

Delivery of hatching larvae to estuaries by an amphidromous river shrimp: tests of hypotheses based on larval moulting and distribution

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SUMMARY

1. Amphidromous shrimps live and breed in freshwater rivers and streams, but their larvae require development in sea water. Larvae may hatch upstream and then drift to the sea, although in some species females have been reported to migrate to the coast before larvae are released. Here, we tested the relative importance of larval drift and female migration in *Macrobrachium ohione* (Decapoda: Palaemonidae) in a distributary of the Mississippi River in Louisiana, U.S.A.
2. Newly hatched (stage-1) larvae are nonfeeding and will not moult to stage 2 (first feeding stage) without encountering salt water. A factorial experiment was conducted in the laboratory to test the effects on moulting to stage 2 of (i) time spent by stage-1 larvae in fresh water before (ii) exposure to and maintenance in water of different salinity. Larvae kept in fresh water for 1 or 3 days before a change to saline water at 6 or 10 ppt showed a greater frequency of moulting than those kept for longer (5 days) in fresh water or changed to less saline water (2 ppt). Non-moulting larvae died or were moribund within 11 days of hatching.
3. The relative abundance of stage-1 larvae was measured with plankton tows at two locations in the river c. 150 km apart, one near the sea and one upstream. Larval abundances near the sea were significantly greater than those upstream.
4. The results indicate that hatched larvae of *M. ohione* have a limited period in which to drift in fresh water before reaching water sufficiently saline to stimulate moulting to the first feeding stage. Female migrations may play an important role in delivering larvae of amphidromous species from large continental river systems in which distances to the sea are great, while larval drift alone may be sufficient in species living in short streams, like those found in many small mountainous tropical islands.

Keywords: amphidromy, *Macrobrachium ohione*, larvae, migration, shrimps

Introduction

Although most caridean shrimps (Crustacea, Decapoda) are marine, there are numerous freshwater species, especially in the families Atyidae and Palaemonidae (subfamily Palaemoninae) (Bauer, 2004; De Grave, Cai & Anker, 2008). The life history of many of

these species is completely adapted to fresh water. In such species, the extended planktonic development of their marine ancestors has been replaced with abbreviated or direct development, in which embryos hatch as advanced larval stages or juveniles which do not require salt water ('freshwaterisation'; Jalihal, 1993; Mashiko & Shy, 2008). However, there are a number of tropical and subtropical freshwater shrimps with an amphidromous life history, in which breeding and spawning occur in fresh water but larval development takes place in brackish or fully marine waters

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(McDowall, 1992, 2007). After larval development in estuaries or the open sea, the newly metamorphosed juveniles (postlarvae) find river mouths or freshwater inlets and migrate into the adult riverine habitat (Ling, 1969; Hunte, 1978; Hamano & Hayashi, 1992; Hamano & Honke, 1997; Holmquist, Schmidt-Gengenbach & Yoshioka, 1998). An amphidromous lifestyle potentially allows freshwater species to disperse among coastal rivers and streams via marine planktonic larvae (Hunte, 1978; McDowall, 2007).

Stage-1 larvae of amphidromous shrimps will not moult to stage 2, the first feeding-stage, without encountering salt water (e.g. Dugan, Hagood & Frakes, 1975; Hunte, 1977, 1978, 1980; New & Valenti, 2000; Bauer & Delahoussaye, 2008). Delivery of newly hatched (stage-1) larvae to salt water for development may occur by larval drift. Females with brooded embryos remain upriver, releasing stage-1 larvae into the flow, which then carries the larvae to estuaries or the open sea (Hunte, 1978). When this occurs, plankton samples of rivers and streams with amphidromous shrimps contain stage-1 shrimp larvae during the reproductive season (March *et al.*, 1998, 2003). However, in some species, females may assist larval delivery to salt water by making a downstream hatching migration, carrying incubated embryos nearer to the coast, where larvae are released a short distance from, or directly into, brackish water estuaries. The latter method has been suggested especially for *Macrobrachium* spp. inhabiting large continental river systems, in which the distances between the adult habitat and the sea can be great (Ling, 1969; Ismael & New, 2000). Further, a close relative of *Macrobrachium*, *Cryphiops caementarius* (Molina) in Peru, has been reported to show a downstream hatching migration by females (Hartmann, 1958).

Six species of the freshwater genus *Macrobrachium* inhabit coastal rivers that empty into the Gulf of Mexico or the southeastern Atlantic coast of the United States. It is believed that they are amphidromous because of their restriction to habitats with connection to the sea (Hedgpeth, 1949; Bowles, Aziz & Knight, 2000) and because the larvae of these species require brackish water for development (Dugan, 1971; Dugan *et al.*, 1975; Bauer & Delahoussaye, 2008). An amphidromous life history is of particular interest in one of these species, *Macrobrachium ohione* (Smith), which formerly sustained large populations over 1000 km from the sea in the upper Mississippi and

Ohio river systems (Anderson, 1983; Bowles *et al.*, 2000; Bauer & Delahoussaye, 2008) although they are now rare there. However, some increase in population density was reported in the unimpounded Mississippi River, between the confluences of the Missouri and Ohio Rivers, after the flood of 1993, although no gravid females were observed (Barko & Hrabik, 2004). An upstream juvenile migration, presumably from a downstream estuary, has been recently studied in *M. ohione* in the Atchafalaya River (Louisiana), a tributary of the lower Mississippi River, which empties via Atchafalaya Bay into the Gulf of Mexico (Bauer & Delahoussaye, 2008).

Bauer & Delahoussaye (2008) reported evidence on *M. ohione* from the Atchafalaya River indicating a female hatching migration down towards the Atchafalaya Delta (AD) and estuary. Monthly population sampling in the AD and two other sites upstream showed that females of reproductive size were found in the AD only during the reproductive season (March–August) but were present at upstream locations at other times of the year. Reproductive adults of *M. ohione* were present in a coastal estuary (Galveston Bay, Texas) only during the reproductive season, and their subsequent disappearance from the estuary at other times of the year was reported by Reimer, Strawn & Dixon (1974). Furthermore, Bauer & Delahoussaye (2008) showed that, during the reproductive season, the proportion of reproductive-sized females carrying embryos near hatching was much greater at sampling sites in or near the estuary than 150 km upstream. These and other observations strongly suggested that females with developing embryos move downstream to or near the Atchafalaya estuary to release the stage-1 larvae.

Here, we investigated the possible roles of larval drift and female hatching migration in delivering larvae to salt water in the Atchafalaya River, Louisiana, U.S.A. We determined the time that stage-1 larvae of *M. ohione* can remain (i.e. drift) in fresh water and still successfully moult when they are subsequently maintained in salt water. We also studied the effects of different salinity on moulting success. The hypothesis of larval release near coastal estuaries predicts higher larval abundances in the estuary than farther upstream. We tested this prediction by sampling larvae with plankton nets in the Atchafalaya River estuary and 150 km upstream.

Methods

Factorial experiment on larval moulting requirements

Preliminary experiments on stage-1 larvae by Bauer & Delahoussaye (2008) showed that newly hatched (stage-1) larvae survived well in fresh water for 5 days, after which larvae swam more weakly, became fouled with debris and microbes, and mortality increased. In contrast, hatching larvae placed directly into salt water (15 ppt) suffered little mortality and began to moult to stage 2 after 4 days with nearly all larvae moulted by day 6–7. In this present study, we performed a factorial experiment to determine (i) how long larvae can remain in fresh water, as they would drifting downriver, and still moult successfully to stage 2 upon (ii) subsequent exposure to and maintenance in water of different salinity. This experiment was designed to address the question of how far upriver (how many days drifting distance) larvae might be released by females and still develop successfully once reaching salt water.

Reproductive females were collected during spring 2008, using baited river-shrimp traps (Bauer &

Delahoussaye, 2008) hung from a dock into the Atchafalaya River at Butte La Rose (= BLR; 30°19.834'N, 91°41.631'W), 146 km upstream from the estuary (Atchafalaya Delta, AD) (Fig. 1). Females incubating embryos were either obtained directly from the field or from females mated in the laboratory and then maintained separately on a water table with recirculation inside perforated 5-L perforated containers at a water temperature of 23 °C and a light : dark photoperiod of 13 h : 11 h. The water temperature used was derived from the average ($n = 5$) of water temperatures taken at BLR during the main hatching season (late April to June) in 2006 (Bauer & Delahoussaye, 2008); the photoperiod is that found at BLR in early May.

Experimental replicates ($n = 22$) were conducted individually from May to August 2009 as females incubating embryos near hatching became available; each of the 22 females that supplied larvae for individual replicates were transferred to a non-perforated hatching bucket containing 2–3 L fresh water, and supplied with gentle aeration. The bucket was checked daily for hatched larvae. After hatching, the phototactic larvae were concentrated for collection by

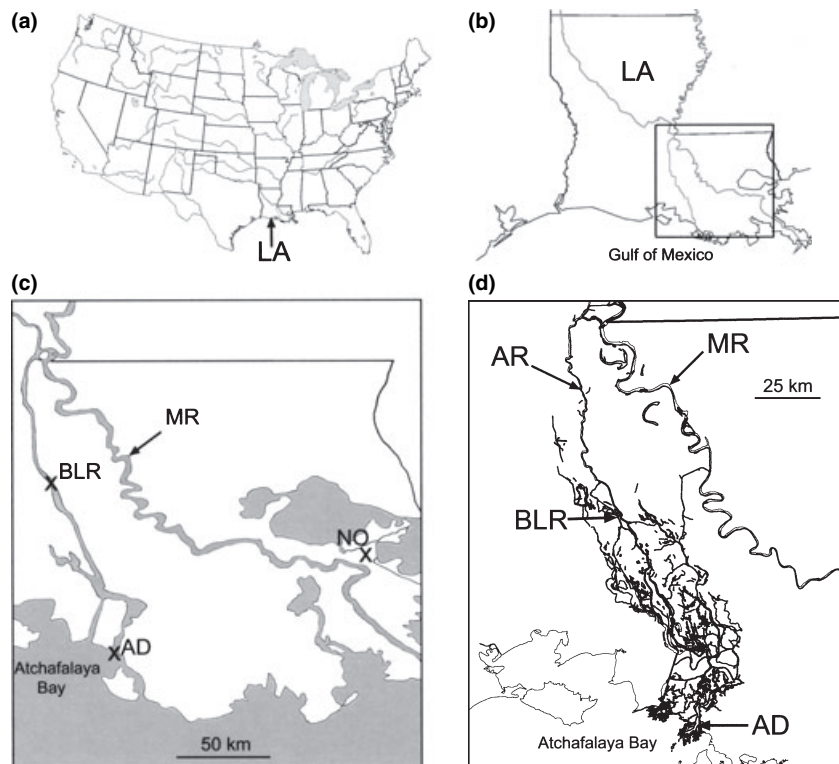


Fig. 1 Atchafalaya River and Delta with location of sampling sites. (a) location of Louisiana within the United States; (b) area (box) of Louisiana with Atchafalaya and lower Mississippi River systems illustrated in (c) & (d); (c) diagram of Atchafalaya and lower Mississippi River main channels with sampling sites on the Atchafalaya River; (d) map of Atchafalaya River with detail on its bayous and side channels. AD, Atchafalaya Delta; AR, Atchafalaya River; BLR, Butte La Rose; LA, Louisiana; MR, Mississippi River; NO, New Orleans.

illuminating one side of the bucket with a table lamp in a darkened room. For each experimental replicate, larvae released from the same female were first transferred to a 250-mL culture dish containing fresh water (0 ppt) using a large-bore pipette (20-mm diameter with 7-mm opening). Larvae viewed under a dissecting microscope were then transferred to nine individual treatment culture dishes (20 larvae per dish, deriving from each replicate female, see below) using small plastic pipettes cut to a 3–4 mm bore diameter. During experiments, larvae were maintained in the culture dishes inside an incubator at 23 °C and a 13 h : 11 h light: dark photoperiod, the same as that used for hatching. Culture dishes were provided with slow gentle aeration (c. 1 bubble s⁻¹) delivered with a glass Pasteur pipette (1-mm diameter tip) attached to an airline and aerator. Fresh water used to maintain females and in larval experiments was supplied from a carbon-dechlorinating water tank system. Salt water used in experiments was prepared from a commercial synthetic seawater mixture.

The factorial design included two factors, each with three levels: (i) time spent in fresh water (1, 3 or 5 days) before (ii) exposure and subsequent maintenance in seawater (2, 6 or 10 ppt). Thus, there were nine different treatments (days × salinity) in each replicate. Larvae used for each of the 22 replicates were supplied by a different female. In each replicate, 20 newly hatched stage-1 larvae were placed and maintained in fresh water in each of nine treatment dishes for the time in days (1, 3 or 5) designated for a particular treatment. At the end of that time, 50% of the fresh water was removed with a pipette and replaced with salt water of a concentration twice that of the designated salinity to produce the appropriate salinity (2, 6 or 10 ppt) in which the larvae were then maintained. Observations on mortality and moulting to stage 2 were recorded every 2 days; after each of these observations, sufficient fresh or salt water was added to culture dishes to adjust for salinity changes due to evaporation or other water loss. Stage-2 larvae of caridean shrimps, with stalked eyes, are easily distinguished from stage-1 larvae in which eyes are sessile (Bauer, 2004; Fig. 3 in Bauer & Delahoussaye, 2008). Observation on all replicates continued for at least 11 days, after which all larvae had either moulted to stage 2, died or were moribund.

Relative larval abundances

If females make a downstream hatching migration, one might expect to find significantly more stage-1 larvae near the head of the estuary than upstream. We tested this prediction by measuring the relative abundances of stage-1 larvae at an upstream (BLR) and downstream (AD) location (Fig. 1) in June 2008. Plankton tows were taken during the day (mid-morning to mid-afternoon) on 6 June at both sites, and again on 20 June at BLR and 23 June at the AD, periods in which females capable of releasing stage-1 larvae have been recorded previously (Truesdale & Mermilliod, 1979; Bauer & Delahoussaye, 2008). Plankton samples were not taken at night because of logistical problems (dangerous boating conditions during the spring flood/hatching season on the Atchafalaya River in 2008). To obtain a representative sample of larval abundance at each site and sampling date, two consecutive tows were taken at each of three different locations relative to the river bank: 'bank' (c. 5 m from the bank), 'main channel' (~ equidistant from each bank), and 'midway' between the bank and the main channel of the river. Each tow was taken for 5 min with a standard plankton net (0.5 m mouth diameter, 310- μ m mesh); the plankton net was submerged to within 1 m of the water surface. Net contents were preserved in 5% formalin and later washed with water before storage in 70% ethanol.

All caridean shrimp larvae were sorted from samples and identified to species. *Macrobrachium ohione* was the only species of that genus found throughout the year in the Atchafalaya River (Bauer & Delahoussaye, 2008). Although Taylor (1992) reported that *M. ohione* is the only *Macrobrachium* species to occur in the Mississippi River drainage, other species have been reported in Louisiana (e.g. Bowles *et al.*, 2000). One of us (R. T. Bauer, pers. obs.) has found only one specimen each of *Macrobrachium olfersii* (Wiegmann) and *Macrobrachium carcinus* (Linnaeus) out of thousands of shrimps from trap samples taken from 2005 to the present. There is no evidence that other *Macrobrachium* species have reproductive populations or occur other than rarely in the Atchafalaya River. The only caridean shrimp species that might contribute larvae to the Atchafalaya River plankton is the freshwater species *Palaemonetes kadiakensis* Rathbun (Holthuis, 1952; Barko & Hrabik, 2004) which is common in lakes, ponds, freshwater bayous and

shallow streams in southern Louisiana (R. T. Bauer, pers. obs.). Stage-1 larvae of *M. ohione* and *P. kadiakensis* are easily distinguished (Broad & Hubschman, 1963; Bauer & Delahoussaye, 2008). No *P. kadiakensis* larvae were recognised among the several thousand caridean larvae sorted from plankton samples. All *M. ohione* larvae were removed and counts were recorded for each sample.

Data analysis

The hypotheses of no difference among groups (factor levels) in larval moulting success to stage 2 by time in fresh water, salinity, or interaction in the factorial experiment were analysed with a two-way ANOVA ($\alpha = 0.05$). To conform to ANOVA assumptions, data were arc-sine transformed for the response variable 'moulting success to stage 2' (the proportion of the 20 larvae in each treatment dish moulted to stage 2 by day 11). Pairwise comparisons among the three means each for time in fresh water and salinity were made with one-way ANOVA *post hoc* tests using Bonferroni-adjusted probabilities. Null hypotheses on relative larval abundances in the Atchafalaya River at the AD and BLR were tested using a nonparametric procedure for paired comparisons (Wilcoxon signed rank test).

Results

Factorial experiment on larval moulting requirements

The time (days) spent in fresh water before exposure to salt water, the salinity of water in which larvae were maintained thereafter, and the interaction between these two factors all had a significant influence on moulting from stage-1 (newly hatched) to stage-2 (first feeding) larvae in *M. ohione* (Fig. 2). A shorter time spent in fresh water before exposure to salt water, and higher salinities once in salt, resulted in greater moulting success. After 1 day in fresh water, larvae subsequently exposed to salt water of 6 or 10 ppt began moulting in large numbers 2 days earlier than those first spending 3 or 5 days in fresh water before saltwater exposure. By day 11, larvae that had not moulted to stage 2 died or were moribund. Moulting success by day 11 was similar in the 1- and 3-day treatments, but significantly greater than that in the 5-day treatments (Fig. 2).

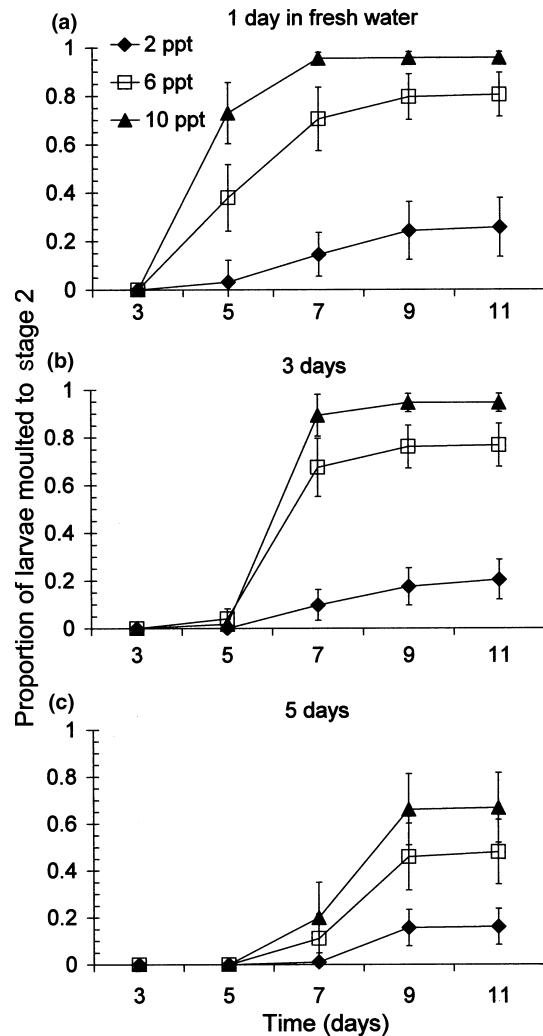


Fig. 2 Time course in the factorial experiment of the stage-1 to stage-2 larval moult for hatching larvae which remained 1, 3 or 5 d in fresh water before maintenance in salt water of 2, 6 or 10 ppt salinity. The mean cumulative proportion ($\pm 95\%$ confidence limits = c.l.) of 20 larvae treatment⁻¹ moulted to stage 2 is shown. The hypothesis of no difference in means for day 11 among treatments was tested with a two-way ANOVA and rejected for days spent in fresh water (d.f. = 2,189; $F = 20.6$, $P < 0.001$), salinity (d.f. = 2,189; $F = 131.4$, $P < 0.001$), and interaction (d.f. = 4,189; $F = 3.1$, $P < 0.016$). Pairwise comparisons of means for days in fresh water ($n = 66$ larvae mean⁻¹) showed that 1-day and 3-day means were not significantly different ($P > 0.95$) but both means were significantly different from that of day 5 ($P = 0.001$ and 0.005 respectively). Means compared among salinities were significantly different ($P \leq 0.001$ in all comparisons).

Salinity had a significant positive effect on moulting success (Fig. 2), with much less moulting in 2 ppt treatments (c. 20% by day 11), than in the 6 and 10 ppt treatments (50–80% and 70–100% respectively).

Relative larval abundances

All shrimp larvae collected in plankton samples were identified as *M. ohione* stage-1 larvae (eyes sessile). For both sampling dates, larval abundance was significantly greater at the AD site (the mouth of the Atchafalaya River estuary) than at the BLR site 146 km upstream (Fig. 3).

Discussion

Our results indicate that stage-1 larvae of *M. ohione* have only a limited period in which they can drift in fresh water to reach water of sufficient salinity for the critical moult to stage 2, the first feeding stage. After 5 days in fresh water, stage-1 larvae become increasingly fouled with microbial growth, swim more weakly, and have a dwindling probability of moulting successfully (Bauer & Delahoussaye, 2008). Larvae held in fresh water 3 or 5 days before salt water was added required an additional 3–4 days after exposure to salt water before they moulted; in the 1-day treatments, moulting occurred more rapidly. Salinity between 6 and 15 ppt appears optimal for stimulating the moult to stage 2 (this study; Bauer & Delahoussaye, 2008).

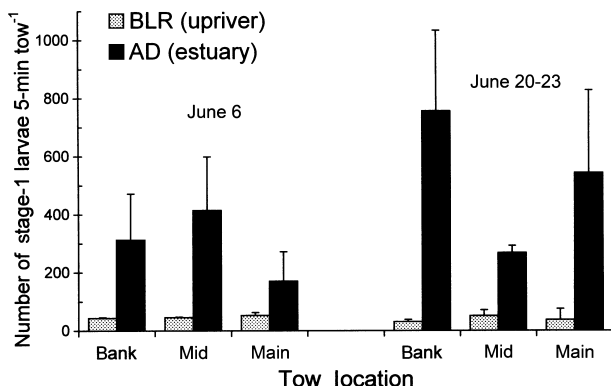


Fig. 3 Comparison of relative larval abundance (number of larvae 5-min tow⁻¹, mean of two replicate samples per tow location \pm standard deviation) by tow location at the Atchafalaya Delta (AD) estuary and the upriver site (Butte La Rose = BLR) during two sampling periods in June, 2008. 'bank', samples c. 5 m from the river bank; 'main', main channel; 'mid', midway between the bank and main channel. The hypothesis of no difference in relative abundance was tested using the Wilcoxon signed-rank test for paired observations, with samples from the two sites paired by date and tow position; the null hypothesis was rejected ($P = 0.002$).

The stage-1 larvae of *M. ohione* are lecithotrophic, i.e. non-feeding and surviving after hatching on ever-decreasing embryonic yolk supplies until their first moult, as are the larvae of other amphidromous shrimps (Hunte, 1977, 1980; Moller, 1978; Jalihal, 1993; Anger, 2001; Bauer & Delahoussaye, 2008; Anger *et al.*, 2009). Females of *M. ohione* must release larvae sufficiently close to the downstream estuary that larvae can survive in the drift without moulting and feeding. The minimum distance that upstream larval release and drift alone can successfully deliver larvae to the estuary also depends on river velocity. Most hatching in *M. ohione* occurs in the Atchafalaya River during the April–June spring flood, in which water velocity in mid-channel averages 2–2.5 km h⁻¹ (Bauer & Delahoussaye, 2008), enabling a larva to drift downstream c. 48–60 km day⁻¹. Females must release larvae at distances no farther than 3 day drift time (c. 144–180 km) from the Atchafalaya Delta (AD) estuary, so that larvae reach salt water in time to continue development. During the seasonal spring flood, however, salinities in the AD (at least near the surface) are very low (usually less than 1 ppt). Stage-1 larvae would still have to travel some unknown distance and time before reaching water saline enough to stimulate moulting. Larvae released by their mothers close to or within the AD would thus have a higher probability of reaching salt water within the 1- to 3-day optimal period.

However, *M. ohione* is abundant in the Atchafalaya River up to 250 km from the AD, as well several hundred kilometres upstream from the Gulf of Mexico in the lower Mississippi River. In the past, there were reproductive populations abundant enough to support commercial fisheries in the upper Mississippi River as far as the Missouri and the lower Ohio Rivers, well over 1000 km from the Gulf of Mexico (McCormick, 1934; Conaway & Hrabik, 1997; Bowles *et al.*, 2000; Barko & Hrabik, 2004). The present study indicates that larvae from populations so far upstream would have little chance for successful development unless females migrated downstream to release larvae within drifting distance of coastal estuaries.

Results from plankton tows are also consistent with downstream larval release in *M. ohione*. Relatively few stage-1 larvae were taken by plankton tows in the Atchafalaya River 150 km upstream (BLR), c. 3 days drifting distance from the AD. On the other hand, tows in the AD yielded relative abundances

significantly greater than those at BLR. Another interpretation of these results might be that stage-1 larvae accumulate in the AD as a result of input from upstream populations. However, the AD is not an enclosed area that might act as a sink or trap for larvae. Rather, it is a dynamic part of the river system with continued outflow out into Atchafalaya Bay and then the open Gulf of Mexico (Perez *et al.*, 2000, 2003).

Two processes may thus play a role in delivery of stage-1 larvae to the sea. In many amphidromous species, ovigerous females may not need to migrate downstream but instead only release larvae that then drift to the sea. This strategy would work well when stream currents are swift (e.g. high gradient streams) and the distance from the release site to the sea is not great, i.e. within a 1–2 day drifting distance (tens of kilometres or less). Most studies indicating larval drift in amphidromous shrimps have been conducted in relatively small, shallow streams on small mountainous tropical islands (especially the Caribbean), with short distances (a few to tens of kilometres) from upstream adult habitat to the sea (e.g. Hunte, 1978; Holmquist *et al.*, 1998; March *et al.*, 1998, 2003; Benstead *et al.*, 1999; Benstead, March & Pringle, 2000; Fievet, 2000). However, studies on some amphidromous palaemonid shrimps from large continental river systems indicate that gravid females migrate downstream to brackish-water estuaries (*Cryphiops caementarius*: Hartmann, 1958; *M. rosenbergii* (De Man): Ling, 1969; Ismael & New, 2000; *M. ohione*: Bauer & Delahoussaye, 2008). Ibrahim (1962) concluded that females of *M. malcolmsonii* Milne Edwards in India do not go all the way to the Godvari estuary but may release larvae as far as 80 km upstream with the river at flood stage. Our plankton sampling indicated limited larval release a few days drifting distance from the AD. Thus, the two processes, larval drift and female hatching migration, are not mutually exclusive.

The proximate (ecophysiological) factors stimulating females to move downstream prior to releasing larvae are unknown. Increasing day length and water temperature frequently stimulate reproductive activity in caridean shrimps (Sastry, 1983; Bauer, 2004). The reproductive season of *M. ohione* in the Atchafalaya and other southeastern U.S.A. rivers begins in April–May, when both photoperiod and river temperature are increasing. In the Atchafalaya and Mississippi Rivers, river height and flow increase from late

summer lows through the winter to maxima in the spring (Bauer & Delahoussaye, 2008), which facilitate larval delivery to salt water. The likely ultimate factor promoting larval delivery to coastal waters during the spring and early summer is the development of favourable conditions (e.g. abundant larval food in the spring plankton) for larval development.

Increasing numbers of studies are being done on the impact of dams, water diversions and other human activities on migrations of amphidromous shrimps (Hamano & Honke, 1997; Holmquist *et al.*, 1998; Benstead *et al.*, 1999; Pringle, Freeman & Freeman, 2000; March *et al.*, 2003). The interruption by dams of female hatching migrations, larval drift and juvenile upstream migrations may be the cause of decreased *Macrobrachium* populations in Texas rivers (Bowles *et al.*, 2000). There are no such barriers in the Atchafalaya River downstream of the hydroelectric dam at the head of the river, which cuts off shrimp populations in the Atchafalaya River from those in the Mississippi River, its source. Dams and impoundments on the lower Ohio River may have contributed to the virtual extinction of *M. ohione* populations once abundant there. Measurements on, and mitigation of, such impacts need to address the details of species life histories including the roles of larval drift and female hatching migrations in delivering larvae to salt water habitats. Previous efforts at using mark–recapture to document a female hatching migration in *M. ohione* were inconclusive (Anderson, 1983), perhaps because the study was conducted late in the reproductive season (G. Anderson, pers. comm.). Although the technology of modern tagging and telemetric techniques (coded wire tags, microchips, radio and acoustic tags and transmitters) has since become more miniaturised and sophisticated (e.g. Linane & Mercer, 1998; Blackburn, 2006; Holden, 2006; Thibault, Dodson & Caron, 2007), we have not yet encountered nor developed the necessary instrumentation and resources for such an effort in *M. ohione*. A direct test, using a tagging or tracking technology, of the role that a female hatching migration plays in larval delivery of amphidromous species is still needed.

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