

Migratory drift of larval freshwater shrimps in two tropical streams, Puerto Rico

J. G. MARCH,† J. P. BENSTEAD,† C. M. PRINGLE† AND F. N. SCATENA‡

†Institute of Ecology, University of Georgia, Athens, GA 30602, U.S.A.

‡International Institute of Tropical Forestry, U.S. Forest Service, Call Box 25000, Rio Piedras, PR 00928, U.S.A.

SUMMARY

1. Migratory shrimps are often major biotic components of tropical stream communities, yet spatial and temporal patterns of their migration have yet to be described. This information is of increasing importance given the continued fragmentation of tropical streams by damming and water abstraction/diversion, which can disrupt migratory life cycles.
2. Larval amphidromous shrimps are released by adult females in freshwater streams. They then drift passively to an estuarine habitat where they metamorphose before migrating back upstream. Drift of larval shrimps was sampled over two to five 24-h periods at each of three sites along two rivers that drain the Luquillo Experimental Forest in Puerto Rico: the Espíritu Santo (10, 135 and 335 m a.s.l.) and the Mameyes (10, 90 and 290 m a.s.l.). A total of seventeen diel samplings were conducted.
3. Shrimp drift increased in the downstream direction in both catchments, and had a significant positive exponential relationship with length of stream channel above each site. There was no significant difference between catchments with respect to mean daily drift rate per km of stream channel. Maximum observed larval shrimp density was $69\,102$ larvae 100 m^{-3} ($1.7\text{ g dry mass } 100\text{ m}^{-3}$), which is high relative to published invertebrate drift studies.
4. The pattern of shrimp drift agreed with the 'risk of predation hypothesis'. In stream reaches with predatory fish, drift of larval shrimps occurred at night and was slight during the day. A nocturnal peak in drift occurred between 19.00 and 22.00 h. At a high-altitude site, where predatory fish were absent, no diel pattern was discernible.
5. The present study provides information on the timing of migratory drift of larval shrimps, which can minimize the adverse effects of water abstraction from streams draining the Luquillo Experimental Forest. Elimination of water withdrawal during peak larval drift after dark will significantly reduce shrimp mortality.

Introduction

Recent studies in tropical stream ecosystems have demonstrated the importance of macrobiota, such as fishes and shrimps, in controlling the structure of aquatic communities (Power, 1990; Flecker, 1992; Pringle *et al.*, 1993; Pringle, 1996; Pringle & Hamazaki, 1998; Rosemond, Pringle & Ramírez, 1998). Many of these macrobiota are migratory during some part of their life cycle (Flecker, 1996; Pringle, 1997). Their

migration represents an important functional linkage between stream headwaters, downstream reaches and estuaries. An understanding of these migration patterns is thus fundamental to tropical stream ecology and conservation.

Migratory amphidromous shrimps (Decapoda: Atyidae, Xiphocarididae and Palaemonidae) are the dominant macroconsumers in many tropical streams. Shrimps can reach high densities (Covich, 1988) and play significant roles in structuring stream commu-

E-mail: jmarch@sparrow.ecology.uga.edu

nities. In some montane streams of Puerto Rico, for example, atyid shrimps reduce sediment cover and algal standing crop on the substratum, and alter insect and algal community composition (Pringle *et al.*, 1993; Pringle & Blake, 1994; Pringle, 1996). Omnivorous *Macrobrachium* spp. (Palaemonidae), which can attain body lengths of 25 cm as adults (Chace & Hobbs, 1969), are the top predators and significantly affect benthic community composition (Crowl & Covich, 1994).

All species of shrimps in Puerto Rico undergo extended larval development and are migratory (Covich & McDowell, 1996; Johnson *et al.*, in press). Adult female shrimps release planktonic larvae (length <2 mm; Fig. 1) that drift downstream from freshwater to the estuary, where they spend 50–110 days before migrating back upstream as metamorphosed post-larvae (Chace & Hobbs, 1969; Hunte, 1979). Very little is known of the ecology of estuarine larval stages, although shrimp larvae evidently provide an important food resource for both marine and freshwater fishes (Corujo, 1980). While laboratory rearing of several species has confirmed that these shrimp larvae require brackish water to develop successfully (Lewis & Ward, 1966; Hunte, 1975), no studies have focused on the migratory drift of larval shrimps to estuarine habitat (but see Füreder, 1994; Pringle & Ramírez, 1998).

Although migratory drift of shrimp larvae has not previously been studied, invertebrate drift has received considerable attention since Müller (1954) demonstrated its significance (see reviews by Waters, 1972; Müller, 1974; Brittain & Eikeland, 1988; Allan, 1995). Most studies have focused on aquatic insect taxa that dominate the drift in temperate streams. Other taxa also drift, however, including molluscs (McKillop & Harrison, 1982), leeches (Elliot, 1973), larval fish and salamanders (Brown & Armstrong, 1985; Bruce, 1985), meiofauna (Palmer, 1992), diatoms (Muller-Haekel, 1971), and juvenile (Barnes & Shiozawa, 1985) and adult freshwater shrimps (Koetsier & Bryan, 1995). Drift studies in tropical streams have also primarily focused on patterns of insect drift (Hynes, 1975; Dudgeon, 1983; Flecker, 1992).

Migratory drift of larval crustaceans, however, is a fundamentally different process from that of insect drift. The causes of insect drift include, among other things, catastrophic floods (Bird & Hynes, 1981), inadvertent dislodgement while foraging (Elliot,

1967), the search for patchy resources (Townsend & Hildrew, 1976), and escape from predators (Peckarsky, 1980). In contrast, larval crustaceans, specifically amphidromous freshwater shrimps, drift to reach estuarine habitat as part of their life cycle. Drift distance consequently differs: insect drift in general, ranges from less than 2 m to as much as several hundred metres during large spates (see review in Brittain & Eikeland, 1988), whereas amphidromous shrimp larvae ultimately must drift many kilometres to reach estuaries.

An understanding of the downstream migration of amphidromous shrimps is extremely important in tropical areas where the natural flow of rivers to estuaries is being increasingly disrupted by damming and water abstraction. Increasing human population and associated demand for fresh water in these regions have resulted in widespread construction of dams and water intakes (Pringle & Scatena, in press) and the island of Puerto Rico is no exception (Hunter & Arbona, 1995). This study was conducted in the Luquillo Experimental Forest (LEF), which is located in the north-east corner of Puerto Rico near the rapidly growing San Juan metropolitan area (Fig. 2). Of the nine major rivers that drain the LEF, all but one have large water intakes on the main stream channel (Naumann, 1994). Thirty water intakes on these major rivers and their tributaries withdraw 50% of the water leaving the forest on an average day (Naumann, 1994).

In order to manage these river ecosystems effectively and to mitigate the potentially adverse effects of dams and water abstraction, resource managers need a better understanding of the ecological requirements of the biota (Christensen *et al.*, 1996). This paper presents the first detailed study of migratory drift of larval freshwater shrimps. The objectives of the study were to determine at what time of day larval shrimp migration occurs and to describe changes in the magnitude and periodicity of larval drift along an altitudinal gradient in two adjacent catchments. This information can guide decisions on the timing and magnitude of water abstraction from streams draining the Luquillo Experimental Forest, Puerto Rico.

Study sites

This study was conducted in two adjacent catchments, the Espíritu Santo and Mameyes, which



Fig. 1 Scanning electron micrograph of *Macrobrachium* sp. shrimp larva. Larva is transparent in life with dark eye spots and scattered chromatophores. Scale bar is 500 μm .

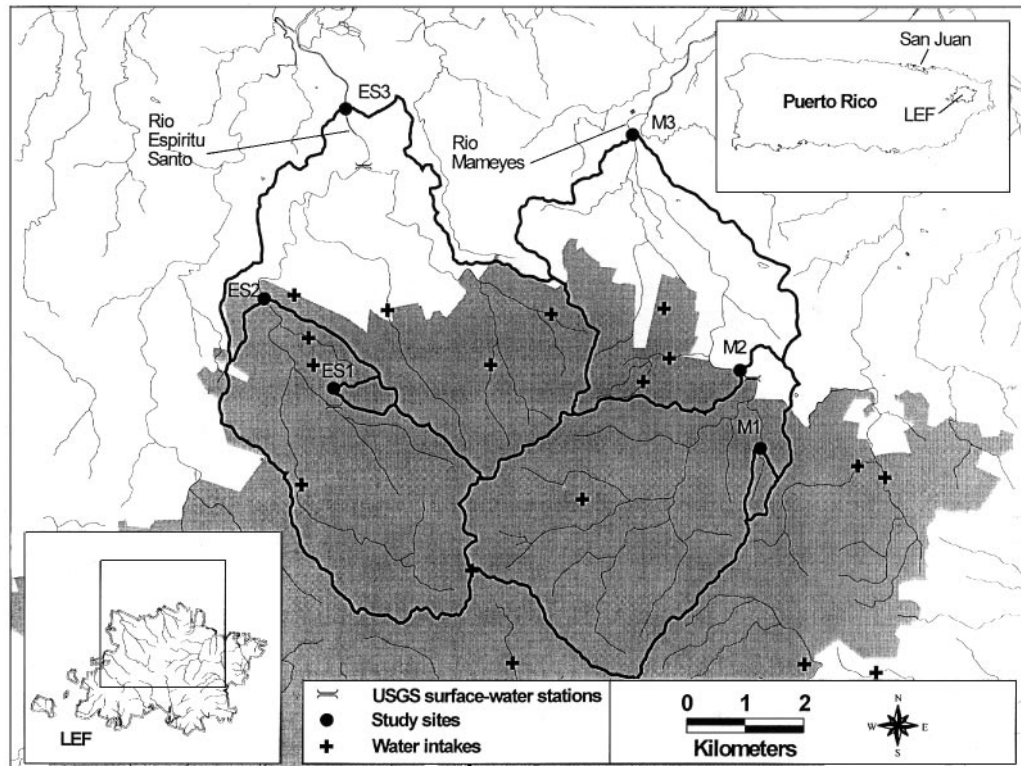


Fig. 2 The Espiritu Santo and Mameyes catchments in the Luquillo Experimental Forest (LEF) showing the location of the park in the north-east corner of Puerto Rico, near the San Juan metropolitan area. Also shown in the figure are the location of sampling sites, LEF boundary, United States Geological Survey (USGS) gage stations, and water intakes. ES, Espiritu Santo; M, Mameyes; 1, high-altitude site; 2, mid-altitude site; 3, low-altitude site.

Table 1 Descriptive statistics of each site where 24-h diel studies were conducted

Catchment	Stream order	Altitude (m a.s.l.)	Stream width (m)	Number of 24-h sampling days	Drainage area (km ²)	Total stream length above site (km)
Espiritu Santo	1	335	4	4	0.41	0.7
Espiritu Santo	3	135	15	2	13.73	16.4
Espiritu Santo	4	10	19	5	33.08	38.9
Mameyes	1	290	3	2	0.39	1.0
Mameyes	3	90	18	2	17.63	23.1
Mameyes	3	10	16	2	30.73	41.1

drain the northern part of the Luquillo Experimental Forest (LEF) and surrounding lowlands (Fig. 2). These catchments are characteristic of Caribbean montane streams (i.e. steep gradients and highly variable discharge; Ahmad, Scatena & Gupta, 1993). Ten species of freshwater shrimps inhabit the rivers of the LEF: *Macrobrachium carcinus* (L), *M. faustinum* (De Saussure), *M. crenulatum* Holthuis, *M. acanthurus* (Wiegmann), *M. heterochirus* (Wiegman), *Atya lanipes* Holthuis, *A. scabra* (Leach),

A. innocous (Herbst), *Micratya poeyi* (Guérin-Méneville) and *Xiphocaris elongata* (Guérin-Méneville). A more detailed description of stream communities in the LEF can be found in Lugo (1986) and Covich & McDowell (1996).

To describe larval migration patterns, three sites along an altitudinal gradient in both the Espiritu Santo and Mameyes catchments were chosen (Fig. 2 and Table 1). The two high-altitude sites were first-order streams within the LEF that drained primarily

tabonuco forest [dominated by *Dacryodes excelsa* Vahl. (Burseraceae)]. In the Espíritu Santo catchment a waterfall at ≈ 200 m a.s.l. excludes predatory fish from upper reaches. The two mid-altitude sites were third-order streams that also drain tabonuco forest. The low altitude Espíritu Santo site was a fourth-order reach of the Espíritu Santo, where the stream drained tabonuco forest as well as neighbouring residential areas. A small dam (1.2 m in height) is located ≈ 1 km downstream of this site. The low-altitude site on the Mameyes was third-order. At this location, the Mameyes also drained tabonuco forest and residential areas. The Mameyes is the only river draining the LEF with no dam on its main stem.

Methods

Between 25 June and 2 September 1995 invertebrate drift was sampled over at least two 24-h periods at each site. Initially, diel patterns of drift were determined by sampling every 3 h from 07.00 h to 01.00 h. Four preliminary sampling days revealed an increase in larval drift during the evening, therefore, on subsequent days ($n = 13$), hourly samples were taken from 16.00 h to 01.00 h to encompass peaks in migratory drift. Insect drift studies have shown peaks both at dusk and dawn (Brittain & Eikeland, 1988), so on all days samples were also taken at dawn, 05.30 h. During the study, sunrise ranged from 05.50 to 06.10 h and sunset was between 18.38 and 19.05 h. To determine variation in daily drift patterns, sampling efforts were concentrated at the low-altitude site (five sampling days) and at the high-altitude site (four sampling days) in the Espíritu Santo catchment. A total of seventeen 24-h sampling days were conducted.

Samples were collected by placing two drift nets (363- μ m mesh, opening dimensions 30×45 cm) in mid-channel positions for timed 5- to 20-min periods depending on flow conditions. Nets were removed from the stream before clogging caused backwelling. Depth and flow velocity were measured to calculate the volume of water sampled. Depth was measured to the nearest 0.5 cm. Flow was measured twice (once during a 5-min sample) to the nearest 0.01 m s^{-1} at five points directly in front of the net with a Marsh-McBirney® flow meter. Samples were preserved immediately in 70% ethanol and transported to the laboratory, where larval shrimps were stained with

Rose Bengal and counted using a dissecting microscope at low power ($20\times$). Samples with high larval densities were subsampled (1/8, 1/32 or 1/64) using the technique of Waters (1969). Two subsamples were counted and averaged. There is no existing key to identify larval freshwater shrimps; therefore, larvae were not separated taxonomically. Drift densities (numbers of larvae 100 m^{-3}) were calculated by dividing the number of animals found in the net by the amount of water sampled.

Discharge data (15-min intervals) were obtained from the United States Geological Survey (USGS) gauging stations nearest the sampling sites for the dates of each diel study (Fig. 2). Discharge at each site was then estimated by multiplying the discharge at the USGS gauging station by the relative difference in drainage area between the gauge and the sampling sites [discharge at site = discharge at USGS gauge (drainage area at site/drainage area at USGS gauge)]. Drift rate (number of larvae s^{-1} passing the site) was calculated by multiplying the drift density (larvae m^{-3}) by discharge at that site.

The mean biomass of shrimp larvae was also calculated. Shrimp larvae were collected at the low-altitude site in the Espíritu Santo River and preserved in 20% formalin. In the laboratory, three samples of 200 larvae were placed in aluminium pans. Each pan was dried at 60°C for 24 h and weighed. Shrimp biomass was expressed as g dry mass 100 m^{-3} of water.

To analyse patterns in larval shrimp migration among sites and between catchments, the stream length above each site and the drainage area at each site were calculated from USGS digital elevation models (DEM) and digital line graphs using Arc-view (v. 3) software (ERSI, 1996). The drainage area was delimited from the contours of a vector coverage produced from the DEM. The stream lengths were taken directly from the digital line graphs for all except the high altitude Espíritu Santo site. This site is not identifiable on the 1 : 20 000 topographical maps or the digital line graphs and had to be estimated using the crenulations of the topographical contours. Additional details describing the methods used to characterize these watersheds can be found elsewhere (Civco, Garcia & Warner, 1995).

To compare the migratory drift of freshwater shrimps with that of other invertebrate taxa, the results were expressed as drift density (larvae 100 m^{-3}) and

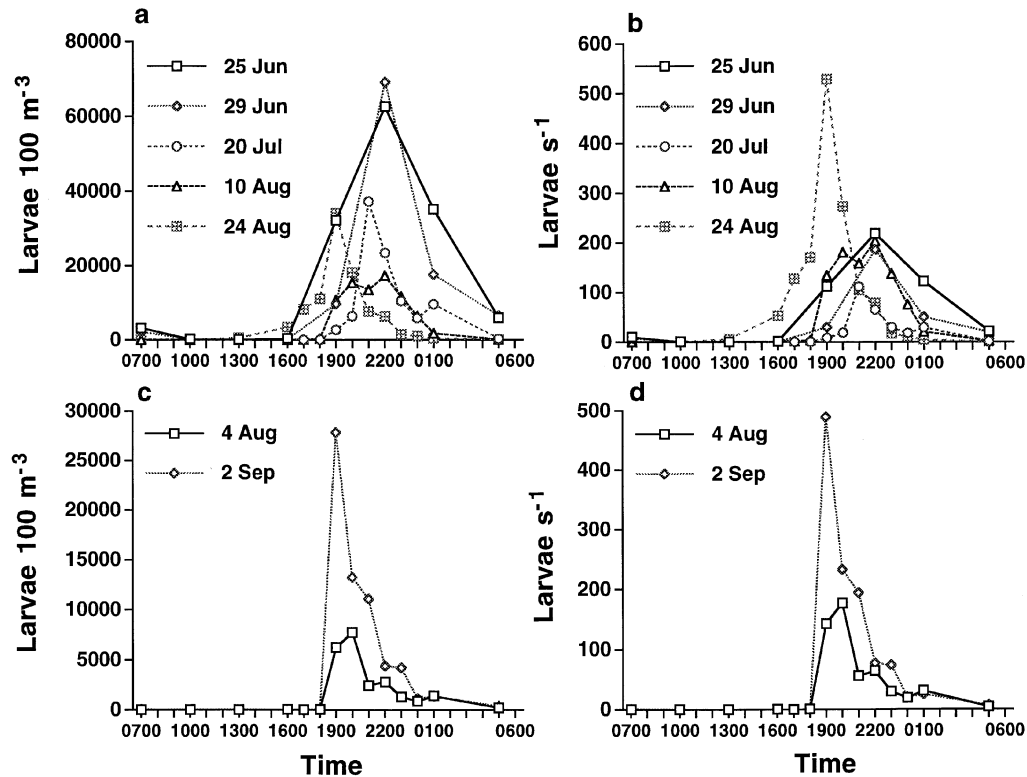


Fig. 3 Comparison of (a, c) drift density and (b, d) drift rate of shrimp larvae over 24-h sampling periods at the low-altitude site in both the Espírito Santo (a,b) and Mameyes (c,d). Each line at each site represents a 24-h study.

drift rate both as larvae s^{-1} and larvae day^{-1} (the number of larvae passing a point s^{-1} and day^{-1}). The daily drift rate (larvae day^{-1}) was estimated by calculating the area under each diel drift curve. Because daily drift rates were correlated to the amount of stream habitat upstream, the data were standardized to mean daily drift rate per river km upstream and then analysis of variance (ANOVA) was used to test for differences in the magnitude of drift between the catchments.

Results

Diel periodicity

At the low and mid-altitude sites in both catchments, larvae were scarce in the drift during the day, increased dramatically after 16.00 h, peaked at night between 19.00 and 22.00 h, and returned to very low numbers by 05.30 h (Figs 3 and 4). At the high-altitude site in the Mameyes catchment, larvae also exhibited diel periodicity. However, the peak in larval drift occurred at 05.30 h on 2 August, and

on 28 August no larvae were found throughout the 24-h study (Fig. 5). Variable patterns were observed at the high-altitude site in the Espírito Santo (Fig. 5). The highest observed migratory drift occurred in the early morning (05.30 h, 21 August; 07.00 h, 25 July), as well as before dusk (17.00 h, 11 July) and after dusk (20.00 h, 7 August). Furthermore, at this site drift was observed during the day at 10.00 h (25 July) and 13.00 h (11 July) (Fig. 5).

Altitudinal differences in drift

The magnitude of larval shrimp migration increased in the downstream direction in both catchments (Table 2; Figs 3–5). Mean daily drift rates at low-altitude sites were more than 64 000 (Espírito Santo) and 33 000 (Mameyes) times greater than mean daily drift rates at high-altitude sites (Table 2). All sites exhibited large daily variations in the magnitude of larval shrimp migration. At the high-altitude site in the Mameyes, mean daily drift rate ranged from 0 to 189 larvae day^{-1} while the range was 21–115 larvae

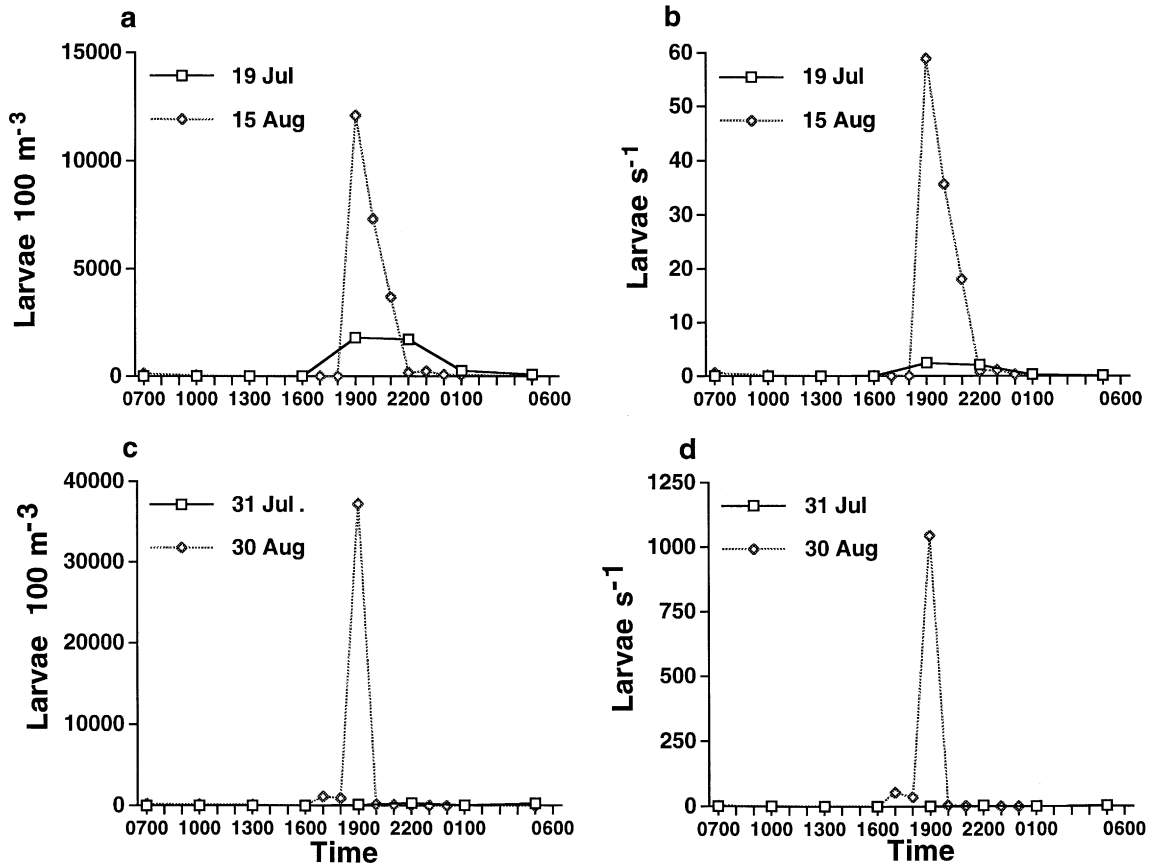


Fig. 4 Comparison of (a, c) drift density and (b, d) drift rate of shrimp larvae over 24-h sampling periods at the mid-altitude site in both the Espiritu Santo (a,b) and Mameyes (c,d). Each line at each site represents a 24-h study.

Table 2 Mean and range of number of larvae migrating over 24-h diel studies (daily drift rate, larvae per day) for each site in the Espiritu Santo and Mameyes catchments

	Rio Espiritu Santo			Rio Mameyes		
	High altitude (n=4)	Mid altitude (n=2)	Low altitude (n=5)	High altitude (n=2)	Mid altitude (n=2)	Low altitude (n=2)
Mean number of larvae migrating over 24-h diel study (daily drift rate)	58	238,997	3,731,079	95	2,106,976	3,171,015
Range of number of larvae migrating over 24-h diel study	21–115	54,775–423,220	1,213,988–5,497,783	0–189	65,999–4,147,952	2,113,629–4,228,401

day⁻¹ in the Espiritu Santo. At the mid-altitude sites the mean daily drift rate was 2106976 and 238997 larvae day⁻¹ in the Mameyes and Espiritu Santo, respectively. The mean daily drift rate at the low-altitude sites ranged from 2113629 to 4228401 larvae

day⁻¹ in the Mameyes and from 1213988 to 5497783 larvae day⁻¹ in the Espiritu Santo (Table 2). There was a highly significant positive exponential relationship between daily drift rate and stream length above each site ($P < 0.00001$, $r^2 = 0.88$; Fig. 6).

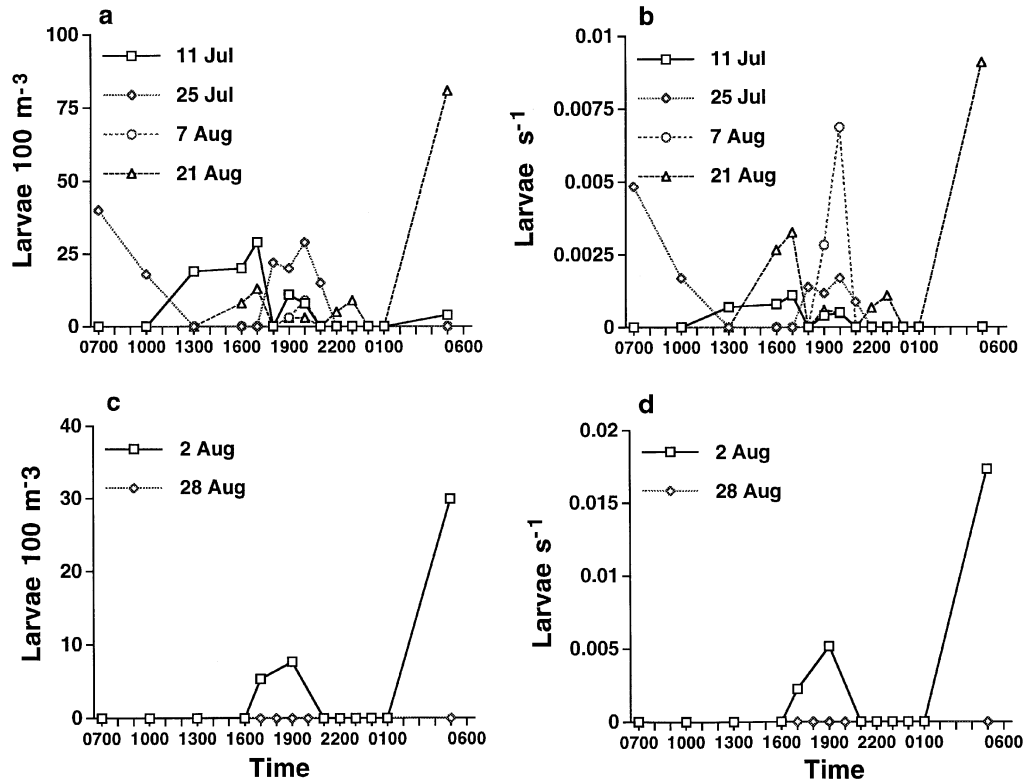


Fig. 5 Comparison of (a, c) drift density and (b, d) drift rate of shrimp larvae over 24-h sampling periods at the high-altitude site in both the Espíritu Santo (a,b) and Mameyes (c,d). Each line at each site represents a 24-h study.

Catchment differences in drift

Both the Mameyes and Espíritu Santo exhibited large variations in daily drift rate among sampling dates and sites (Table 2; Figs 3–5). The Mameyes had higher daily drift rates than the Espíritu Santo at the high and mid-altitude sites, whereas the Espíritu Santo had a higher rate at the low-altitude site (Table 2). To account for the effects of different stream length above each site, the daily drift rates were standardized per total length of stream channel above each site. There was no significant difference between catchments with respect to mean daily drift rate per km of stream channel upstream ($P=0.76$).

Effects of discharge on drift

Discharge patterns were typical of the region and varied considerably throughout the study period. An increase in discharge diluted drift density, although no relationship was found between discharge and daily drift rate. Linear regressions of daily drift rate and mean discharge at the time of sampling were

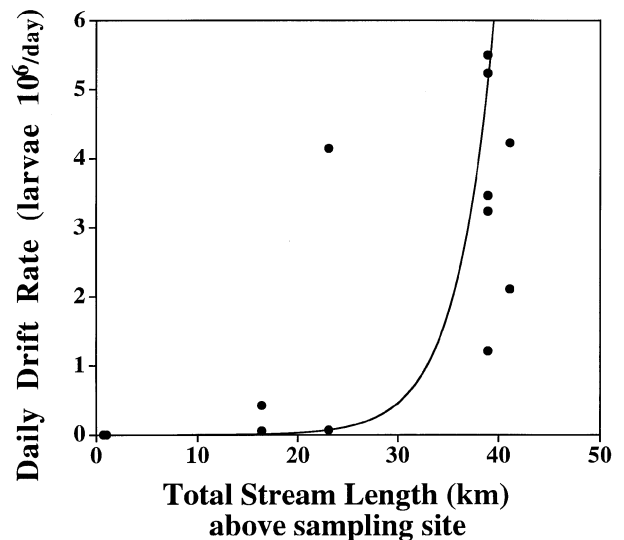


Fig. 6 Relationship between daily drift rate and total stream length above the site ($n=17$, $Y=0.00014 10^{0.1175X}$, $r^2=0.88$, $P<0.00001$).

insignificant at both the Espíritu Santo high-altitude site ($n=4$, $P=0.93$) and the Espíritu Santo low-altitude site ($n=5$, $P=0.56$).

Larval shrimp biomass

The mean biomass of a larval shrimp was calculated to be 2.47×10^{-5} g dry mass $\pm 2.89 \times 10^{-7}$ (SD). The daily drift rates observed in this study resulted in a mean export of 92 g dry mass day⁻¹ of shrimp larvae from the Espiritu Santo and 78 g day⁻¹ from the Mameyes.

Discussion*Diel periodicity*

The finding that the migratory drift of larval freshwater shrimps exhibited diel periodicity (i.e. occurred predominantly at night) is consistent with both laboratory observations of egg-bearing adult shrimps that released larvae at night (e.g. Graziani, Chung & Donato, 1993) and *in-situ* drift studies in lowland Costa Rican streams (Füreder, 1994; Pringle & Ramírez, 1998). Nocturnal periodicity has often been reported for aquatic insect larvae (e.g. Waters, 1962; Hynes, 1975; Flecker, 1992; Brewin & Ormerod, 1994; Pringle & Ramírez, 1998) and is thought to be an adaptation to avoid predation by visually feeding fishes (Allan, 1978; Flecker, 1992). This 'risk-of-predation' hypothesis may also apply to adult shrimps and the release of their larvae in streams draining the Luquillo Experimental Forest. The mountain mullet, *Agonostomous monticola* (Bancroft), a visually feeding predatory fish, is common in the low and mid-altitude reaches of both the Mameyes and Espiritu Santo and is also present at the high-altitude site in the Mameyes (Lugo, 1986; J. G. March, personal observation). Studies have indicated that the freshwater *A. monticola*, as well as estuarine fish, consume freshwater shrimp larvae (Corujo, 1980; Cruz, 1987).

The lack of marked diel periodicity at the high-altitude Espiritu Santo site is noteworthy. This was the only site in this study where the mountain mullet was absent. This lack of periodicity appears to support the 'risk-of-predation' hypothesis. However, unlike insect larvae that may only drift a few metres, amphidromous shrimp larvae must drift considerable distances to an estuary, a journey which in these catchments includes downstream reaches containing mountain mullet. For this reason it was predicted a priori that migratory drift would exhibit diel periodicity at fishless high-altitude sites. Alternatively, the

lack of nocturnal periodicity observed at the Espiritu Santo high-altitude site may have been an artefact of the very low drift magnitude measured at this site (Fig. 5). One female shrimp can release over 25 000 larvae (Graziani, Chung & Donato *et al.*, 1993) and therefore the few larvae sampled at this site may have originated from a single individual. These drifting larvae may have been released at night and delayed in dead zones (*sensu* Lancaster, Hildrew, & Gjerlov, 1996), caused by coarse woody debris or eddies, resulting in diurnal drift. Although it was not possible to differentiate larvae among species it is unlikely that differences in drift patterns between high-elevation sites are a result of different species, as adult shrimp communities are composed of the same taxa at both sites (J. March, unpublished data).

An important factor potentially affecting diel patterns of migratory drift is distance from the estuary. Not only must shrimp larvae reach the estuary, but they must do so rapidly after being released by females. Laboratory studies observed 100% mortality of amphidromous shrimp larvae that were kept in freshwater more than a few days after release (Lewis & Ward, 1966). Because very low numbers of larvae drifting during the day were observed and substantial numbers of larvae could not be found in the benthos, it seemed plausible that most larvae drift to the estuary in one night. To estimate the potential time it takes larvae to drift to the estuary, the distance of each site in the Mameyes catchment from the estuary was calculated (high 8.6 km, mid 6.9 km, and low altitude 1.4 km) and the mean water velocity was used (0.1 m s^{-1}) across pools and riffles during low flow conditions (Ortiz-Zayas, 1998). Under these low flow conditions, travel time from the high-, mid-, and low-altitude sites to the estuary is 23.9 h, 19.2 h and 3.9 h, respectively. Only larvae released 4.3 km from the estuary would be able to reach it in a single night at this flow velocity. However, during moderate and high flows (mean velocity greater than 0.2 m s^{-1}), larvae released in the headwaters could reach the estuary in a single night. Similarly, studies conducted in lowland Costa Rica (more than 50 km inland) have noted the presence of shrimp larvae in nocturnal drift; however, larvae were not found in benthic samples (Pringle & Ramírez, 1998). In Costa Rica and other continental areas, however, where distance to the estuary can be greater than 50 km, it seems impossible for larvae to reach

estuaries in a single night. Indeed, some species of freshwater shrimps complete their entire life cycle in freshwater (Pereira & Garcia, 1995). Furthermore, within-species variation in the degree of amphidromy has been shown to be a function of distance of the population from the ocean (Odinetz Collart & Rabelo, 1996). Unfortunately, information on the diurnal behaviour of larvae is lacking for both amphidromous and completely freshwater shrimp populations. Clearly, more investigations need to address the patterns of migratory drift in populations many kilometres from the ocean.

Altitudinal differences in drift

Increased larval shrimp drift was observed with increasing stream order, and a significant positive exponential relationship between total stream length above a given site and daily drift at that site. These larvae are not able to swim against the current, so it can be assumed that larvae captured at a high-altitude site were derived only from that particular high-altitude tributary. In contrast, the low-altitude sites contained larvae originating from tributaries throughout the entire catchment. Furthermore, the drift density increased in the downstream direction, indicating that the density ($n\ m^{-2}$) of females releasing larvae may also increase downstream.

The magnitude of migratory drift of freshwater shrimps is impressive relative to previously published invertebrate drift studies. The present study measured a peak drift density of 69 102 larvae $100\ m^{-3}$. As part of a concurrent study on the effects of water abstraction on migratory drift (Benstead *et al.*, in press), a peak larval drift density was recorded of 277 284 individuals $100\ m^{-3} \approx 1\ km$ downstream from the low-altitude site in the Espírito Santo. This drift density is higher than any reported in the literature, surpassing the 250 000 meiofaunal organisms $100\ m^{-3}$ in Goose Creek, Virginia (U.S.A.) reported by Palmer (1992). In terms of biomass, 277 284 individuals $100\ m^{-3}$ is equivalent to 6.84 g DM $100\ m^{-3}$, which is considerably higher than the peak of 0.308 g DM $100\ m^{-3}$ that Palmer (1992) found and the 0.246 g DM $100\ m^{-3}$ of insects reported from drift in the Ogeechee River in Georgia (U.S.A.) (Benke, Parsons & Dhar, 1991).

Catchment differences in drift

No difference in mean daily drift rate of larval shrimps between the two catchments was found when account was taken of the relative lengths of streams above each site. The Mameyes might be predicted to have higher shrimp densities because it has a similar drainage area to the Espírito Santo and has no dam on its main stem (i.e. the dam and associated water intake may increase the mortality of freshwater shrimp larvae). Alternatively, the Espírito Santo catchment might be expected to exhibit greater shrimp densities because of the presence of waterfalls that exclude many fish predators from upstream reaches (i.e. in the absence of fish predators the shrimp community may reach higher densities). In any case, while differences between the two rivers may exist it was not possible to detect them statistically. This may be because of the number of diel studies conducted (six in the Mameyes, eleven in the Espírito Santo).

Variability in drift

Several factors may have contributed to the extreme spatial and temporal variability in drift rate at each site, between sites and between catchments. One factor is the sampling regime. It was only possible to sample one site per 24-h sampling period. Less variability among sites in a catchment and between catchments may have been observed if all sites had been sampled simultaneously. Simultaneous sampling would also decrease the variability in discharge which may affect daily drift rate. Another factor contributing to the observed variation in migratory drift may be species-specific drift patterns. The larvae of the ten shrimp species present in these streams are not yet distinguishable. Differences in shrimp community composition between catchments could result in differing patterns of larval drift. Genetic analysis or rearing studies may aid in future differentiation between larvae of different shrimp species.

Another important factor affecting drift of amphidromous shrimp larvae may be discharge. In this study no significant relationship was found between daily drift rate and discharge at a site. However, at the low-altitude site in the Espírito Santo catchment the relationship was positive, although not significant.

This positive relationship may be expected because estuarine conditions are necessary for development of these larval shrimps, thus it may be advantageous for females to release larvae during high-discharge events.

An aspect of migratory drift that was not addressed in this study is seasonality. Migratory drift of larval shrimps was observed throughout the summer. Johnson *et al.* (in press) trapped adult shrimps in the catchments used in the present study and found egg-bearing shrimps present throughout the year. However, the proportion of the community that was ovigerous was highest during the months of September to December, suggesting that the drift rates observed in the present study may be less than the annual maximum.

Future research and management implications of migratory drift

It is hoped that this paper will provide a stimulus for future studies on amphidromous shrimp larvae. Many aspects of this topic need to be explored further. The ability to differentiate among the different species and a better understanding of diurnal larval behaviour and seasonal drift patterns are needed.

Although many aspects of shrimp migratory drift merit further investigation, this study provides useful and important information to aquatic resource managers. Enhanced knowledge of the life history characteristics of amphidromous shrimps has allowed incorporation of the marked diel periodicity of shrimp drift in low-altitude streams into models which present options for mitigating the effects of dams and water withdrawals. In a companion study, Benstead *et al.* (in press) used data collected at the low-head dam in the Espírito Santo and a 30-year discharge record to calculate the mean entrainment of larvae into the water intake, as well as the effects of different intake management strategies. Mean daily entrainment mortality was estimated at 34–62%, depending on the estimates of abstraction rate. However, with elimination of water withdrawal during peak nocturnal drift (20.00–01.00 h), larval shrimp mortality as a result of water abstraction could be reduced to 11%, with only a 21% decrease in the amount of water abstracted.

This study also provides important information on the relative numbers of shrimp larvae and the timing

of migration at high- altitude relative to low-altitude sites. There are currently twenty-one dams and water intakes on high-altitude tributaries and nine at low altitudes outside the forest's boundaries. Managers of the LEF are under increasing pressure to allow more damming and water abstraction and they must designate potential locations for new dams (E. Garcia, personal communication). The results of the present study can be used by water resource managers to make more informed decisions regarding the location and operation of dams and associated water withdrawals along stream continua; for example, given the significant positive exponential relationship between total stream length above a given site and drift at that site, managers might consider establishing water intakes on low order, low altitude streams. This would result in entrainment of fewer shrimp than a water intake on the main stem. However, alternatives to increased damming and water abstraction should be explored, as, on an average day, 50% of the water leaving the forest is currently withdrawn (Naumann, 1994). Naumann estimates that the amount of water withdrawn is $219\,614\text{ m}^3\text{ day}^{-1}$. Based on this estimate of water withdrawal, a conservative estimate of drift density would be $13\,913\text{ larvae }100\text{ m}^{-3}$ (mean nocturnal drift density for the low-altitude sites). Assuming that the rate of water withdrawal is constant throughout the daytime, losses of $15.3 \times 10^6\text{ larvae day}^{-1}$ are calculated, which is 377 g DM day^{-1} of larval shrimp biomass. Assuming this conservative drift density, as well as the size of entrained larvae, remains constant all year, 5.5×10^9 larvae (137.6 kg DM) would be lost per year to water withdrawals.

Effects of water withdrawals on shrimp populations may impact on the entire stream ecosystem, from headwaters to the estuary. Entrainment of migratory shrimp larvae may cause a decrease in recruitment to upstream populations and previous studies have shown that significant differences exist in algal and insect community structure in stream headwaters in the absence of shrimps (Pringle, 1996). Furthermore, the loss of 137.6 kg of shrimp larvae per year may also negatively affect the food resource base of higher trophic levels in estuarine and coastal areas. Corujo (1980) completed a survey of the Espírito Santo estuary and found that over half of the fish species analysed had shrimp larvae in their guts. In addition, water abstraction is not the only anthropogenic factor affecting shrimps. Overharvesting of shrimps by the

growing human population, as well as increases in waste water discharge into the estuary, may also affect shrimp populations. It is recommended that managers consider the entire ecosystem, including the river and estuary, when developing management plans for migratory shrimp species.

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