis and Fester, 1991; Ross, 1983). This diversity offers a unique opportunity to understand the conditions driving the diversity of anatomical, physiological and behavioral traits of resource-specialist (e.g. symbiotic) species.

As in many other groups of marine invertebrates, symbiosis has independently evolved several times among crustaceans from tropical and temperate habitats. Shrimp, crabs, lobsters, amphipods and isopods from distant monophyletic clades use other macro-invertebrates, including sponges, corals, sea anemones, oysters, sea urchins, and ascidians (among others), as refuge, direct or indirect food source, and mating arenas (Ross, 1983; Thiel and Baeza, 2001). The diversity of host use patterns of symbiotic crustaceans is remarkable. Some species dwell on their hosts as solitary individuals (*Allopetrolisthes spinifrons* dwelling on the sea anemone *Phymactis papillosa* — Baeza et al., 2001). Other
species are found as heterosexual pairs (Pinixa transversalis—Baeza, 1999; Alpheus armatus—Knowlton, 1980; Pontonia marginata—Baeza, 2008). Even other species form large unstructured aggregations (the sea urchin dwelling crab Liopeolitrois mira—Baeza and Thiel, 2000; the clown shrimp Thor amoebinoïdes—Baeza and Piantoni, 2010) and a few establish small structured groups within their hosts (the eurous shrimp Synalpheus regalis—Duffy, 1996; the polygamous isopod Paracerceis sculpa—Shuster and Wade, 1991). During the last decade, a few formal ideas have been proposed to explain the variety of refuge use patterns and mating systems of organisms adapted to live in discrete and discontinuous habitats such as symbiotic crustaceans (Baeza, 2008; Baeza and Piantoni, 2010; Baeza and Thiel, 2003, 2007; Thiel and Baeza, 2001). Theory suggests that host characteristics, including abundance, distribution, body size (relative to symbiotic dwellers) and morphology (structural complexity) together with predation risk off refuges (hosts) are important in determining the host-use pattern and reproductive strategies of symbiotic crustaceans (Baeza, 2008; Baeza and Thiel, 2003, 2007; Thiel et al., 2003).

Symbiotic crustaceans are expected to live as heterosexual pairs in/on hosts and exhibit monogamy (monogamy here defined sensu Wickler and Seibt 1983) as pairs of conspecifics spending extensive periods of time together when their hosts are large enough to support two (e.g., two) but not more conspecifics, when hosts are relatively rare, and when predation risk away from hosts is high (Baeza, 2008; Baeza and Thiel, 2007). Under these circumstances, movements among hosts are constrained and host monopolization is favored in male and female symbionts due to host scarcity and its value in offering protection against predators (Baeza and Thiel, 2007). Because spatial constraints allow only a few adult symbiotic individuals to cohabit in/on the same host, both adult males and females maximize their reproductive success by sharing “their” dwelling with a member of the opposite sex (Baeza, 2008). These monogamous species should display low sexual dimorphism in body size and weaponry (e.g., chelipeds used for intra-sexual aggression). The low intensity of sexual selection characteristic of monogamous regimes is expected to relax selection for large body size and weapons in males (Baeza, 2008; Baeza and Thiel, 2007; Shuster and Wade, 2003).

A powerful approach to test the importance of host traits in driving the evolution of monogamy in symbiotic crustaceans is to tag and maximize their reproductive success by sharing a monogamous mating system (Baeza, 2008, 2010; Baeza and Thiel, 2003, 2007; Knowlton, 2010). A monogamous mate is often the first mate of a female, and the number of shrimps per host was recorded. The carapace length (CL) and the length of the largest (major) of the second pair of chelipeds of all shrimps from each host were measured under the stereomicroscope to the nearest 0.1 mm. Next, the number of shrimps per host was recorded. The carapace length (CL, mm) and the length of the largest (major) of the second pair of chelipeds of all shrimps from each host were measured under the stereomicroscope to the nearest 0.168 mm. Also, the sex of each shrimp was determined based on external characters; in males a gonopore (located on the coxae of the fifth pair of walking legs) and appendices masculinae on the base of the endopod of the second pleopods. Each female shrimp was identified by the presence or absence of brooded embryos (ovigerous or non-ovigerous). The embryo mass was inspected under a stereomicroscope and the embryos were classified based on the following characters: stage I: embryo with uniformly distributed yolk and no eyes; stage II, embryo with yolk clustered and visible but not reported living in male–female pairs, in relatively small and scarce hosts from tropical environments (Baeza and Thiel, 2007; Thiel and Baeza, 2001). In contrast, various other symbiotic species inhabiting relatively large, structurally complex, and abundant hosts are not monogamous (Baeza and Piantoni, 2010).

The aim of this study is testing the hypothesis that symbiotic crustaceans inhabiting relatively small, structurally simple, and rare hosts in environments with high predation pressure (i.e. tropical shallow subtidal) should be monogamous. We used as a model the Caribbean shrimp Pontonia mexicana (Palaeonidae, Pontoniinae) which dwells in the mantle cavity of the amber pen-shell Pinna carnea (cf. Fransen, 2002). The pen-shells used as host by this shrimp represent small and discrete refuges that should be relatively easy to protect and defend against intruders (Baeza, 2008; Fransen, 2002). Also, it is highly probable that movement among pen-shells in the subtidal is costly for both male and female shrimps because of the risk of predation by the omnivorous fishes and crabs common in these tropical environments (Randall, 1967). Environmental constraints such as these that limit the ability of shrimps to switch among the relatively small and scarce pen shells in search of sexual partners should favor monogamy and no or reduced sexual dimorphism in P. mexicana (cf. Baeza, 2008; Baeza and Thiel, 2007).

2. Materials and methods

2.1. Study site

The association between the shrimp P. mexicana and the amber pen-shell P. carnea was analyzed in the shallow subtidal of Las Cabeceras, Isla Cubagua (N 10° 49’ W 64° 12’), Venezuela. The study site is dominated by the seagrass Thalassia testudinum. Pen-shells are found either solitary or in pairs half-buried in the sand among sea grass blades between 4 and 10 m depth (Fig. 1). Occasionally, fire corals, large brain coral heads of Diploria labyrinthiformis and sponges from various unidentified species (e.g., Xestospongia spp., Clathria spp., and Aplysina spp.) are found interspersed at the seagrass bed. During sampling, species of omnivorous/predatory fish (known to prey on crustaceans—Randall, 1967) observed at the locality included various species of search-and-catch (e.g., wrasses Halichromes spp.) and sit-and-wait predators (the toad fishes Amphilichthys spp., the scorpionfish Scorpaena plumieri).

2.2. Collection of hosts and shrimps

Individuals of the pen-shell P. carnea were collected with SCUBA between June and September, 2008. Each encountered pen-shell was collected (regardless of their size), immediately placed in a plastic bag, and transported to the laboratory. In the laboratory, pen-shells were gently cracked open with a hammer, their valves were stored, and all shrimps found within the host individuals were frozen or fixed for further examination. The shell length (SL, the longest point along a line parallel to the umbo) of the left or right valve of each P. carnea individual (depending on which valve remained intact after cracking it open) was measured with a manual caliper to the nearest 0.1 mm. Next, the number of shrimps per host was recorded. The carapace length (CL, mm) and the length of the largest (major) of the second pair of chelipeds of all shrimps from each host were measured under the stereomicroscope to the nearest 0.168 mm. Also, the sex of each shrimp was determined based on external characters; in males a gonopore (located on the coxae of the fifth pair of walking legs) and appendices masculinae on the base of the endopod of the second pleopods. Each female shrimp was identified by the presence or absence of brooded embryos (ovigerous or non-ovigerous). The embryo mass was inspected under a stereomicroscope and the embryos were classified based on the following characters: stage I: embryo with uniformly distributed yolk and no eyes; stage II, embryo with yolk clustered and visible but not
well-developed eyes; stage III, embryo with well-developed eyes, free abdomen, and thoracic appendages.

Lastly, we measured host abundance. For this purpose, four different transects (4×22 m) were randomly placed at the study site and a single SCUBA diver counted all host individuals found within each transect.

2.3. Host use pattern of P. mexicana in pen-shells P. carnea

We examined the host use pattern of P. mexicana that included the description of its population distribution, male–female association pattern, and host–shrimp body size relationships. First, we tested whether or not the distribution of P. mexicana in its host differed significantly from a random distribution by comparing the observed distribution (number of individuals per host) with the Poisson distribution (Elliot, 1983). Significant differences between the distributions were examined using a Chi-square test of goodness of fit (Sokal and Rohlf, 1995). In the case where 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 for false discovery rate (Rice, 1989). If shrimps were found as pairs in the same host, then we determined whether the sexes were randomly distributed when comparing the observed distribution with the binomial distribution. A Chi-square test of goodness of fit was used to inspect for significant differences between these distributions (Sokal and Rohlf, 1995). Lastly, we examined whether the presence of eggs and the developmental stage of the embryos brooded by females affected male presence/absence. A Chi-square test of independence was used to detect significant differences between the frequencies of occurrence of males with females carrying embryos in different stages (Sokal and Rohlf, 1995).

2.4. Sexual dimorphism in P. mexicana

We described the extent of sexual dimorphism with respect to body and major cheliped size in P. mexicana. In caridean shrimps from the genus Pontonia, the fifth pair of thoracic appendages bears the largest of the two pair of chelipeds (Fig. 1c). In crustaceans, these structures serve as weapons during intra-sexual interactions (Hartnoll, 1978, 1982). We examined whether the size of this largest cheliped in the second pair of pereiopods increased linearly with body size in males and females of P. mexicana. The relationship between the length of the propodus of the largest second cheliped and body size of shrimps (CL, mm) was examined using the allometric model $y = ax^b$ (Hartnoll, 1978, 1982). The slope $b$ of the log-log least-squares linear regression represents the rate of exponential increase ($b > 1$) or decrease ($b < 1$) of the cheliped with a unit increase in body size of shrimp. To determine if the relationship deviated from linearity, a t-test was used to test if the estimated slope $b$ deviated from the expected slope of unity (Sokal and Rohlf, 1995). If the cheliped grows more or less than proportionally with a unit increase in body size of shrimps, then the slope should be greater or less than unity, respectively (Hartnoll, 1978).

3. Results

3.1. Host use pattern of P. mexicana in pen-shells P. carnea

A total of 120 pen-shells P. carnea were collected from Isla Cubagua, Venezuela. The SL of the pen-shells varied between 130 and 390 mm with a mean (± SD) of 284.5 (± 45.1) (Fig. 1, 2). The average density of the pen-shells was 0.059 (± 0.027) individuals m$^{-2}$ (range: 0.023–0.083). Pen-shells were most commonly found either solitarily or in pairs during our collections in the natural environment. We never observed pen-shells in aggregations of three or more individuals at the seagrass bed.

P. mexicana was found in 93.3% (112 out of 120) of the pen-shells collected at Isla Cubagua. Most pen-shells without shrimps were small (< 20 cm SL) but some medium sized pen-shells also lacked shrimp (Fig. 2). The smallest pen-shells with shrimp had an SL of 13 cm.

The number of shrimp P. mexicana per host varied between 0 and 2 with a mean of 1.62 ± 0.61. The population distribution of P. mexicana on pen-shells did not display a random pattern (observed versus expected Poisson distribution, Chi-square test of goodness of fit,
\( \chi^2 = 23.71, \text{df} = 2, P < 0.0001 \). More pen-shells harbored two shrimps compared to the number expected by chance alone and fewer pen-shells with zero or one shrimp were observed compared to the number expected by chance alone (decomposition of the Chi-square test of goodness of fit: \( \chi^2 = 110.92, \text{df} = 1, P < 0.0001 \), sequential Bonferroni \( \alpha = 0.025 \)). Invariably, all shrimps inhabiting hosts as pairs were heterosexual couples (Fig. 3). Taking into consideration the binomial distribution and the total number of males and females in the population, the number of hosts harboring heterosexual pairs expected by chance alone would have been 41. Therefore, shrimps were found as heterosexual pairs more frequently than expected by chance alone (Fig. 3).

There was a weak but positive correlation between the size of males and females in a pair (t-test: \( t = 3.45, \text{df} = 1.80, P < 0.0009 \) (Fig. 3). In 90% of these heterosexual pairs (74 out of 82 pairs), the male was smaller than the female. On average, females were 1.27 mm (±1.03) larger than their male companions. Of the females found with a male in the same host, 75 out of 82 (91.5%) were brooding embryos. Six out of the seven non-brooding females seemed to be close to spawning as their ovaries were full of vitellogenic oocytes visible through the carapace. The proportion of paired brooding and paired non-brooding females differed significantly from a 1:1 ratio (\( \chi^2 = 54.74, \text{df} = 1, P < 0.0001 \)). Males were paired with a brooding female more frequently than expected by chance alone. Of the brooding females cohabiting with males, 18, 20, and 37 carried embryos in stage I, II, and III, respectively. The proportion of females with embryos at different developmental stages differed significantly from each other (\( \chi^2 = 8.72, \text{df} = 2, P < 0.0128 \)). Males cohabited with females carrying late stage embryos more frequently than with females carrying early or intermediate embryos.

Of the 30 shrimps inhabiting the pen-shells solitarily, 19 were males and 11 were non-ovigerous females. Among these solitary shrimps, sex ratio did not differ significantly from an expected 1:1 ratio (\( \chi^2 = 1.64, \text{df} = 1, P = 0.2003 \)). However, the power of this latter test was low (1 - \( \beta = 0.2491 \)). Solitary and paired males and females did not differ significantly in body size (paired versus solitary males, 9.68 ± 1.9 and 9.98 ± 0.93 mm CL, respectively, Mann–Whitney test [variances were heterogeneous], M-W = 786, N = 19 and 82, respectively, \( P = 0.9549 \); solitary versus paired females, 11.29 ± 0.84 and 11.29 ± 0.93 mm CL, respectively, t-test [variances were homogeneous], \( t = 0.0005, N = 11 \) and 82, respectively, \( P = 0.9996 \)).

A weak but positive, statistically significant correlation between host size and shrimp size was recorded for both males and females (\( r^2 = 0.2813, t \)-test; \( t = 6.194, \text{df} = 1.99, P < 0.0001 \), and \( r^2 = 0.176, t = 4.41, \text{df} = 1.91, P < 0.0001 \), for males and females, respectively) (Fig. 4).

3.2. Sexual dimorphism in P. mexicana

The carapace length of male and female shrimps varied between 3.25 and 12.0 mm (mean ± SD: 9.94 ± 1.17) and between 9.1 and 13.0 mm (11.29 ± 0.8), respectively. Significant differences in CL between the sexes were detected (males–females: t-test; \( t = 9.3, P < 0.0001 \), indicating sexual dimorphism with respect to body size (Fig. 5)).

The major cheliped differed with respect to the status and degree of allometry depending on sex. In males and females, the slope of the relationship between shrimp body size and major cheliped size was significantly <1, i.e., negatively allometric (Table 1; Fig. 5). Nevertheless, claw relative growth was greater in males than in females (general linear model, intercept: \( F = 923.98, \text{df} = 1.3, P < 0.001 \)).

4. Discussion

The symbiotic shrimp P. mexicana is “socially” monogamous; shrimps inhabited host individuals as heterosexual pairs more frequently than expected by chance alone. Nonetheless, P. mexicana does not appear to feature long-term (e.g., maybe lifetime) monogamy, as was expected, considering our theoretical considerations and as suggested for other crustaceans that most commonly inhabit their hosts as heterosexual pairs (P. domestica— Courtney and Couch, 1981;
First, males paired most frequently with brooding females carrying late stage embryos, and thus, these females were close to molt and become sexually receptive. In monogamous species in which pairing appears to be long-term, males occur with females in the same host, independent of the reproductive condition of the female (Pontonia transversalis—Baeza, 1999; Pontonia margarita—Baeza, 2008; Pontonia sp.—Aucoin and Himmelman, 2010; hermaphrodite–hermaphrodite pairs of Lysmata pedersenii—Baeza, 2010). In promiscuous or polygamous species in which pairing is only temporal and males abandon females soon after insemination, males most commonly associate with females close to molting and spawning a new batch of unfertilized eggs (Bauer and Abdalla, 2001; Diesel, 1986, 1988; van der Meeren, 1994). This last pattern agrees with that observed in P. mexicana and disagrees with what is expected for a long-term monogamous species.

A second indication of short-term pairing rather than long-term monogamy in P. mexicana is the weak relationship between host body size and shrimp body size. If males and females of P. mexicana were staying within host individuals for long periods of time, a tight correlation between host and shrimp size would have been found (as reported in various other monogamous symbiotic crustaceans—Adams et al., 1985; Baeza, 1999, 2008). In contrast, a loose relationship between host and symbiont size (as that found in P. mexicana) is usually reported for species in which males and/or females shift among hosts rather frequently (e.g., the sea urchin dwelling crab Liopetrolisthes mitra—Baeza and Thiel, 2000; Thiel et al., 2003).

A third indication of short-term pairing in P. mexicana is the poor correlation between the body size of males and females found as pairs within pen shells. Size-assortative pairing has been reported before for various other long-term monogamous free-living and symbiotic crustaceans (Adams et al., 1985; Baeza, 1999, 2008; Mathews, 2002). In the symbiotic and monogamous Pontonia margarita and Pinnixa transversalis, the size of the male explains 63.8% and 77.6% of variation in female size, respectively (Baeza, 1999, 2008). In contrast, only 13% of male body size explains variation in female body size in P. mexicana. The loose correlation between the size of males and females forming pairs and between host size and shrimp size suggest that males and/or females of P. mexicana have a short-term association with their individual hosts, and consequently, with the other shrimp inhabiting the same host.

A fourth line of reasoning suggesting that heterosexual pairing in P. mexicana does not last too long is the observed pattern of sexual dimorphism. On the one hand, in agreement to that reported for other socially monogamous shrimp species (e.g., Pontonia margarita—Baeza, 2008; Pontonia sp.—Aucoin and Himmelman, 2010), males of P. mexicana were, on average, smaller than females and the major cheliped did not exhibit positive allometry. Small size in males of monogamous species is expected due to the low intensity of male–male competition in this mating system (Baeza and Thiel, 2007; Shuster and Wade, 2003). On the other hand, although the major cheliped did not exhibit positive allometry, males of P. mexicana had a major cheliped larger than that of females at any given body size. Such sex-specific difference in resource allocation to major cheliped disagrees with our prediction of low sexual dimorphism in terms of weaponry in this species. Large claws in males are uncommon in monogamous crustaceans but

**Table 1**

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Fig. 4. Relationship between valve length of the pen shell Pinnia cerasus and carapace length of males (above) and females (below) of the symbiotic shrimp Pontonia mexicana (see Results for further details).

Fig. 5. Size frequency distribution of body size (above) and relative growth of major cheliped length as a function of carapace length (below) in males and females of Pontonia mexicana. Measurements are in mm. Linear regression equation obtained from previous log–log transformation of the data is shown for each sex in Table 1.
common in non-monomymous shrimps where males compete for females through agonistic interactions (Baeza and Thiel, 2007; Bauer, 2004; Correa and Thiel, 2003). The larger chelips in males of *P. mexicana* (compared to females) suggest that at least some males might be switching among hosts in search of receptive females (see below) and might indeed be competing for receptive females via overt aggression. If some males do switch among hosts (see below), when resident and intruder males meet, cheliped size most probably determines the winner of the agonistic interaction and access to receptive females (Rahman et al., 2002, 2003).

An additional or alternative explanation for the larger major cheliped in males than in females of *P. mexicana* is division of labor between the sexes with respect to refuge defense if pairs of shrimps do defend hosts individuals against natural enemies (e.g., predators, competitors). Host defense has been documented before in other symbiotic crustaceans, including socially monomymous shrimps (e.g., *Alpheus armatus* defend its anemone host *Bartholomea annulata* from intrusion by the predatory polychaete *Hermodice carunculata*—Smith, 1977). However, division of labor between sexual partners has not yet been explored in symbiotic monomymous shrimps, but it occurs in symbiotic eusocial shrimps (Duffy et al., 2002). The possibility of division of labor driving sexual dimorphism in weaponry remains to be addressed in *P. mexicana* and other marine invertebrates.

Overall, *P. mexicana* is indeed a “socially” monomymous species; as expected, shrimp are found in their hosts as heterosexual pairs more frequently than expected by chance. However, our data also suggests that this heterosexual pairing does not last long. Indeed, our observations fit with the notion that males in this species might be switching among hosts and roaming in search of receptive females. Such a male mating strategy might explain why males cohabited with females carrying late stage embryos (i.e., soon to molt and become receptive) more frequently than with females carrying early or intermediate embryos and the loose correlation between the size of receptive females (Rahman et al., 2002, 2003). The larger chelipeds in males of *P. mexicana* (compared to females) suggest that at least some males share their hosts with individuals of the opposite sex with more frequency than expected by chance alone. Our study partially supports the notion that dissimilar host use patterns in closely related symbiotic species are explained by differences in abundance, relative size and habitat of their respective refuge (e.g., hosts) (Baeza, 2008, 2010; Baeza and Piantoni, 2010; Baeza and Thiel, 2003). On the other hand, the discrepancies between theoretical expectation and our empirical results (mainly with respect to shrimp and host body size, male–female association pattern, and sexual dimorphism) argue in favor of new more complex models capable of predicting more accurately the mating system of symbiotic species. Indeed, other conditions that might favor short- or long-term monomony (i.e., “territorial cooperation” hypothesis — Wickler and Selbst, 1981; “mate-guarding” hypothesis — Grafen and Ridley, 1982) remain to be addressed in *P. mexicana*. Other shrimps of the subfamily Pontoniinae, including species from the genera *Pontonia, Ascidonia*, *Dactylyona* and *Brueon*, inhabit hosts with differing biology and ecology (e.g., various bivalves, gastropods, tunicates — Courtney and Couch, 1981; Fransen, 2002; Baeza, 2008; Aucoin and Himmelman, 2010). Because of the differing ecology of the host species, shrimps in this subfamily are expected to display dissimilar host use patterns, mating systems and social behaviors. Therefore, shrimp from the subfamily Pontoniinae might be used as model systems to study the importance of environmental conditions in shaping the mating system and social behavior of marine invertebrates inhabiting discrete refuges.

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