AMPHIDROMY AND MIGRATIONS OF FRESHWATER SHRIMPS. II. DELIVERY OF HATCHING LARVAE TO THE SEA, RETURN JUVENILE UPSTREAM MIGRATION, AND HUMAN IMPACTS

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ABSTRACT

Hatching (Stage-1) larvae of amphidromous shrimps do not feed and must reach salt water within a few days to molt to Stage 2, the first feeding instar. Stage-1 larvae are transported from to the sea after upstream hatching by drifting in stream flow or are carried to estuaries for hatching by females migrating downstream. Hatching usually occurs during seasons or periods of high stream flow. After development in the sea, newly metamorphosed benthic postlarvae (juveniles) must find stream mouths and migrate upstream to the adult freshwater habitat. Such migrations are striking, occurring during periods of low but continuous flow, with many juveniles walking or swimming alongside the shore at night. The migratory behavior is a positive rheotaxis, with downstream river flow the directional cue. Juveniles are capable of climbing over or around low obstacles in their path provided that there is some downstream flow. Both larval drift and juvenile migrations are blocked by high dams without passageways and by the reservoirs behind them. Water extraction from streams is a significant source of larval mortality. Human impacts can be mitigated by appropriate conservation measures, e.g., restriction of water extraction during periods of larval abundance, and construction of passageways up and around dams and reservoirs to allow juvenile migration to upstream habitats.

INTRODUCTION

Amphidromy is a life history pattern defined by diadromous migrations (Bauer, 2011, this volume). Here, I address two major aspects of amphidromy, the delivery of larvae to the sea and the return upstream juvenile migration, as well as human impacts on these migrations.

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New frontiers in crustacean biology: 157-168

DELIVERY OF LARVAE TO THE SEA

Research on amphidromous shrimps has long indicated that females hatch their larvae into stream flow, with larvae drifting more or less passively to downstream estuarine or marine habitats (fig. 1) (Hunte, 1978; Hamano & Hayashi, 1992; March et al., 1998, 2003; Benstead et al., 1999, 2000; Bauer & Delahoussaye, 2008). Many amphidromous species inhabit streams in which distances from the adult habitat to the sea are relatively short, a few to dozens of kilometers, e.g., Caribbean islands, Japan, Taiwan, Costa Rica). Stage-1 (hatching) larvae of amphidromous species are lecithotrophic, i.e., do not feed, instead utilizing yolk remaining from embryonic development. Such larvae must molt to Stage 2 (first feeding stage) before their food stores are used up or face starvation (Rome et al., 2009). Thus, Stage-1 larvae have a limited period, usually a few days, to drift to the saline waters which will trigger molting to Stage 2. In amphidromous species in streams with a 1-3 days drifting distance to the sea, larvae can simply be released upstream to drift to the sea.

However, in river systems on large land masses, distances from the adult habitat to the sea may be hundreds of kilometers or more (Bauer & Delahoussaye, 2008). Such distances may be well beyond the drifting capacity of Stage-1 larvae. Females may have to assist larval delivery by migrating downstream to or near coastal waters where hatching then occurs. Various observations have indicated such migrations in different *Macrobrachium* species on continental land masses, e.g., *M. rosenbergii* (cf. Ling, 1969), *M. malcomsonii* (cf. Ibrahim, 1962), and *M. ohione* (cf. Bauer & Delahoussaye, 2008). Females of the palaemonid *Cryphiops caementarius* migrate from as much as 100 km upstream to enter brackish water to hatch embryos for larval development in coastal waters (Hartmann, 1958). In such species, how long (far) can a non-feeding (Stage-1) safely drift in fresh water until reaching the sea and still molt successfully to Stage 2, the first feeding stage? This question was addressed with a factorial experiment on larval development in *M. ohione* by Rome et al. (2009). High survival and molting occurred in treatments in which larvae were maintained in fresh water 1 or 3 d before transfer to saline water of 6 or 10 (but not 2) ppt. On the other hand, larvae maintained 5 d in fresh water before transfer had poor survival and molting at all salinities. Thus, *M. ohione* larvae hatched within or very near the estuary have the greatest chance of continuing larval development.

In many amphidromous species, release of larvae coincides with high stream flows which facilitate both female downstream migration or rapid larval drift to the sea (fig. 2A). In palaemonid species in continental large

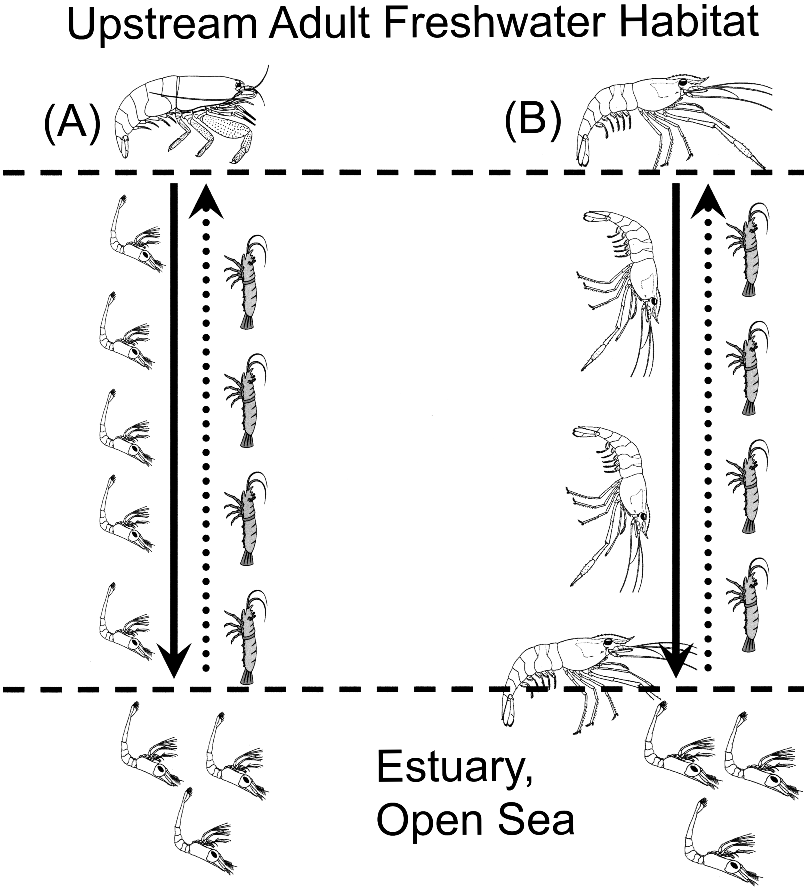

Fig. 1. Migrations of amphidromous shrimps. A, upstream females hatch larvae (upside-down swimmers) which then drift in stream flow down to the sea; B, females incubating embryos migrate down to river mouths to hatch larvae. In both A and B, after planktonic development in salt water, larvae metamorphose to benthic postlarvae which then migrate as young juveniles upstream to the adult freshwater habitat.

rivers systems, female migration to or near estuaries occurs during the river's seasonal flood (Hartmann, 1958; Ibrahim, 1962; Bauer & Delahoussaye, 2008). In amphidromous species which depend only on river flow to deliver larvae to the sea, hatching by upstream females usually occurs during periods or seasons of high stream flow. In Central America, distances to the sea are relatively short, and hatching and larval drift apparently occur during the rainy season, when stream flows are high (Ingo Wehrtmann and Luis Rólier, pers. comm.). Likewise, freshwater shrimps in high gradient streams on the mountainous island of Puerto Rico tend to have their peak reproduction when

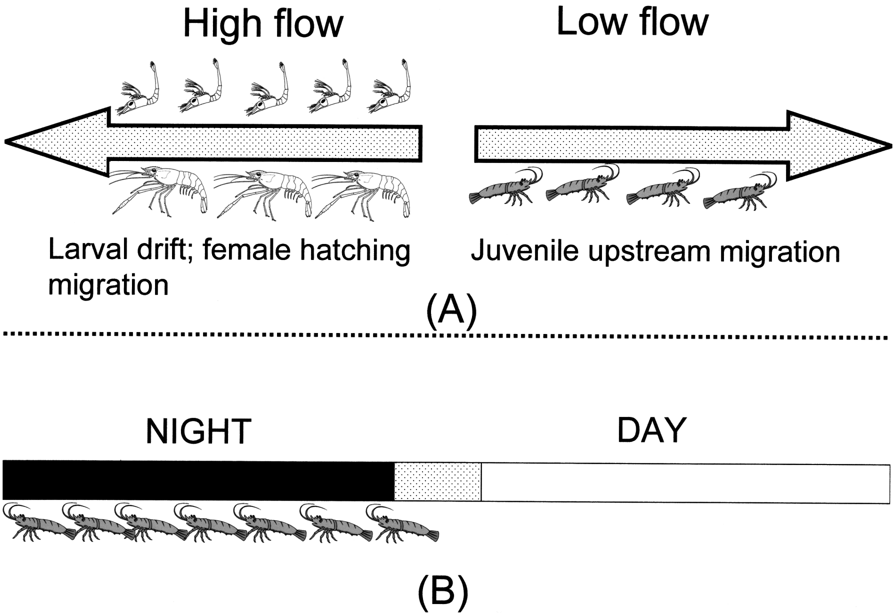

Fig. 2. Major factors affecting the timing of amphidromous shrimp migrations. A, larval release and drift to the sea, as well as female downstream hatching migrations in species which have them, tend to occur during seasonal periods of high downstream flow; juvenile upstream migrations take place during low stream flow, when flow resistance to upstream movement is lower; B, juvenile migrations occur at night in the relative absence of light; migrating juveniles will avoid (move away from) strong illumination (e.g., floodlights) on shore structures and bridges.

river flow is high (Johnson et al., 1998). On Miyako-jima Island (Ryukyus, Japan), two amphidromous carideans from an anchialine cave habitat release larvae when freshwater levels of small cave pools rise sufficiently, due to seasonal precipitation, to allow larval exit from the caves into the sea for development (Yoshihisa Fujita, pers. comm.).

RETURN UPSTREAM MIGRATION BY JUVENILES

After larval development, the newly-metamorphosed individual must find the mouth of a stream and migrate back up to the adult habitat (fig. 1). In carideans, the zoeal larva swims with natatory thoracic exopods; in the last larval (decapodid) stage, the young shrimp has functional pleopods (swimerets) but retains natatory exopods. When the latter are lost completely, the individual is a juvenile; transitional stages in which these degenerate are postlarvae (Anger, 2001). Young individuals migrating upstream in *M.*

rosenbergii and *M. ohione* are juveniles (Ling, 1969; pers. obs., respectively) as is likely in other amphidromous species.

Juveniles migrate upstream from the sea at night (fig. 2B) (Ibrahim, 1962; Hamano & Hayashi, 1992; Benstead et al., 1999; Bauer & Delahoussaye, 2008; Kikkert et al., 2009). The ultimate cause of nocturnal migration is avoidance of predation by visually hunting fish and birds (e.g., Kikkert et al., 2009), with reduction in light intensity the proximate factor. However, Kikkert et al. (2009) analyzed the influence of cloud cover and moonlight on juvenile migrations of three species (from 3 families) and did not always find the expected positive or negative effects. During the day, migrating juveniles may be resting, feeding, and molting in protected habitat along the river bank. The latter is suggested by the increase in size (growth) with increasing distance upstream from the sea observed in migrating juveniles of various amphidromous species (Hartmann, 1958; Bauer & Delahoussaye, 2008; Kikkert et al., 2009; Ingo Wehrtmann and Luis Rólier, pers. comm.).

Migrating juveniles are usually found along the stream bank in very shallow water or in the splash zone, often with their bodies partially or completely out of the water (e.g., Hamano & Honke, 1997; Benstead et al., 1999). They move upstream by a combination of swimming, walking, and crawling along the bottom. Juveniles of various amphidromous species have been observed crawling up vertical or near-vertical natural barriers such as low waterfalls and brush piles as well as artificial barriers such as low weirs and dams (e.g., Ibrahim, 1962; Ling, 1969; Hamano & Hayashi, 1992; Benstead et al., 1999; Kikkert et al., 2009). When juveniles encounter an obstacle, they can crawl up or around it along the wet edges of the obstacle (Benstead et al., 1999). There must be some flow over the barrier for movement to occur (e.g., Hamano & Hayashi, 1992; Benstead et al., 1999, Fièvet, 1999; March et al., 2003). On the other hand, in *Macrobrachium ohione*, which occurs in large deep rivers, migrating juveniles swim near the surface in a band or swarm within 1-2 m of the river bank, sometimes right along the edge of the water (Bauer & Delahoussaye, 2008). The unidirectional flow of water downstream is the probable cue that stimulates a positive rheotaxis in migrating juveniles, whether they are crawling or swimming.

An obvious hypothesis to explain juvenile migrations along the stream edge is that water velocity is lowest there (fig. 3). Downstream flow (the directional cue) is present, but less energy is required to move against it. When encountering an obstacle, juveniles seek areas of low flow to climb up or around it (Benstead et al., 1999). Perhaps for the same reason, juvenile migrations generally

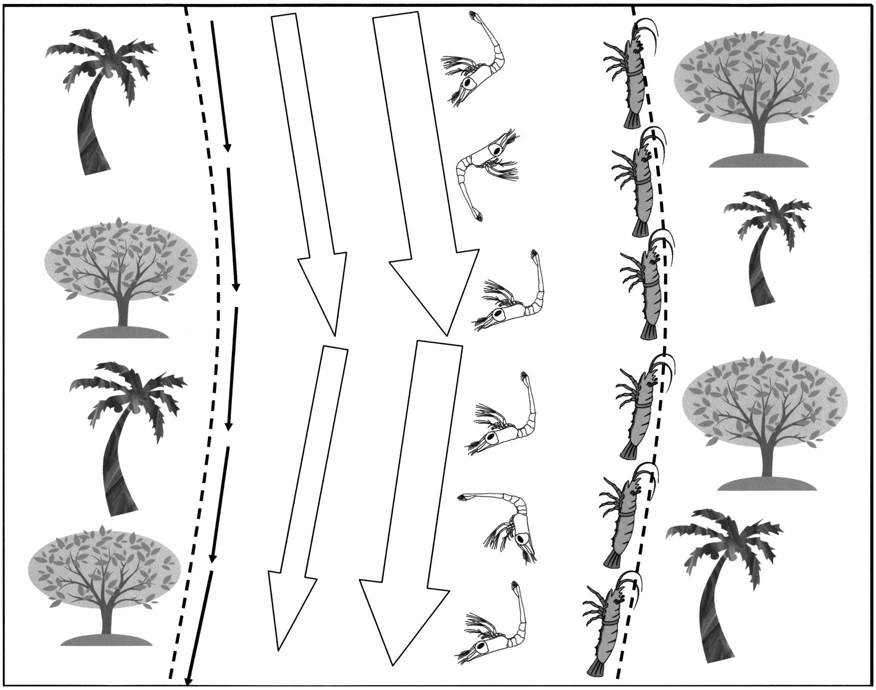

Fig. 3. Relationship between the midchannel to shore stream velocity and location of larval and juvenile migrations of amphidromous shrimps. River velocity (width of downstream pointing arrows) is greatest towards midstream and diminishes towards the shore where it is minimal. Larvae drift downstream in the bulk flow of the stream; juveniles migrate along the shore where river flow offers the least resistance to upstream movement while still retaining a directional cue for juveniles to follow.

take place when stream flows are seasonally low (but not absent) (fig. 2A). In *Macrobrachium malcolmsonii*, the migration takes place in the River Godavari from August to February, when the river is lower and water velocity is slowing from highs of the previous June–September monsoon flood (Ibrahim, 1962). Similarly, the upstream migration of *Cryphiops caementarius* occurs during the low flow periods in Peruvian coastal streams from June–September (austral winter) (Hartmann, 1958). Peak juvenile migrations of *M. ohione* in the Atchafalaya River coincide with decreasing water velocity that occurs during the summer in the lower Mississippi River system (Bauer & Delahoussaye, 2008). Juveniles of various *Macrobrachium* spp. on the Pacific coast generally migrate upstream during the seasonal dry season, when stream flow was reduced (Ingo Wehrtmann and Luis Rólier, pers. comm.).

Differences among species in migratory response to stream velocities are related to differences in body morphology and degree of resistance to high flows. Kikkert et al. (2009) analyzed juvenile migrations of amphidromous species from three different genera and families in Puerto Rico. Migrations of two of them (*Xiphocaris elongata*; *Macrobrachium* spp.) were negatively correlated with high flows, as might be expected, but not those of a third (*Atya* spp.). *Xiphocaris elongata* is a slender shrimp whose body is held high off the substratum by long slender legs (Fryer, 1977) and thus is most easily displaced downstream by high flows. *Atya* spp. have a much stouter, heavier body which hangs down close to the substratum between robust, short legs better adapted for clinging. The juveniles of *Macrobrachium* spp. are intermediate in overall morphology and climbing behavior.

OCCURRENCE AND REDUCTION OF HUMAN IMPACTS

The most dramatic and significant human alteration of amphidromous shrimp habitat is the blocking of migratory routes by high dams (spillway height > 15 m; March et al., 2003) (fig. 4). Headwaters above high dams without any spillway discharge or fishway (fish ladder, passageway, ramp) completely lack amphidromous shrimps, which were present in equivalent streams without dams (e.g., Holmquist et al., 1998). Horne & Besser (1977) trapped *Macrobrachium* spp. at different points along the San Marcos and Guadalupe Rivers in Texas. Several high bottom-release dams had been built along the 325 km length of the river, and 3 of 4 *Macrobrachium* spp. now occur only downstream of the dam nearest the river mouth. Only 1 species, *M. carcinus*, which apparently can crawl around dams, occurs throughout the length of the river system (Horne & Besser, 1977).

Juveniles are capable of climbing low-incline, man-made passageways with water flow (see below). Although juveniles can surmount low dams with flow, the latter are still a partial impediment to migration. The juveniles encountering an obstacle tend to accumulate below it, attracting predators such as birds and fishes, including migrating predatory fishes which are blocked from moving upstream (Benstead et al., 1999) (fig. 4).

Although no construction of new dams and elimination of unnecessary ones is the best alternative to blockage of amphidromous migrations, passage around such barriers is possible. Various studies have shown that juvenile shrimps migrating upstream will climb up fish ladders or other suitable constructed ramps (Hamano et al., 1995; Hamano & Honke, 1997; Benstead et al., 1999; Fièvet, 1999). Japanese researchers have conducted experimental studies showing that the ideal “shrimp ladder” is a ramp with an inclination

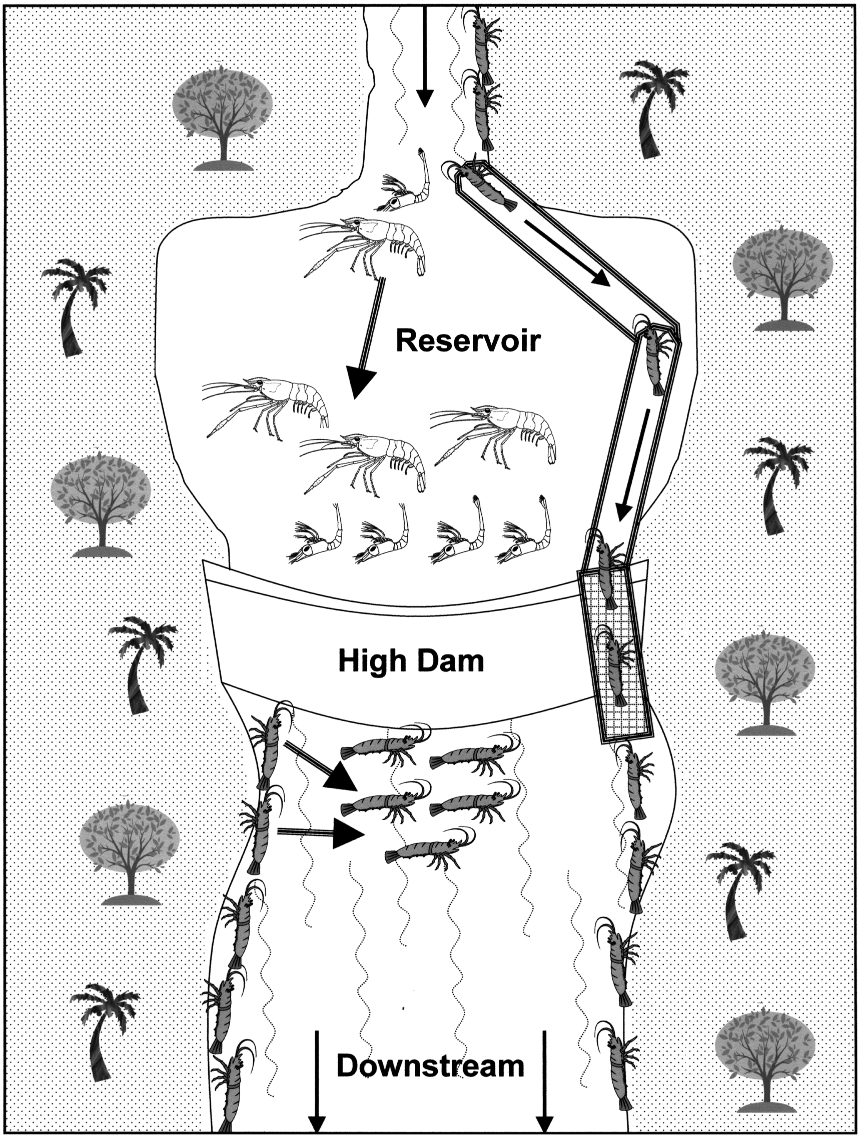

Fig. 4. Human impacts on amphidromous shrimp migrations. Stage-1 larvae (upside-down swimmers) released in upstream headwaters (top of figure) by females in one species, and adult females (unshaded, upright) of another species migrating downstream to hatch in coastal waters, are trapped (arrow with double line) in the reservoir upstream of the high dam. Juveniles (shaded) of both species migrating upstream after larval development are blocked (left stream bank) and accumulate (arrows with double lines) downstream of the dam; on the right side of the stream, a shrimp ramp (rectangle with mesh fill) allows juveniles to climb up and over the dam. If a channel with directional flow (solid arrows) is provided, juveniles may be able to bypass the still waters of the reservoir and move into the headwaters upstream of the reservoir.

of $\leqslant 50°$, a flow of water at speeds of $\leqslant 65$ cm sec^{-1}, and a flooring with sufficient purchase for the tips of the shrimps' walking leg (~0.5 mm mesh, e.g., lined with artificial sponge scrubber mesh, or constructed with cellular concrete). Hamano & Honke (1997) showed how floodlight illumination of one bank can be used to direct migrating shrimps, which avoid such light, to the opposite bank below a dam equipped with a fishway. Pompeu et al. (2006) reported that juvenile migraters enter and are transported to the upstream side of power plant dam with a fish lift (elevator). If dams or other obstacles are low enough, continual or periodic flow over the structure will stimulate juvenile movement over them. No studies, however, have addressed the issue of how adult females moving downstream to release larvae, in those species which do so, might be able to continue downstream past dams. Whether or not they would be able to find and migrate down shrimp or fish ladders is unknown.

Other structures along the bank, such as wharves, jetties, revetments, wing dikes and other river control structures may block or interrupt the migration route of juveniles. Flow patterns downstream of such structures may be complex and confuse the directional response of migrating juveniles. The decline in the once-abundant populations of the amphidromous *M. ohione* in the upper Mississippi and lower Ohio Rivers might due to such interruption of juvenile recruitment to upstream populations (Bauer & Delahoussaye, 2008; Bauer, 2010). The actual effect of along-bank structures on juvenile migrations needs to be tested.

The reservoirs behind high dams are also a problem for amphidromous shrimps. Even if juvenile migraters pass by a high dam via a "shrimp ladder", the lack of directional flow in the reservoir may confuse them and prevent further movement upstream. For this reason, Holmquist et al. (1998) recommended the construction of side channels between the shrimp ladder and upstream flow to circumvent the reservoir (fig. 4). Many reservoirs are stocked for recreational fishing with species predatory on shrimps (Holmquist et al., 1998). Reservoirs of high dams without frequent spillway discharge must also act as traps for shrimp larvae drifting down from upstream, preventing the larvae from continuing on to the sea (fig. 4). Although likely, this source of significant larval mortality has not been studied (March et al., 2003). In species in which females migrate downstream to hatch larvae, the reservoir-dam complex may block the migration (fig. 4).

Reservoirs behind dams are often the site for extracting water to use in municipal water systems and agriculture. The large volumes of water removed contain large numbers of larvae (Benstead et al., 1999; March et al., 2003).

Intake screens to keep out large fish and debris do and can not have a mesh small enough to block tiny shrimp larvae from entering. However, various measures can be taken to greatly reduce this source of larval mortality (Benstead et al., 1999; March et al., 2003). In tropical streams, at least, females release larvae in the early evening, i.e., in the ∼3 h after sunset (March et al., 1998). Limiting extraction of water from a reservoir above a dam for 3-5 h in the early evening would greatly reduce larval mortality (March et al., 2003). A knowledge of the species reproductive season would make this limitation necessary only during that period of the year. Reduction of all water extraction by water conservation measures and elimination of wasteful water usage would further limit larval mortality (March et al., 2003).

Amphidromous shrimps are important components of the ecosystems in which they occur. Within the freshwater (juvenile and adult) portion of their life cycle, they serve both as primary and secondary consumers. In tropical island streams, biomass of these shrimps is significant. Although the ecology of amphidromous shrimps in continental river systems is much less studied, given their often high abundance and use in artisanal fisheries, they must also have important ecological roles in their habitats. Larvae delivered to and developing in estuaries and nearshore coastal waters must represent a measurable and possibly significant energy transfer from the freshwater to the marine environment. Having grown in size and energy content during development in the sea, the upstream migrating juveniles must likewise represent an important energy input from marine habitats into freshwater streams, their adult habitat. Amphidromous shrimps, as adults, are often the focus of local artisanal fisheries. For these reasons, the considerable human impacts on amphidromous species should be reduced as much as possible. An understanding of their migrations is essential in identifying and mitigating human impacts on these species.

ACKNOWLEDGEMENTS

I am grateful to editor Akira Asakura for organizing the 2009 Tokyo Crustacean meetings at which the symposium on migration of freshwater shrimps, which stimulated this paper, was presented. This research was supported by NOAA grant No. NA06OAR4170022 (R/SA-04) to RTB and Louisiana State University. This is Contribution number 139 of the University of Louisiana Laboratory for Crustacean Research.

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First received 16 December 2009.
Final version accepted 13 January 2010.