

LIFE HISTORY MIGRATIONS OF THE AMPHIDROMOUS RIVER SHRIMP  
*MACROBRACHIUM OHIONE* FROM A CONTINENTAL LARGE RIVER SYSTEM

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A B S T R A C T

The hypothesis of an amphidromous life history pattern, with a female hatching migration from the river to an estuary, larval development in saltwater, and a return upriver migration by postlarvae (juveniles) was tested in the river shrimp *Macrobrachium ohione* in the Atchafalaya River, Louisiana, U.S.A. in 2006. A possible female migration from the river to the Atchafalaya Delta estuary (AD) to hatch incubated embryos was tested by comparing reproductive status of females sampled monthly from stations 146 km (Butte La Rose = BLR), 42 km (Berwick = BR), and 0 km from AD. Females only occurred in traps at AD only during the reproductive season (March to August) but were present throughout the year at other stations. The highest percentages of prehatching females occurred at the AD and BR stations while prehatching females were relatively rare at the upriver BLR station. Salt water requirements for larval development were tested by incubating first stage larvae from individual hatches in freshwater and saltwater (15 ppt) treatments (n = 10). The first stage (nonfeeding) larvae did not molt to second stage (feeding) larvae in freshwater, with significant mortality beginning after day 5. In saltwater, survival was high and most hatching larvae molted to stage 2 after 4-5 days of hatching. An upstream migration of juveniles began in mid-July 2006 and continued until October. Juvenile migrators were observed swimming near the surface from approximately one hour after sunset until at least early morning in a band of hundreds to thousands of individuals 1-2 m wide along the shore. Body size of migrators increased from downstream to upstream, suggesting that juveniles are feeding and growing during the migration. Hypotheses about whether formerly abundant far northern populations migrated to and from the sea are discussed. The decline of the species in the northern part of its range might be partially explained by human impacts on the juvenile migration and subsequent upstream recruitment.

KEY WORDS: amphidromy, Atchafalaya River, juveniles, *Macrobrachium*, migration

INTRODUCTION

Among the animals reported to make life-history migrations are various species of freshwater caridean shrimps (Bauer, 2004). All caridean females attach fertilized eggs beneath the pleon and then incubate the developing embryos for varying periods of time, after which the embryos hatch, usually as swimming larvae. In two large caridean families, some (Palaemonidae, especially species of *Macrobrachium*) or nearly all (Atyidae) species have invaded the freshwater environment. Some species are completely adapted to freshwater, especially those living in bodies of water without access to the sea. In such species, the planktotrophic larval development of the ancestral marine carideans has become direct, i.e., with hatching as a juvenile, or abbreviated, with just a few non-feeding larval stages of short duration.

However, many atyids and some freshwater palaemonids (*Macrobrachium* spp.) still require full larval development in saline waters, either brackish-water estuarine or full salinity nearshore habitats (Hunte, 1977, 1978; Hayashi and Hamano, 1984; Holmquist et al., 1998; March et al., 1998; Benstead et al., 2000). In some species, the upstream freshwater adult females release the larvae which drift to the saline larval habitat downstream (Hamano and Hayashi, 1992; March et al., 1998; Benstead et al., 1999, 2000). Some species of *Macrobrachium* are assumed, based on saline larval development and anecdotal field observations, to migrate to estuaries to hatch larvae [southeast Asian *M. rosenbergii* (De Man, 1879): Ling, 1969; Ismael and New, 2000; continental USA spp., Bowles et al., 2000]. After larval development, the newly settled benthic

juveniles (= postlarvae and subsequent early juvenile instars) must migrate back up into the adult freshwater riverine habitat at distances ranging from a few to many kilometers. This type of diadromous life cycle, in which there is recurring life history migration between freshwater and the sea that is not for the purpose of breeding (which occurs at some other stage of life cycle) was termed amphidromy by McDowall (1992).

The upstream migrations of juvenile amphidromous shrimps have now been observed in many locations around the world, e.g., Caribbean and other tropical islands (Holmquist et al., 1998; March et al., 2003; Covich et al., 2006), Brazil (Pompeu et al., 2006), Japan (Hamano and Hayashi, 1992), Australia (Lee and Fiedler, 1979) and India (Ibrahim, 1962). In these migrations, small juvenile shrimps swim upstream or walk and climb upstream in very shallow water along the bank, in the wetted splash zone along the bank just outside of the water. They are capable of climbing up or around cascades, low vertical walls and dams, as well as taller dams as long as there is an inclined surface with a suitable downstream water flow (Hayashi and Hamano, 1984; Hamano et al., 1995; Holmquist et al., 1998; March et al., 2003). The effect of river control structures and other human impacts, such as artificial lighting, on juvenile migrations has been the focus of an increasing number of studies in recent years (Hamano et al., 1995; Hamano and Honke, 1997; Holmquist et al., 1998; March et al., 1998; Benstead et al., 1999, 2000; Fievet, 2000; Pompeu et al., 2006).

*Macrobrachium ohione* (Smith, 1874) occurs in river systems flowing into the Gulf of Mexico and the Atlantic



Fig. 1. Reproductive female of *Macrobrachium ohione*; scale bar = 12 mm.

coast of the U.S. from Virginia to Florida (Holthuis, 1952; Hedgpeth, 1949; Bowles et al., 2000). This species has been reported throughout the Mississippi River System (MRS) as far north as the Missouri River and up into the Ohio River (from where it was described) from Illinois to Ohio (Holthuis, 1952; Barko and Hrabik, 2004). In the lower Mississippi River and its major Louisiana distributary, the Atchafalaya River, *M. ohione* is abundant (Huner, 1977; Bauer, personal observation) and appears to be a major prey item of river fishes. Reproductive females (Fig. 1) are from 30 to 90 cm total length while males are much smaller than females. Local commercial fishermen make extensive sets of traps to catch the shrimps for baiting trotlines and for sale in bait shops to recreational fishermen. Historically, the species was abundant enough to support a commercial fishery for bait and human consumption throughout the range of the species (McCormick, 1934; Gunter, 1937; Hedgpeth, 1949; Truesdale and Mermilliod, 1979; Bowles et al., 2000). By the middle of the last century, however, the abundance declined drastically in the upper MRS, and now *M. ohione* only occurs sporadically in these areas (Conaway and Hrabik, 1997; Barko and Hrabik, 2004). Possible causes for the decline in abundance include overfishing, river channelization, habitat loss, and chemical pollution (Bowles et al., 2000; Barko and Hrabik, 2004). The decline of this ecologically and commercially important species may be a result of human impacts on its probable amphidromous life cycle. An understanding of the life cycle of the species is essential for reduction of such impacts in attempts to restore the species to its former abundance and ecological/commercial importance in the MRS and other river systems.

Review papers on *Macrobrachium* in the United States (Hedgpeth, 1949; Bowles et al., 2000) suggest that coastal populations of *M. ohione* and other species of *Macrobrachium* in U.S. river systems are amphidromous. As in other *Macrobrachium* with apparently planktotrophic larvae, this assumption is derived from their distribution (all occur in rivers connecting to the sea) and their apparent

requirement of saline water for larval development in populations relatively near the sea. Initial studies on larval development of *M. ohione* were done on southeastern USA on species of *Macrobrachium*, including *M. ohione*, by Dugan (1971) and Dugan et al. (1975). Although informative and valuable in the context of possible aquaculture development, they were not designed to address questions about a migration hypothesis. Valuable information on reproduction and growth from size frequency studies on *M. ohione* from the Atchafalaya River was gathered by Truesdale and Mermilliod (1979). Reimer et al. (1974) sampled *M. ohione* in an estuarine habitat in Texas (Galveston Bay) throughout the year. Shrimps were only found from March through June, with greatest abundances of females incubating embryos in April and May. These observations suggested a seasonal movement (migration) of females from the river into the estuarine habitat, possibly for hatching of larvae from incubated embryos.

The objective of this study was to test the hypothesis of amphidromous life history migrations in *M. ohione*, i.e., a downstream hatching migration by females and an upstream juvenile migration after estuarine larval development. To test predictions from this hypothesis, measurements were done on the temporal and spatial distribution of reproductive females in the Atchafalaya River, USA. An experiment on the early larval development tested the prediction from amphidromy of obligate marine development. A post-developmental juvenile migration, another prediction from amphidromy, was searched for, discovered, and is documented and measured for the first time in a species of *Macrobrachium* from North America.

## MATERIALS AND METHODS

### Temporal and Spatial Distribution of Reproductive Females

After a period of preliminary sampling in the spring and summer of 2005, sampling for reproductive females for this study took place at three sites along the Atchafalaya River, Louisiana, USA, from November 2005

through October 2006. The Atchafalaya is a distributary of the Red and Mississippi Rivers, with most of its flow coming from the Mississippi. From its origin in northcentral Louisiana, it flows south into Atchafalaya Bay, an inlet of the Gulf of Mexico (Fig. 2). Three sites were chosen at increasing upstream distances from the Atchafalaya Bay estuary. The northernmost or "upstream" site was at the private dock of the second author (JD) at "Butte La Rose" (BLR) ( $30^{\circ}19.6'N$ ,  $91^{\circ}41.7'W$ ), 146 km north of the river mouth (Atchafalaya Delta = AD), 2.8 km south of the intersection (overpass) of interstate highway 10 and the river. Two "downstream" sites were sampled, one at the dock of a fish market ( $29^{\circ}41.6'N$ ,  $91^{\circ}12.9'W$ ) at Berwick (BW), across the river from Morgan City, Louisiana, 42 km north of AD. The second "downstream" site was at the Atchafalaya Delta Wildlife Management Area (AD) ( $29^{\circ}26.3'N$ ,  $91^{\circ}20.8'W$ ). One sample of migrating juveniles was taken on Aug. 22, 2007, at the Old River Control Complex (252 km from AD), which controls flow of the Red and Mississippi Rivers into the Atchafalaya River. All river distances among sites have been measured to the nearest kilometer from US Army Corps of Engineer charts of the Atchafalaya River.

Sampling for reproductive adults was done with baited shrimp traps constructed from wire mesh "hardware" cloth with 6.4 mm mesh size. The goal was to obtain a sample of ~200-300 adult shrimps each month, abundance permitting. Traps were composed of a barrel of hardware cloth, 76-90 cm in length, compressed at the closed end and with a wing-shaped funnel at the open end, with an inner funnel opening of 2-3 cm. Traps were variously baited with fish scraps, commercial crayfish bait, or perforated cans of dog or cat food, all of which appeared equally effective in attracting shrimps to the trap. Three traps were set for a period of three consecutive nights during the first or second week of each month at the upstream BLR and downstream BW sites. Trap samples were taken in the first week of each month at BLR and BW. Samples were taken every two weeks at the AD site because preliminary sampling in 2005 showed that abundance was seasonal and more variable than at the other sites. Sampling at AD was conducted by staff of the Louisiana Department of Wildlife and Fisheries (LDWF). Surface salinity at the BLR and BW sampling site was 0 ppt at all times but varied from 0 to 1.6 ppt at AD during the sampling period.

#### Reproductive Condition of Females

Basic observations on size and sex were made on all shrimps captured in the traps, and reproductive condition of females was recorded. A standard measure of body size, carapace length (CL = chordal distance in mm from the posterior edge of the eye orbit to the mid-dorsal edge of the carapace, e.g., Bauer, 1986), was recorded. Shrimps were sexed by the presence (male) or absence (female) of the appendix masculina on the inner ramus of the second pleopod (Bauer, 2004). Reproductive condition of females was recorded. The degree of ovarian maturation could be observed through the translucent exoskeleton of the carapace and was measured on a scale of 1-4 (Bauer, 1986), with 1 = no ovarian development observable, 2 = ovary developing but not extending into the carapace space above the cardiac stomach, 3 = ovary extending into and up to half of the carapace space, and 4 = ovary extending into more than half of that space (usually filling the space just prior to spawning). Occurrence and developmental stage of incubated embryos (Bauer, 1986) below the female pleon was recorded as 0 (no embryos present), 1 (newly spawned, all yolk, no blastodisc visible), 2 (blastodisc present, no eye pigmentation), 3 (pigment or eye development visible, cephalothorax and pleon not separated), and 4 (embryo near hatching, little yolk, carapace and pleon separate). The size of the smallest female incubating embryos below the pleon (8.9 mm CL) was used as the size definition of a reproductive female. Females captured in traps ranged from 3.9 mm to 25 mm CL, males from 1.8 mm to 17.0 mm CL. Total length is approximately  $3 \times$  CL, so that trap mesh was appropriate for catching reproductive females.

#### Embryo Incubation Period

Measures of incubation period (spawning and egg attachment until embryo hatching) were done on females in the laboratory. In April 2006 and 2007, 22 non-incubating females with mature ovaries were captured and maintained with males on a shallow laboratory water tables system (240 cm  $l \times$  66 cm  $w \times$  15 cm  $ht$ ) with circulation of freshwater through an oyster gravel reservoir filter. Shrimps were maintained at 22-23°C water temperature, a 13h: 11h day: night photoperiod, and *ad libitum* feeding with commercial catfish food pellets. Females were checked daily for spawning (embryos attached under the pleon); spawned females were maintained individually in perforated buckets and checked daily for hatching (disappearance of incubated embryos). Time from spawning to hatching (days) was recorded.

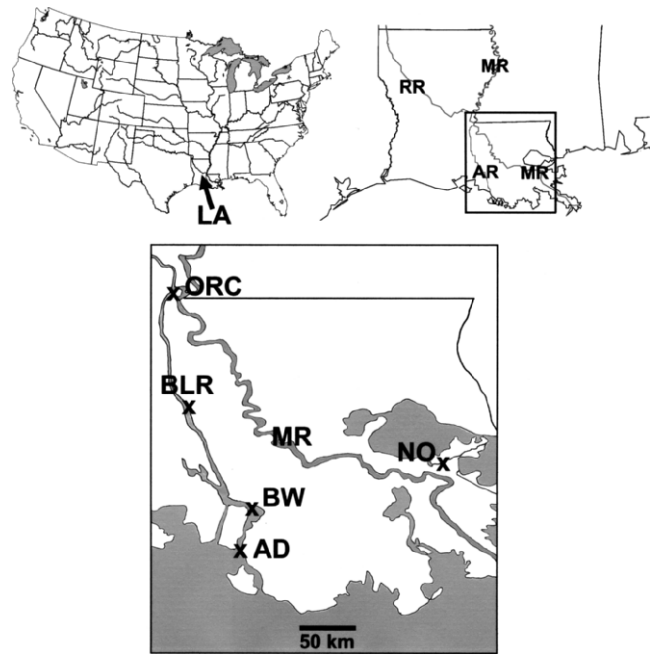


Fig. 2. Map of sampling sites on the Atchafalaya river (below), with location of sampling area in the United States of America (upper left) and state of Louisiana (upper right). AD, Atchafalaya Delta; AR, Atchafalaya River; BLR, Butte La Rose; BW, Berwick; LA, Louisiana; MR, Mississippi River; ORC, Old River Control complex; RR, Red River.

#### Larval Studies

In amphidromous shrimps, hatching (first stage) larvae may be released far upstream in freshwater or females might carry the embryos for hatching near or in brackish or saltwater habitats. First stage (stage 1) larvae in species of *Macrobrachium* with extended saline development are non-feeding (Ling, 1969; Dugan et al. 1975; Moller, 1978), so the molt to stage 2 (first feeding) larvae is critical to the continued development of several instars. In this study, the survival of stage 1 larvae and molting success to stage 2 was compared between freshwater and saltwater treatments. In each of 10 replicates, a female with advanced (stage 4) embryos was maintained individually in a 38 l aquarium with recirculating freshwater and checked daily for hatching. The top and 3 sides of the aquarium were covered with black plasticine. When first observed, newly hatched stage 1 larvae were concentrated at the uncovered end of the aquarium with the light of a small lamp after turning off the water circulation. Larvae were gently pipetted out into a culture dish with freshwater from which 30 were pipetted individually out into treatment culture dishes (250 ml), filled either with freshwater or "saltwater" at a salinity of 15 ppt. The latter salinity, simulating an estuarine environment, was that used in aquaculture studies on the larval development of *Macrobrachium* (Ling, 1969; Dugan et al., 1975). Culture dishes were maintained in a laboratory incubator with a photoperiod of 13h light: 11h dark and a temperature of 29°C (following Dugan, 1975). Water in each treatment culture dish was very gently aerated ( $\sim 1$  air bubble  $sec^{-1}$ ) using a Pasteur pipette connected by air hose to an exterior pump. During each daily observation of the treatments, half the water volume was changed, and dead individuals or those molting to stage 2 were removed, preserved, and recorded. Stage 2 larvae were distinguished by their stalked eyes (Fig. 3B) from stage 1, in which the eyes are sessile (Fig. 3A).

Plankton sampling for larvae, both day and night, was done concurrently with sampling for juveniles (see below) at BLR and BW except in February and March, when day samples were not taken. Day plankton samples only were taken at AD by LDWF personnel twice per month. In total, 21 day samples were taken at AD; 9 day and 19 night samples at BW, and 9 day and 18 night samples at BLR. A 16 cm mouth diameter 240  $\mu m$  mesh plankton net was hung from the docks of sampling sites and allowed to sample river flow for 10 min. The plankton sample was preserved in 10% formalin and later concentrated, washed, and stored in 70% ethanol for later examination.



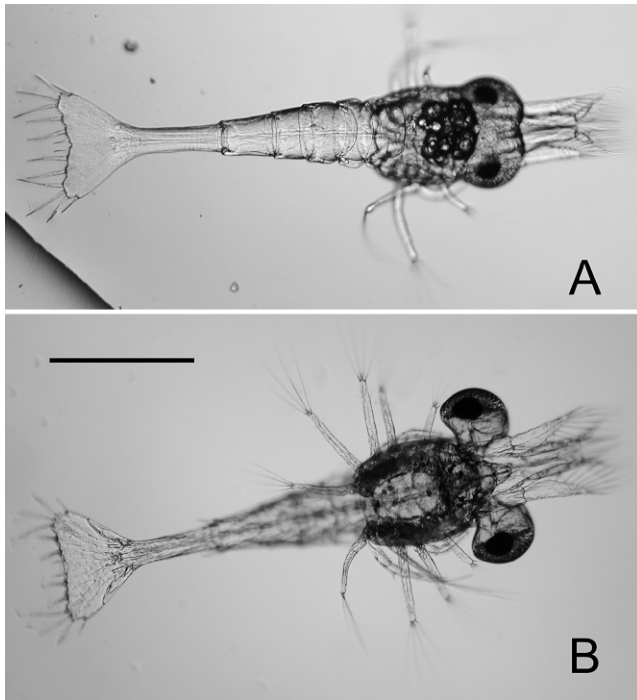


Fig. 3. Early larval stages of *M. ohione*. Note sessile eyes in stage 1 (A) and stalked eyes in stage 2 (B). Scale bar = 0.6 mm.

#### Juvenile Migration

Preliminary observations on the mass upstream movements of juveniles (small reproductively immature individuals ~3-7 mm CL) at night during the summer and early fall of 2005 allowed development of a sampling plan for the present study. Juveniles were sampled at upstream BLR and downstream BW by a long-handled rectangular dipnet (23 × 48 cm) with 1 mm mesh. A sample consisted of all shrimps taken in two 2 m sweeps through the water column for 2 m just adjacent to the dock with the net mouth just below the water surface. "Day" samples were taken at various times in late morning or early afternoon, while "night" samples were taken at various times from at least one hour after sunset until one hour after midnight. Juvenile samples were taken twice a month during the reproductive season (females with embryos; April-August, based on 2005 preliminary observations and Truesdale and Mermilliod, 1979) and two months beyond. From November 2005 to March 2006 (non-reproductive season), only one sample was taken each month at BLR and BW. At BLR, weekly nighttime samples were taken during the period of juvenile migration.

The size (carapace length) of at least 50 individuals (or all sampled if  $n < 50$ ) from several juvenile samples were measured. When  $n > 50$ , ~50 individuals were separated by randomly choosing a quadrat from a dissecting pan in which the sample had been poured and shaken to disperse the specimens. The procedure was repeated until the sample size was reduced to ~50 individuals.

#### Statistical Analyses

The Kendall concordance test (Tate and Clelland, 1957) was used to test the null hypothesis of no joint variation (coefficient of concordance,  $W = 0$ ) among months in measures of breeding intensity by sampling site. Testing of the hypothesis of no difference in body size (carapace length) among females or juvenile migrators from different locations and/or dates were done with  $t$ -tests (2 samples compared) or one-way ANOVA (three samples compared) when assumptions for those tests were met using SYSTAT 10.2 (2002). Multiple comparison post hoc tests were based on Student's  $t$ -statistic (Bonferroni; SYSTAT 10.2, 2002). When assumptions of normality, equal variances, and independence of means were not met, the non-parametric Kruskal-Wallis (Mann-Whitney for two samples) was used. The significance level was set at 0.05 for all tests except multiple post hoc tests for the Kruskal-Wallis (K-W), in which the significance level was set at 0.017 (Bonferroni procedure for 3 pairs of samples).

Table 1. Trap sample sizes of *Macrobrachium ohione* at different sites during the sampling period. Number of females is given to the left, males to the right of the comma in each table cell.

Site Month	Butte La Rose	Berwick	Atchafalaya Delta
Nov. 2005	42, 10	11, 1	0
Dec.	88, 25	5, 0	0
Jan. 2006	48, 26	1, 0	0
Feb.	100, 48	27, 13	0
Mar.	169, 37	286, 30	15, 3
Apr.	299, 79	229, 7	60, 58
May	247, 53	161, 151	122, 49
June	177, 39	84, 13	86, 35
July	161, 35	20, 16	57, 65
Aug.	119, 13	36, 4	11, 1
Sep.	130, 6	8, 1	0
Oct.	130, 26	38, 10	0

## RESULTS

### Temporal and Spatial Distribution of Reproductive Females

Females were taken from all locations throughout the year except at the Atchafalaya Delta (AD) site in which no shrimps were taken during fall and winter samples (Table 1). Females incubating embryos below the pleon occurred in samples from April through August (Fig. 4A). The proportion of reproductive-sized females ( $\geq 8.9$  mm CL) incubating embryos at any developmental stage increased significantly from upriver to downstream sites (BLR < BW < AD) (Fig. 4A) (Kendall concordance test;  $W = 0.76$ ;  $0.05 > P > 0.01$ ). Likewise, the proportion of reproductive females incubating embryos near hatching (with stage 3-4 incubated embryos) also tended to be higher in the seaward sampling sites (Fig. 4B), although this tendency was not statistically significant ( $W = 0.48$ ;  $0.20 > P > 0.10$ ). The proportion of reproductive females near spawning (stage 3-4 ovarian development) was higher at the downstream sites (Fig. 4C) ( $W = 0.64$ ,  $P = 0.05$ ).

There was a gradient in mean female size among sites during April through August, months with incubating and hatching females, with female size increasing seaward (BLR < BW, AD) ( $W = 0.92$ ,  $P < 0.01$ ) (Fig. 5). A more detailed view of female size data shows that mean female sizes were not significantly different between BLR and BW in February ( $t_{56} = 1.21$ ,  $P = 0.23$ ) nor among sites in March (ANOVA  $F_{2, 467} = 1.72$ ,  $P = 0.181$ ). From April through September, however, significant differences were found among sites (April:  $n = 588$ , K-W = 252.0,  $P < 0.001$ ; May: ANOVA  $F_{2, 527} = 209.6$ ,  $P < 0.001$ ; June: ANOVA  $F_{2, 344} = 64.1$ ,  $P < 0.001$ ; July:  $n = 238$ , K-W = 36.9,  $P < 0.001$ ; August:  $n = 166$ , K-W = 6.9,  $P = 0.031$ ; September:  $n = 138$ , K-W = 290.5,  $P = 0.036$ ). In April, May, and June, all sites were significantly different from each other; in July, AD and BW were significantly different from BLR but not from each other; in August, there were no significant difference in paired comparisons of sites, although the overall K-W test was significant ( $P = 0.031$ ).

### Spawning Pattern

Female caridean shrimps often produce more than one brood during a breeding season (Bauer, 2004). A subsequent brood may be produced soon after hatching of the first, in which

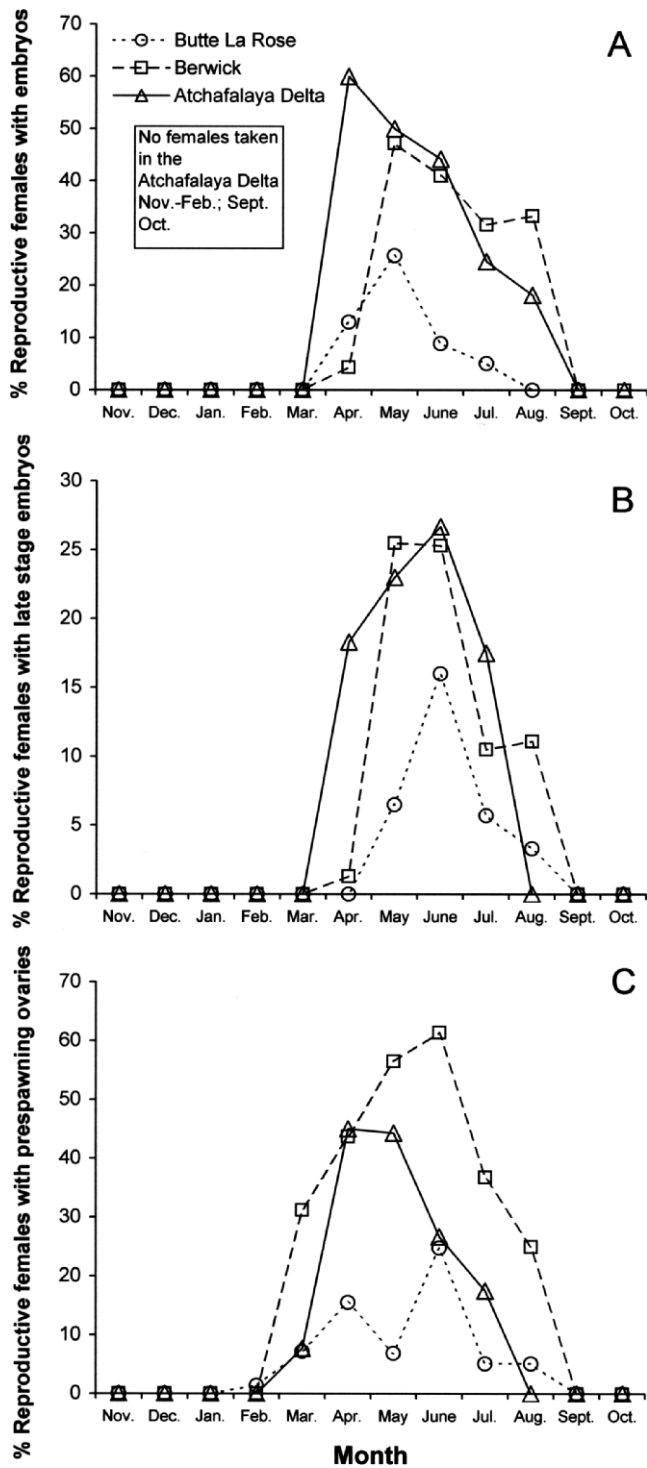


Fig. 4. Percentage of reproductive-sized females at the three sampling sites: A, carrying embryos; B, carrying late-stage (near hatching) embryos; C, with mature ovaries.

case females with prehatching embryos will show ovarian maturation. Many of the prehatching females (with stage 3-4 embryos) were observed with prespawning ovaries (ovarian stage 3-4) (Fig. 6). The positive association of ovarian maturation stage with embryonic stage of development is significant (Pearson  $\chi^2 = 274.4$ , 9 *df.*,  $P < 0.001$ ,  $n = 383$

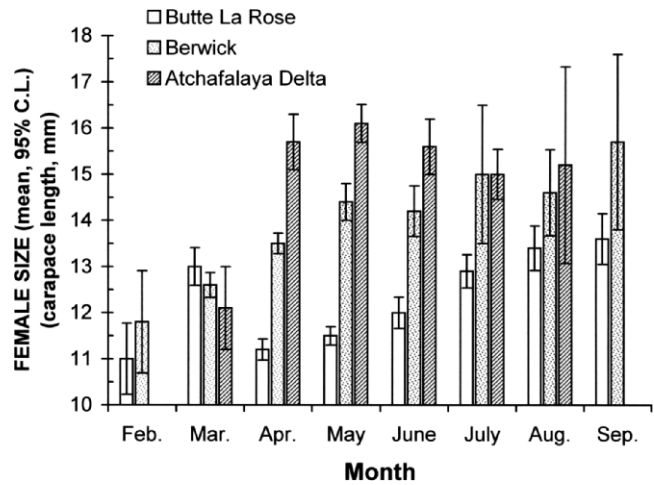


Fig. 5. Mean body size (carapace length) of females at the three sampling sites; error bars are 95% confidence limits (C.L.) on the means.

incubating females). However, some females near hatching did not have mature ovaries, indicating that a subsequent spawn was not imminent.

Period of Embryo Incubation

The number of days that embryos were incubated, i.e., from spawning to hatching, was measured at 22-23°C, water temperatures found at collecting sites in May when females were first incubating embryos at all sites. The median duration of incubation in 22 females was 18 d (95% confidence limits = 17 d, 18 d; minimum = 15 d, max = 20 d).

Larval Studies

In the freshwater treatments ( $n = 10$ ), none of the stage 1 larvae molted to stage 2 (Fig. 7A), with median survivorship declining gradually to day 5 after hatching with a sharper drop to 50% survivorship at day 7 (Fig. 7B). Qualitatively,

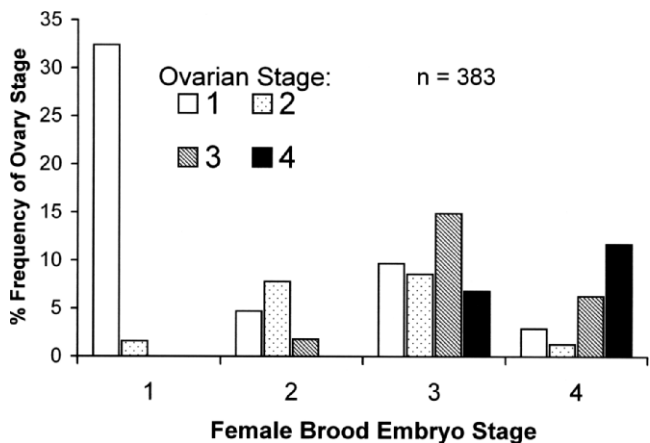


Fig. 6. Ovarian stages of females incubating embryos of different developmental stages. Ovarian stages range from 1 (no ovarian development) to 4 (ovaries full of eggs, near spawning); embryo developmental stages range from 1 (recently spawned and fertilized eggs) to 4 (embryo near hatching).

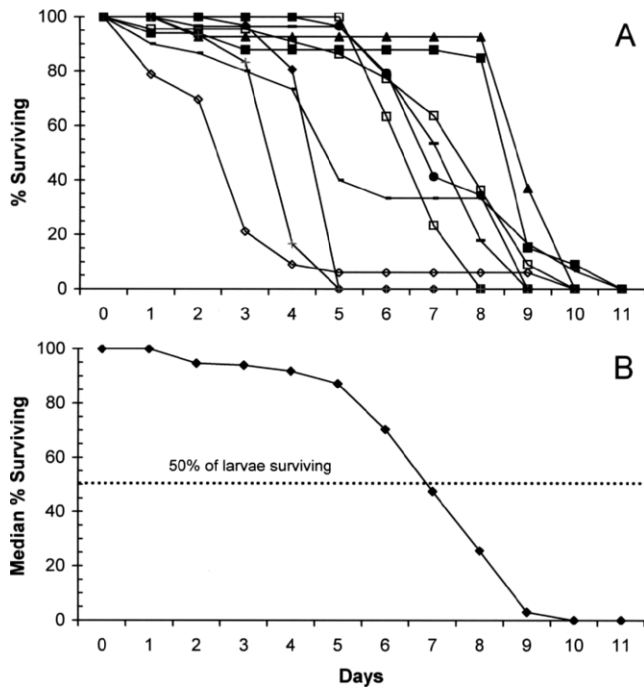


Fig. 7. Survival of stage 1 larvae in freshwater (10 replicates,  $n = 30$  larvae replicate<sup>-1</sup>). A, Percent survival in individual replicates; B, Median survivorship per day in all replicates.

larvae began to swim more weakly and became noticeably fouled with debris and filamentous microbes at about the fifth day of culture. In the “seawater” (15 ppt salinity) treatments, survivorship was high and larvae began molting to stage 2 (first feeding stage) on day 5 after hatching, with most molted to stage 2 by day 8 (Fig. 8A-B).

Although the “usual” components of river plankters, e.g., copepods and cladocerans, were collected in plankton samples, shrimp larvae were not taken in any of the 76 plankton samples taken during the study at all sites during the year of study.

#### Juvenile Migration

Preliminary observations in July–August 2005 had revealed a spectacular mass swimming of juveniles near the surface at night in a band ~1–2 m wide along side the river bank (Fig. 9A–B). Sampling for these small immature individuals (“juveniles”) was conducted throughout the year at one downstream site (BW) and the upstream site (BLR). Juveniles were taken only by night samples (Fig. 10A–B). Some juveniles were collected from March to October at both sites, but a large distinct peak in juvenile abundance was documented in mid-to-late July (Fig. 10A–B). The peak at BW, 42 km upstream of AD, took place two weeks earlier than at BLR, 146 km upstream of AD. During the peak period of abundance, juveniles could be observed swimming near the surface. Outside of this period (April to June, Sept.–Oct.), juveniles were not observed swimming although they were sometimes collected by the near-surface dipnet sweeps (Fig. 10A–B). Adults of reproductive size were never collected by this sampling effort.

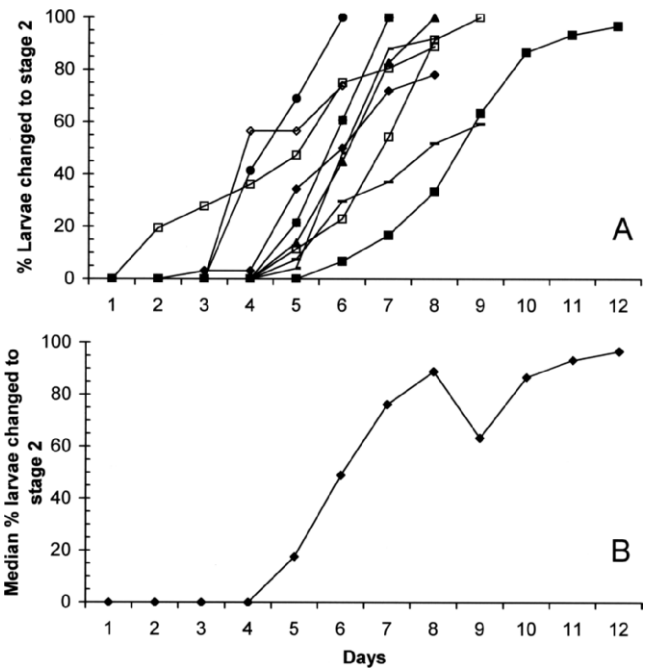


Fig. 8. Change of stage 1 to stage 2 larvae in 15 ppt seawater (10 replicates,  $n = 30$  larvae replicate<sup>-1</sup>). A, Percent change day<sup>-1</sup> in individual replicates; B, Median percent change day<sup>-1</sup> in all replicates.

In Fig. 10C, the timing of the peak migration in mid-July is compared to the temporal pattern of stream velocity in the Atchafalaya River. Monthly means of daily measures of river velocity at a mid-channel station near the BW sampling site in 2006 (Fig. 10C) show that the peak juvenile migration occurred when river flow was decreasing but not at its minimum. A comparison of the 2006 flow pattern with 2000–2005 values (grand monthly means) indicates that the 2006 pattern observed is similar to that observed the previous five years in the Atchafalaya River.

To test the hypothesis that juvenile migrators farther upstream (BLR) are larger than those further downstream (BW), juvenile size (carapace length) was compared between sites in samples taken on or close to the same day (Fig. 11). Size was significantly different in samples taken at both sites on June 19 ( $n = 66$ ,  $K-W = 540$ ,  $P < 0.001$ ) and July 19 ( $t_{55} = 7.92$ ,  $P < 0.0001$ ) as well as between July 5 BW vs. July 13 BLR ( $t_{97} = 2.12$ ,  $P = 0.036$ ) and July 26 (BW) vs. July 31 (BLR) ( $t_{97} = 9.68$ ,  $P < 0.001$ ). Additionally, a sample of migrating juveniles was obtained in 2007 from the northernmost location on the Atchafalaya River (where it joins the Red and Mississippi Rivers) at the Old River Control (ORC) complex in northern Louisiana. The mean size of juveniles in that sample is significantly larger than that found in the other locations (Fig. 11; 95% confidence limits of the ORC mean does not overlap with those from other locations).

#### DISCUSSION

The gradient in reproductive intensity and body size in females from upstream to downstream indicates a migration



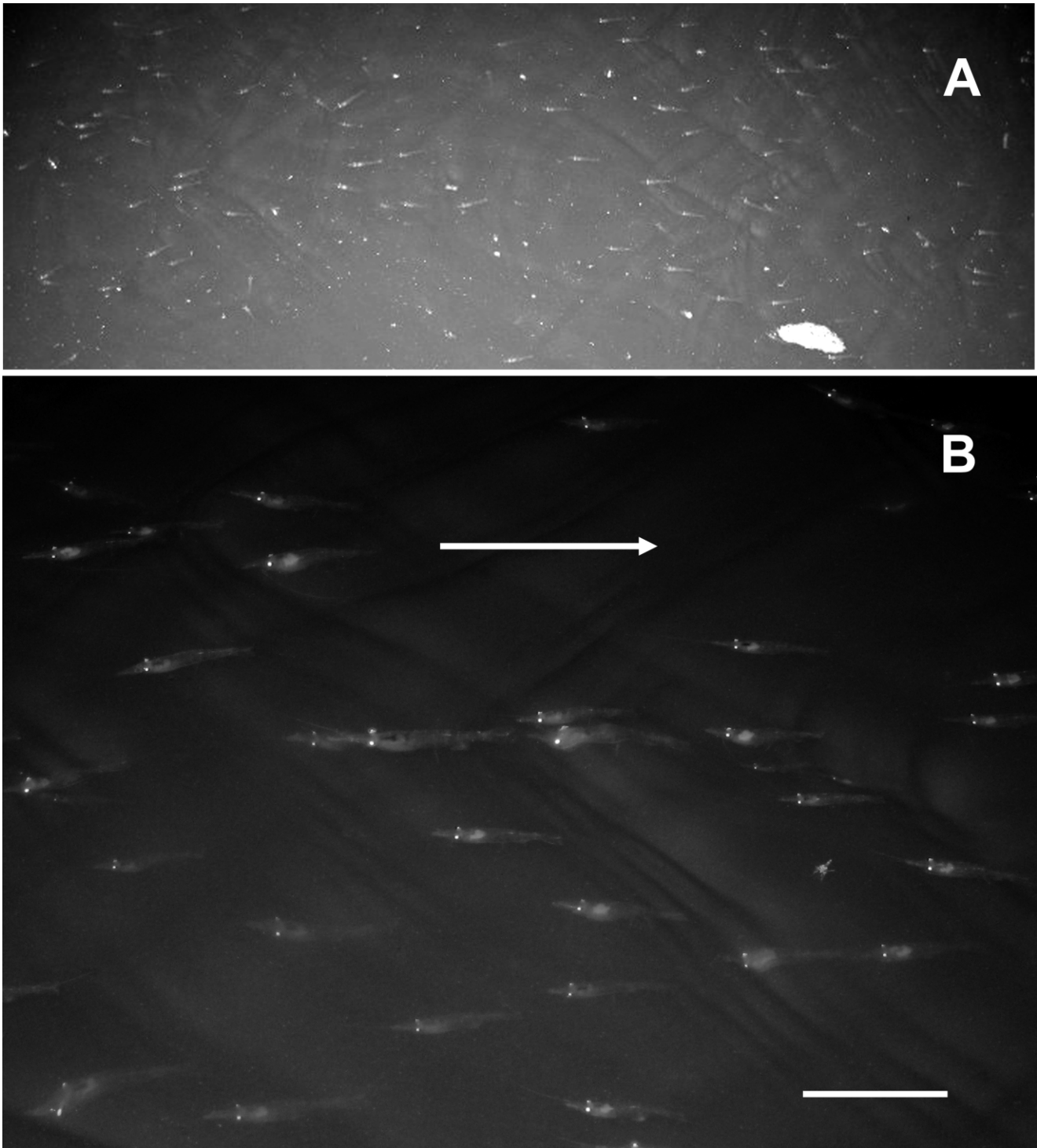


Fig. 9. Juveniles migrating upstream just below the water surface, shown at (A) lower and (B) higher magnification. Scale bar in B represents 20 mm; arrow shows direction of river flow in (A) and (B).

of larger females towards the estuary as they become reproductive, with the largest influx in the early spring. Local fishermen report that “the shrimp are running” during the early spring, i.e., they find marked increases in their trap catches for use as fish bait, an anecdotal observation that concurs with the results on spatial and temporal distribution of reproductive females in this study. Truesdale and

Mermilliod (1979), who estimated growth and maturation of *M. ohione* from length frequency distributions, proposed that the majority of reproductive females were 1-year old shrimps, spawned the previous year, with many surviving into fall or early winter, and many fewer surviving to reproduce a second year. Our study confirms that once females have hatched their first brood in or near the estuary

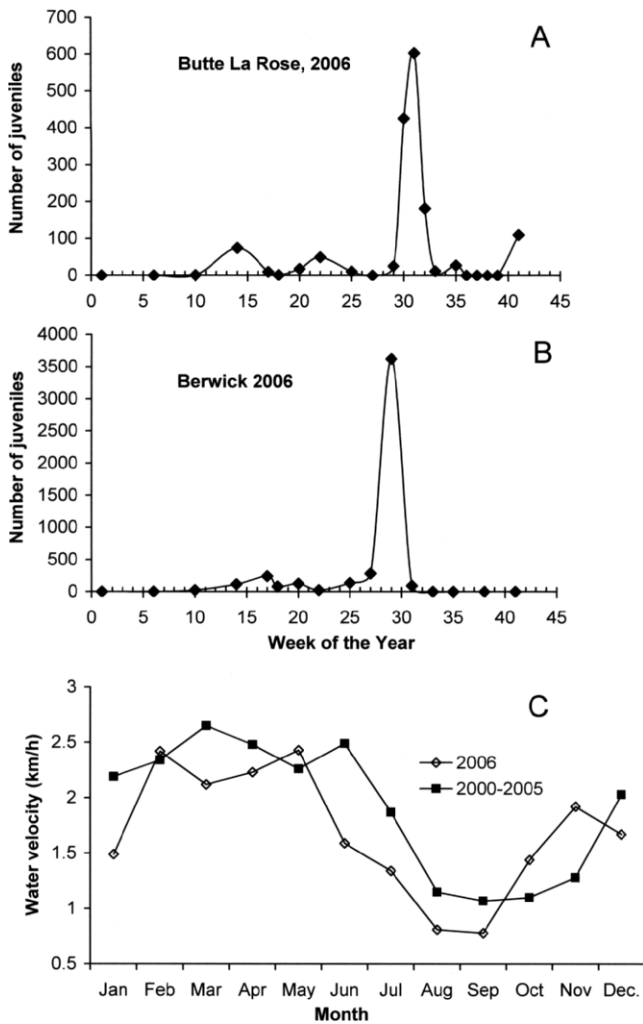


Fig. 10. Abundance of juvenile migrators in standard night net samples: A, Butte La Rose (upstream location); B, Berwick (downstream location); C, Monthly pattern of river velocity in the lower Atchafalaya River. River velocities are from a United States Geological Survey (USGS) station in the lower Atchafalaya River near Berwick, Louisiana. Given are monthly means of daily measures at this station for 2006 and also grand mean monthly values for the years 2000-2005. Data courtesy of David Walters, USGS (river flow data are unpublished and subject to possible minor revision).

in the early to mid-spring, they may stay and hatch a second brood. It is not known whether and how far the surviving post-hatching females migrate back up into the freshwater river environment.

Larval studies reported here confirm earlier studies by Dugan (1971, 1975) that *M. ohione* larvae require saltwater development and give additional details on survival and molting of hatching larvae in fresh and saltwater. Although embryos readily hatch to typical planktonic stage 1 larvae in freshwater, they are unable to molt to the essential stage 2, the first feeding stage which would allow continued development. However, the present study shows that stage 1 larvae, which utilize leftover embryonic yolk for metabolic needs, can survive at least 5 days before significant mortality begins, apparently both from starvation and a buildup of fouling, with the latter removed by molting

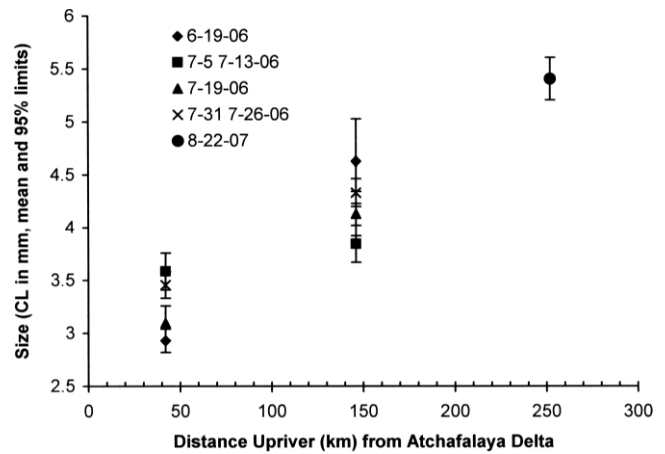


Fig. 11. Size (carapace length: mean in mm and 95% confidence limits) of 2006 juvenile migrators from a downstream site 42 km (Berwick) and the upstream site 146 km (Butte La Rose) from the Atchafalaya Delta (AD). Also included for comparison are results from a sample taken far upstream in the Atchafalaya River (252 km from AD) in 2008 at the Old River Control complex.

to stage 2 in the saltwater treatments before reaching lethal levels. If larvae only have to reach seawater before molting, a female *M. ohione* might not have to reach water with significant salinity before hatching embryos. Instead, it might only need to get close enough to the estuary so that hatching and subsequent river drift will carry the larva within approximately 5 days into estuarine water with the sufficient salinity needed for development. Such a pattern of larval release was suggested, based on distribution of incubating females, for *M. malcolmsonii* (H. Milne Edwards, 1844) in India (Ibrahim, 1962). At river velocities found from April through June, when most hatching probably takes place, a larva of *M. ohione* could conceivably reach Atchafalaya Bay from a considerable distance upstream. Larval drift to estuaries from upstream river hatching sites occurs in amphidromous atyids and species of *Macrobrachium* on neotropical islands (Hunte, 1978; March et al., 1998; Benstead et al., 1999). However, adult females live considerably closer to the sea in these locations so that larvae can arrive in brackish water after only 1-2 days of drift.

However, the absence of larvae in plankton samples argues against upriver release of larvae. It is possible that the plankton sampling in this study along the bank using river drift may not have been adequate to sample larvae; perhaps most larvae occur in mid-channel where flow is greatest, as suggested for smaller shallow rivers in Puerto Rico (March et al., 2003). Future studies on larval distribution for location of hatching sites should include sampling in the main channel of the river as well as out in Atchafalaya Bay.

Given the larval necessity for saltwater development and the observed distribution of reproductive adults, there seems little doubt that the mass upstream swimming of juveniles during the summer is a migration of newly developed juveniles from the estuary up into the adult freshwater habitat. Estimates from observations done in this study and from related species are useful for making a preliminary model about the timing of this migration. Based on results



from this study, mid-April (April 15) will be taken at the beginning of the spawning season. After spawning, embryos are incubated 18 days prior to hatching (in this study, at 22-23°C, temperatures similar to those at the study sites, April-May). Once hatched, the larvae go through a developmental period. An extended planktonic larval development is likely for Atchafalaya River *M. ohione*, based on the small size of its embryo (<1 mm long axis, Truesdale and Mermilliod, 1979; Bauer, personal observation), indicative of extended development (Bauer, 2004) and the morphology of the stage 1 and 2 larvae observed in this study, which show no signs of the abbreviated or direct development of completely freshwater, non-amphidromous freshwater shrimp species (Bauer, 2004). Developmental time (hatching to settling postlarva = 1<sup>st</sup> juvenile instar) was given by Dugan (1971) for *M. ohione* at 36-79 days. The newly settled juveniles must then migrate from the estuary upstream into the freshwater river habitat for the next phase of their life cycle. In *M. rosenbergii* from Southeast Asia, the juveniles began to swim upstream at ~14 d after settlement (Ling, 1969). Swimming speeds have not been formally analyzed, but preliminary observations from video analysis of juvenile swimming in the Atchafalaya River by a collaborator (Brad Moon, UL Lafayette) indicate that swimming speed is ~1 km h<sup>-1</sup>. Juvenile swimming only occurs at night, and we have made direct observations of swimming juveniles from 2100 to at least 0200 h. If it is assumed that the larvae swim through the night (1 hour after sunset to one hour before sunrise), i.e., ~8 h during midsummer, they could progress ~8 km d<sup>-1</sup>. Using the Atchafalaya Delta sampling site (AD) as a starting point, a juvenile could swim the 146 km to the upriver Butte La Rose (BLR) sampling site in 18 days. Thus, an embryo spawned near the Atchafalaya Delta ~April 15 would take 18 d (incubation) + 36-79 d (larval development to juvenile) + 14 days (to begin upstream swimming) + 18 days (swimming time, AD to BLR) = 86 days (July 10) to 125 days (August 22) to arrive as a juvenile at BLR. In both 2005 (preliminary observations) and 2006 (this study), juvenile migrators were first observed swimming at the surface on July 12 at BLR, concordant with this simple model. The occurrence of the juvenile peak at the BW site, 104 km downstream, two weeks before the BLR peak, is agreement with these estimates. The model also agrees with growth estimates from Truesdale and Mermilliod (1979), of 71-129 days for an individual of *M. ohione* to attain a size of 25 mm, similar in size to the swimming juveniles collected in this study. Although temporal variations in river flow were similar from 2000-2006, they may vary considerably during longer time periods, thus affecting the timing of the juvenile migration. Juveniles might be delayed or delay swimming upstream by stronger currents.

Juvenile migrator size at the upstream BLR site was significantly larger than that at the downstream BW location, indicating that juveniles are growing as they migrate upriver. A single sample taken far (250 km) upstream in 2007 yielded the largest juvenile migrators. Juveniles were never found swimming along the bank during the day. These observations suggest that, during the day, the juveniles are on the bottom, possibly among shore

vegetation and other structure along the shore, feeding, molting, and growing.

Various aspects of the juvenile migration appear to be specific adaptations evolved by this (and other) amphidromous species. The shrimps swim adjacent to the bank, where river velocity is lowest and where presumably less energy is required to swim upstream, i.e., against the current. The juvenile migration may be timed to midsummer because seasonal river flows are declining during this time period, making swimming upstream less strenuous. Interestingly, the peak of migration was not during the period of lowest river flow in 2006 (and in 2005, Bauer, personal observation) perhaps because the flow along the bank is too slow to serve as an upstream directional cue. Juveniles engage in migratory upstream swimming only at night, perhaps to avoid predation from visually hunting predators such as fishes and birds. Nocturnal activity to avoid predation is a common decapod crustacean adaptation (Bauer, 1985).

The number and biomass of juveniles moving upriver is impressive. Preliminary estimates of abundance within the swarm of juvenile migrators reach 5-6000 m<sup>-2</sup>. The exchange of biomass, energy, and nutrients between the estuary and the river must be ecologically significant. Juveniles of *M. malcolmsonii* from the River Godvari in India (Ibrahim, 1962) are the basis of a fishery for the dried shrimp industry, indicating a juvenile migration similar or greater in scope than that observed in this study.

The distribution of *M. ohione*, past and present, and its amphidromous life cycle suggest a life history puzzle that has long been of interest (Gunter, 1937; Anderson, 1983). This species still occurs as far north as southern Missouri in the Mississippi River, 1560 km from the Gulf of Mexico (Conaway and Hrabik, 1997; Barko and Hrabik, 2004; Bauer, personal observation). It was historically abundant not only in the upper Mississippi but also up into most of the Ohio River, which flows into the Mississippi from the eastern United States, with distances to the Gulf of Mexico of up to 3100 km. Do (did) females from these populations migrate such a long distance to hatch embryos and do the tiny juveniles migrate such a long distance back upstream? Such a migration would be similar in scope to other long range migrators such as many insects, birds, and catadromous eels in the genus *Anguilla* (Dingle, 1996), and would be remarkable for an animal of such a relatively short life span (~1-2 years; Truesdale and Mermilliod, 1979).

Besides a long distance female hatching and juvenile return migration (amphidromy), two other hypotheses might also explain the past abundance of *M. ohione* in the northern Mississippi and in Ohio Rivers. One hypothesis is that that northern populations are non-migratory (reviewed in Anderson, 1983) with a higher degree of "freshwaterization" (Jalihal et al., 1993), i.e., local adaptation to a completely freshwater life cycle with probable reproductive isolation from southern populations. Abbreviated or direct larval development, indicated by a significant increase in embryo size, would be the key adaptation, and has occurred in other *Macrobrachium* spp. (e.g., Mashiko, 1992; Jalihal et al., 1993). Anderson (1983) considers this

unlikely and supported the long-distance migration hypothesis, i.e., amphidromy in populations far upriver.

Another intriguing hypothesis that might explain the past and present far-northern distribution of *M. ohione* is suggested by the distribution of salines (salt springs, surface salt deposits) in the Upper Mississippi and Ohio rivers (fig. 1 in Brown, 1980). Relatively large areas surrounding the mid-lower Ohio Rivers and upper Mississippi south of St. Louis in Missouri are documented as having or having had salines. It is possible that drainage by or through these salines into northern rivers created low salinity areas in or near the rivers that would have supported the extended marine planktonic development characteristic of *M. ohione* from coastal rivers. Females in the far northern part of the *M. ohione* distribution might have migrated much shorter distances to such low salinity "larval nursery areas" rather than the great distances to the Gulf of Mexico. Correspondingly, return dispersal of juvenile migrators would occur over much shorter, more biologically realistic distances. Although admittedly speculative, this hypothesis needs to be investigated and tested.

The juvenile migrations of *M. ohione* observed in the Atchafalaya River may be important in understanding the decline and extirpation of northern populations in the upper Mississippi and Ohio Rivers if those populations are or were amphidromous as well. Although many factors may be involved in the decline of this species (Bowles, 2000; Barko and Hrabik, 2004), one that has not been seriously considered is interruption of an upstream juvenile migration, such as that observed in the Atchafalaya river population. River control structures, such as those separating the Atchafalaya River from the Mississippi beginning in the 1960's, may completely block migrating juveniles from moving further upstream and recruiting into upstream areas. Even complete blockage of the juvenile migration may not be necessary to rob upstream populations of recruitment. Riverbank structures such as revetments, wing dikes, wharfs, etc. greatly change the intensity and direction of flow along the river bank where juvenile migration takes place (Hamano and Hayashi, 1992; Hamano and Honke, 1997; Bauer, personal observation). Migrating juveniles of amphidromous shrimps require the directional cue of downstream flow to orient and move upstream (positive rheotaxis; Hamano and Honke, 1997). Impoundments and reservoirs behind dams remove this directional cue (Holmquist et al., 1998). Likewise, structures such as wing dikes that extend many meters out from the river bank create a complex water flow that may confuse and disperse migrating juveniles moving upstream just along the bank. If the juvenile migration can be demonstrated and its characteristics and cues studied, factors that impede the migration might be mitigated, perhaps aiding in the conservation of existing populations and in the restoration of those in northern parts of the *M. ohione* range.

Although this study concentrates on the "what" and "how" of amphidromy in *M. ohione*, the "why" or evolutionary cause (ultimate factor) explaining the occurrence of migration in the life cycle is of considerable interest. Dispersal of larvae among river systems is promoted by marine larval development in amphidromous

species (Hunte, 1978; Bauer, 2004), and certainly the geographic distribution of *M. ohione* is broad, as is that of other amphidromous species, e.g., North American species of *Macrobrachium* (Bowles et al., 2000). Escape from predation is a selective advantage of amphidromy in atyid and palaemonid shrimps on tropical islands in mountain streams flowing rapidly over steep slopes (Puerto Rico: Covich et al., 2006). Waterfalls are upstream barriers to predatory fishes but not to amphidromous shrimps, so that upstream shrimp populations are exposed to lower or no fish predation (Covich et al., 2006). However, there were no such upstream barriers to fish predators in the broad large river systems in which *M. ohione* occurs, at least not until significant human impact began in the 19<sup>th</sup> century. The ecological context in which shrimp amphidromy occurs and has evolved may vary widely among river systems according to size, flow characteristics, and geographic location (tropical island vs. tropical continental vs. warm temperate continental, e.g., Mississippi/Atchafalaya River system). Comparison of amphidromy in shrimps in these different ecological situations will reveal much about the evolution of this life history pattern.

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