Revista Mexicana de Biodiversidad

Revista Mexicana de Biodiversidad 97 (2026): e975872

Ecology

Reproduction and prevalence of *Probopyrus pandalicola* (Isopoda, Bopyridae) in Yucatán, southeastern Mexico

Reproducción y prevalencia de Probopyrus pandalicola *(Isopoda, Bopyridae) en Yucatán, sureste de México*

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Received: 27 February 2026; accepted: 28 July 2026

Abstract

This study provides data on size at sexual maturity, fecundity, embryo size, brood loss, and prevalence of the isopod *Probopyrus pandalicola,* parasite of *Palaemon mundusnovus,* at Sisal, Yucatán, Mexico. A total of 3,549 specimens of *P. mundusnovus* were captured, of which 214 were found to be infested by *P. pandalicola*. The prevalence of the parasite was 6.03% and the sex ratio of infested hosts was skewed to females (χ^2 = 57.57, p < 0.05). The size at sexual maturity estimated was 3.51 ± 0.54 mm total length (TL). Mean fecundity of ovigerous females with embryos in the first stage of development was 927 ± 516 embryos, ranging from 37 to 2,722 embryos in females between 3.48 and 5.40 mm TL, respectively. The female size and fecundity showed a significant correlation (r^2 = 0.70), whereas fecundity varied among specimens of similar size. Newly extruded embryos had a mean length of 0.14 ± 0.02 mm, increasing its volume by 116.66% throughout their development. The estimated embryo loss during incubation was 22.17%. This is the first study of *P. pandalicola* for the Atlantic coast of Mexico.

Keywords: Bopyrids; Reproduction; Sexual maturity; Fecundity; Embryo loss

Resumen

Este estudio aporta datos sobre reproducción como talla de madurez sexual, fecundidad, tamaño, pérdida de embriones, y prevalencia del isópodo parásito *Probopyrus pandalicola* de epecímenes obtenidos en Sisal, Yucatán, México. Un total de 3,549 especimenes of *P. mundusnovus* fueron capturados, de estos, 214 estuvieron infestados por *P. pandalicola*. La prevalencia del parásito fue 6.03% con tendencia mayor de infestación hacia las hembras (χ^2 = 57.57, p < 0.05). La talla de madurez sexual se estimó en 3.51 ± 0.54 mm de longitud total (LT). La fecundidad promedio de las hembras ovígeras con embriones en el primer estadio de desarrollo fue de 927 ± 516, con un rango de 37 a 2,722 embriones en hembras de 3.48 y 5.40 mm LT, respectivamente. Se obtuvo una correlación significativa

ISSN versión electrónica: 2007-8706; Universidad Nacional Autónoma de México, Instituto de Biología. Open Access bajo la licencia CC BY-NC-ND (4.0) https://doi.org/10.22201/ib.20078706e.2026.97.5872

entre la talla de las hembras y la fecundidad ($r^2 = 0.70$), pero ésta varió en especímenes de talla similar. Los embriones recientes tuvieron un tamaño promedio de 0.14 ± 0.02 mm; a través del desarrollo su volumen aumentó 116.66%, y la pérdida embrionaria durante la incubación fue de 22.17%. Este estudio representa la primera contribución sobre *P. pandalicola* en la costa Atlántica de México.

Palabras clave: Bopíridos; Reproducción; Madurez sexual; Fecundidad; Pérdida de embriones

Introduction

Crustaceans exhibit a great variability of reproductive strategies that allows them to adapt to particular environmental situations and to increase progeny survival (Martínez-Mayén & Román-Contreras, 2013; Terossi et al., 2010). The study of the reproductive biology of organisms is important since it provides an approximation on the ecology and life history of populations. Thus, information on aspects such as fecundity and size at sexual maturity provides important parameters to understand the life cycle of a species (Pescinelli et al., 2020).

Fecundity, i.e., the number of embryos produced by a female in a given period, indicates the reproductive potential of a species, usually varies as a function of female body size and can be influenced by biological and environmental factors (Ramírez-Llodra, 2002; Sastry, 1983). The size (length or volume) of eggs is considered an indicator of energy investment in embryonic development and provides information for understanding reproductive strategies (Bauer, 1991; Torati & Mantelatto, 2008). Likewise, the size at sexual maturity is a key parameter of any species as it indicates the stage at which an organism has the potential to start reproducing and generate offspring (Martínez-Mayén & Román-Contreras, 2003).

Bopyrid isopods are obligate ectoparasites that typically invade the branchial chambers or the abdomen of caridean shrimps and other decapod crustaceans (Burgos & Itani, 2024; Jay, 1989; Rasch & Bauer, 2015). The males are tiny with a typical isopod body shape, while the females have distorted bodies and are much larger in size (Cericola & Williams, 2015; Román-Contreras, 2008). These parasites feed on the hemolymph and tissues of their hosts (Boyko et al., 2013; Briggs et al., 2017; Sherman & Curran, 2015), and can cause branchial atrophy, modification of sexual characters, sexual sterilization, a reduction in metabolic rate, and partial inhibition of the growth (Beck, 1980; Brinton & Curran, 2015; de Barros et al., 2020; Sherman & Curran, 2015; Van Wyk, 1982). Bopyrid isopods usually infest juvenile shrimp (Beck, 1980; Rasch & Bauer, 2015), and exhibit a complex life cycle that requires a calanoid copepod as an intermediate host and a decapod crustacean as a definitive host (Bortolini-Rosales et al., 2021).

On other hand, the bopyrid prevalence can have a significant impact on the shrimps because the infested individuals are removed from the reproductive population before they reach the sexual maturity (Chaplin-Ebanks & Curran, 2007), which cause a decrease in their populations (Romero-Rodríguez & Román-Contreras, 2013).

Probopyrus pandalicola is a branchial parasitic isopod, widely distributed along the Atlantic coast from New Jersey, USA, to Brazil (Román-Contreras & Martínez-Mayén, 2011). In Mexico, this species is distributed in Tamaulipas, Tabasco, Campeche, Yucatán, and Quintana Roo (Martínez-Mayén & Romero-Rodríguez, 2024, and literature cited herein). It infests mainly caridean shrimp of the genera *Macrobrachium* and *Palaemon* (Martínez-Mayén & Romero-Rodríguez, 2024; Román-Contreras, 1993), important species in transferring primary production to higher trophic levels in their ecosystems (Anderson, 1985).

Information on *P. pandalicola* in Mexico is limited to taxonomic checklists (Aguilar-Perera, 2022; Martínez-Mayén & Romero-Rodríguez, 2024; Román-Contreras, 2008), regional faunal inventories and local distribution data (Castellanos-Osorio et al., 2024; Markham et al., 1990; Rodríguez-Almaraz et al., 2000; Román-Contreras & Martínez-Mayén, 2011). Thus, the purpose of this study was to provide data on the size at sexual maturity, fecundity, embryo size, loss of embryos and prevalence of *P. pandalicola* infesting the shrimp *Palaemon mundusnovus* in the southeastern Gulf of Mexico.

Materials and methods

Specimens of *Palaemon mundusnovus* parasitized with *Probopyrus pandalicola* (Fig. 1) were collected during 1 diurnal sampling in a wetland known as La Ciénega (21°10.85’ N, 89°58.52’ W) in Sisal, Yucatán, Mexico on April 28th, 2009 (Fig. 2). Shrimps were collected from patches of submerged vegetation and roots of riparian shrubs with a spoon-shaped net (mesh size 1 mm). Immediately after sampling, all specimens were preserved in 96% ethanol. Water temperature during sampling was 30°C. Salinity was not measured, but Zaldívar-Jiménez et al. (2012) recorded a mean value

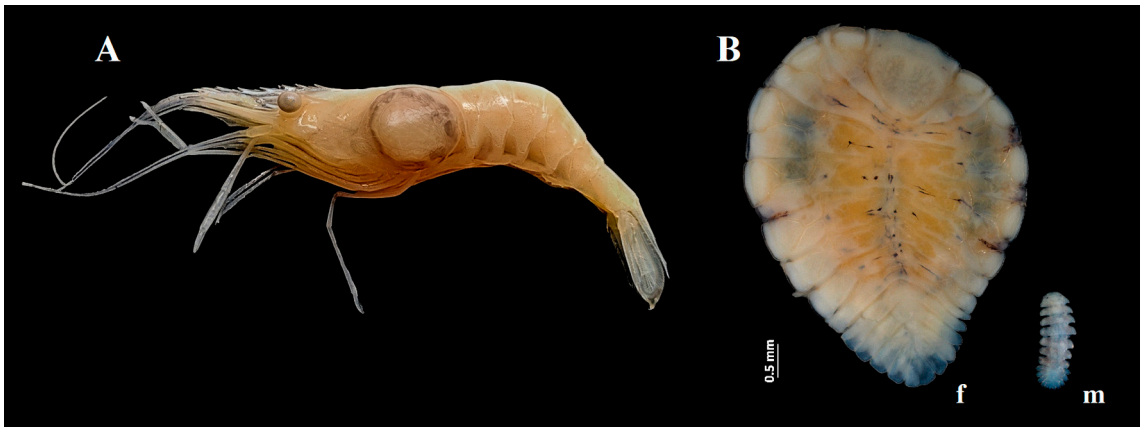

Figure 1. A, *Palaemon mundusnovus* parasitized with *Probopyrus pandalicola*; B, female (f) and male (m) of *P. pandalicola*.

of 36.5 ups at the same time and under similar conditions to those of this study.

The shrimp and parasitic isopods were identified following the taxonomical criteria proposed by Holthuis (1952) and Markham (1985), respectively. The size of the infested shrimp, taken as carapace length (CL), was measured from the postorbital margin to the mid-posterior end of the carapace with a digital caliper (± 0.01 mm accuracy). The specimens were sexed considering the presence (male) or absence (female) of the appendix masculina in the endopods of the 2nd pair of pleopods. The parasites were detached from their hosts, and only in females of *P. pandalicola* the total length (TL) was measured from the anterior margin of the cephalon to the posterior end of the pleotelson (Cash & Bauer, 1993).

The prevalence was calculated as the number of individuals of a host infected with the parasite divided by the host examined, expressed in percentage (Margolis et al., 1982). Host sex selectivity was evaluated with a chi-square test (Rasch & Bauer, 2015).

The entire brood mass of each ovigerous female was removed from the marsupium with fine forceps, and the development of the embryos was categorized into stages I, II and epicaridium larvae following Beck (1980), and Cash and Bauer (1993) for *P. pandalicola*. All embryos were counted directly, but the fecundity reported here refers to the total number of embryos in stage I to avoid underestimation related to the embryo loss during embryogenesis (García-Guerrero & Hendrickx, 2005; Wehrtmann et al., 2012); one ovigerous female with 37, and other carrying 50 embryos were not used in the regression analyses between the fecundity vs total length. From each brood mass, 10 embryos were randomly chosen, and their minor (d_1) and major (d_2) diameters were measured to calculate their volume with the formula $V = \pi$

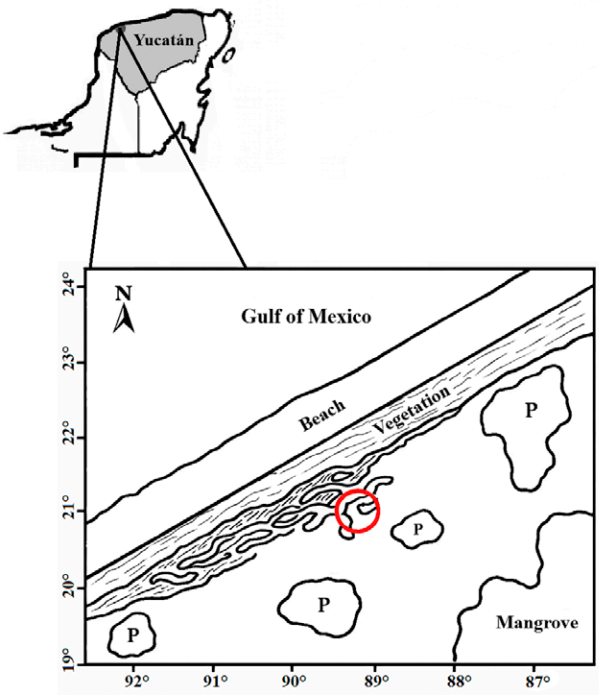

Figure 2. Study area; sampling site is indicated by the red circle. P, Peten mangroves.

$(d_1)^2 * (d_2)/6$, used for bopyrids by Romero-Rodríguez and Román-Contreras (2013).

Size at sexual maturity (TL_{50}) was calculated, considering all the ovigerous females (Romero-Rodríguez & Román-Contreras, 2013; Tallack, 2007), with the logistic equation $P = 1/(1 + \exp[-(a + b \times TL)])$, which relates the proportion of females (P) in each size class with total length (TL), and a and b are the parameters calculated for

the regression between *P* and TL. The size corresponding to 50% sexually mature females was obtained from the relationship TL_{50} = -(*a*/*b*) and using interpolation (Oh et al., 2002; Pescinelli et al., 2020).

The change in embryo volume between stages I and II was evaluated with a one-way ANOVA. The variation in the number of embryos (stage I) with respect to the total length of the female parasite was calculated with simple linear regression analyses. The parameters that describe the equation between these variables were obtained with the least-squares method.

Results

At the sampling site, a total of 3,549 specimens of *Palaemon mundusnovus* were captured, of which 214 were found to be infested by *Probopyrus pandalicola*. Host size varied from 2.79 to 6.35 mm CL. The mean size of *P. pandalicola* females was 3.19 ± 0.70 mm TL (range 1.75-5.64 mm TL), 66 females were ovigerous, with a mean size of 3.90 ± 0.56 mm LT, ranging from 2.98 to 5.64 mm TL, being more abundant at the size class of 3.13-4.04 mm TL (Fig. 3). Bopyrid prevalence in the study area was 6.03%, with significant differences (χ^2 = 57.57, $p < 0.05$) between the number of females (163) and males (51) infested.

Considering all ovigerous females, the number of embryos varied from 37 to 2,722 (Table 1) with a mean fecundity of 927 ± 516 (n = 66). The mean fecundity of females with embryos in the first stage of development was 961 ± 555 (n = 50) and was correlated significantly (*t*-test = 10.52, $p < 0.05$) with female size. Fecundity increased with parasite body size, but not progressively since some smaller females had a higher fecundity than larger ones, also the number of embryos varied in specimens of similar total length (Fig. 4).

Embryos in stage I were spherical in shape, whitish and had evenly distributed yolk, those in stage II were oblong in shape, brown and pronounced segmentation, the epicaridium larvae had a darker color, fully defined eyes and well-developed appendages. Only 1 developmental stage was found in each embryo mass of the females. The average lengths of the *P. pandalicola* embryos were 0.14 ± 0.02 mm and 0.23 ± 0.02 mm at stages I and II, respectively, and the mean size of the epicaridium larvae was 0.25 ± 0.01 mm. Mean embryo volume ranged from 0.0012 mm^3 in stage I to 0.0026 mm^3 in stage II, which represent an increase of 116.66% (F = 778.10, $p < 0.05$). Fecundity decreased 22.17% between stages I and II.

The smallest *P. pandalicola* ovigerous female was 2.98 mm TL, which can be considered the size at first reproduction for this species in the study area. The relationship between TL and the proportion of ovigerous females is represented by the equation P = 1/(1 + exp [-2.5337 + 8.8974*TL]), thus the estimated size at functional sexual maturity, at which 50% of the females are sexually mature, was 3.51 ± 0.54 mm TL (Fig. 5).

Discussion

In *Palaemon*, species infested by *Probopyrus pandalicola*, the levels of prevalence varied from 0.5% to 100% (Beck, 1979; Morris, 1948). The wide variability in parasite prevalence may be the result of interactions between various environmental factors and the abundance and behaviour of the stages in the life cycle of both the parasite and host (Jay, 1989; Pralon et al., 2018), as well as the size of the sample analyzed (Romero-Rodríguez & Román-Contreras, 2013).

The parasite infested mainly female hosts, which agrees with studies by Beck (1979) and Morris (1948) for this species, and other bopyrid species (Jay, 1989; Rasch & Bauer, 2015; Romero-Rodríguez & Román-Contreras, 2013; Truesdale & Mermilliod, 1977; Vargas-Ceballos et al., 2016). The higher infestation of females could represent advantages to the parasite, such as increased longevity and hence, the production of a greater number of spawnings, likewise female hosts have a longer life expectancy than male hosts (Beck, 1979; Romero-Rodríguez & Román-Contreras, 2013; Schuldt & Rodrigues-Capitulo, 1985), but also sex-selectivity could be related to their abundance in the population (Beck, 1979), which coincides with the results obtained in this study since the females predominated over the males in a ratio of 3.1: 1.

In the study area, *P. pandalicola* begins to produce embryos at 2.98 mm TL, similar value to the 3 mm TL reported by Beck (1980) for the same species in Florida, USA, but higher than the 2.1 mm TL reported by Brinton and Curran (2015) in Georgia, USA, and the 2.80 mm TL reported by Román-Contreras (1993) for *P. pacificensis* in Guerrero, Mexico. According to Jordá and Roccatagliata (2002), female bopyrids ingest large amounts of hemolymph of the infested shrimp, and this allows females to reach early maturity. Walker (1977) estimated that females of *P. pandalicola* can ingest about 25% of the hemolymph of *Palaemon pugio* (cited as *Palaemonetes pugio*) daily, which influences the growth as well as the embryo production of the parasites as a result of the stable, nutrient rich environment provided by the host (Baeza et al., 2018; Jennings & Calow, 1975; Poulin, 1996).

Table 1
Number of embryos per stage of development in *Probopyrus pandalicola* females.

Stage	n	Mean total length (mm)	Number of embryos-range	Number of embryos mean ± sd
I	50	4.0 ± 0.60	37-2,722	961 ± 555
II	13	3.67 ± 0.35	106-1,185	748 ± 358
Epicaridium	3	3.57 ± 0.23	1,043-1,297	1,144 ± 135

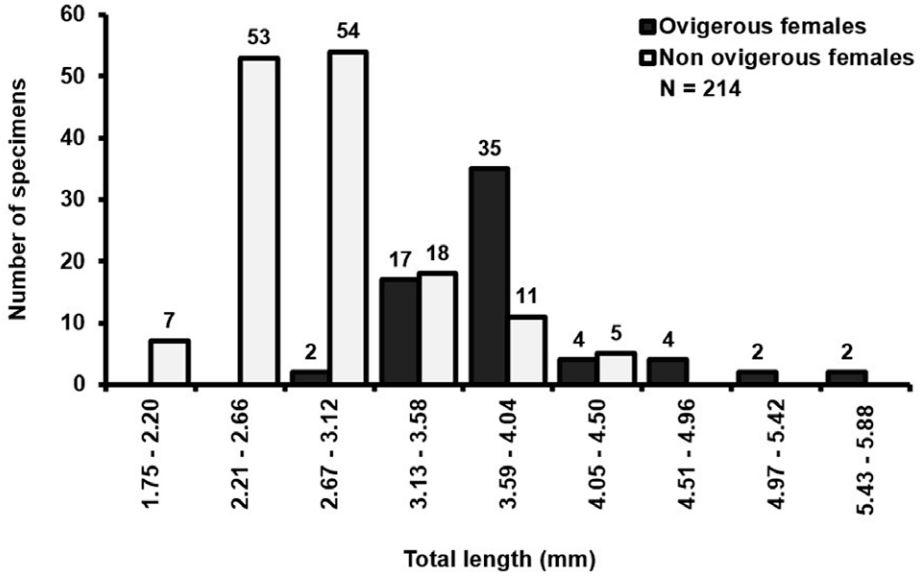

Figure 3. Size-frequency distribution of *Probopyrus pandalicola* non-ovigerous females and ovigerous females. The number of individuals is shown above each size-class bars.

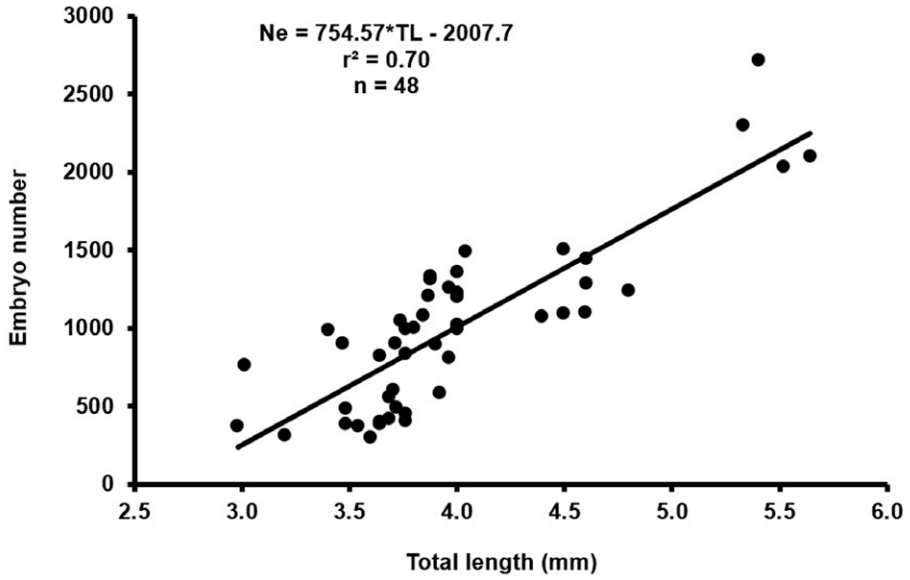

Figure 4. Relationship between numbers of embryos (*N*e) and total length (TL) in *Probopyrus pandalicola* ovigerous females with embryos in stage I of development.

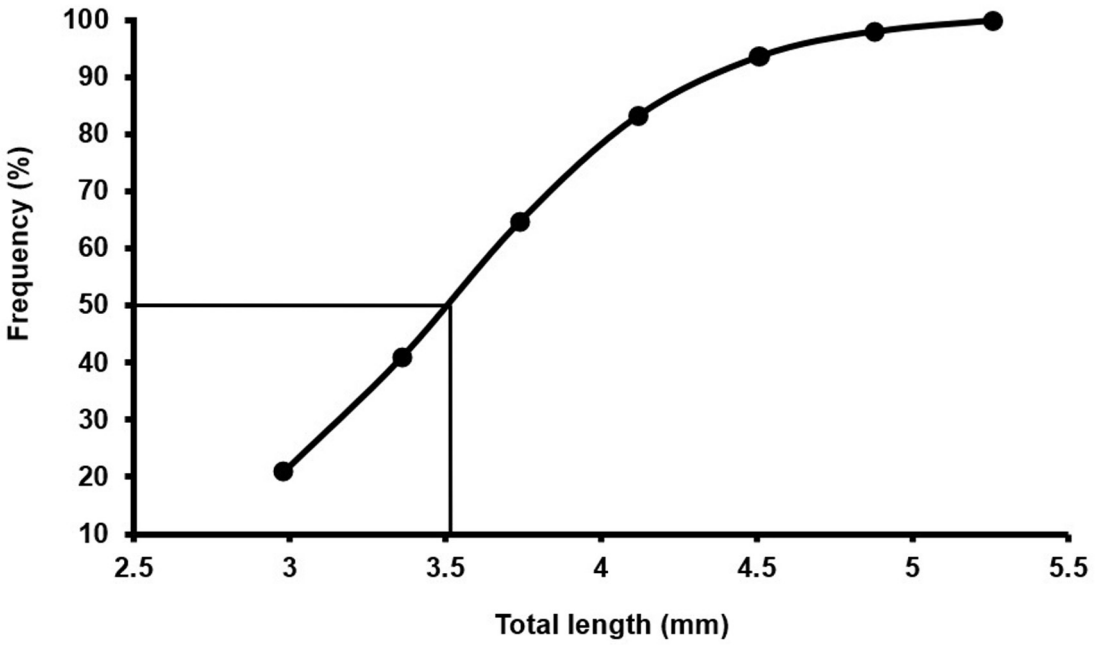

Figure 5. Logistic function between the proportion and total length (TL) of *Probopyrus pandalicola* ovigerous females. TL50 corresponds to 50% of the size at functional sexual maturity.

There are no reports on size at sexual maturity for any species of the genus *Probopyrus* obtained with the method used in this study; however, maturity is associated with the mean size of the ovigerous females (Roa et al., 1999; Martínez-Mayén & Román-Contreras, 2003). The results of the present study agree with this statement since their mean size was 3.90 mm, similar to the 3.51 mm TL calculated for the sexual maturity, while Beck (1980) reported in the same species mean values that ranged between 5.2-5.4 mm TL. Such discrepancy in size at the sexual maturity in conspecific species may be associated with local environmental abiotic or biotic factors, season of the year in which the study took place (Rasch & Bauer, 2015), and the size and number of specimens sampled (Waddy & Aiken, 2005). In other bopyrids such as *Cryptione elongata africana* (mentioned as *Pseudione elongata africana*), Penha-Lopes et al. (2012) calculated sizes at sexual maturity of 4.15 and 4.58 mm TL in distinct localities, while Rasch and Bauer (2015) recorded sizes at sexual maturity of 1.09 and 1.63 mm TL for *Urobopyrus processae* in 2 different years.

In bopyrid isopods, fecundity is generally related to female size because larger hosts harbor larger parasites which produce a higher number of embryos (Beck, 1980; Rasch & Bauer, 2015). The variation in the number of embryos among female parasites of similar size registered is similar to that reported for *P. pandalicola* (Beck, 1980), *Argeia pugettensi*s (Jay, 1989), *Bopyrinella thorii* (Romero-Rodríguez & Román-Contreras, 2008), *Athelges takanoshimensis* (Cericola & Williams, 2015) and *U. procesase* (Rasch & Bauer, 2015). Bourdon (1968) and Beck (1980) suggested that this variation is due to the size of the outpocketing in the host carapace caused by the parasite that limits the space available for the embryos. Likewise, sometimes a parasite produces more embryos than what the marsupium or the host's branchiostegite can contain (Romero-Rodríguez & Román-Contreras, 2008; Schuldt & Rodriguez-Capitulo, 1985). This variation in fecundity could, in part, explain the moderate correlation value (r^2 = 0.70) between parasite size and fecundity registered.

The fecundity of *P. pandalicola* obtained was lower than that reported for the same species in other regions (Table 2). These differences may be attributable to environmental conditions such as temperature, in this respect, Beck (1980), and Brinton and Curran (2015) studying different populations of *P. pandalicola* recorded ranges of this parameter between 16-24 ºC in Florida, and of 11-31.6 ºC in Georgia, USA, respectively, with higher fecundity values than those of the present study (Table 2). Other factors that could also affect the fecundity are the salinity, presence of toxic elements (Penha-Lopes et al.,

2012; Ramírez-Llodra, 2002), embryo size (Martínez-Mayén et al., 2020), and embryo mortality (Cericola & Williams, 2015; Oh et al., 2002). However, the difference in the number of *P. pandalicola* embryos recorded in this study with respect to other localities is most probably due to the wider range of parasite sizes analyzed in previous studies (Table 2).

Embryo size is important in the reproductive strategy of a species, as it is often related to the duration of embryonic development (Steel & Steel, 1975). It has been suggested that bopyrid isopods produce embryos smaller than 0.2 mm in diameter (Table 2) and exhibit complex life cycles involving at least 2 hosts (Romero-Rodríguez, 2014; Strömberg, 1971), while other epicarideans (e.g.,

Table 2

Fecundity and embryo size (stage I) of branchial bopyrids parasitizing diverse shrimp species. Cited as: [a)]*Hippolyte curacaoensis*, [b)]*Palaemonetes carolinus*, [c)]*Palaemonetes paludosus*, [d)]*Palaemonetes pugio*.

Species	Female size (mm)	Fecundity	Embryo size (mm)	Embryo volume (mm^3)	Host(s)	Location	Reference
Argeia pugettensis	4.2-9.0	1,600-38,300	-	-	*Crangon franciscorum*	Humboldt Bay, California, USA	Jay (1989)
Boypyrella harmopleon	4.25	1,405	0.14	0.0012	*Synalpheus hemphilli*	Southwestern Gulf of Mexico	Romero-Rodríguez & Álvarez (2020)
Bopyrina abbreviata	1.15-2.35	131-1,548	0.102	0.0005	*Hippolyte zostericola*	Laguna de Términos, Campeche, Mexico	Romero-Rodríguez & Román-Contreras (2013)
Bopyrina ocellata	1.5-3.1	330-1,410	-	-	*Hippolyte* spp.	Europe (several localities)	Bourdon (1968)
Bopyrina ocellata	-	61-596	0.133	-	*Hippolyte obliquimanus*[a)]	Brazil (several localities)	Tsukamoto (1981)
Bopyrinella thorii	1.87-3.52	83-1,036	0.113	-	*Thor floridanus*	Bahía de la Ascensión, Mexican Caribbean	Romero-Rodríguez & Román-Contreras (2008)
Boypyrione sinalphei	-	-	0.12	0.0008	*Synalpheus brooksi*; *Synalpheus elizabethae*	Arrecife Alacranes, Yucatán, Mexico	Romero-Rodríguez & Álvarez (2020)
Epipenaeon ingens ingens	7.2-26.8	83,360	0.1479	-	*Penaeus aztecus*	Antalya Bay, Turkey	Deval & Koçanci (2021)
Munidion pleuroncodis	-	11,134	0.166	0.0022	*Grimothea planipes*	Isla Socorro, Colima, México	Romero-Rodríguez & Álvarez (2023)
Parabopyrella lata	5.71-6.83	2,181-5,998	-	0.0311	*Lysmata boggessi*	Homosassa Springs, Florida, USA	Baeza et al. (2018)
	3.17	168	0.17	-	*Alpheus normanni*	Puerto Morelos, Quintana Roo, Mexico	Romero-Rodríguez & Álvarez (2020)
Parabopyrella thomasi	4.19	1,802	0.14	0.0013	*Tozeuma carolinense*	Bahía de la Ascensión and Bahía del Espíritu Santo, Quintana Roo, Mexico	Romero-Rodríguez & Martínez-Mayén (2018)
Probopyrus bithynis	5.5-7.5	5,241	0.14-0.160	-	*Macrobrachium ohione*	Atchafalaya River, Louisiana USA	Truesdale & Mermilliod (1977)

Table 2. Continued

Species	Female size (mm)	Fecundity	Embryo size (mm)	Embryo volume (mm^3)	Host(s)	Location	Reference
Probopyrus floridensis	-	1,545	0.178	-	*Macrobrachium potiuna*	Ilha do Cardoso, São Paulo, Brazil	Rocha & Bueno (2000)
Probopyrus markhami	-	-	0.179	0.0028	*Macrobrachium americanum*	Río Verde, Oaxaca, Mexican Pacific coast	Romero-Rodríguez & Álvarez (2023)
Probopyrus pacificensis	-	-	0.163	0.0019	*Palaemon hiltoni; Palaemon ritteri*	Sonora and Colima, Mexican Pacific coast	Romero-Rodríguez & Álvarez (2023)
	7.0-9.0	5,390-11,800	-	-	*Macrobrachium tenellum*	Laguna Coyuca, Guerrero, Mexico	Román-Contreras (1993)
Probopyrus pandalicola	3.4	-	0.15	-	*Palaemon vulgaris*[b)]	Progreso, Yucatán, Mexico	Pearse (1936, as *Probopyrus creaseri*)
	3.0-7.5	350-11,850	0.15	-	*Palaemon paludosus*[c)]	Wakulla County, Florida, USA	Beck (1980)
Probopyrus pandalicola	2.1-5.5	391-4,596	-	-	*Palaemon pugio*[d)]	Savannah, Georgia, USA	Brinton & Curran (2015)
	2.98-5.64	37-2,722	0.14	0.0012	*Palaemon mundusnovus*	Sisal, Yucatán, Mexico	Present study
Schizobopyrina striata	3.27	-	0.120	0.0008	*Periclimenes infraspinis*	Isla Alcatraz, Bahía de Kino, Sonora, México	Romero-Rodríguez & Álvarez (2023)
Schyzobopyrina urocaridis	1.78-2.12	205-304	0.120	0.0008	*Phycomenes siankaanensis*	Bahía de la Ascensión and Bahía del Espíritu Santo, Quintana Roo, Mexico	Romero Rodríguez & Martínez-Mayén (2017)
Urobopyrus processae	1.50-3.90	85-3,096	0.159	0.0014	*Ambidexter simmetricus*	St. Joseph Bay, Florida, USA	Rasch & Bauer (2015)

Entoniscoides okadai) produce larger embryos (ca. 0.2 mm) similar in size to an epicaridium larva, and have an abbreviated larval development (Miyashita, 1940; Strömberg, 1971).

The mean length of the *P. pandalicola* embryos in stage I recorded here concurs with values reported for this species by Pearse (1936) and Beck (1980), as well as by Truesdale and Mermilliod (1977) for *Probopyrus bithynis* (Table 2), whereas *Probopyrus floridensis*, *Probopyrus markhami* and *P. pacificensis* produce larger embryos (Table 2). In addition, *P. pandalicola* embryos are similar in size to those of other branchial bopyrids, for which data are available (Table 2). The mean size of the epicaridium larvae recorded here (0.25 mm) resembles that reported by Beck (1980) (0.25-0.30 mm) for *P. pandalicola*, and that recorded for *P. insularis* (0.18-0.25 mm) by Román-Contreras and Bourdon (2001), while Romero-Rodríguez and Álvarez (2023) recorded a value of 0.284 mm for *P. markhami*.

The size and development of the *P. pandalicola* embryos did not vary within a brood, as was recorded by Morris (1948) and Beck (1980) for this species and for other bopyrids like *Aparapenaeon japonica* (Hiraiwa, 1936, cited as *Parapenaeon japonica*), *Epipenaeon ingens* (Owens & Glazebrook, 1985), *Probopyrus ringueleti* (Schuldt, 1993), *B. thorii* (Romero-Rodríguez & Román-Contreras, 2008), *Bopyrina abbreviata* (Romero-Rodríguez & Román-Contreras, 2013) and *U. processae*

(Rasch & Bauer, 2015). This phenomenon appears to be common in the Bopyridae (Bourdon, 1968; Schuldt, 1993; Strömberg, 1971) and is due to the male releasing sperm directly onto the external surface of the gonopores and the eggs being fertilized as they pass through them (Burgos & Itani, 2023).

Comparatively, the embryo volume of *P. pandalicola* is smaller than that of *P. markhami* and *P. pacificensis* (Table 2), although the value calculated in this study lies within the range recorded for other bopyrid species (Table 2). Embryo volume increased more than twice over the incubation period (116.66 %), and this value corresponds well with the range of 2-180% recorded for crustaceans (Pandian, 1994). Romero-Rodríguez and Román-Contreras (2013) documented a 60% increase in embryo volume for *B. abbreviata*, while *U. processae* and *Parabopyrella thomasi* embryos increased in volume by 51.03% and 38.46%, respectively (values of increase in volume calculated from data of Rasch and Bauer [2015] and Romero-Rodríguez and Martínez-Mayén [2018], respectively). This increase during incubation is mainly due to embryo growth, biochemical changes and water uptake for the embryo (Clarke, 1993; Pandian, 1970).

Brood loss during the incubation period in crustaceans is a common feature that may be caused by several physical and biological factors (for a review see Kuris, 1991). The only bopyrid embryo loss documented is the 7.21% calculated by Romero-Rodríguez and Román-Contreras (2013) in a population of *B. abbreviata*, which is considerably lower than that obtained in this study for *P. pandalicola* (22.17%) but fit well with the range of 4-50% recorded for other crustaceans that incubate embryos in the marsupium (Pandian, 1994). One possible reason for egg loss in *P. pandalicola* may be an increase in embryo volume during incubation, when the ovigerous mass exceeds the available space of marsupium of parental females, and consequently, some embryos may be discarded (Balasundaram & Pandian, 1982; Kuris, 1991; Ramírez-Llodra, 2002). Another reason may be that embryos may become detached through the first oostegites by the movement of the maxillipeds during embryo grooming by the female parasite, as was observed by Burgos and Itani (2024) in the case of *Bopyrus crangorum* infesting *Palaemon serrifer*. Also to be considered is the loss of embryos resulting from the handling of specimens during the collection and processing of specimens (Cericola & Williams, 2015).

The present study is the first one on *P. pandalicola* from the Atlantic coast of Mexico. Although this study was restricted to a single sampling, our results increase the current understanding of this parasite, and future studies will be carried out to obtain additional information regarding the dynamics, structure and biology, in order to identify possible differences among populations of this species.

Acknowledgements

This paper is part of the first author's undergraduate thesis. We thank the authorities of the Instituto de Ciencias del Mar y Limnología, UNAM for financing the field work, Andrés Reda Deara (Estación El Carmen, ICMyL, UNAM) and Ramiro Román Contreras for their help with the field work, and Nuno Simões (Unidad Multidisciplinaria de Docencia e Investigación-Sisal, Facultad de Ciencias, UNAM) for the facilities provided during our stay in Sisal, Yucatán, and the two reviewers for the valuable suggestions that improved the manuscript.

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