

Review

Amphidromy in shrimps: a life cycle between rivers and the sea

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ABSTRACT. Amphidromy is a diadromous life history pattern, common in tropical and subtropical freshwater caridean shrimps, in which adults live, breed and spawn small-sized embryos in freshwater but have extended larval development (ELD) in marine waters. Most completely freshwater species spawn large embryos with either direct or abbreviated larval development (ALD). An important benefit of amphidromy is dispersal among river systems via marine larvae, which increases their access to alternative habitats. Thus, amphidromous species have much broader geographic distributions than closely related completely freshwater ones with ALD. ALD and freshwater ELD species appear to have evolved from amphidromous species with marine ancestors. Delivery of larvae to the sea in many amphidromous species is accomplished by upstream hatching and river drift of larvae to the sea. In other species, the females themselves apparently migrate down to marine waters to spawn. After development, the postlarvae must find a river mouth and migrate upstream to the adult habitat. Migrations occur at night, with juveniles swimming or crawling along the river or stream bank. Larvae are released during the wet or flood season of the year, while juvenile migrations take place during the dry or low-flow season. Both larval downstream and juvenile upstream movements are disrupted by human impacts such as dams and other forms of river control. Although much progress has been made in understanding the evolution and ecology of amphidromy, research is still needed on all aspects of shrimp amphidromy, especially in Latin America with its diverse freshwater shrimp fauna.

Keywords: Caridea, diadromy, larvae, juveniles, migration, streams, rivers.

Anfidromía en camarones: un ciclo de vida entre los ríos y el mar

RESUMEN. La anfidromía es un ciclo de vida común en camarones tropicales y subtropicales de agua dulce, en que los adultos viven, se aparean y desovan embriones pequeños en agua dulce, pero tienen un extenso desarrollo larval (DLE) en aguas marinas. Especies con embriones grandes tienen un desarrollo larval abreviado o directo (DLA), y pasan toda su vida en agua dulce. Un beneficio importante de la anfidromía es la dispersión en los ríos por medio de larvas marinas. Por eso, las especies anfidrómicas tienen distribuciones geográficas más amplias que las especies de agua dulce sin larvas marinas. Al parecer, las especies con DLA han evolucionado de especies anfidrómicas con antepasados marinos. La llegada de larvas al mar en algunas especies anfidrómicas ocurre por la deriva de larvas por la corriente del río. En otras especies, las hembras migran río abajo para liberar sus larvas en agua salada. Después del desarrollo larval en el mar, las postlarvas tienen que buscar una desembocadura de un río y luego, migrar río arriba al hábitat de los adultos. Las migraciones ocurren durante la noche, con los juveniles nadando o siendo transportados por la corriente del río. La eclosión de las larvas ocurre durante la temporada de lluvia (flujo alto), pero las migraciones de juveniles río arriba, ocurren durante la temporada seca (flujo lento). El impacto humano en las migraciones se relaciona con el control de las aguas en los ríos (*e.g.*, las represas). Aunque hay bastante progreso en la comprensión de la evolución y ecología de la anfidromía, aún se necesitan muchas investigaciones sobre este tema, especialmente en Latinoamérica con su variada fauna de camarones de agua dulce.

Palabras clave: Caridea, diadromía, larvas, juveniles, migración, transporte, ríos.

INTRODUCTION

The life cycles of many aquatic species are divided between freshwater and marine habitats, a life history pattern termed diadromy. In such species, an individual begins life in one habitat and soon migrates to the other, where it spends the majority of its life feeding and growing to reproductive maturity. The individual then migrates back to the habitat of its birth, thus completing the life cycle. These migrations are ecologically important because migrating organisms are temporally variable components of different ecosystems, affecting habitat, productivity, and trophic relationships at different times of the year. Migrations promote export and import of productivity between freshwater and marine habitats. Human activities greatly impact migrations, e.g., blockage of migratory routes of diadromous fishes and invertebrates by damming of rivers and streams (Dingle, 1996; Holmquist *et al.*, 1998; March *et al.*, 2003; Merz & Moyle, 2006). The presence or absence of migration among populations of species with wide geographic ranges has an important impact on dispersal and the population genetics of a species.

The best known and studied types of diadromy are anadromy and catadromy. In anadromy, the individual hatches out in freshwater streams or lakes, spending a short part of the life cycle there, then migrates out to sea, where it may spend several years before returning to fresh water where mating and spawning takes place (e.g., Pacific salmon, *Oncorhynchus* spp.; Hasler *et al.*, 1978). In catadromy, the opposite occurs, as shown by the classic case of *Anguilla* eels (Schmidt, 1923). In these fishes, individuals are hatched in the middle of the ocean, float as larvae with currents to continents where they enter rivers and spend several years in fresh water, growing and maturing before returning to the sea to mate and spawn.

Another form of diadromy, termed amphidromy, occurs in many fishes, shrimps, and some gastropod snails inhabiting tropical and subtropical freshwater habitats (e.g., Pyron & Covich, 2003; Kikkert *et al.*, 2009; Thuesen *et al.*, 2011). Although found in species from coastal rivers of continents, it is particularly common on small mountainous oceanic islands (McDowall, 2010). In freshwater amphidromy (McDowall, 1992, 2007), the individual grows, mates and spawns in freshwater streams or rivers but the planktonic larvae develop in brackish-water estuaries or fully marine coastal waters. Upon completion of larval development, the individual settles to the bottom as postlarva and must find the mouth of a freshwater stream or river to migrate upstream to the adult habitat (Fig. 1). Amphidromy in shrimps has

received much attention in the last two decades with the discovery of marine larval development in freshwater species (e.g., shrimps; Hunte, 1977, 1978, 1980). Research on the ecology of tropical streams has indicated the importance of these shrimps in stream food webs and ecosystem function (leaf shredders, algal consumers) (Crowl *et al.*, 2006; Cross *et al.*, 2008; Synder *et al.*, 2011). The construction of dams and other human impacts on rivers in these areas has interrupted the downstream delivery of larvae to the sea, as well as the return upstream migrations of juveniles returning from the sea. Such impacts have severely damaged species diversity and ecological function in the affected tropical streams (Holmquist *et al.*, 1998; March *et al.*, 2003; Synder *et al.*, 2011).

Caridean shrimps are one of the most important groups of amphidromous organisms. Although the majority of carideans are marine, approximately 25% of the 3,400 described species live in freshwater (De Grave *et al.*, 2008; De Grave & Fransen, 2011). Most freshwater carideans are in the families Atyidae, Xiphocarididae and Palaemonidae (especially the genus *Macrobrachium*), and it is in these groups that amphidromous life cycles have evolved (Bauer, 2004). In the completely freshwater shrimp families Euryrhynchidae, Typhlocarididae, Desmocarididae, and Kakaducarididae, as well as in many freshwater species of Palaemonidae, amphidromy is not known: embryos are large in size, and larval development is known to be or appears to be abbreviated or direct (Bauer, 2004).

The life history of some freshwater species is completely adapted to freshwater in that all stages of the life cycle occur there. The extended planktonic development of most marine species is abbreviated in these freshwater species, with hatching from large embryos as advanced larvae and few subsequent larval stages, or is direct with the embryo hatching out as a postlarvae or small juvenile (Hayashi & Hamano, 1984; Magaelhães & Walker, 1988; Jalihal *et al.*, 1993) (Fig. 2). To sustain extended incubation and embryonic development before hatching in these species, mature oocytes (eggs) must contain considerable amounts of yolk. Thus, females spawn relatively few large eggs. On the other extreme, in the life history spectrum of freshwater shrimps, are amphidromous species, whose larvae require extended planktonic development in saline waters. Larval development occurs in the brackish water of estuaries and coastal bays or in the open sea. In amphidromous species, females spawn many small eggs, which hatch at a much less advanced larval stage than those of species with abbreviated or direct development (Bauer, 2004) (Figs. 2 and 3).

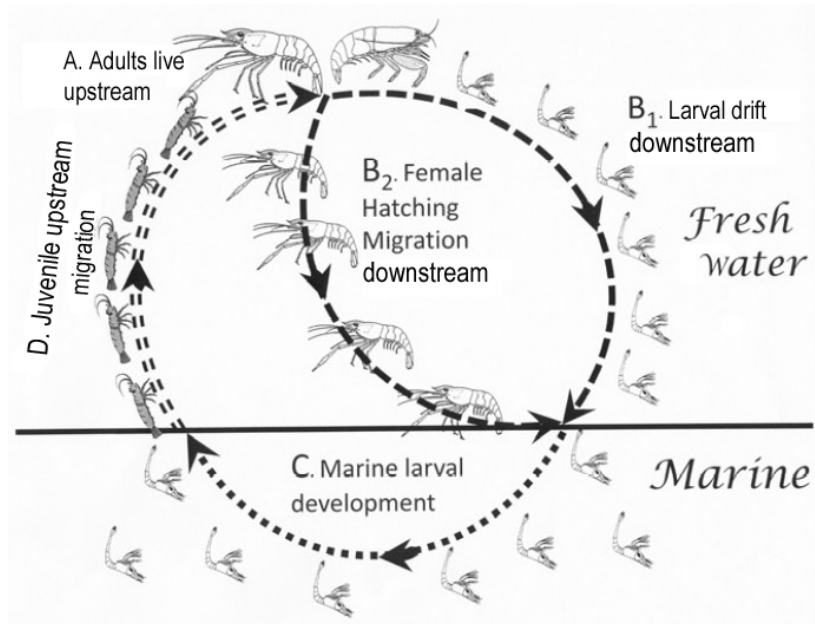


Figure 1. Amphidromous life cycle in caridean shrimps: adults live and breed upstream in fresh water. Females deliver first stage larvae either by releasing them into the stream current (drift) or by migrating downstream to hatch them in the sea. After larval development in the sea, the postlarvae and juveniles enter a stream or river and migrate upstream to the adult freshwater habitat.

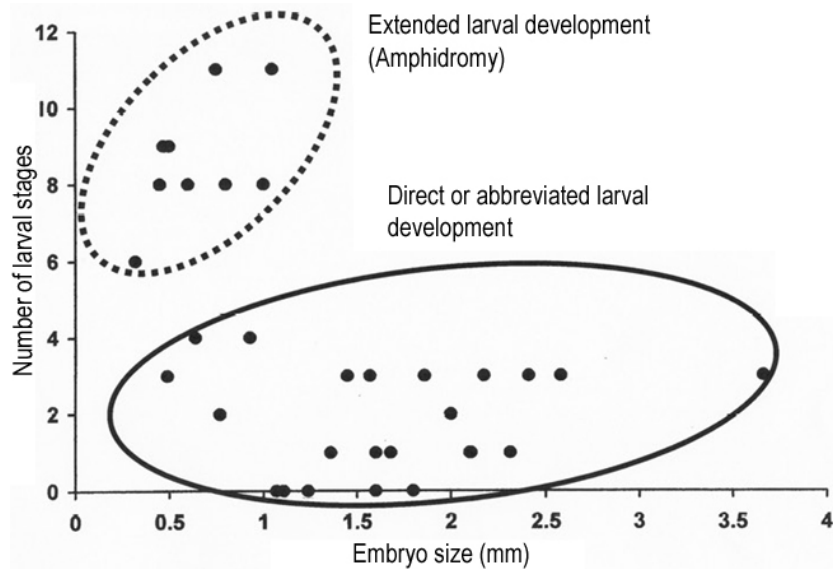


Figure 2. The relationship between embryo size and the number of larval stages in freshwater shrimps (modified from Bauer, 2004; original data from Hayashi & Hamano, 1984; Magalhães & Walker, 1988 and Jalihal *et al.*, 1993). Each data point represents one species. Species with extended larval development are generally amphidromous, while those with abbreviated or direct larval development have a completely freshwater life cycle.

Although most freshwater species with small eggs have extended larval development in the sea, there are a few freshwater species which have taken another life history route. In these species, extended development occurs in fresh water (Fig. 3). The environmental conditions which lead to this latter condition are a

stable freshwater environment in which nutrient supplies are plentiful and abundant larval food (*i.e.*, plankton) occurs. Examples of such extended larval development in plankton-rich freshwater habitats are far-upstream river populations of *Macrobrachium amazonicum*, in upper Amazonian floodplains in

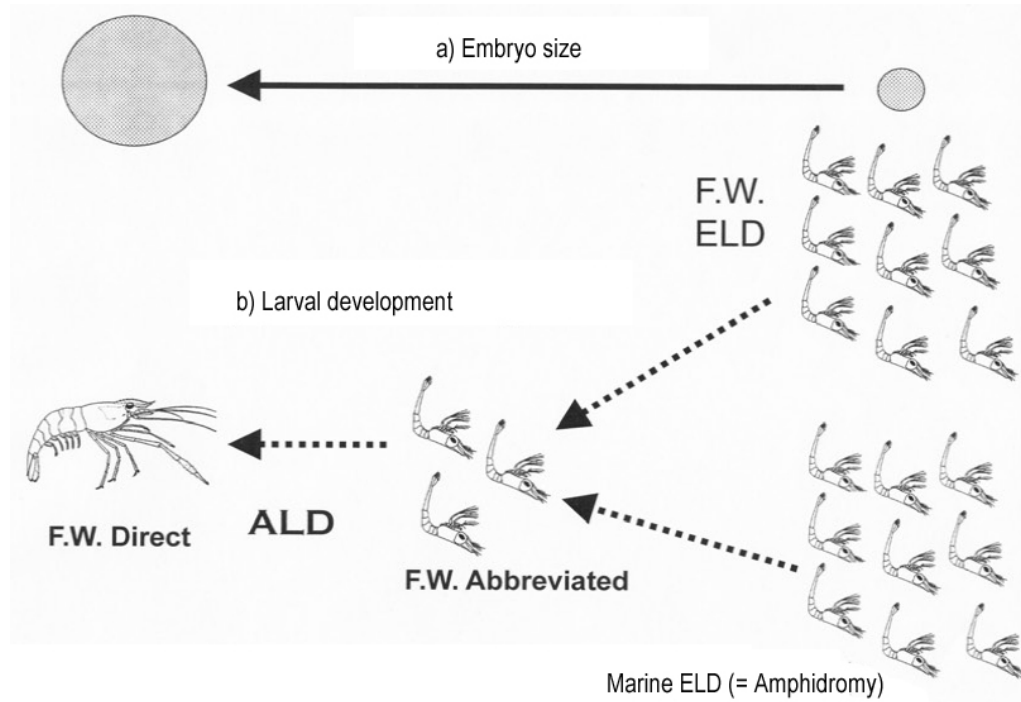


Figure 3. The relationship between embryo size, larval development and life history in freshwater shrimps. Species with small eggs and extended larval development (ELD) are generally amphidromous, although some ELD species are completely freshwater. Freshwater species with large embryos and abbreviated or direct larval development (ALD) are descended from ELD species.

South America (Magaelhães, 1985; Magaelhães & Walker, 1988) as well as those of *M. niloticum* in Lake Chad, Africa (Walker, 1992). Several species of *Limnocaridina* spp., two *Caridella* spp. (Atyidae) and *Macrobrachium moorei* (Palaemonidae) in Lake Tanganyika, Africa, have extremely small eggs (Mashiko *et al.*, 1991) indicating extended planktonic development. Given the distance (several thousand kilometers) from Lake Tanganyika to the only accessible marine environment, the Atlantic Ocean, it is quite probable that this extended development occurs in fresh water, *i.e.*, the lake itself, a large, ancient and stable lacustrine habitat. Thus, the process of adaptation of primitive marine species to the fresh water environment (“freshwaterization,” Jaliha *et al.*, 1993) has taken three principal routes: (1) the reduction or loss of larval stages (direct or abbreviated larval development, both termed “ALD” in this paper), (2) retention of the extended planktonic development in the sea (ELD) of the marine ancestor, or less commonly, (3) the adaptation of ELD to freshwater.

Studies on the occurrence, evolution, and human impacts on amphidromous species are being published at an accelerating rate. The purpose of this manuscript, stimulated by a presentation at the decapod crustacean session of the “Primer Congreso Latinoamericano

sobre Macroinvertebrados de Agua Dulce” (February 2012, San José, Costa Rica), is to amplify and update previous short reviews on amphidromy (Bauer, 2011a, 2011b). The objectives of this paper are to review, in caridean shrimps, the evolutionary costs and benefits, the evolutionary origins, and the migrations associated with amphidromy, and to give suggestions for future research on amphidromy in Latin America. The impact of human activities on amphidromy has been recently reviewed (Bauer, 2011b) and will not herein be treated extensively.

Historical perspective

An amphidromous life history was suspected in various freshwater shrimp species for some time before being confirmed by recent studies. Species with distributions restricted to freshwater habitats (rivers and streams) with a connection to the sea, such as North American *Macrobrachium* spp. (Hedgepeth, 1949) and the atyid and *Macrobrachium* species of Caribbean islands (Chace & Hobbs, 1969) were thought to have marine larval development. Studies on larval development of Caribbean atyid and *Macrobrachium* species by Hunte (1977, 1980), on North American *Macrobrachium* spp. by Dugan *et al.* (1975) and the atyid *Caridina japonica* (Hayashi &

Hamano, 1984) demonstrated the need for saltwater larval development in many freshwater shrimps. The upstream movement (migration) of newly-metamorphosed postlarvae and small juveniles from river mouths was first inferred (*e.g.*, Hartmann, 1958; Chace & Hobbs, 1969; Hunte, 1978) or reported anecdotally (*e.g.*, Ibrahim, 1962; Ling, 1969). Direct observations on juveniles migrating upstream and climbing up over obstacles (*e.g.*, low weirs) were made by Lee & Fiedler (1962) and Hamano & Hayashi (1992). Beginning in the late 1990's, both qualitative and quantitative observations and studies on juvenile migration increased considerably (*e.g.*, Holmquist *et al.*, 1998; Benstead *et al.*, 1999, 2000; Fievet, 1999a, 1999b; Bauer & Delahoussaye, 2008; Kikkert *et al.*, 2009). The accumulating literature indicates that generalizations about amphidromous migrations often vary depending on the nature of the stream system (high *versus* low gradient streams; small island streams with short distances from headwaters to the sea *vs* large rivers on continents with shrimp populations at relatively greater distances from the sea). The type of stream system may have important consequences on the mode of delivery of larvae to the sea as well as the characteristics of the subsequent upstream migration (see below).

Evolutionary origins of amphidromy

Amphidromy would appear to be a very risky life history strategy for freshwater shrimps. Species living in mountain streams on tropical islands release their larvae to drift down rapidly flowing, turbulent streams to the sea for larval development (Benstead *et al.*, 2000). Other species on large continents have populations far from the sea, and females apparently must migrate long distances down to estuaries to release larvae (Hartmann, 1958; Bauer & Delahoussaye, 2008). After an extended series of larval stages in an estuary or coastal marine waters, the postlarvae settles to the bottom and must seek the mouth of a freshwater stream or river and migrate, often many kilometers, and in some cases climbing up and past cascades and waterfalls, to reach the adult habitat. Would it not make more "evolutionary sense" for a species to simply reduce or eliminate the number of larval stages, *i.e.*, evolve away from the marine ELD of their ancestors to the ALD found in so many freshwater species? As McDowall (2007) has rhetorically proposed, why bother with amphidromy? Of course, freshwater species which become landlocked must evolve away from marine ELD or become extinct. For those many species in which the adults live in bodies of water with access to the sea, why do they still "bother" with marine development and the risks that

migrations from the sea involve? Below, I discuss some of the possible selective pressures (costs and benefits) which may be involved in the evolution of amphidromy in shrimps.

For freshwater shrimps that live in fast-flowing bodies of water, release of larvae that would go through a long series of stages would simply mean that they would be washed away from the adult habitats. In populations kilometer within tens of kilometers to the sea, the larvae would arrive in the sea within a day or two. Thus, the stage is already set for amphidromy in such species. In species living in stable lentic environments, ELD can potentially continue to occur as long as there is a healthy plankton community to provide larval food. Physiologically, there is no barrier for larvae to adapt to freshwater conditions, because it has occurred as indicated above for *Limnocaridina* spp. and *Macrobrachium niloticum* in large African lakes and shown in *M. amazonicum* populations living thousands of kilo-meters from the sea in floodplain lakes (Magaelhães, 1985). However, a much more common ecological situation is that many lentic freshwater habitats are plankton-poor, and thus ALD has evolved in these species (Walker, 1992). The hatching stage is either a postlarvae, so that the planktonic environment is avoided completely, or the few larval stages that do occur are nonfeeding lecithotrophic larvae which sustain themselves with yolk left over from the embryo, which is large compared to amphidromous species and richly supplied with yolk (Figs. 2 and 3).

Caridean shrimps are primarily a marine group. What might have been the selective pressures that led to the invasion of freshwater habitats? Freshwater habitats may have been simply an empty ecological niche that shrimps invaded with sufficient benefits to overcome the physiological problems of adaptation to freshwater. The freshwater stream systems of tropical rainforests and habitats, in which many amphidromous shrimps live, are rich in organic matter from leaf fall, twigs and fruit, which sustains a productive detritus-based food web (Covich & McDowall, 1996; Crowl *et al.*, 2006). In Caribbean island streams, atyid shrimps, with their unique scraping and filtering chela brushes, are important harvesters of detritus and periphyton. *Xiphocaris elongata* is a somewhat more generalized consumer (primarily a leaf-shredder) and, at a higher tropic level, *Macrobrachium* spp. is omnivorous scavengers and predators (Covich & McDowall, 1996). Entry of the marine ancestors of amphidromous species into freshwater habitats might have been due both to past competition with the diverse caridean fauna of marine habitats, as well as invasion into a relatively unoccupied but resource-rich habitat. By the

time the xiphocaridid/atyid caridean lineage entered fresh water (early to late Jurassic: Ortmann, 1902; Hobbs & Hart, 1982; Bracken *et al.*, 2010), other ecologically-equivalent consumers, the insects and their larvae, must have been well-established. However, Fryer (1977) has suggested that the insect fauna of streams co inhabited by atyid shrimps is depauperate, presumably because of competition with the shrimps for the same detritus-based resource, an hypothesis that has received some equivocal support (Vinson & Hawkins, 1998).

A major benefit for freshwater shrimps in the headwaters of streams on mountainous tropical islands is that there are few or no fish predators there (*e.g.*, Covich *et al.*, 2009; Blob *et al.*, 2010; Hein *et al.*, 2011). Covich *et al.* (2009) demonstrated that the amphidromous shrimps *Atya lanipes* and *Xiphocaris elongata* inhabiting stream headwaters escape from fish predation. *Xiphocaris* living in deep pools below barriers, where fish are present, show morphological responses to fish predation (larger size, elongate rostra). The shrimps are capable of crawling up or around barriers such as large steep waterfalls, either as adults or during their juvenile migrations (discussed below) while their fish predators cannot move up the cascades. On the other hand, McDowall (2007) suggested that an overall escape from predation by marine and estuarine fishes may have been an initial selective pressure favoring invasion of fresh water by groups that were capable of moving upstream. McDowall (2007) also pointed out that the fresh water fish fauna (including predators) is highly impoverished, at least on island streams where amphidromous species are abundant.

An obvious advantage of amphidromy is the potential for dispersal (Hunte, 1978; Covich, 2006; McDowall, 2007). Streams and rivers from which larvae originated are recolonized by marine larvae which can also invade previously uninhabited streams (Hunte, 1978), some of which may be far from the stream of larval origin (Cook *et al.*, 2009). Amphidromous (ELD) species generally have broader geographic ranges than non-amphidromous species in the same taxon. Gene flow among populations of the same species tends to be greater in amphidromous or presumed (small egg size) amphidromous species (Page *et al.*, 2005, 2007, 2008; Cook *et al.*, 2006; Mashiko & Shy, 2008). For example, Mashiko & Shy (2008) studied four species of *Macrobrachium* in the western Pacific. Small egg (presumably ELD) species had generally broader geographic ranges and greater genetic homogeneity than large-egg (ALD) species. Page & Hughes (2007) showed, using the COI mitochondrial gene, that in *Caridina* spp. (Atyidae)

from eastern Australia those species with the smallest eggs (presumably ELD) have the least intraspecific divergence and largest geographic distribution, whereas those with the biggest eggs (direct or ALD) have the most genetic divergence and restricted distributions. Medium-sized egg species are intermediate in these characteristics. *Cryphiops caementarius* (Palaemonidae), a river shrimp with a broad geographic range along the west coast of South America, was shown by Hartmann (1958) to have marine larvae. Dennenmoser *et al.* (2010) demonstrated, using haplotypes of a mitochondrial gene, high gene flow among separate river populations over a distance of several hundred kilometers. The biogeography and distributional patterns of Caribbean and Pacific atyid shrimps appears, in large part, to be a product of larval dispersal or lack thereof (Page *et al.*, 2008; Cook *et al.*, 2009, 2012). “Estuary hopping” (larval movement among nearby estuaries), or limited dispersal in the open sea, has allowed gene flow among Indo-Australian populations of the river shrimp *Macrobrachium rosenbergii* (De Bruyn & Mather, 2007). The literature is becoming replete with similar examples, which clearly show the dispersal advantage of amphidromy.

Given the above discussion, on the costs and benefits of amphidromy *versus* ALD, one might ask the question: which is ancestral (plesiomorphic) and which is derived (apomorphic)? The Atyidae are almost exclusively fresh water shrimps with life histories ranging from amphidromy to completely fresh water (ALD). Various authors (Chace & Hobbs, 1969; Carpenter, 1977; Hobbs & Hart, 1982) presumed the atyid ancestor was an amphidromous species with immediate marine ancestors. This issue has been addressed by results from various recent studies using molecular phylogenetic techniques. The genus *Paratya* from the Pacific has both amphidromous and ALD fresh water species. A phylogenetic analysis of the genus by Page *et al.* (2005) supports the hypothesis of amphidromy as ancestral in this group. Cook *et al.* (2006) found that *Paratya australiensis* from eastern Australia, in which some populations are restricted to freshwater while others are amphidromous, is probably a complex of cryptic species. The phylogeographic analysis of these authors indicates that amphidromic populations have colonized various stream systems, giving rise to repeated evolution from amphidromic coastal populations to strictly freshwater populations (or cryptic species) of *Paratya*, presumably with some form of ALD.

The view of amphidromy as plesiomorphic is not universally held, stemming primarily from suggestions

by Pereira (1989) and Pereira & Garcia (1995), and the opposite might be true for another important freshwater group, the speciose genus *Macrobrachium* (Palaemonidae). They argued that because various purportedly primitive freshwater palaemonid genera had ALD in their life cycle, ELD must be derived. According to this hypothesis, the ancestor of *Macrobrachium* was a freshwater species with ALD, which then gave rise to descendants which either retained ALD or developed ELD (either amphidromous or, more rarely, completely fresh water. Pereira (1989), went even further in making the case that all the marine palaemonids are derived from a freshwater palaemonid (presumably with ALD). This development would entail a life cycle with ALD evolving into one with ELD. However, there is nothing in the larval development of *Macrobrachium* spp. with ELD that is noticeably different from that of other marine shrimps. One would suppose that ELD derived secondarily from ALD would show some set of unique or different larval characteristics, when compared to other marine species with ELD. No such features have been reported, although many descriptive studies on caridean larvae have been published. Williamson (1982) stated, in his review of decapod larvae, that ALD may certainly be regarded as a departure from the ancestral condition in Decapoda. The sequence of ELD (marine ancestor) to ALD (freshwater *Macrobrachium* ancestor) to a morphologically similar ELD (amphidromous *Macrobrachium* spp.), again seems unlikely simply on the basis of both developmental constraints and the principle of parsimony.

Mapping of ALD and ELD species on molecular phylogenies of *Macrobrachium* potentially provides good tests of the “ELD first” vs “ALD first” hypotheses. Using the mitochondrial 16S rRNA gene, Murphy & Austin (2005) constructed a phylogeny from a worldwide sample of 30 species. When amphidromy and ALD were mapped on the phylogeny, five primarily amphidromous lineages contained derived ALD species, supporting the “amphidromy as primitive” view in these lineages. However, the most basal lineages in the overall tree were ALD species, supporting the Pereira & García (1995) hypothesis, that ALD is primitive in *Macrobrachium*. This study used a limited sample of the more than 238 *Macrobrachium* spp. (De Grave *et al.*, 2009). Another analysis of 46 Asian species, based on three nuclear and two mitochondrial genes (Wowor *et al.*, 2009), supported the ELD as primitive and showed independent origins of ALD in various clades. This result agreed with less conclusive work by Liu *et al.* (2007), based on a single mitochondrial gene, which

supported the hypotheses that (a) *Macrobrachium* spp. originated from marine ancestors and subsequently invaded freshwater multiple times and (b) that the ALD of land-locked species represents adaptive convergence from different ELD ancestors. Furthermore, none of the supposedly primitive freshwater species from other palaemonid genera used as out-group species, included in the Liu *et al.* (2007) analysis, were in a basal position in the phylogeny, which does not agree with the Pereira and García hypothesis. On the other hand, Pileggi & Mantelatto (2010) analyzed a sample of 58 north and south American *Macrobrachium* species, using two mitochondrial genes, to produce a phylogeny on which the distribution of ELD and ALD life history trait could be mapped. Although the authors suggested that the phylogeny did indicate some support of the Pereira and García hypothesis, they considered the results inconclusive. Pileggi & Mantelatto (2010) felt that the question, as addressed by phylogenetic studies, remains open but may be resolved as more species are sampled and included in these phylogenetic studies.

Another way to address this issue is to look at variation in embryo size (as an indicator of ELD and ALD), in different populations of the same species, especially in the same river system. An example of such variation is that presented by the brackish/freshwater *Palaemonetes varians* complex, in which populations living in waters of different salinities show variation in embryo size. Sollaud (1923, 1924), proposed that such populations were subspecies, which he named *P. varians* var. *microgenitor* (small embryos; marine brackish), *P. varians mesogenitor* (medium embryos, freshwater brackish) and *P. varians macrogenitor* (large embryos, fresh water). Holthuis (1950), was able to find sufficient morphological differences between these subspecies to raise them to the level of species (*P. varians*, *P. mesogenitor*, and *P. antennarius*, respectively). Chow *et al.* (1988), reported on genetic variation in egg size and other characters in 20 Japanese populations of *Palaemon paucidens*, with large-embryo populations, living in lakes and ponds, while small-embryo populations occurred only in rivers, *i.e.*, with access to the sea. The two types of populations showed genetic (allozyme) differences and mating incompatibility. Similarly, Mashiko & Shy (2008) found small-embryo and large-embryo populations of *Macrobrachium nipponense* in different locations along the western Pacific. Some populations varied in embryo size in the same river system, with small-egg populations in estuarine environments and large-egg populations in upstream freshwater streams and ponds. They were able to show that these populations were capable of

and showed evidence of hybridization, indicating incipient speciation. Finally, *Macrobrachium amazonicum*, a South American species with a very extensive geographic distribution, shows great variation in life history traits, from coastal-amphidromous (ELD) to far-inland populations, with both ALD and freshwater ELD, as well as variation in several other morphological and life history traits (Hayd & Anger, 2013; Vergamini *et al.*, 2011). Such genetically similar populations are obviously in the process of speciation or are morphologically cryptic species, and it would be of great interest to determine their phylogenetic sequence to help resolve the ELD-ALD controversy of amphidromous and freshwater shrimps.

In summary, the weight of all current evidence from physiological, developmental, and phylogenetic considerations supports the hypothesis of multiple invasion of marine species giving rise (a) to first ELD species requiring brackish or marine water development, which then (b) gave rise to ALD species, or, more rarely, to species which were able to adapt ELD to plankton-rich lentic freshwater habitats.

Transfer of larvae from freshwater to the sea

The larvae of amphidromous shrimps require saline waters to complete development. As the adult females live, mate and primarily spawn in upriver freshwater habitats, the larvae have to be delivered to river mouths for development to brackish water estuaries or high salinity coastal waters. Earlier workers on amphidromous shrimps hypothesized that upstream females hatch their larvae directly into stream flow, after which the larvae drift more or less passively to downstream estuarine or marine habitats (Chace & Hobbs, 1969; Hunte, 1978; Hamano & Hayashi, 1992). More recent studies on the larval biology of such species have definitively demonstrated such larval drift (Holmquist *et al.*, 1998; March *et al.*, 1998; Benstead *et al.*, 1999). Most of these species occur in tropical and subtropical stream habitats in which distances from the adult habitat to the sea are relatively short, *i.e.*, a few to dozens of kilometers, *e.g.*, Puerto Rico, other Caribbean and small oceanic Indo-Pacific islands; large islands (*e.g.*, Japan, Taiwan) and continental locations relatively close to the sea (coastal stream systems in Costa Rica, *e.g.*, Pringle & Ramirez, 1998; Covich, 2009).

Stage-I larvae of amphidromous caridean species are lecithotrophic, *i.e.*, do not feed. Instead, the larvae utilize yolk droplets remaining from embryonic development as a nutritional resource. Such larvae must molt to Stage II (first feeding stage) or sometimes Stage III (Anger & Hayd, 2010) before their food stores are used up or they will starve to death (Rome *et al.*, 2009 and references therein).

Thus, Stage-I larvae have a limited period, usually a few days, to drift downstream in freshwater to saline waters, which trigger molting to Stage II and the commencement of feeding. For females of amphidromous species on small oceanic islands or other locations in which the adult habitat is 1-2 days larval drifting distance to the sea, larvae can easily arrive at the sea before starvation precipitates mortality.

There are other patterns as well, at least in *Macrobrachium* spp., in amphidromous species living far from the sea. *Macrobrachium amazonicum* in South America is composed of populations ranging in distribution from coastal to far inland locations in two (northern and southern) hydrologically separate river systems across tropical South America (Anger & Hayd 2010). These populations have differences in life history and sexual dimorphism which indicates that they may consist of incipient or sibling species (Vergamini *et al.*, 2011; Hayd & Anger, 2013). In the Pantanal (upper Paraguay basin) wetland populations, planktonic larvae develop completely in the relatively stable plankton-rich freshwater wetlands. Anger & Hayd (2010) compared the dependence on larval lecithotrophy of early larval stages between a Pantanal population and one from northeastern Brazil, in which larvae drifting from upstream Amazon River populations arrive and develop in low salinity estuaries. They found that Pantanal larvae were hatched with lower amounts of embryonic yolk reserve and were less dependent on lecithotrophy than the Amazon River estuarine larvae. Pantanal Zoea I could survive without food for 8-9 days versus 14-15 days in the Amazonian larvae. Furthermore, Pantanal Zoea I larvae were facultatively lecithotrophic but Zoea III (and beyond) larvae completely planktotrophic. Amazonian estuarine larvae, which require salinity (optimally 10 ppt) to reach and continue into zoeal stages, can survive without food through Zoea III, occasionally molting to Zoea IV after which obligate planktotrophy begins (Anger & Hayd, 2009, 2010). The greater dependence on lecithotrophy in Amazonian larvae is likely an adaptation to the very long drift times in moving river water from upstream hatching sites to coastal estuaries. Pantanal populations have evolved further away from lecithotrophy as development occurs completely in a plankton-rich more stable lentic habitat (Anger & Hayd, 2010). These authors hypothesized that the continued albeit limited dependence on lecithotrophy in the Pantanal larvae is a vestige of the more extensive lecithotrophy evolved in coastal marine ancestors invading riverine freshwater habitats.

Interestingly, in the North American *M. ohione*, which inhabits rivers emptying into the Gulf of

Mexico and southeastern Atlantic coast of the United States, larvae show a lower dependence on lecithotrophy than any of the *M. amazonicum* populations from South America studied by Anger & Hayd (2010). Zoeae I are completely lecithotrophic, but all yolk reserves are used or disappear after the molt to Zoea II which, as in later stages, is completely planktotrophic (Bauer & Delahoussaye, 2008 and references therein). There is no difference in the degree of lecithotrophy between coastal (Atchafalaya river, only 250 km in length) and far-upstream populations in the Mississippi river (Olivier *et al.*, 2012). This variation in the degree of larval lecithotrophy between *M. ohione* and *M. amazonicum* populations is perhaps a good reminder that selection does not act equally on the same traits in populations presumably derived from different ancestral stocks.

Not all amphidromous species or populations deliver larvae to the sea via river drift. In river systems on continents or other large land masses, distances from the adult habitat to the sea may be hundreds or thousands of kilometers from the sea, *e.g.*, *M. rosenbergii* (Ling, 1969), *M. malcomsoni* (Ibrahim, 1962), *Macrobrachium ohione* (Bauer & Delahoussaye, 2008; Olivier & Bauer, 2011), and *M. amazonicum* (Magaalhães & Walker, 1988). Such distances may be beyond the drifting capacity of Zoea-I larvae. In such species, females may have to assist larval delivery by migration down into or near coastal estuaries or nearshore marine habitats in order to release larvae. Various observations or studies on the distribution of reproductive (prehatching) females have indicated such migrations in different *Macrobrachium* species on continental land masses, *e.g.*, *M. rosenbergii* (Ling, 1969); *M. malcomsonii* (Ibrahim, 1962), *M. ohione* (Reimer *et al.*, 1974; Bauer & Delahoussaye, 2008; Olivier & Bauer, 2011), and *Cryphiops caementarius*, a probable species of *Macrobrachium* (Pileggi & Mantelatto, 2010). Females incubating embryos of these species appear in coastal estuaries or nearshore coastal waters during the reproductive season which is coincident with the high water or flood season of the rivers that the adults inhabit. The females then disappear from the estuaries soon after the end of the peak reproductive season, presumably reentering the river and moving back upstream.

These species vary in the degree of migration from upstream freshwater habitats to downstream saline habitats. In *C. caementarius* from Peru, Hartmann (1958) demonstrated with population sampling that only females migrate down from as much as 100 km upstream to enter the river mouths where wave action mixes coastal waters with river water to produce brackish water. Entry into the river mouth apparently

occurs well before hatching of embryos because the young postlarvae first appear there, indicated that larval development occurs in coastal waters. Hartmann's work was supported subsequently by Dennenmoser *et al.* (2010) with population genetics, based on mitochondrial DNA haplotypes, showing long-distance dispersal and mixing among coastal populations via the sea. Anecdotal observations on *M. rosenbergii* suggest that brooding females migrate downriver from as far as 200 km upstream into upper estuaries where hatching and larval development occur (Ling, 1969). Reimer *et al.* (1974), carefully documented the appearance of *M. ohione* in the Galveston Bay estuary (Texas, USA), during the reproductive season, and the disappearance of individuals from the estuary afterwards. Bauer & Delahoussaye (2008), sampling *M. ohione* at upstream and downstream locations in the Atchafalaya River (Louisiana, USA), found a similar result. Reproductive-sized adult females with embryos were only found in the Atchafalaya Delta estuary during the spring and early summer reproductive season. The proportion of reproductive females with embryos near hatching was much higher in the Atchafalaya Delta (estuary) than 150 km upstream. Rome *et al.* (2009) sampled larvae in the river and found a much greater abundance of hatching (Stage I) larvae within the estuary than at the upstream location, supporting the view that most females are hatching larvae in the estuary. The females of populations of *M. ohione*, in the lower Mississippi River, have similar migrations as indicated by the upstream-downstream distribution of females bearing embryos near hatching (Olivier & Bauer, 2011).

In several *Macrobrachium* species, from mountainous Atlantic and Pacific coasts of Costa Rica, no evidence of downstream female migration has been found (I. Wehrtmann, *pers. comm.*). Compared to species such as *M. ohione* in the Atchafalaya and Mississippi Rivers, the distances from upstream populations to the sea in this Central American *Macrobrachium* spp. are relatively short. Here, as with species from small tropical islands and other near-coast continental amphidromous shrimps, current flow can carry hatched larvae from upstream to the sea within 1-2 days, within the non-feeding time limits of Stage-I lecithotrophic larvae.

In many amphidromous species, hatching and/or release of larvae coincides with high river or stream flows which facilitate both female migration, when it occurs, and rapid larval drift to the sea (Fig. 4). In palaemonid species in continental large river systems, female migration and hatching occur during the river's seasonal flood. Hartmann (1958) showed that females

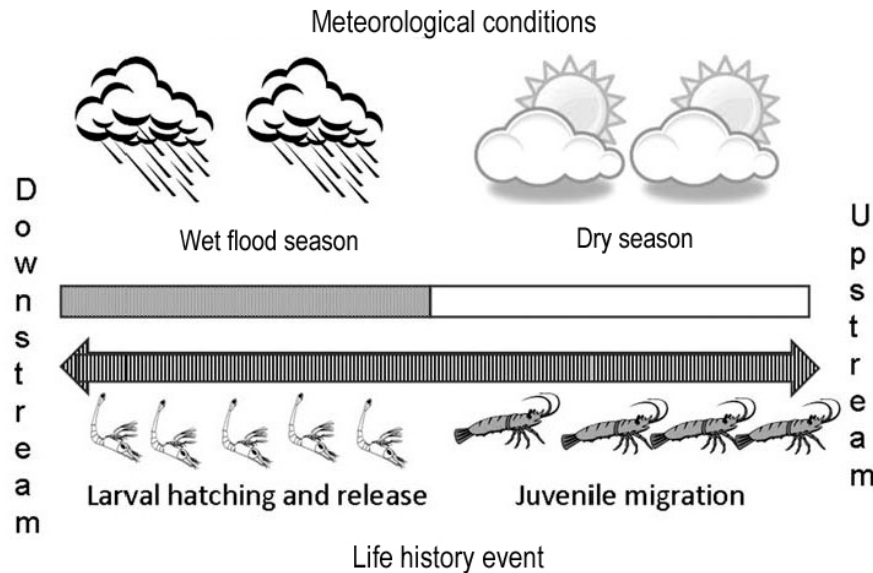


Figure 4. Larval delivery to the sea by stream drift or female migration occurs during the wet (rainy, flood) season of the year, while the upriver juvenile migration after marine larval development occurs during the dry (low-flow) season.

of the palaemonid *Cryphiops caementarius* make their downstream migration to the sea during the Austral summer (December-March) when, swollen by summer rains, Peruvian coastal rivers are at flood stage. In *M. malcolmsonii*, females move down to about 80 km upstream of the Godavari estuary to release larvae. At this distance, stream flow during the seasonal river flood, when hatching occurs, should be sufficient to deliver drifting larvae to the estuary in 1-2 days. Above it was noted that, in *M. ohione* from the Mississippi River system, the female hatching migration and larval release occur during the spring flood. In Central America, a relatively narrow isthmus divided by a mountain chain, distances to the sea are relatively short, and hatching and larval drift apparently occur during the rainy season, when stream flows are high (I. Wehrtmann, *pers. comm.*). Likewise, freshwater shrimps in high gradient streams on the mountainous island of Puerto Rico tend to have their peak reproductive season during the wet season of the year, in which stream flows are higher (Covich *et al.*, 1996; Heartsill-Scalley *et al.*, 2012).

Return upstream migration by juveniles

After passing through several larval stages in an estuary or the open sea, the planktonic larva becomes benthic as it metamorphoses to the more shrimp-like postlarvae, a transitory stage little different from the subsequent juvenile stages (Anger, 2001; Bauer, 2011b). In *M. rosenbergii*, the small juvenile rapidly undergoes further molts and growth, and within 1-2

weeks shows signs of migratory behavior. Little is known about where the metamorphosis from planktonic larva to benthic postlarva takes place, but the latter must soon find the mouth of a river or freshwater stream and begin its trek up to the adult freshwater habitat. The stimuli used by these individuals to enter river mouths have not been studied.

Sufficient research on the upstream juvenile migrations has been done to make some generalizations about them. One is that juveniles can be observed moving upstream at night (Ibrahim, 1962; Hamano & Hayashi, 1992; Benstead *et al.*, 1999; Bauer & Delahoussaye, 2008; Kikkert *et al.*, 2009). This is not surprising, as nocturnal activity by small shrimps, potential prey of larger predators, is quite common. A reasonable hypothesis for the ultimate cause of the nocturnal activity of shrimps is avoidance of predation by visually hunting fish and birds (*e.g.*, Kikkert *et al.*, 2009). The most important proximate factor stimulating migration would obviously seem to be highly reduced light intensity at night. Lesser variation in light levels, *e.g.*, by cloud cover or moonlight, seem to have little effect on juvenile migrations, as shown by Kikkert *et al.* (2009) in three species from different families of amphidromous shrimps. Bauer (2011b) suggested, based largely on a lack of observation of movement during the day, that migrating juveniles are quiescent in protected habitat along the riverbank, resting, feeding, and molting. Support for this hypothesis was given 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). However, in *M. ohione*, day and night trapping shows continued upstream movement along the bottom during the day, very unlike the swimming near the water surface observed only at night (T. Olivier & P. Hartfield, *pers. obs.*). More detailed observations need to be made on both day and night behavior and distribution to test more completely the hypothesis of nighttime-only juvenile migrations.

Not all upstream migrations by shrimps are necessarily young juveniles just coming up from the sea. An upstream “mass migration” by *M. australiense*, a completely freshwater species, was observed by Lee & Fiedler (1979). It was composed by subadults and some reproductive individuals. Like juvenile migrations, the shrimps were on the move at night, crawling and walking upstream. Likewise, Fievet (1999b), witnessed an upstream migration of *Xiphocaris elongata* on the Caribbean island of Guadeloupe composed by individuals too large to be young juveniles coming up from the sea. The movement was unusual, in that it occurred during the day, and appeared to be stimulated by a sudden release of water over the weir on which the shrimps climbed. It may be that such movements of subadults or young adults occur when they have been prevented from moving up past a particular point by low or interrupted stream flow, and then are stimulated by a later return of flow. Alternately, shrimps displaced downstream by previous high flows might be returning back upstream with such movements.

The migration of juveniles occurs near the bank where the velocity of flow is the slowest and requires the least energy output by the small juvenile to move upstream against it. There has to be some flow to serve as the directional cue which will trigger the positive rheotaxis on the juvenile, so that they move upstream. The exact location of the narrow band of migraters along the bank depends on the type of stream or river. In the steep, shallow, rapidly flowing streams, characteristic of the mountainous tropical islands on which amphidromous shrimps are often abundant and diverse, a narrow column of juveniles may be observed swimming and walking in the very shallow water, *e.g.*, splash zone, just along the bank (Kikkert *et al.*, 2009). When reaching the rapid flow of the frequently encountered cascades, the juveniles may leave the stream completely and crawl up and around the obstruction in the wetted area on the side of the bank (Ibrahim, 1962; Ling, 1969; Hamano & Hayashi, 1992; Hamano & Honke, 1997; Holmquist *et al.*, 1998; Benstead *et al.*, 1999; Fievet, 1999a;

Benbow *et al.*, 2002; March *et al.*, 2003; Kikkert *et al.*, 2009). However, there must be some flow or the juveniles become confused (Benstead *et al.*, 1999). The microflow pattern in climbing habitats may be quite erratic and occur in short bursts, changing the climbing environment found by the juveniles (Benbow *et al.*, 2002). As a result, juveniles often move upward in short jumps as the immediate microflow quickly waxes and wanes. The opportunistic crawling and climbing ability of these juveniles can be utilized to get them above artificial man-made obstacles (dams, weirs), using shallow inclined “shrimp ramps” equipped with a slow flow (see review in Bauer, 2011b).

The response of juveniles to obstacles and flow encountered, as they move upstream, also varies with body morphology of the species. The more robust *Atya* spp., such as *A. scabra* and *A. innocuous*, with a stout, somewhat dorso-ventrally flattened shape, and short stout legs, are less easily dislodged by flow than *Macrobrachium* spp. and especially *Xiphocaris elongata* juveniles, with their slender and delicate built legs (Kikkert *et al.*, 2009).

On the other extreme of juvenile migration is the environment confronting migrating juveniles in the larger, deep, and low-sloped coastal rivers found on continents or large islands. In *M. ohione* from the southeastern United States, juveniles swim near the surface at night in a band or swarm within 1-2 m of the river bank, sometimes just along the water’s edge (Bauer & Delahoussaye, 2008). Although juveniles have been at times observed in very shallow water by this author (RTB), they do not slowly crawl on the bottom or outside of the water, and are seldom forced to do so in these large rivers. In laboratory experiments, they are capable of crawling slowly up and over an appropriately constructed ramp (T. Olivier, *pers. comm.*). Climbing by upstream migrating juveniles, when confronted with a low dam or weir, has been observed in *M. malcolmsonii* (Ibrahim, 1962, in the river Godvari, India) and *M. rosenbergii* (Ling, 1969 in Malaysia).

Although some river or stream flow is necessary to provide migrating juveniles with the stimulus needed to direct them upstream, too much flow may be equally detrimental. Juvenile migrations generally take place when stream flows are seasonally low (Fig. 4). In *M. malcolmsonii*, migration takes place in the river Godavari, from August to February, when river flow is slowing from the previous June-September monsoon flood (Ibrahim, 1962). When flow completely stops in some portions of the river, the upstream migration is halted. Similarly, the upstream migration of *Cryphiops caementarius* occurs during low flow

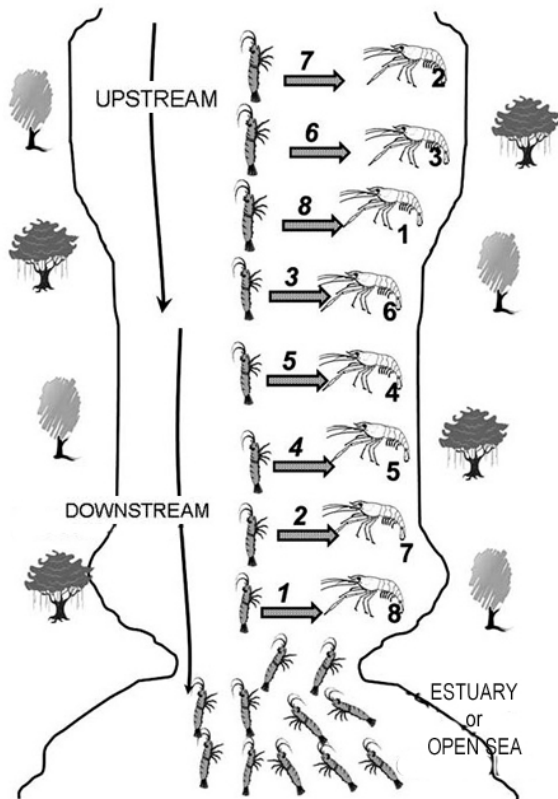


Figure 5. Hypothesis of density-dependent recruitment of upstream-migrating juveniles into resident populations in a large continental river system. The relative density of resident river populations (unfilled upright shrimps) is given by non-italicized numbers, and the rate of recruitment of migrating juveniles (filled shrimps) by italicized numbers from 1 (lowest) to 8 (highest). Note that the density in resident populations decreases gradually upstream during juvenile migration season but not necessarily in a linear fashion. The rate of recruitment and density of resident populations are inversely correlated.

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). A similar pattern has been observed in *Macrobrachium* species in Costa Rica, in which the juvenile migration occurs during the dry season, when the river flows are slowest (I. Wehrmann, *pers. comm.*).

Future research on amphidromy in Latin America

Most research on amphidromy has been conducted on a few Caribbean islands, Australia, Japan, Hawaii, and

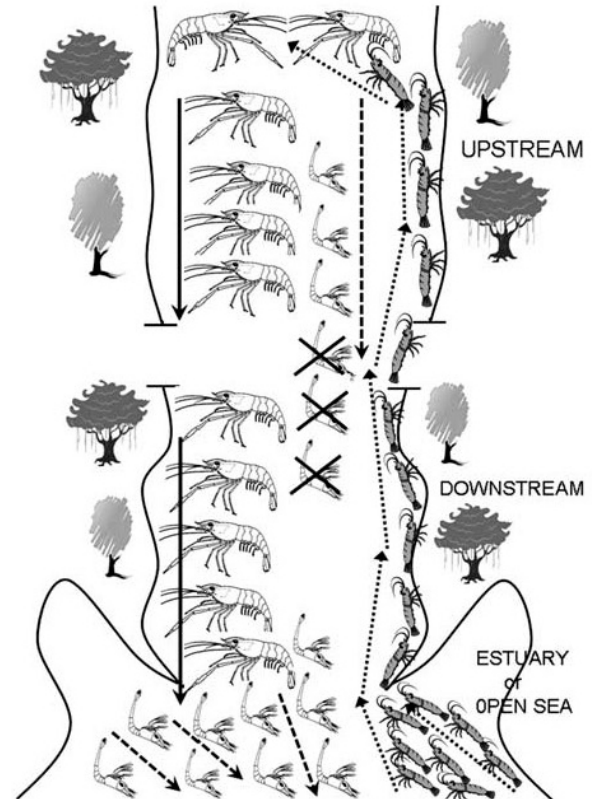


Figure 6. Hypothetical Source-Sink dynamics of an amphidromous shrimps in a large continental river system. Females (unfilled upright shrimps) of far-upstream populations become mature, spawn, and begin downstream migration (solid lines), but must release larvae (upside-down shrimps) before arriving at saline water downstream (estuary or open sea). These non-feeding stage-I larvae drift downstream (dashed lines), but do not survive (X) to arrive at the sea because their yolk reserves are not sufficient for the trip. Downstream females migrate down to the sea and release larvae which develop there. After metamorphosis, the now benthic postlarvae/juveniles (filled shrimps) migrate (dotted lines) along the shore, feeding and growing as they move upstream, and recruit into (are the source of) both downstream and upstream populations.

some other Pacific and Indo-Pacific localities. In Latin America, excluding Puerto Rico, where much research on amphidromous shrimps has been done, relatively little work on amphidromous species has taken place until recently (see papers above). Subtropical and tropical Latin America (used in the broadest sense: countries south of the United States) is home to an incredibly rich and diverse array of amphidromous species as recent studies are showing. Yet very little has been forthcoming from the large Caribbean islands of Hispaniola (Haiti and the Dominican Republic),

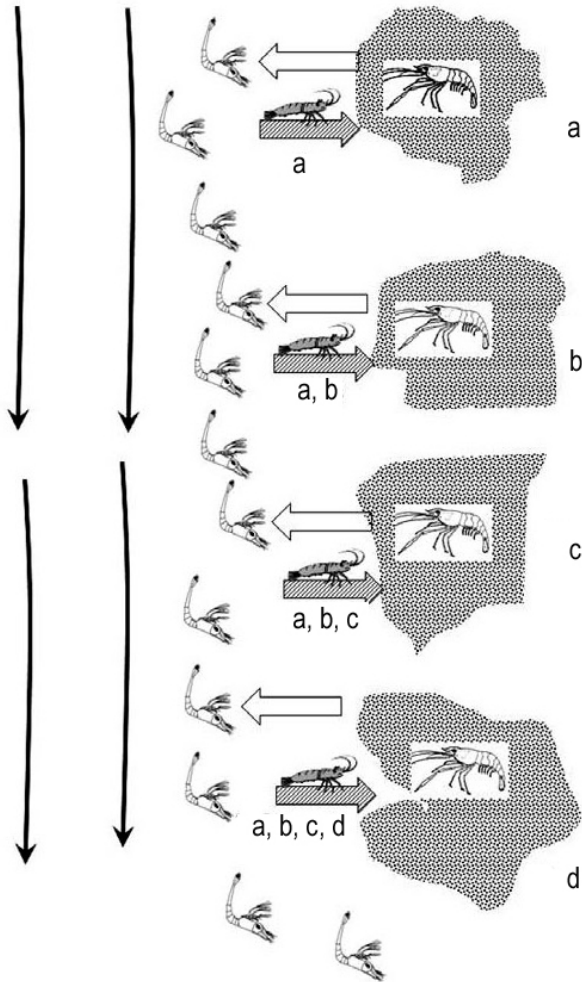


Figure 7. Hypothetical Source-Sink dynamics of an amphidromous shrimp inhabiting a chain of ocean islands located within an offshore current system. Females (unfilled upright shrimps) from Island A produces larvae (upside down swimmers), some of which are retained by local currents and recruit as juveniles (filled shrimps) back to Island A, and some of which continue on downstream in the offshore current to recruit on islands downstream. The process is repeated sequentially at each island. If there are no landmasses downstream of Island D, larvae from upstream islands swept downstream by the prevailing offshore current will not survive.

Cuba, and Jamaica, which presumably are home to a rich amphidromous shrimp fauna. The huge and largely unexplored tropical rainforest areas of the Orinoco Basin, Amazonia, the Pantanal, and other areas of tropical South America, as well suitable areas in Mexico and Central America hold large numbers of freshwater and amphidromous shrimps. However, basic descriptions of the life history of such species, such as those given in papers cited above from

Amazonia and the Pantanal, are largely lacking. Thus, there is a tremendous potential for Latin American biologists to ask and answer basic questions about amphidromy and its evolution in shrimps.

In addition to basic life history information, *i.e.*, type of larval development, delivery of larvae to the sea by stream drift or female migration, and juvenile upstream migrations, there are a number of other potentially productive areas of research. What are the patterns of larval release and the return juvenile migration, and how are they related to proximate factors such as precipitation, water flow and other meteorological conditions? Where do larvae go when they are delivered from freshwater into the marine environment? Is there local retention of larvae and reinvasion of the same stream system by its resident population or is there wide dispersal at sea? The increasing literature on population genetics in amphidromous species has often revealed widespread panmixia, but not in all cases (*e.g.*, Weese *et al.*, 2012; also see Hunte, 1978). It would be of great interest to document the distribution nearshore and in the open sea of the larval stages of different species in a particular region. Likewise, various interesting questions could be answered rather easily if just the first stage larvae of different species were identifiable and distinguishable. This could be a relatively simple project in which first-stage larvae are easily collected from hatching females in the laboratory and then figured and described, with the result of an identification key. As only first-stage larvae will be found in stream plankton collections, enumeration of the relative abundance of the different species, based on such a key, would give valuable data for the temporal pattern of reproduction and larval release in a complex of amphidromous species in a particular stream system.

How do the newly metamorphosed postlarvae travel to and gather in river mouths in order to begin the upstream juvenile migration? As most studies indicate migration at night only, what are the juveniles doing during the day? What are the stimuli or environmental factors which cause some juveniles to recruit into one area of the stream, and others to continue onwards? Is there some density-dependent mechanism controlling this process in which a juvenile decides to recruit to a particular location or to continue upstream to a less densely populated area (Fig. 5)? Is this related to the existence of “sink” (non-reproducing) populations of amphidromous shrimps, recruited from juveniles produced by females of coastal (downstream) populations? According to this hypothesis, individuals recruit and grow to maturity so far upstream that when females mature and spawn,

they are too far from the sea for their first-stage larvae to make it to saline water in time to molt to the Stage-II (first feeding stage) and survive (McDowall, 2010; Bauer, 2011a) (Fig. 6). Conversely, if some populations on oceanic islands are so far downstream in oceanic current systems that they are populated from larval or juvenile recruits from upstream source populations (Fig. 7), can they ever contribute to the next generation except perhaps locally?

These and many other questions about amphidromy related to invasion of freshwater by marine species, occupation, and distribution within freshwater habitats should keep the growing body of Latin American aquatic biologists occupied for some time to come. I look forward to this information and perhaps to having the good fortune to participate in such studies.

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