Invertebrate Biology



Invertebrate Biology 129(4): 344–352. © 2010, The American Microscopical Society, Inc. DOI: 10.1111/j.1744-7410.2010.00210.x

Infection of adult migratory river shrimps, *Macrobrachium ohione*, by the branchial bopyrid isopod *Probopyrus pandalicola*

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Abstract. Macrobrachium ohione is a migratory (amphidromous) river shrimp (Decapoda, Caridea) that may be parasitized by the branchial parasite *Probopyrus pandalicola* (Isopoda, Bopyridae). The parasite disrupts gonadal maturation and spawning in female shrimps, resulting in the total loss of reproduction. Shrimps are usually infected by bopyrid parasites during the late zoeal or early postlarval stages; in this study, we investigated the apparent parasite infection of adult shrimps. We analyzed the relationships between parasite body size (total length) and host shrimp body size (carapace length) to test the hypothesis that parasite infection of adult shrimps occurs during the shrimps' reproductive migrations. The results presented here indicate that infection of adult shrimps is common in M. ohione in the Atchafalaya and Mississippi Rivers, Louisiana, USA. In the two upriver sites sampled, Butte La Rose (BLR) and River Bend (RB), parasite size was not associated with host body size. In these locations, many parasitized adult M. ohione were infected with immature P. pandalicola (40.3% in BLR and 51.2% in RB), indicating that the shrimps were adults at the time of infection. A possible explanation is that when female shrimps enter the estuary to hatch larvae, they molt and spawn another brood. The smaller male shrimps that accompany the females downstream are also assumed to molt and continue growth. The intermediate host of the parasite is an estuarine copepod, and thus the parasite cryptoniscus larva that infects the host shrimp is primarily estuarine as well. Newly molted shrimps have soft cuticles, which may facilitate their infection by parasite cryptonisci. Our conclusion is that most infections of adult shrimps occur during their migration into estuarine waters, the primary habitat of infective parasite larvae, and that host vulnerability is probably increased following host ecdysis.

Additional key words: Caridea, Bopyridae, Probopyrus bithynis

Introduction

Macrobrachium ohione SMITH 1874 (Ohio shrimp) is a freshwater shrimp in which embryo-incubating females and males migrate from the upriver adult habitat down to brackish-water estuaries to release hatching larvae. The larvae must be exposed to saline water (optimally 10–15‰) in order to complete their development (Bauer & Delahoussaye 2008; Rome et al. 2009). After larval development in the sea, the resulting postlarvae move back into estuaries and then migrate as young juveniles upriver to the adult freshwater habitat, where growth to adulthood and breeding occur. This diadromous life-history pattern is termed amphidromy (McDowall 1992).

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The Ohio shrimp is endemic to coastal rivers in the central and southeastern United States, and previously occurred in abundance in the Mississippi River System (MRS) from as far north as the Missouri and lower Ohio Rivers down to the Gulf of Mexico (Holthuis 1952; Huner 1977; Taylor 1992; Bowles et al. 2000; Barko & Hrabik 2004). Population density has drastically declined in the upper MRS from that of the 1930s (Taylor 1992; Conaway & Hrabik 1997). Relatively few *M. ohione* (\sim 9) have been reported in the Ohio River since 1977 (Taylor 1992; Conaway & Hrabik 1997; Poly & Wetzel 2002). This decline is primarily attributed to anthropomorphic habitat disturbance, e.g., the effects of dams, levees, and wing dikes (Bowles et al. 2000; Barko & Hrabik 2004). In the lower MRS, particularly in Louisiana, M. ohione is still abundant and an important bait shrimp; in the past, it sustained a commercial food fishery in both the lower and the upper MRS (Huner 1977; Truesdale & Mermilliod 1977).

Parasitism in amphidromous shrimps

Probopyrus pandalicola PACKARD 1879 is a bopyrid isopod parasite that is found on M. ohione (it is sometimes referred to as Probopyrus bithynis RICHARDSON 1904: see Van Name 1936; Truesdale & Mermilliod 1977; Dale & Anderson 1982; then synonymized with P. pandalicola by Markham 1985). The epicaridium (hatching) larvae of this parasite must find and infect brackish-water calanoid copepods (specifically Acartia tonsa DANA, 1849; Dale & Anderson 1982), their intermediate hosts. Once attached to the copepod, an epicaridium metamorphoses into a microniscus larva, which then metamorphoses into a cryptoniscus larva. The cryptoniscus then quickly detaches from the copepod and searches for a definitive host, in this case, an individual of M. ohione. Sex determination is apparently environmental. The first cryptoniscus larva to infect a shrimp becomes a female. A subsequent cryptoniscus larva that enters the branchial chamber of an already infected host will attach to the female parasite and becomes a male (Anderson 1975; Overstreet 1978; Dale & Anderson 1982; O'Brien & Van Wyk 1985).

Bopyrids usually infect very young shrimps (zoeal and early postlarval stages, Anderson 1990) and then grow together with the hosts (Van Name 1936; Pike 1960; Beck 1979; Truesdale & Mermilliod 1977), resulting in positive linear correlations between parasite and host sizes (Van Name 1936; Pike 1960; Beck 1980; Cash & Bauer 1993). Pike (1960) suggested that the hardened adult cuticle is not pliable enough to accommodate the rapid growth of a newly settled bopyrid parasite. Shrimp zoea and postlarvae molt frequently and hence often have soft cuticles, in comparison with young adult shrimps. The soft branchiostegite (gill cover) possibly allows for easy parasite attachment to the host (Anderson 1990).

Recent collections of specimens of M. ohione from two Louisiana rivers yielded a number of large shrimps with relatively small, immature female P. pandalicola. This indicated that these shrimps may have been infected not as late-stage zoeal larvae or early postlarvae, but as adults. In this study, we investigated the hypothesis that individuals of M. ohione are frequently infected as adults. We tested this hypothesis by analyzing variation in parasite and host body size in estuarine and upriver populations of M. ohione. Our results on possible infection of adult shrimps are interpreted in light of the seasonal migration of reproductive adults to estuaries in this amphidromous species.

Materials and methods

Specimens of *Macrobrachium ohione* were collected every 2 weeks during 2008 with 6.4 mm mesh hard-



Fig. 1. Map of sampling sites on the Atchafalaya River (AR) and Mississippi River (MR), Louisiana, USA. AD, Atchafalaya Delta Wildlife Management Area (29°25'N, 91°18'W); BLR, Butte La Rose (146 km north of the Atchafalaya River mouth at 30°19'N, 91°41'W); PAL, Pass a Loutre Wildlife Management Area in the Mississippi River delta (29°12'N, 89°02'W); RB, River Bend (411 km upriver from the Mississippi River mouth at 30°43'N, 91°21'W).

ware cloth shrimp traps described in Bauer & Delahoussaye (2008). Four sample sites (two delta and two upriver locations) were chosen in two MRS rivers (Atchafalaya and lower Mississippi) in southern Louisiana, USA. Traps were set and collected by the Louisiana Department of Wildlife and Fisheries in the Atchafalaya River Delta Wildlife Management Area (AD) (29°25'N, 91°18'W) and the Pass a Loutre Wildlife Management Area (PAL) in the Mississippi River Delta $(29^{\circ}12'N, 89^{\circ}02'W)$. The traps set in the upriver sites were collected by T.J. Olivier at Butte La Rose (BLR) (146 km north of the Atchafalaya River mouth at 30°19' N, 91°41'W) and at River Bend (RB) (411 km upriver from the Mississippi River mouth at 30°43'N, 91°21'W) (Fig. 1). Samples were initially preserved in 10% freshwater formalin, washed with tap water, and then transferred to 70% ethanol for permanent storage.

Parasitized shrimps were removed from collections for observation. Shrimps with large parasites were easily detected by a conspicuous bulge in the carapace of the host as well the obvious pigmentation of the female parasite or its brood (Fig. 2). The presence of a small, immature female parasite could be recognized by a pattern of spots or "freckles" on the host's branchiostegite (gill cover) consistent with the site on

Fig. 2. An adult *Macrobrachium ohione* parasitized by the bopyrid *Probopyrus pandalicola*. F, mouth parts of female parasite; L, unreleased larvae in female's marsupium; M, male parasite attached to female pleotelson. Scale bar = 4 mm.

the inner branchiostegite to which the female parasite attaches (Figs. 3A,B, 4A,B). This freckling may be due to the scarring of the branchiostegite caused by the female parasite's attempts to attach. Crustacean cuticles scar with brown-black pigmentation when damaged (Stevenson 1985).

Host shrimp body size was measured as carapace length (CL, mm), the distance from the posterior edge of the eye orbit to the posterior middorsal edge of the carapace. Female parasite body size was measured by the total length (TL, mm), the distance from the anteriormost edge of the cephalon to the posteriormost edge of the telson. The degree of development of female parasite oostegites and marsupium (brood pouch), absence or presence (and degree of development) of parasite embryos, and the degree of development of the presumptive male parasite were also recorded.

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Variation in parasite body size with host body size was investigated using linear regression analysis on the two delta populations (AD and PAL) as well as on all upriver subgroups. Female parasite TL (dependent variable) was regressed on host CL (independent variable). The 2008 biweekly data were pooled for each site and tested for normality using the Shapiro–Wilk test. The hypothesis that the slope (*b*) of the regression line is zero was tested with linear regression using a significance level of $\alpha = 0.05$. All data were tested with SAS On Demand software (SAS Institute Inc., Cary, NC, USA). Graphs were generated using Microsoft Excel, 2007.

Results

Parasitized shrimps were found at all sites. At AD, two of 447 (0.4%) female and six of 253 (2.4%) male shrimps were parasitized; at BLR, 85 of 714 (11.9%) females and 54 of 598 (9.0%) males were parasitized. At PAL, 90 of 1930 (4.7%) females and 16 of 116 (13.8%) males were infected, while at RB, 31 of 347 (8.9%) females and 12 of 359 (3.3%) males carried bopyrids.

In the delta populations (AD, PAL), most parasitized shrimps had fully mature female and male parasite pairs infesting the branchial chamber. However, populations in each of the upriver sites (BLR and RB) had parasites in varying stages of maturity. Each of these upriver populations was divided into three subgroups (A, B, and C). The divisions were based on the level of maturity of the female parasites (degree of development of oostegites and marsupia) as well as the absence or the degree of development of the male parasites. The upriver subgroups (BLR-A and RB-A) consisted of immature female parasites averaging 3.59 mm TL, with underdeveloped oostegites (no marsupia); these female parasites were unaccompanied by males and occurred on hosts of average CL 12.45 mm (Fig. 3). Subgroups BLR-B and RB-B included immature female parasites averaging 5.14 mm TL, with underdeveloped oostegites (no marsupia), and accompanied either by a cryptoniscus larva or an immature presumptive male on hosts of average CL 12.55 mm. Presumptive males. intermediate in morphology between the cryptoniscus and mature male, averaged 0.76 mm TL (Fig. 4). Subgroups BLR-C and RB-C included shrimps averaging 12.22 mm CL with mature female parasites averaging 7.40 mm TL, with fully formed oostegites and marsupia and accompanied by mature male parasites averaging 1.75 mm TL (Fig. 5, Table 1).

Parasitized shrimps from the sampled deltas (AD, PAL) were infected with fully mature female and male parasite pairs (equivalent to the upriver Subgroup C) in

one branchial chamber (three of 195 shrimps in the upriver samples were infected in both gill chambers); only one female parasite in AD was unaccompanied by a male. In these delta populations, female parasite size was highly correlated with host body size. Regressions of parasite on host size were significant in both the AD and the PAL populations ($R^2 = 0.8115$, p = 0.0023, n = 8; $R^2 = 0.5844$, p < 0.0001, n = 106, respectively) (Fig. 6).

Variation in female parasite TL with host body size (CL) was examined in the two upriver populations, Atchafalaya (BLR) and the Mississippi (RB), each of which consisted of three subgroups (Fig. 7). In the upriver subgroups with immature female parasites and no male parasites (BLR-A and RB-A), variation in female parasite TL was not significantly explained by host CL ($R^2 = 0.0275$, p = 0.3201, n = 38; $R^2 = 0.0134$, p = 0.6932, n = 14, respectively). In one of the subgroups that contained immature female and immature male parasites (RB-B), the variation in female parasite TL was not significantly explained by host CL $(R^2 = 0.0068, p = 0.8456, n = 8)$, but was in the other (BLR-B; $R^2 = 0.3440$, p = 0.0105, n = 18). Variation in female parasite TL was significantly explained by host CL in the subgroups with fully mature female-male parasite pairs (BLR-C, $R^2 = 0.3869$, p<0.0001, n = 83and RB-C, $R^2 = 0.7739$, p<0.0001, n = 21) as well as in both delta populations (AD and PAL; see above).

Discussion

The results presented here indicate that specimens of the amphidromous river shrimp, Macrobrachium ohione, may be infected in the adult stage. It is commonly stated in the literature that cryptoniscus larvae of the bopyrid Probopyrus pandalicola attach to the smallest host (shrimp) size classes (Van Name 1936; Pike 1960; Beck 1979, 1980; Truesdale & Mermilliod 1977). Anderson (1990) showed, in P. pandalicola infecting the shrimp Palaemonetes pugio HOLTHUIS 1949, that the first cryptoniscus larva to find a definitive host (a zoea larva or early postlarva) enters the cephalothorax of the host within 24 h of contact with the host. It becomes an endoparasite, probably entering the host hemocoel. After $\sim 1-2$ weeks, the parasite emerges into the host branchial chamber (Anderson 1990), attaches to the shrimp's branchiostegite as an ectoparasite, and then becomes an adult female (Anderson 1975; Overstreet 1978; Dale & Anderson 1982; O'Brien & Van Wyk 1985). Subsequent cryptoniscus larvae that enter the branchial chamber of already infected hosts will attach to the female parasites, never becoming endoparasites (Anderson 1990), and will become males (Anderson



Fig. 4. Representative of upriver Subgroup B host-parasite complex. A. View of adult Macrobrachium ohione carapace with patterned scarring ("freckling," F) on the branchiostegite indicating infection by an immature female Probopyrus *pandalicola*. Scale bar = 2 mm. **B**. Higher magnification of freckling on host branchiostegite. Scale bar = 1 mm. C. An immature female parasite accompanied by an immature male. M, accompanying cryptoniscus/presumptive immature male; O, underdeveloped oostegites. Scale bar = 1 mm.

1975; Overstreet 1978; Dale & Anderson 1982; O'Brien & Van Wyk 1985) within 24 h after contact with the females (Anderson 1990). A male may remain with the same female, and thus host, throughout its lifetime (Cash & Bauer 1993).

Anderson (1990) suggested that the hosts become more resistant to parasite larval attachment over time. The host is most susceptible to infection as a zoea larva or early postlarva because these stages molt frequently, which may aid attachment (Anderson 1990). However, our results suggest that adult M. ohione can be infected as adults, in spite of low molting rates, because of their seasonal reproductive migration from upriver down into estuaries in which the parasite infective stage is likely to be abundant. Bauer & Delahoussaye (2008) found that adult females in the Atchafalaya River (e.g., BLR) migrate to the AD estuary, release larvae from the brood they are incubating, and then molt, mate, spawn, and later release a second brood in the AD estuary. This process apparently also occurs in the PAL estuary (T.J. Olivier, pers.

comm.). If females produce more than two broods in the estuary and thus undergo further posthatching/ premating molts, the opportunity for infection is further increased. Adult males are abundant in the estuaries only during the hatching season, indicating that they too make the downstream reproductive migration to the estuary (population abundance data in Bauer & Delahoussaye 2008), where infection may occur following ecdyses.

At the end of the spring/summer hatching season, the adults then migrate back to the freshwater adult habitat (Truesdale & Mermilliod 1977). Our study shows that some of the returning shrimps have become infected with bopyrid parasites. The reason why members of Subgroups BLR-A and RB-A are unaccompanied by cryptonisci or immature presumptive males may be because, as Anderson (1990) found, it takes a few weeks for the female to transform from an endo- to an ectoparasite. If the host shrimp migrates out of the estuary and away from other cryptonisci of *P. pandalicola*, a potential

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Fig. 5. Representative of upriver Subgroup C host–parasite complex. A. View of adult *Macrobrachium ohione* with bulging carapace indicating infection by a mature female and a mature male (M) *Probopyrus pandalicola*. The female parasite has well-developed oostegites (O). Scale bar = 2 mm. B. Typical mature male *P. pandalicola*. Scale bar = 0.5 mm. C. Typical mature female parasite (without a brood in the marsupium, allowing the fully developed oostegites [O] to be easily viewed). Scale bar = 1 mm.

male will not be present to settle onto the female. Patterns observed in members of Subgroup B (immature female accompanied by a cryptoniscus or an immature male) have a similar explanation. In this scenario, the male or the female shrimp molts and is infected early during its stay in the estuary, giving the female cryptoniscus time to develop to an immature female stage and for a presumptive male cryptoniscus to pair up with it. As with members of Subgroup A, these infected shrimps began the return trip to adult freshwater habitat, where they were collected (in our study) at BLR and RB with the female parasite more developed than in Subgroup A and accompanied by a cryptoniscus or an immature male. The C subgroup adults are shrimps infected as larvae or postlarvae in the estuaries so that the female parasite and its host grow larger together, displaying the typical positive linear correlation between parasite and host size that is reported in the literature (Van Name 1936; Pike 1960; Beck 1979, 1980; Truesdale & Mermilliod 1977; Anderson 1990; Cash & Bauer 1993).

Beck (1979) found specimens of P. pandalicola infecting the freshwater grass shrimp Palaemonetes paludosus GIBBES 1850 as far as 33 km upstream. These shrimps do not migrate to saline waters to spawn, as do adults of *M. ohione*, indicating that some cryptonisci of P. pandalicola leave their estuarine intermediate hosts' habitat and actively swim upstream (13-33 km) in search of the definitive hosts (Beck 1979). It is unlikely that cryptonisci of P. pandalicola are able to reach populations of M. ohione in the MRS as far upstream as BLR (146 km north of the Atchafalaya River mouth), and especially not as far as RB (411 km north of the Mississippi River mouth). Rather, it is more probable that individuals of M. ohione infected as adults encounter infective parasites when the shrimps migrate into the estuary to reproduce. In three upriver subgroups (BLR-A, RB-A, and

Table 1. Sample size (*n*), average carapace length (CL) of host shrimps (*Macrobrachium ohione*), and average total length (TL) of the parasite *Probopyrus pandalicola* from two Louisiana delta sites (AD, Atchafalaya River Delta; PAL Pass a Loutre, Mississippi River Delta) and two upriver sites (BLR, Butte La Rose, on the Atchafalaya River; RB, River Bend, on the Mississippi River). Subgroup A (BLR-A; RB-A) consists of shrimps infested with immature female parasites (underdeveloped oostegites, no marsupium) that are unaccompanied. Subgroup B (BLR-B; RB-B) includes shrimps with immature female individuals of *P. pandalicola* (with underdeveloped marsupia, and accompanied by either a cryptoniscus or an immature presumptive male). Subgroup C (BLR-C; RB-C) contains shrimps with mature female parasites (with fully formed oostegites and marsupia) and mature male parasites.

	п	Mean shrimp CL (mm)	Mean female parasite TL (mm)	Mean male parasite TL (mm)
AD	8	10.6	6.54	1.21
BLR-A	38	12.4	3.52	
BLR-B	18	12.6	5.17	0.76
BLR-C	83	11.9	7.49	1.85
PAL	106	9.2	6.51	1.25
RB-A	14	12.5	3.65	
RB-B	8	12.5	5.10	0.75
RB-C	21	12.6	7.30	1.64



Fig. 6. Variation in the total length of female specimens of the parasite *Probopyrus pandalicola* as a function of their host shrimp (*Macrobrachium ohione*) carapace length, in two Louisiana delta sampling sites. Shrimps were infected with mature female parasites (with fully formed oostegites and marsupia) which were accompanied by mature male parasites. **A.** Atchafalaya River Delta ($R^2 = 0.8115$, p = 0.0023, n = 8); **B.** Pass a Loutre, Mississippi River Delta ($R^2 = 0.5844$, p < 0.0001, n = 106). CL, carapace length; TL, total length.

RB-B), there was no significant correlation between female parasite size and host size (Fig. 7), suggesting that these hosts were very recently infected and the parasites had not yet had time to grow and fill the host branchial cavity. A possible explanation is that these adult female shrimps went into the estuary to hatch their broods. After spawning, the females molted, and the resulting soft cuticle may have facilitated bopyrid cryptoniscus attachment. Adult males also migrate into the deltas and undergo growth molts that expose them to infection. It should be noted, however, that there is much debate as to whether P. pandalicola is a single species as synonymized by Markham (1985) or three (P. pandalicola, Probopyrus bithynis, and Probopyrus floridensis RICHARDSON 1904) as concluded by Dale & Anderson (1982). If much-needed DNA work on *Probopyrus* systematics concludes that the bopyrids infecting adults of M. ohione are members of P. bithynis and not of P. pandalicola, then this comparison may be less appropriate.

There are at least two possible reasons that immature female parasites were not found on adult M. *ohione* from the delta sites. One is that at the time of collection, the presumptive female cryptoniscus was still an endoparasite and had not yet emerged from the host hemocoel into the brachial chamber, thus eluding detection. The second possibility is the female parasite had not yet metamorphosed from the cryptoniscus form and thus had not attempted to attach to the host branchiostegite. This would result in a lack of freckling, and infections would be overlooked when samples were sorted.

Macrobrachium ohione is a shrimp of both ecological and commercial interest, although in recent

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Fig. 7. Variation in total length of female specimens of the parasite Probopyrus pandalicola as a function of their host shrimp (Macrobrachium ohione) carapace length, in two Louisiana upriver sampling sites. Subgroup A consists of specimens of M. ohione infested with immature female parasites (underdeveloped oostegites, no marsupia) that are unaccompanied by male parasites. Subgroup B includes shrimps with immature female P. pandalicola (with underdeveloped oostegites, no marsupia) that are accompanied by either a cryptoniscus larva or an immature presumptive male parasite. Subgroup C consists of shrimps with mature female parasites (with fully formed oostegites and marsupia) that are accompanied by mature male parasites. A. Butte La Rose (BLR), on the Atchafalaya River. BLR-A: $R^2 = 0.0275$, p = 0.3201, n = 38; BLR-B: $R^2 = 0.3440$, p = 0.0105, n = 18; BLR-C: $R^2 = 0.3869$. p < 0.0001, n = 83. B. River Bend (RB), on the Mississippi River. RB-A: $R^2 = 0.0134$, p = 0.6932, n = 14; RB-B: $R^2 = 0.0068$, p = 0.8456, n = 8; RB-C: $R^2 = 0.7739$, p < 0.0001, n = 21). CL, carapace length; TL, total length.

decades (since the 1930s), abundances and the commercial fishery have declined considerably, particularly in far-upstream populations of the MRS (Huner 1977; Bowles et al. 2000). Besides anthropomorphic degradation of habitat, natural factors may also be affecting the sizes of populations of *M. ohione*. The bopyrid parasite *P. pandalicola* (referred to as *P. bithynis* by Truesdale & Mermilliod 1977) considerably reduces the reproductive capacity of populations of M. ohione. Members of P. pandalicola (and other epicaridean isopods) are parasitic castrators that prevent ovarian maturation and spawning in female hosts (Pike 1960; Anderson 1977; Beck 1979; O'Brien & Van Wyk 1985). The energy that the host shrimp normally expends into reproduction and growth is apparently diverted to the maintenance and reproductive output of its bopyrid parasite. Bopyrids do not cause permanent gonad destruction, only a temporary cessation of function (Pike 1960), but as the parasite may live as long as its host (Beck 1980), this would result in lifetime sterility. There is also evidence that bopyrid parasitism may increase the mortality rates of young hosts in heavily parasitized populations (Anderson 1990). It is thus important to understand how individuals of M. ohione are parasitized, especially in light of its migratory life history. Further studies are also necessary to better understand the impact of parasitism on the host.

Acknowledgments. We thank Tyler J. Olivier for making, setting, and collecting shrimp traps at BLR and RB. We thank James Delahoussave and William Spell (Entergy Corporation River Bend Power Plant) for access to and sampling at the BLR and RB sites, respectively. We greatly appreciate the help of Cassidy Lejeune, Todd Baker, Jonathon Winslow, and Harold Prosperie, Louisiana Department of Wildlife and Fisheries, for arranging the collection of shrimps at the AD and PAL sites. This research was supported by the Louisiana Sea Grant College Program with funds from the National Oceanic and Atmospheric Administration Office of Sea Grant, Department of Commerce, under Grant No. NA06OAR4170022 with funds from UROP grant to Nicholas Rome and RTB, as well as Project No. R/SA-04 to RTB and Louisiana State University. Statements, findings, conclusions, and recommendations are those of the authors and do not necessarily reflect the views of Louisiana Sea Grant or the US Department of Commerce. This is Contribution #140 of the University of Louisiana at Lafayette's Laboratory for Crustacean Research.

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