

Estuarine Larval Development and Upstream Post-Larval Migration of Freshwater Shrimps in Two Tropical Rivers of Puerto Rico

Key words: amphidromy; estuaries; freshwater shrimps; migration; Puerto Rico; tropical rivers.

MIGRATORY FRESHWATER SHRIMPS REPRESENT IMPORTANT LINKS between the headwaters and estuaries of many tropical rivers. These species exhibit amphidromous life cycles in which larvae are released by females in upper reaches of rivers; first stage (*i.e.*, newly hatched) larvae drift passively to coastal environments where they develop and metamorphose into postlarvae that subsequently migrate back upstream to adult (freshwater) habitat. Recent studies in rivers draining northeastern Puerto Rico and Costa Rica's Caribbean slope have been the first to document migratory drift of first stage larval freshwater shrimps (March *et al.* 1998, Pringle & Ramírez 1998, Benstead *et al.* 1999). While we now have information about the migratory drift of first stage shrimp larvae and the effects of damming and water abstraction on larval migration, no information exists on the location of larval development (*i.e.*, whether estuarine, fully marine, or both). We also lack data on subsequent recruitment of metamorphosed postlarvae to upstream populations of adults and the factors that control upstream migration.

In 1996, we conducted short-term estuarine sampling to determine if developing (post-first stage) freshwater shrimp larvae were present in the estuaries of two rivers (Espíritu Santo and Mameyes) that drain the Luquillo Experimental Forest (LEF) in northeastern Puerto Rico. We also used simple traps to examine upstream migration of post-larval freshwater shrimps and its relationship to river discharge in the same two rivers. The Espíritu Santo and Mameyes are similar in size and mean discharge, and both support diverse assemblages of amphidromous freshwater shrimps. Ten species are found in the two study watersheds: *Atya lanipes*, *A. innocous*, *A. scabra*, *Micratya poeyi*, *Xiphocaris elongata*, *Macrobrachium carcinus*, *M. heterochirus*, *M. crenulatum*, *M. faustinum*, and *M. acanthurus* (Covich & McDowell 1996). The rivers differ with respect to hydrological modification. At the time of this study, the Río Mameyes was the last free-flowing river draining the LEF (*i.e.*, no dams or major water abstraction). The Espíritu Santo has a low-head dam and water intake (constructed in 1984 for municipal water supply) located on its main stem (fifth order), *ca* 4 km from the coast at 5 m elevation.

For sampling of developing larvae, seven stations were chosen in each estuary between the upper tidal limit (distinguished by salinity >1 ppt above streambed at high tide) and the river mouth. Stations were *ca* 100 and 200 m apart in the Mameyes and Espíritu Santo, respectively. The Mameyes estuary was sampled for larvae on two occasions (5 and 6 September 1996); the Espíritu Santo estuary was sampled once (4 September 1996). All sampling took place during the day. At each of the seven stations, we took one vertical plankton tow (net diameter 0.5 m; mesh 363 μ m) through the entire water column at both the river margin (2–3 m from the bank) and the center of the channel. Depth was recorded at each sampling site. Salinity was measured at 0.5-m depth intervals. Samples were preserved immediately in 70 percent ethanol and transported to the laboratory where larvae were counted, measured (carapace length), and sorted into 1-mm size classes using a stereomicroscope. We used published larval descriptions (*e.g.*, Choudhury 1971, Hunte 1979) to check that larvae were derived from freshwater species.

We sampled upstream migration of metamorphosed larvae using a trapping method adapted for post-larval shrimps (A. Burky, University of Dayton, pers. comm.; design available from the first author). Traps (150 \times 150 \times 80 mm) were constructed from transparent 2-mm Plexiglass® sheets with 1-mm wire mesh at the upstream end; paired oblique baffles formed a 7 mm wide, vertical entrance at the opposite end. The trapping site in the undammed Mameyes was situated *ca* 500 m above the upper tidal limit; in the Espíritu Santo traps were placed *ca* 750 m upstream of the low-head dam (to incorporate potential effects of the dam on upstream migration). We set traps ($N = 4-6$) in both rivers simultaneously on 28 occasions between 16 July and 6 September 1996. Traps were tethered to stakes in shallow riffle areas close to the bank with the mesh end facing upstream. Traps were set at dusk and collected the following morning; postlarvae were transported to the laboratory in the traps, identified to genus (Chace & Hobbs 1969; *M. poeyi* was grouped with *Atya* spp.), and counted.

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TABLE 1. Summary of estuarine sampling results, September 1996.

River	Date	Mean density (larvae/m ³)	Size classes present (mm carapace length)
Espíritu Santo	4 Sept. 1996	11.15	<1, 1-2, 2-3
Mameyes	5 Sept. 1996	2.67	<1, 1-2
Mameyes	6 Sept. 1996	20.05	<1, 1-2, 2-3, 3-4, 4-5

Numbers of postlarvae were expressed as mean number caught per trap on each night and compared between rivers using a one-way ANOVA. Mean daily discharge data were obtained from the nearest U.S. Geological Survey gauging stations (gauges 50063800 and 50065500 for the Espiritu Santo and Mameyes, respectively) and adjusted for watershed area using methods described in March *et al.* (1998) to obtain approximate discharge values for each post-larval sampling site. To investigate potential effects of river discharge on timing of upstream migration, we performed regression analyses using mean number of postlarvae per trap and a suite of discharge variables. The regression models were separated into two types. First, mean number of postlarvae per trap was regressed against mean daily discharge on single days for each of one to five days previous to trap retrieval. Second, mean number of postlarvae per trap was regressed against mean discharge during D days previous to trap retrieval ($D = 2-5$). We chose this suite of variables to incorporate potential time lags between discharge-mediated migration cues and migratory movement of postlarvae. All statistical analyses were performed using JMP (SAS 1994).

We found post-first stage larval shrimps in both estuaries, although they were present at low densities relative to other planktonic organisms (*e.g.*, calanoid copepods). Most larval shrimps (79–98% on each sampling date) were in the smallest size class (<1 mm carapace length; *i.e.*, first stage). Three size classes were found in the Espiritu Santo estuary, with two size classes present on the first sampling date in the Mameyes and five on the second sampling occasion (Table 1). Although these data do not preclude the possibility of fully marine development of freshwater shrimp larvae, the presence of several larval stages in the two estuaries suggests that at least a proportion of larvae (and species) develop to post-larval stage in estuarine habitat. A vertical gradient in salinity was present at all our sampling sites (0.1–28.8‰ at the surface, 0.3–35.1‰ at the riverbed). Developing larvae in our vertical tow samples therefore were sampled from water ranging greatly in salinity. Although laboratory rearing studies have demonstrated the importance of salinity for larval development of amphidromous freshwater shrimps (*e.g.*, Choudhury 1971), our data cannot shed light on salinity preferences under natural conditions.

Several large peaks in upstream post-larval migration were recorded, particularly in the Mameyes during the latter half of the study period (Fig. 1). The relative post-larval abundance of the three genera differed between the streams (Table 2). The most commonly caught postlarvae in the Espiritu Santo were *Atya* spp., followed by *Xiphocaris* and *Macrobrachium* spp. In contrast, postlarvae trapped in the Mameyes were predominantly *Macrobrachium* spp. and *Xiphocaris*, with *Atya* spp. occurring quite rarely. Numbers of migrating *Macrobrachium* spp. and *Xiphocaris* were far higher in the Mameyes than the Espiritu Santo; the Espiritu Santo exceeded the Mameyes only in abundance of *Atya* spp. (Table 2). Numbers of migrating postlarvae were significantly higher in the Mameyes than in the Espiritu Santo ($P = 0.028$, $F_{1,54} = 5.11$; Fig. 1 and Table 2).

Most peaks in migration appeared to be associated with recent (previous 1–4 d) increases in discharge (Fig. 1); however, the relationship was not clearly defined, as many storm flows were not accompanied by a concomitant increase in post-larval migration. Despite this, regression analysis of mean number of postlarvae per trap against discharge on the previous day indicated a highly significant relationship and explained the most variation in upstream migration among the regression models ($R^2 = 0.37$, $F_{1,26} = 15.09$, $P = 0.0006$, $N = 28$) in the Mameyes. No significant relationship was found with any model in the Espiritu Santo ($R^2 = 0.03$, $F_{1,26} = 0.91$, $P = 0.35$, $N = 28$ for the model using previous day's discharge).

This is the first study to quantify relative rates of upstream migration for post-larval freshwater shrimps from estuarine habitat (*cf.* Fièvet 1999). Our conclusions are constrained by the low number of sampling dates. In addition, estimations of absolute numbers for migrating postlarvae are impossible to make because our trapping method provided only a relative measure of post-larval migration (*i.e.*, between sampling dates and rivers). Nevertheless, our results indicate that the timing and magnitude of upstream

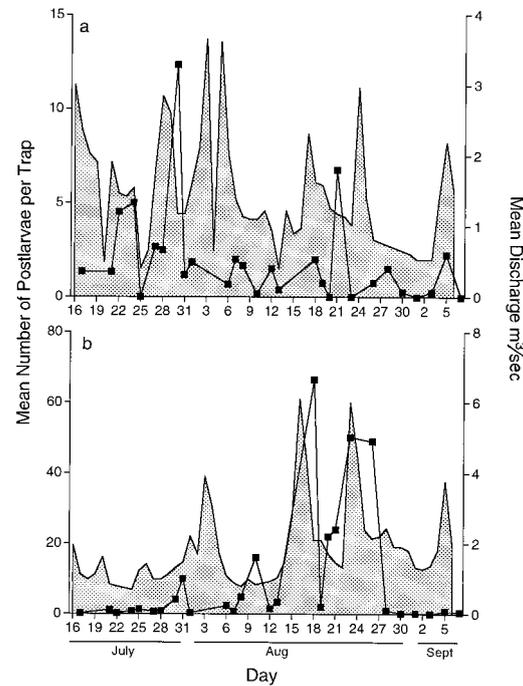


FIGURE 1. Mean number of postlarvae caught per trap (black squares) in (a) the Espiritu Santo and (b) the Mameyes from July to September 1996. Shading indicates mean daily discharge (m^3/sec). Note differences in y-axis scales.

post-larval migration from larval habitat may be partly controlled by peak discharges, as observed in other diadromous species (Drinkwater & Frank 1994).

Clearly, further work is needed to understand the life histories of amphidromous freshwater shrimps. In particular, research is needed to address the factors controlling the development, distribution, and mortality of larval stages. Work is also needed to elucidate the relationship between discharge and upstream post-larval migration and to assess if other factors are important in determining migratory behavior (*e.g.*, tidal cues). Finally, we need to understand the potential effects of damming and water abstraction on recruitment of postlarvae into adult populations upstream. During our short study, numbers of migrating postlarvae were significantly higher in the free-flowing Mameyes than in the dammed Espiritu Santo. It appears that reductions in post-larval recruitment potentially could occur in dammed rivers through direct mortality of larval shrimps during migratory drift (by entrainment into water intakes; Benstead *et al.* 1999) or through negative impacts on estuarine larval habitat (mediated by reductions in freshwater inputs), or both. Large reductions in adult densities upstream of dams and water intakes may have ecosystem-level consequences because of the important processes controlled by these migratory organisms (Pringle 1996, 1997; Holmquist *et al.* 1998; Benstead *et al.* 1999; Pringle *et al.* 1999).

TABLE 2. Mean numbers of *Atya*, *Xiphocaris*, and *Macrobrachium* postlarvae (± 1 SE) caught per trap per night in the two study streams during summer 1996.

River	Total no. of trap nights	<i>Atya</i> spp.	<i>Xiphocaris elongata</i>	<i>Macrobrachium</i> spp.
Espiritu Santo	143	0.98 ± 0.24	0.80 ± 0.36	0.14 ± 0.03
Mameyes	144	0.26 ± 0.09	4.25 ± 2.14	4.94 ± 2.45

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