

Infestation of two shrimp species of the genus *Palaemon* Fabricius, 1798 (Decapoda, Palaemonidae) by an isopod of the genus *Probopyrus* Giard & Bonnier, 1888 (Bopyridae) from the Brazilian southeast coast

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ABSTRACT

We determined the infestation rate of *Probopyrus* sp. in populations of *Palaemon pandaliformis* (Stimpson, 1871) and *P. northropi* (Rankin, 1898) in the Ubatumirim River, localized in a mangrove ecosystem on Ubatumirim Beach, northern coast of the state of São Paulo, Brazil. Samplings were carried out monthly from April 2003 to March 2004. Monthly prevalence varied from 0 to 4.94 % for *P. pandaliformis*, and from 0 to 4.54 % for *P. northropi*. This is the first record of *Probopyrus* sp. infesting the studied species in this region. Species of *Probopyrus* (Giard and Bonnier, 1888) seem to have a high plasticity with regard to palaemonid hosts, as they can be parasites of shrimps in both *Palaemon* (Fabricius, 1798) and *Macrobrachium* (Spence Bate, 1868). The linear relationships between the parasite and host sizes suggest that the parasite infests both hosts early in their development. We concluded that the infestation of *Probopyrus* sp. has little impact on *Palaemon* populations, mostly due to the low prevalence of infestation.

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ectoparasitism, prevalence, host, palaemonid, Brazil.

INTRODUCTION

Caridean shrimps of the genus *Palaemon* Fabricius, 1798 are components of estuarine food webs (Bass and Weis, 1999; Mortari and Negreiros-Fransozo, 2007). These crustaceans have their lives adversely affected in many ways when parasitized by isopods belonging to the family Bopyridae (Ocaña-Luna *et al.*, 2009).

Bopyrid isopods are obligate hematophagous ecto- and holoparasites of crustaceans (Chaplin-Ebanks and Curran, 2007; Boyko and Williams, 2009; Williams and Boyko, 2012). They have complex life cycles that require a decapod as a definitive host, and a calanoid copepod as an intermediate host (Anderson, 1990; Lester, 2005; Oliveira and Masunari, 2006; Boyko and Williams, 2009; Sherman and Curran, 2015). An adult female bopyrid is typically found attached to the gills inside the branchial chamber, while the dwarf adult male is often found attached to the ventral side of the female bopyrid (Beck, 1980; Choong *et al.*, 2011; Sherman and Curran, 2015). Parasites induce visible lateral swellings on the carapace of the host and this deformation on the branchiostegite region characterizes the host-parasite relationship (Choong *et al.*, 2011).

Bopyrids feed on the host's haemolymph and disrupt the normal mechanical functioning of the gills, impairing the respiration and metabolism of shrimps (Choong *et al.*, 2011; Dale and Anderson, 1982). Shrimps parasitized by bopyrids may become reproductively impaired as both male and female individuals may become sexually sterile or show reduced fecundity, and male individuals can become somewhat feminized due to their reduced chelae length (Bass and Weis, 1999). Female shrimps often suffer parasitic castration by having the full maturation of their ovaries inhibited (Rocha and Bueno, 2000). Thus, the deleterious effects of bopyrid infestation may act as an important factor regulating some decapod populations (Varisco and Vinuesa, 2011).

Among caridean shrimps, the family Palaemonidae is the main group with species acting as hosts for bopyrid isopods of the genus *Probopyrus* Giard and Bonnier, 1888, whose distribution is therefore tied to that of the Palaemonidae (Masunari *et al.*, 2000). According to Lemos de Castro and Brasil-Lima (1974), on the Brazilian coast there are three species of *Probopyrus*: *Probopyrus bithynis* Richardson, 1904, *P. palaemoni* Lemos de Castro and Brasil-Lima, 1974 and *P. floridensis* Richardson, 1904. As the same authors emphasize, *P. bithynis* infests several palaemonid species, including *Palaemon pandaliformis* (Stimpson, 1871) and *Palaemon northropi* (Rankin, 1898), while *P. palaemoni* has been recorded parasitizing *P. pandaliformis*. Nevertheless, despite the wide geographical distribution and phylogenetic divergencies showed by *P. pandaliformis* and *P. northropi* (see Carvalho *et al.*, 2017 for details), extending from Central America to Southern South America (Holthuis, 1952), these species have never been recorded carrying bopyrid parasite on the northern coast of São Paulo State, Brazil.

Palaemon pandaliformis and *P. northropi* are abundant in the estuaries located along the southeastern Brazilian coast (Anger and Moreira 1998). They play an important role in the food web serving as prey for numerous predators. Presence of bopyrid ectoparasites in populations of those shrimps can potentially affect local reproduction. Thus, our study aimed to report for the first time the infestation of *Probopyrus* sp. in populations of *P. pandaliformis* and *P. northropi* from the Ubatuba region, northern coast of the state of São Paulo, Brazil. In addition, we commented on some aspects of their host-parasite relationships.

MATERIAL AND METHODS

Specimens of *P. pandaliformis* and *P. northropi* were collected monthly from April 2003 through March 2004, in the Ubatumirim River (23°20'17.8"S

44°53'2.2"W), localized at a mangrove ecosystem of Ubatumirim Beach, in the northern coast of the state of São Paulo, Brazil. The mangrove forest of Ubatumirim is mostly composed of vascular plants (*i.e.*, *Avicennia shaueriana*, *Laguncularia racemosa* and *Rhizophora mangle*) as reported by Colpo *et al.* (2011). We conducted the samplings in the morning, during low tide, collecting samples within a 10 m stretch along the riverbank. We used a sieve (3 mm mesh), passing it under the submerged vegetation. For further information about sampling procedures see Mortari *et al.* (2009).

We utilized plastic bags to pack samples, which were labeled with the date and site of the collection. Specimens were taken to the laboratory where they were identified according to Melo (2003), and preserved in 70% ethanol for later analysis. Voucher specimens were deposited in the crustacean collection of the Department of Zoology, IB, UNESP, Botucatu (NEBECC AD # 0001; AD # 0002). Carapace length (CL = from the posterior margin of the orbit to the posterior margin of the carapace) of each shrimp was measured under a stereomicroscope provided with a micrometer scale (mm). Sex evaluation was based on the presence (male) or the absence (non-ovigerous female) of an *appendix masculina* on the endopods of the second pair of pleopods.

Parasites were identified under a dissecting microscope, according to available literature (Lemos de Castro and Brasil-Lima, 1974; Richardson, 1904). Photographs of the ectoparasite and its host were taken with a Zeiss Stemi SV6 stereoscopic microscope. Parasites (female and male) were measured for total length (TL) and width (TW) to the nearest 0.01 mm with a stereoscopic microscope, provided with a micrometer scale. Male parasites are symmetrical in shape and were measured from the anterior edge of the cephalon to the posterior edge of the pleotelson, while females are asymmetrical in shape and were measured along the longest side from the anterior margin of the body to the end of the pleotelson (Cash and Bauer, 1993). Immature and mature parasites were differentiated according to Conner and Bauer (2010). The use of the term "prevalence" followed Margolis *et al.* (1982), and expressed the

percentage of infested shrimps present in the sampled population. Linear regressions of parasite body size (TL, dependent variable) *vs.* host body size (CL, independent variable) were calculated by using the least square method, with a significance level of 5% (Wilkinson, 1988).

RESULTS

We examined 2,878 *P. pandaliformis* (CL ranging from 1.5 to 5.8 mm) and 486 *P. northropi* (CL ranged from 1.9 to 9.6 mm), from which seventeen were from the former species (CL: 3.12 – 4.49 mm) and five from the latter one (CL: 3.75 – 5.74 mm) that were parasitized by *Probopyrus* sp. (Figs. 1A-B; Tab. 1). The monthly prevalence was low throughout the study and varied from 0 to 4.94% (mean value = 0.8 ± 1.39) for *P. pandaliformis* and from 0 to 4.54% (mean value = 0.8 ± 1.63) for *P. northropi* (Tab. 2). All bopyrid isopods removed from their hosts matched the morphological characteristics described by Richardson (1904) for *Probopyrus* sp. (Fig. 1C). Only four parasites were breeding (females with eggs in the marsupium). Two of those specimens, obtained in November 2003, were parasitizing *P. pandaliformis*, and the other two, obtained in August 2003 and November 2003, were parasitizing *P. northropi* (Tab. 1). Unfortunately, most eggs of the breeding females were lost, so the determination of fecundity was not possible. However, we could observe that the eggs were still at an early stage of development, as they were full of yolk and with no evidence of developing embryos. Each female had a dwarf male of yellow coloration attached to its pleon (Fig. 1D). In the present study, infestation by *Probopyrus* sp. was observed mostly in males of *P. pandaliformis* (Tab. 1). We found a positive correlation between the TL of the parasites and the CL of the shrimp hosts (*P. northropi* $n = 5$; $R^2 = 0.97$; $p < 0.01$; *P. pandaliformis* $n = 17$; $R^2 = 0.54$; $p < 0.01$) (Fig. 2). We also found the proportion of parasitized specimens varied during the study period for both host populations. There were no bopyrids for at least five months of the year for either host species (see Tab.2).

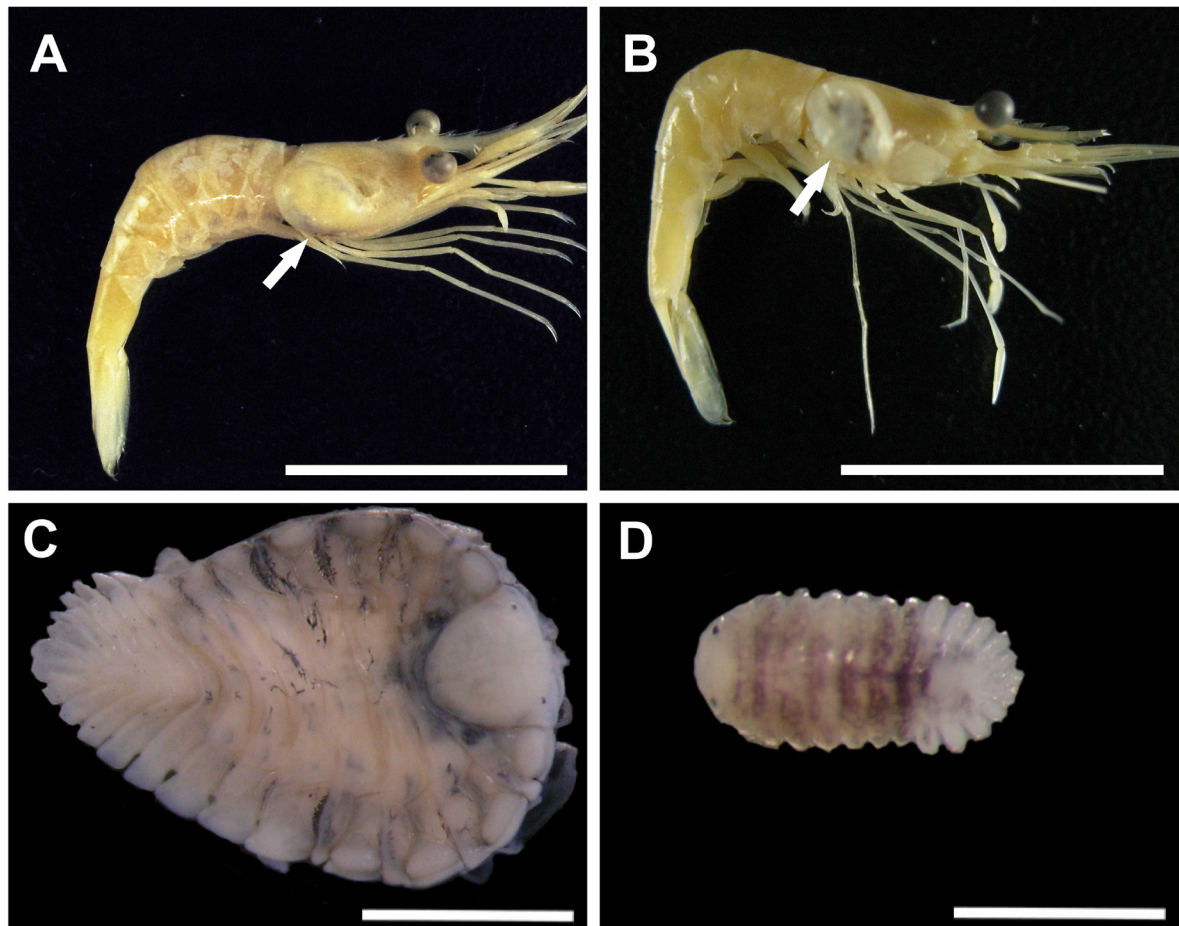


Figure 1. Lateral view of *Palaemon northropi* (A) and *Palaemon pandaliformis* (B) infested by *Probopyrus* sp. (arrow). Scale bar = 5 mm. Female of *Probopyrus* sp. (dorsal view) (C). Scale bar = 1 mm. Male of *Probopyrus* sp. (dorsal view) (D). Scale bar: 0.5 mm.

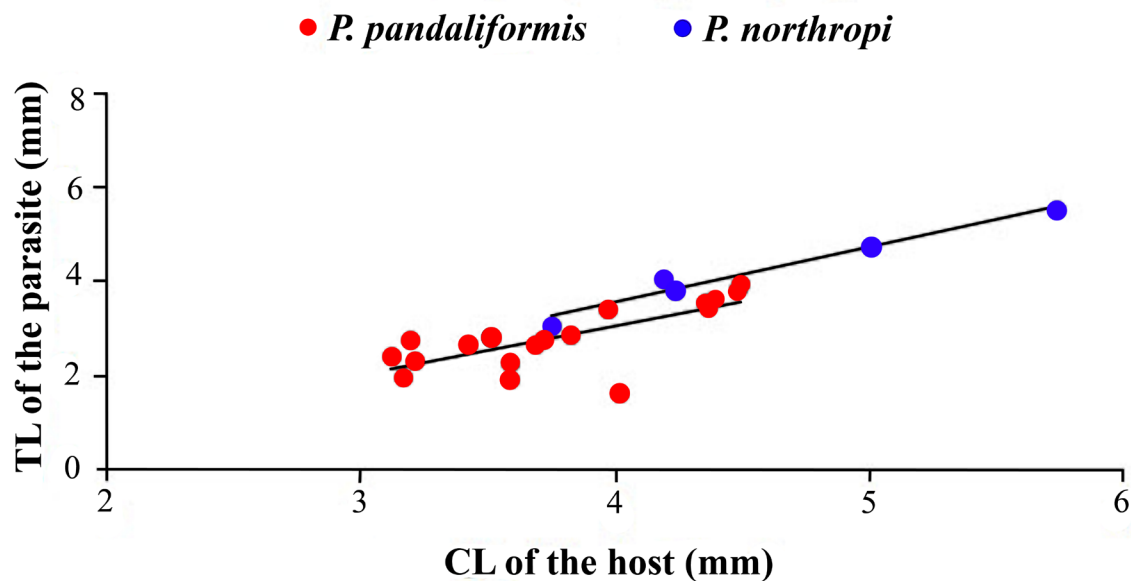


Figure 2. Relationship between carapace length (CL, mm) of the hosts *Palaemon northropi* and *P. pandaliformis* and total length (TL, mm) of their parasite, *Probopyrus* sp. Linear regression equation for *P. pandaliformis* size and probability value: $TL = 1.051 CL - 1.1306$ ($p = 0.0003$; $r^2 = 0.54$). Linear regression equation for *P. northropi* size and probability value: $TL = 1.172 CL - 1.116$ ($p = 0.002$; $r^2 = 0.97$).

Table 1. Number of specimens and carapace length (CL) of males (M) and females (F) of *Palaemon pandaliformis* and *P. northropi* infested by *Probopyrus* sp. Developmental stage, total length (TL) and total width (TW) of males and females of *Probopyrus* sp.

Host shrimp data		Parasite data						
data		Females			Males			
	Sex	CL (mm)	Month	TL (mm)	TW (mm)	Developmental stage	TL (mm)	TW (mm)
<i>P. pandaliformis</i>	M	4.48	nov/03	3.88	2.95	ovigerous		
	M	3.82	nov/03	2.86	2.12	ovigerous	0.72	0.18
	M	3.97	nov/03	3.41	2.38	mature female	1.02	0.42
	M	4.35	nov/03	3.55	3.1	mature female	1.33	0.57
	M	3.21	aug/03	2.33	1.86	mature female	0.75	0.18
	M	3.42	oct/03	2.67	1.82	mature female	0.82	0.27
	M	3.51	oct/04	2.82	2.02	mature female	0.96	0.36
	M	4.36	sep/03	3.48	2.77	mature female	1.01	0.48
	M	3.58	sep/04	2.27	1.64	mature female		
	M	4.38	sep/04	3.63	2.74	mature female	1.16	0.54
	M	3.19	sep/04	2.8	3.51	mature female	1	0.49
	M	3.12	mar/04	2.45	1.81	mature female	0.74	0.18
	M	4.49	jun/03	3.96	2.95	mature female	0.92	0.28
	M	3.58	jul/03	1.96	1.43	mature female	0.73	0.19
	M	3.71	jul/03	2.77	2.08	mature female		
	M	3.16	jul/03	1.98	1.46	mature female		
M	3.68	jul/03	2.66	1.99	mature female			
<i>P. northropi</i>	M	4.23	dec/03	3.83	2.82	mature female	0.86	0.36
	M	4.19	aug/03	4.05	2.99	ovigerous	0.95	0.45
	M	3.75	aug/04	3.09	2.32	mature female		
	F	5.74	nov/03	5.56	3.87	ovigerous	1.61	0.63
	F	5	nov/03	4.74	3.13	mature female	1.38	0.5

Table 2. Prevalence of *Probopyrus* sp. in *Palaemon* species at the Ubatumirim River estuary, southeast coast of Brazil.

Date	<i>P. pandaliformis</i>			<i>P. northropi</i>		
	N	Parasite	Prevalence (%)	N	Parasite	Prevalence (%)
Mar-03	191	1	0.52	0	0	0
Apr-03	230	0	0	10	0	0
May-03	314	0	0	57	0	0
Jun-03	285	1	0.35	39	0	0
Jul-03	83	4	4.94	65	0	0
Aug-03	235	1	0.42	44	2	4.54
Sep-03	241	4	1.65	131	0	0
Oct-03	286	2	0.7	51	0	0
Nov-03	391	4	1.02	46	2	3.63
Dec-03	221	0	0	43	1	2.05
Jan-04	231	0	0	0	0	0
Feb-04	170	0	0	0	0	0

Table 3. List of palaemonid shrimps infested by *Probopyrus* sp. (Isopoda, Bopyridae).

USA = United States of America; SP = state of São Paulo; ES = state of Espírito Santo; PR = state of Paraná.

Host shrimp	Geographic location	Reference
<i>Macrobrachium potiuana</i>	Paranaguá, PR, Brazil	Masunari et al., 2000
<i>Macrobrachium potiuana</i>	Cananéia, SP, Brazil	Rocha & Bueno, 2000
<i>Palaemon northropi</i>	Ubatuba, SP, Brazil	Present study
<i>Palaemon pandaliformis</i>	Ubatuba, SP, Brazil	Present study
<i>Palaemon paludosus</i>	Florida, USA	Richardson, 1904
<i>Palaemon paludosus</i>	Guarapari, ES, Brazil	Lemos de Castro & Brasil-Lima, 1974
<i>Palaemon paludosus</i>	Florida, USA	Dale and Anderson, 1982
<i>Palaemon paludosus</i>	Georgia, USA	Lemos de Castro & Brasil-Lima, 1974
<i>Palaemon pugio</i>	Alabama, USA	Sheehan et al., 2011
Unidentified palaemonid	São Vicente, SP, Brazil	Carvalho, 1942

DISCUSSION

We record here, for the first time, the infestation of *P. pandaliformis* and *P. northropi* by *Probopyrus* sp. on the southeast coast of Brazil. According to Ocaña-Luna *et al.* (2009), bopyrids of the genus *Probopyrus* typically infest palaemonid prawns from the following genera: *Macrobrachium* Spence Bate, 1868 and *Palaemon*. In South America, the association of *P. floridensis* with the host *Palaemon paludosus* (Gibbes, 1850) (as *Palaemonetes exilipes*) has been reported by Lemos de Castro and Brasil-Lima (1974), and the same parasite infested *Macrobrachium potiuna* (Muller, 1880) according to Masunari *et al.* (2000), and Rocha and Bueno (2000). Two more palaemonid species are here recorded as hosts of a *Probopyrus* species. Information on host specificity of bopyrids and their geographic distribution are scarce for most species (Romero-Rodríguez *et al.*, 2017). Even when studies have addressed ecological information of the hosts, reports about their parasites were often neglected or omitted (Romero-Rodríguez *et al.*, 2017). Williams and Boyko (2012) mentioned that the absence of some parasitic groups, in certain areas, might be related to the lack of sampling.

Ectoparasitism in palaemonid shrimps by *Probopyrus* sp. is not host species-specific, or even host genus-specific, since infestations by species of *Probopyrus* have been reported for five different host species (Tab. 3). The same pattern was verified for *Probopyrus bithynis* (as *P. pandalicola* Packard, 1879) that was recognized to infest several *Macrobrachium* species (Markham, 1985). Infestation on *Palaemon* species has been previously reported for *P. pandaliformis* by both *P. palaemoni* and *P. bithynis* (Dale and Anderson, 1982; Markham, 1985). The latter parasite also infests *P. northropi*, as mentioned by Lemos de Castro and Brasil-Lima (1974).

We cannot accurately identify the species of the *Probopyrus* specimens obtained, mainly because we only had adult individuals. Dale and Anderson (1982) described *Probopyrus* larvae from northwest Atlantic and found that it is possible to distinguish three species based on larval features: *P. pandalicola*, *P. floridensis* and *P. bithynis*. According to Markham (1985), these species cannot be distinguished in the adult stage.

Although the relationship of *Probopyrus* with a palaemonid host has already been reported in the state of São Paulo (Rocha and Bueno, 2000), our study

expanded the distribution of this bopyrid genus, adding a new locality on the southeast region of Brazil, in the Ubatumirim River. In general, the range of distribution of *Probopyrus* sp. is narrower than that of its host species (Ocaña-Luna *et al.*, 2009). In the present study, the distribution area of *Probopyrus* sp. was extended to the northern coast of São Paulo State, although the parasite distribution remains more limited than that of its hosts.

The mean prevalence of *Probopyrus* sp. in both *Palaemon* species hosts during monthly samplings was relatively low, as it was also found by Rocha and Bueno (2000). On the other hand, Masunari *et al.* (2000) found a higher value of prevalence for *P. floridensis* in *M. potiuna*. According to these authors, monthly infestation varied from 1.1% to 91.7% throughout the year, when taking into account all life cycle stages of the parasites, in Paranaguá Bay, state of Paraná, Brazil. The differences between our results and those from other studies in the South Atlantic area might be related to numerous factors, such as density of cryptoniscid larvae, massive recruitment of hosts during specific periods of the year, natural mortality of shrimps, and the annual life cycle of the parasites. Further studies should be done to make a detailed examination of this host/parasite relationship. We found that the proportion of parasitized specimens varied during the study period for both host populations. There was an absence of bopyrids for at least five months of the year for both host species. As noted by Masunari *et al.* (2000), we suspect that the reproduction of *Probopyrus* sp. occurs once a year in the Ubatumirim estuary. However, our data on monthly prevalence do not support the conclusion that the parasite's reproduction is seasonal for both shrimp species from the study area.

In the present study, infestation by *Probopyrus* sp. occurred mostly in males of *P. pandaliformis*, differently from studies conducted on other carideans, in which parasite prevalence was either higher in female hosts (Chaplin-Ebanks and Curran, 2007; Rasch and Bauer, 2015) or equivalent for both sexes (Jarrin and Shanks, 2008). With respect to *P. northropi*, it is not possible to conclude on its host sex-specific prevalence due to the low number of parasites found in the collected specimens.

In other decapod species with sexual dimorphism associated with body size, bopyrid infestation can be higher in larger hosts (Jordá and Roccatagliata,

2002). When there are no apparent morphological differences, the parasites may infest both sexes at the same proportion (Blower and Roughgarden, 1988). Thus, in the case of crustacean hosts, bias for males in a host-parasite system could be attributed to differences in sexual selection pressure. An experimental test with a copepod revealed a male-biased susceptibility to helminth infection attributed to sexual selection (Wedekind and Jakobsen, 1998). Although sexual selection on *Palaemon* species has not been detailed yet, a possible explanation for male bias is that males experience higher intra-sexual selection. Thus, their energetic resources are used up more rapidly, and this can cause a reduced ability to avoid infestation (Wedekind and Folstad, 1994).

Our data indicate that specimens of *P. pandaliformis* and *P. northropi* may be parasitized in the juvenile stage. The size of the hosts correlated positively with the size of the parasites (Fig. 2); the largest specimens of *Probopyrus* sp. (larger than 1 mm TL) were found in larger shrimps (larger or equal to 3.97 mm CL). Cryptoniscid larvae usually infest shrimps during the host's early developmental stages and grow together with the hosts, although this is not always the case; in rare cases, bopyrids may infest older and larger shrimp hosts (Conner and Bauer, 2010). Video observations of *P. pandalicola* infesting *Palaemon pugio* (Holthuis, 1949) suggest that most bopyrids must survive through the ecdysis of the host (Cash and Bauer, 1993).

In summary, our results indicate that there is a low and variable prevalence of *Probopyrus* sp. on both sympatric host populations. Thus, it is suggested that these infestations may not negatively affect the presently studied *Palaemon* species. However, for better understanding the role played by this bopyrid in *Palaemon* population dynamics, further studies in the field and laboratory are still necessary.

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REFERENCES

- Anderson, G. 1990. Postinfection mortality of *Palaemonetes* spp. (Decapoda: Palaemonidae) following experimental exposure to the bopyrid isopod *Probopyrus pandalicola* (Packard) (Isopoda: Epicaridea). *Journal of Crustacean Biology*, 10: 284–292.
- Anger, K. and Moreira, G.S. 1998. Morphometric and reproductive traits of tropical caridean shrimps. *Journal of Crustacean Biology*, 18: 823–838.
- Bass, C.S. and Weis, J.S. 1999. Behavioral changes in the grass shrimp, *Palaemonetes pugio* (Holthuis), induced by the parasitic isopod, *Probopyrus pandalicola* (Packard). *Journal of Experimental Marine Biology and Ecology*, 241: 223–233.
- Beck, J.T. 1980. The effects of an isopod castrator, *Probopyrus pandalicola*, on the sex characters of one of its caridean shrimp hosts, *Palaemonetes paludosus*. *The Biological Bulletin*, 158: 1–15.
- Blower, S.M. and Roughgarden, J. 1988. Parasitic castration: host species preferences, size-selectivity and spatial heterogeneity. *Oecologia*, 75: 512–515.
- Boyko, C.B. and Williams, J.D. 2009. Crustacean parasites as phylogenetic indicators in decapod evolution. p. 197–220. In: J.W. Martin, K.A. Crandall, and D.L. Felder (eds), *Crustacean Issues 18. Decapod Crustacean Phylogenetics*. Boca Raton, FL, CRC Press.
- Carvalho, P.J. 1942. Nota sobre *Probopyrus floridensis* Richardson. *Boletim da Indústria Animal*, 5: 125–133.
- Carvalho, F.L., De Grave, S. and Mantelatto, F.L. 2017. An integrative approach to the evolution of shrimps of the genus *Palaemon* (Decapoda, Palaemonidae). *Zoologica Scripta*, 46: 473–485.
- Cash, C.E. and Bauer, R.T. 1993. Adaptations of the branchial ectoparasite *Probopyrus pandalicola* (Isopoda: Bopyridae) for survival and reproduction related to ecdysis of the host, *Palaemonetes pugio* (Caridea: Palaemonidae). *Journal of Crustacean Biology*, 13: 111–124.
- Chaplin-Ebanks, S.A. and Curran, M.C. 2007. Prevalence of the bopyrid isopod *Probopyrus pandalicola* in the grass shrimp, *Palaemonetes pugio*, in four tidal creeks on the South Carolina-Georgia coast. *The Journal of Parasitology*, 93: 73–77.
- Choong, F.C.; Shaharom, F.; Bristow, G.A.; Rashid, Z.A. and Kua, B.C. 2011. *Probopyrus buitendijki* (Isopoda, Bopyridae), a parasitic isopod on *Macrobrachium rosenbergii* in Timun River, Negeri Sembilan, Malaysia. *Crustaceana*, 84: 1051–1059.
- Colpo, K.D.; Chacur, M.M.; Guimaraes, F.J. and Negreiros-Franozo, M.L. 2011. Subtropical Brazilian mangroves as a refuge of crab (Decapoda: Brachyura) diversity. *Biodiversity and Conservation*, 20: 3239–3250.
- Conner, S.L. and Bauer, R.T. 2010. Infection of adult migratory river shrimps, *Macrobrachium ohione*, by the branchial bopyrid isopod *Probopyrus pandalicola*. *Invertebrate Biology*, 129: 344–352.
- Dale, W.E. and Anderson, G. 1982. Comparison of morphologies of *Probopyrus bithynis*, *P. floridensis*, and *P. pandalicola* larvae

- reared in culture (Isopoda, Epicaridea). *Journal of Crustacean Biology*, 2: 392–409.
- Holthuis, L.B. 1952. A general revision of the Palaemonidae (Crustacea Decapoda Natantia) of the Americas. Part II. The subfamily Palaemoninae. *Allan Hancock Foundation Publications: Occasional Papers*, 12: 1–296.
- Jarrin, J.R.M. and Shanks, A.L. 2008. Ecology of a population of *Lissocrangon stylirostris* (Caridea: Crangonidae), with notes on the occurrence and biology of its parasite, *Argeia pugettensis* (Isopoda: Bopyridae). *Journal of Crustacean Biology*, 28: 613–621.
- Jordá, M.T. and Roccatagliata, D. 2002. Population dynamics of *Leidya distorta* (Isopoda: Bopyridae) infesting the fiddler crab *Uca uruguayensis* at the Río de La Plata estuary, Argentina. *Journal of Crustacean Biology*, 22: 69–82.
- Lemos de Castro, A. and Brasil-Lima, I.M. 1974. Crustáceos isópodes epicarídeos do Brasil IX. Gênero *Probopyrus* Giard and Bonnier. *Revista Brasileira de Biologia*, 34: 209–218.
- Lester, R.L.G. 2005. Isopoda (isopods). p. 138–144. In: K. Rohde (ed), *Ecology of Marine Parasites*. Victoria, Australia, CSIRO Publishing.
- Margolis, L.; Esch, G.W.; Holmes, J.C.; Kuris, A.M. and Schad, G.A. 1982. The use of ecological terms in Parasitology (Report of an Ad Hoc Committee of the American Society of Parasitologists). *The Journal of Parasitology*, 68: 131–133.
- Markham, J.C. 1985. A review of the bopyrid isopods infesting caridean shrimps in the northwestern Atlantic ocean, with special reference to those collected during the Hourglass Cruises in the gulf of Mexico. *Memoirs of the Hourglass Cruises*, 7: 1–156.
- Masunari, S.; Castagini, A.S. and Oliveira, E. 2000. The population structure of *Probopyrus floridensis* (Isopoda, Bopyridae), a parasite of *Macrobrachium potiuna* (Decapoda, Palaemonidae) from the Perequê River, Paranaguá Basin, Southern Brazil. *Crustaceana*, 73: 1095–1108.
- Melo, G.A.S. 2003. *Manual de identificação dos Crustacea Decapoda de água doce do Brasil*. São Paulo, Loyola.
- Mortari, R.C. and Negreiros-Fransozo, M.L. 2007. Composition and abundance of the caridean prawn species in two estuaries from the northern coast of São Paulo State, Brazil. *Acta Limnologica Brasileira*, 19: 211–219.
- Mortari, R.C.; Pralon, B.G.N. and Negreiros-Fransozo, M.L. 2009. Reproductive biology of *Palaemon pandaliformis* (Stimpson, 1871) (Crustacea, Decapoda, Caridea) from two estuaries in southeastern Brazil. *Invertebrate Reproduction and Development*, 53: 223–232.
- Ocaña-Luna, A.; Martínez-Guzmán, L.A. and Sánchez-Ramírez, M. 2009. Nuevos registros del parásito *Probopyrus pacificensis* (Isopoda: Bopyridae) en el sur de Nayarit y norte de Jalisco, México. *Revista Mexicana de Biodiversidad*, 80: 259–261.
- Oliveira, E. and Masunari, S. 2006. Distribuição temporal de densidade de *Aporobopyrus curtatus* (Richardson) (Crustacea, Isopoda, Bopyridae), um parasito de *Petrolisthes armatus* (Gibbes) (Crustacea, Anomura, Porcellanidae) na Ilha do Farol, Matinhos, Paraná, Brasil I. *Revista brasileira de Zoologia*, 23: 1188–1195.
- Rasch, J.A. and Bauer, R.T. 2015. Temporal variation in population structure of the isopod *Urobopyrus processae* Richardson, 1904 (Isopoda: Bopyridae) infesting the branchial chamber of the night shrimp *Ambidexter symmetricus* Manning and Chace, 1971 (Decapoda: Processidae). *Nauplius*, 23: 89–103.
- Richardson, H. 1904. Contributions to the natural history of the Isopoda. *Proceedings of the United States National Museum*, 27: 1–89.
- Rocha, S.S. and Bueno, S.L.S. 2000. *Probopyrus floridensis* Richardson, 1904 (Isopoda, Bopyridae) parasitizing the freshwater prawn *Macrobrachium potiuna* (Muller, 1880), from São Paulo, Brazil. *Nauplius*, 8: 133–140.
- Romero-Rodríguez, J.; Guillén-Hernández, S. and Simões, N. 2017. First report of the parasite crustacean *Leidya distorta* (Isopoda: Bopyridae) on the fiddler crab *Uca spinicarpa* (Decapoda: Brachyura) in Yucatán coasts, Mexico. *Revista Mexicana de Biodiversidad*, 88: 459–463.
- Sheehan, K.L.; Lafferty, K.D.; O'Brien, J. and Cebrian, J. 2011. Parasite distribution, prevalence, and assemblages of the grass shrimp *Palaemonetes pugio*, in southwestern Alabama, USA. *Comparative Parasitology*, 78 (2): 245–256.
- Sherman, M.B. and Curran, M.C. 2015. Sexual sterilization of the daggerblade grass shrimp *Palaemonetes pugio* (Decapoda: Palaemonidae) by the bopyrid isopod *Probopyrus pandalicola* (Isopoda: Bopyridae). *Journal of Parasitology*, 101: 1–5.
- Varisco, M. and Vinuesa, J. 2011. Infestation of the squat lobster *Munida gregaria* (Anomura: Galatheidae) by *Pseudione galacanthae* (Isopoda: Bopyridae) in San Jorge Gulf, Argentina. *Journal of the Marine Biological Association of the United Kingdom*, 91: 1681–1688.
- Wedekind, C. and Folstad, I. 1994. Adaptive or nonadaptive immunosuppression by sex hormones? *The American Naturalist*, 143: 936–938.
- Wedekind, C. and Jakobsen, P.J. 1998. Male-biased susceptibility to helminth infection: an experimental test with a copepod. *Oikos*, 81: 458–462.
- Wilkinson, L. 1988. SYSTAT: The system for Statistics. Evanston, Illinois, Systat Inc..
- Williams, J.D. and Boyko, C.B. 2012. The Global Diversity of Parasitic Isopods Associated with Crustacean Hosts (Isopoda: Bopyroidea and Cryptoniscoidea). *PLoS ONE*, 7: e35350.