

EFFECTS OF A LOW-HEAD DAM AND WATER ABSTRACTION ON MIGRATORY TROPICAL STREAM BIOTA

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Abstract. Migration of large-bodied “macroconsumers” (e.g., fishes, shrimps, and snails) is an important functional linkage between many tropical rivers and their estuaries. Increasingly, this linkage is being severed by dams and water abstraction. The ecological impacts of these activities are poorly understood and are largely being ignored by dam operators. We investigated the direct effects of a water intake and low-head dam on the migration of amphidromous freshwater shrimps between the headwater streams and estuary of the Río Espíritu Santo, Puerto Rico, USA. Both downstream migratory drift of larvae and upstream migration of postlarvae had strong diel patterns, with most activity occurring at night. Unlike large dams on the island, this low-head dam did not act as a complete barrier to the upstream migration of metamorphosed postlarvae. However, the dam did cause large numbers of postlarval shrimps to accumulate directly downstream of the structure. Mortality of drifting first-stage larvae by entrainment into the water intake during downstream migration averaged 42% during the 69-d study period. During low discharges, 100% of the drifting larvae were entrained by the intake. The rate of nocturnal entrainment-induced mortality averaged 233 larvae/s and peaked at 1167 larvae/s. We used our field data and a 30-yr discharge record to model the long-term impacts of different intake management strategies on the entrainment mortality at this dam. The simulation model estimated long-term mean daily entrainment mortality at 34–62%, depending on the amount of water extracted from the river. Monthly differences in mean daily entrainment mortality (27–76% depending on estimates of abstraction) were caused by seasonal variation in discharge. Modeling of mitigation options suggested that daily entrainment mortality of larvae could be reduced to 11–20% if water abstraction was halted for 5 h during evening periods of peak drift. Impacts of the dam and operations can be significantly ameliorated by 3–5 h stoppages in water abstraction during peak nocturnal larval drift, upkeep of a functional fish ladder, and maintenance of minimum flow over the dam. Since the impacts of dams depend on the hydrology and design of specific water intake systems, mitigation strategies must be tailored to individual dams and intakes. However, our approach and results are likely to apply to low-head dams throughout the range of amphidromous species.

Key words: *amphidromy; dams; entrainment; freshwater shrimps; migration; mitigation; modeling; Puerto Rico; stream regulation; tropical rivers; water abstraction.*

INTRODUCTION

The protection of aquatic ecosystem integrity is a central goal of sustainable water resource management (Young et al. 1994). Toward this end, the impacts of dam construction and flow diversion are receiving increased attention from ecologists (Covich 1993, Dynesius and Nilsson 1994, Ligon et al. 1995, Naiman et al. 1995, Rosenberg et al. 1995, Postel et al. 1996, Holmquist et al. 1998, Pringle and Scatena 1998a). Direct ecological effects of these activities include the blocking of migration routes and the loss of navigational cues (Drinkwater and Frank 1994), the fragmentation of habitat with associated isolation of populations (Winston et al. 1991), the mortality of larvae and juveniles at water intakes (Travnicek et al. 1993), alteration of natural hydrologic and geomorphic re-

gimes (Ligon et al. 1995), declines in biodiversity and the alteration of natural food webs (Power et al. 1996, Wootton et al. 1996, Pringle 1997), disruption of riparian plant communities (Nilsson et al. 1997), and shifts in the water chemistry of coastal zones (Humborg et al. 1997).

To date, much of the focus has been on effects of large dams on populations of economically important temperate species (e.g., salmon; see Mills 1989, Lewis 1991, Nehlsen et al. 1991). Published studies on tropical regions are scarce and generally emphasize the impacts of large hydrologic projects (Odinetz Collart 1987, Bonetto et al. 1989, Fearnside 1989, Barthem et al. 1991, Borghetti et al. 1994, Holmquist et al. 1998; see also Goldman 1976, Vaux and Goldman 1990 for reviews). The need for more investigations in tropical regions is pressing for four reasons. First, many of the ecologically and economically important fauna found in tropical rivers are migratory (Welcomme 1979,

Payne 1986, Lowe-McConnell 1987) and are therefore particularly vulnerable to dams and water diversions. Second, although the "golden age" of dam building is apparently over in developed regions of the world (Boon et al. 1992), many developing countries in the tropics are undergoing an increased rate of dam construction and river diversion (Petts 1990, Vaux and Goldman 1990, Allan and Flecker 1993, Sanchez-Sierra 1993, Pringle and Scatena 1998b). Third, there is a widespread but largely undocumented proliferation of small, low-head dams throughout the tropics. These dams are not recorded in the World Register of Dams (Petts 1990), and their ecological effects are poorly understood. Fourth, almost 1.3 billion of the world's population do not have access to potable water (Gleick 1993). Meeting the potable water needs of this (largely tropical) population while maintaining the integrity of aquatic ecosystems will require management based on a thorough, and presently unavailable, understanding of tropical aquatic environments.

Puerto Rico has experienced a rapid rate of development in the last 50 yr and its population density, presently 404 persons/km², is one of the highest in the world (Hunter and Arbona 1995). Because large areas of the developing world are expected to undergo similar transitions from agrarian to industrial economies in the next two to three decades (Berry 1990), studies of human impacts on aquatic environments in Puerto Rico provide insights into the future of many tropical areas. Despite being one of the wettest islands in the Caribbean, Puerto Rico has recently experienced severe water shortages. These water shortages are the legacy of decades of rapid development combined with inadequate maintenance of infrastructure, decreasing reservoir storage capacity caused by siltation, and declining groundwater quality (Hunter and Arbona 1995, Pringle and Scatena 1998a). Increased water demand has placed severe pressure on the island's rivers and streams. River systems near the San Juan metropolitan area, where one-third of the island's population lives, are particularly susceptible to these pressures.

Most of the headwaters of the Luquillo Mountains are within the Luquillo Experimental Forest (LEF), also known as the Caribbean National Forest. The LEF (11 330 ha) is the only tropical forest in the U.S. National Forest system, and was designated a UNESCO Biosphere Reserve in 1976. The nine rivers that drain the forest represent an excellent example of the increasing conflict between water demand and in-stream flow requirements. All but one of the rivers draining the LEF have been dammed at least once along their main channel, and, on an average day, 50% of the stream water draining the forest is appropriated for municipal water supplies (Naumann 1994). Twenty-one water intakes currently operate within the LEF, and nine larger intakes are located outside its boundaries on streams that drain the forest. The long-term impacts of this scale of water diversion on the aquatic fauna of

the forest remain poorly studied. However, monitoring of aquatic populations within the LEF by the U.S. Forest Service suggests that there are significant differences in abundance, diversity, and size-class structure between the communities and populations of migratory biota in streams with and without water diversions (E. García, *unpublished data*).

We examined the effects of a water intake and low-head dam on the migration of freshwater shrimps in the Espíritu Santo river at the base of the Luquillo Mountains in eastern Puerto Rico. We chose to study freshwater shrimps for three primary reasons: (1) they are abundant and widespread members of tropical stream communities; (2) they play important ecological roles in those communities; and (3) aspects of their life cycle (e.g., small drifting larvae) make them extremely vulnerable to effects of water abstraction. We used field measurements and simulation modeling to demonstrate the effects of low-head dams and water abstraction on the migration of tropical amphidromous shrimps and to show how life history ecology can provide rationale for alternative dam operations to reduce impacts on migratory fauna.

NATURAL HISTORY AND STUDY SITE

Puerto Rico's rivers support a diverse community of decapod crustaceans; at least nine species of freshwater shrimps occur in the study watershed (Covich and McDowell 1996): *Atya lanipes*, *A. innocous*, *A. scabra*, *Micratya poeyi*, *Xiphocaris elongata*, *Macrobrachium carcinus*, *Macrobrachium heterochirus*, *Macrobrachium crenulatum*, and *Macrobrachium faustinum*. All are migratory and have a typical amphidromous (sensu McDowall 1992) life cycle in which first-stage larvae (length <2 mm) are released by females at dusk and drift overnight to the river's estuary (March et al. 1998). Young shrimps undergo a 50–110 d period of larval growth in this brackish environment and subsequently migrate back upstream to adult habitat as postlarvae (Hunte 1978, Hobbs and Harte 1982). Upstream migration is completed by swimming and crawling, primarily during nighttime. However, upon encountering a physical obstacle (geomorphic or anthropogenic), postlarvae will leave the water and crawl along the wetted margins of the obstacle; water flow appears to be an essential cue in this crawling movement (J. P. Benstead and J. G. March, *personal observations*).

Among freshwater shrimp populations in the Caribbean and many other regions, an estuarine or marine stage appears to be obligate (i.e., first-stage larvae must reach brackish water to molt into the next larval stage). However, the life cycle of some tropical species is completed within the freshwater environment, especially in areas that are on the order of 10² km from the ocean (see Hughes et al. 1996). In addition, there is evidence of within-species variation in the degree of amphidromy vs. completely freshwater development; this vari-

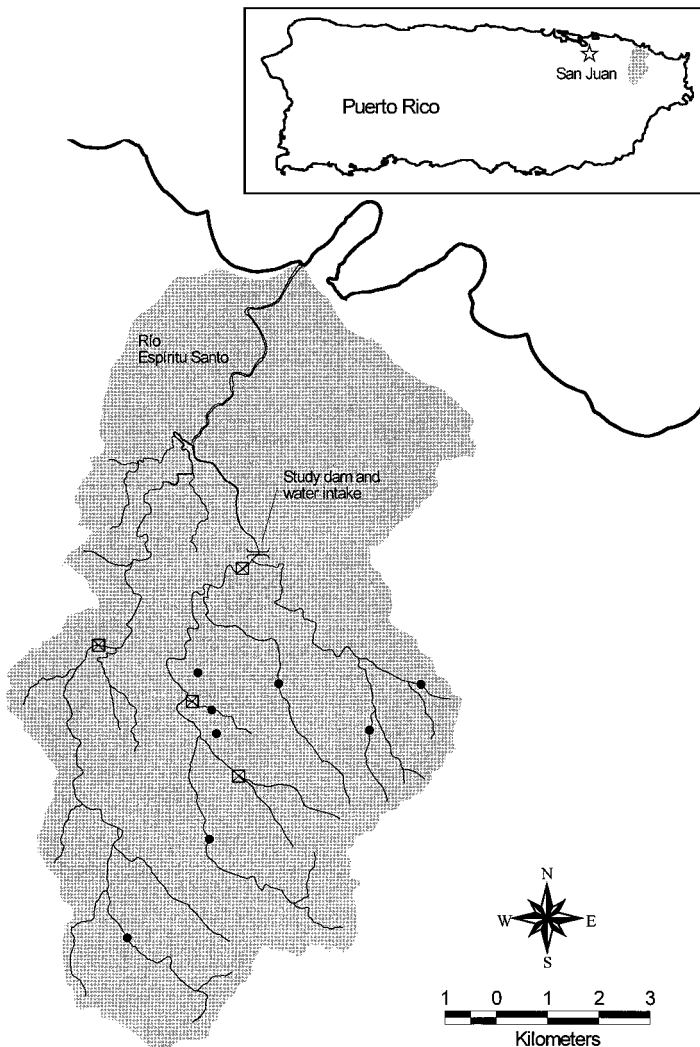


FIG. 1. Map of the Río Espíritu Santo showing the study dam, catchment boundary (shaded), discharge gauging sites (squares), and points of water abstraction (solid circles). Inset shows the location of the Río Espíritu Santo catchment in Puerto Rico.

ation appears to be a function of the distance of adult populations from the ocean (Odinetz Collart and Rabelo 1996). Freshwater shrimps appear to be relatively long lived; adult *Xiphocaris elongata* have been kept for >6 yr in laboratory aquaria (A. Covich, *personal communication*).

In montane streams in Puerto Rico, adult freshwater shrimps dominate faunal biomass and play important ecological roles, including the processing of leaf litter and the assimilation of fine particulate organic matter (Covich 1988), local mediation of sedimentation through bioturbation (Pringle et al. 1993, Pringle and Blake 1994), regulation of nutrient cycling through grazing of algae (Pringle et al. 1993, Pringle 1996), and disturbance (through reduction of biomass) of sessile invertebrate communities (Pringle et al. 1993). Throughout the Caribbean, freshwater shrimps are considered delicacies and are important sources of protein for many rural communities. Related species, which are found in many other areas of the tropics, appear to

perform similar ecological and economic functions (Payne 1986).

The dam chosen for this study is located on the main stem (fifth order) of the Río Espíritu Santo, ~5 km from the coast and 5 m above sea level (Fig. 1, Plate 1). The dam, which is representative of low-head dams in the region, was built by the Puerto Rico Aqueduct and Sewage Authority (PRASA) in 1984 as part of a gravity-fed water distribution system that supplies the local community (B. Ruíz, *personal communication*). The structure, which has a width and height of 20.9 m and 1.2 m, respectively, was the first dam built in Puerto Rico to have a fish ladder. Although this fish ladder was installed to facilitate the upstream movement of migratory biota, the ladder has been closed for over a decade to prevent loss of water from the impoundment. In addition, the intake lacks both screens (which would reduce the entrainment of fish) and a flow-measuring device (to determine the amount of water being withdrawn from the river). These are design flaws common



PLATE 1. The Espiritu Santo dam and water intake, July 1995. Note the defunct fish ladder below, and the triple-barred intake above the dam sill on the right. Photograph by Catherine Pringle.

to many intake structures in Puerto Rico and throughout the Neotropics (F. N. Scatena, *personal observation*). According to PRASA, the intake withdraws an average of 0.91 m³/s from the river (Naumann 1994).

METHODS

Field sampling and measurements

The study area was sampled every third evening during 30 June–7 September 1995. The 24 sampling visits were timed to coincide with the postdusk increase in larval downstream migration and postlarval upstream migration. For each sampling date, we estimated stream discharge, water abstraction, entrainment of larval shrimps, and density of postlarval shrimps swimming below the dam.

Because there were no gauging devices that measured the volume of water entering the intake during our measurements of larval density, the rate of water withdrawal was estimated by multiplying the area of the intake by the average velocity of water entering the intake. The velocity of flow entering the intake was measured at 60% depth using a Marsh McBirney flow meter. Since velocity fields around intakes are complex and tend to increase at the control point of the intake (Henderson 1966), these estimates may underestimate the actual amount of water that is withdrawn from the river. The discharge flowing over the dam (i.e., not going into the intake) was also measured with a Marsh McBirney flow meter and calculated similarly. However, on two occasions the discharge going over the dam was too low to measure with a flow meter and was estimated from a linear regression between flow velocity and depth of water going over the dam ($r^2 = 0.84$, $n = 19$). Total river discharge at the dam site was calculated as the sum of the water entering the intake and discharge flowing over the dam.

Mortality of first-stage larval shrimps due to entrain-

ment was quantified by taking a 10 min drift sample with a standard WildCo drift net (mouth 30 × 45 cm; mesh 363 μm) held just below the water surface and 10–15 cm in front of the intake. Because drift density of larval shrimps varies during the night, with peaks in larval drift during 1900–2300 (March et al. 1998), we took each sample at the same time (1945–1955).

Preliminary observations suggested that the dam acted as an obstacle to upstream migration causing large numbers of postlarvae to accumulate below the dam sill. As a relative measure of the magnitude of upstream migration, we estimated the density of postlarval shrimps swimming below the dam using a plankton tow that was pulled at a constant speed across the width of the entire channel. On each sampling date, we made three oblique tows directly below and parallel to the dam sill. High discharge on 5 of the 24 visits prevented sampling for postlarvae.

We preserved all samples immediately in 70% ethanol. Larval drift samples from the intake were subsampled using a method described by Waters (1969). Two subsamples (1/8, 1/32, or 1/64) were counted under a stereomicroscope, and larval drift density was expressed as no. individuals/m³ of water sampled. Entrainment rate of larval shrimps into the water intake (no. individuals/s) was calculated by multiplying drift density (no. larvae/m³) by volume per unit time (m³/s) of water flowing into the intake. Larval shrimps were not identified, because keys to larval stages have not yet been developed. Postlarval shrimps were counted and identified to genus under a low-power stereomicroscope (Note that *Micratya poeyi* was not distinguishable from *Atya* spp.) Density of postlarval shrimps below the dam was expressed as mean no. individuals/m³ of water sampled.

Simulation modeling

We used our field data and a 30-yr discharge record (1 August 1966–30 September 1996) to model the long-term entrainment of larval shrimps and the impact of various mitigation strategies. Mean daily discharge data were obtained from the nearest continuous recording gauge (U.S. Geological Survey [USGS] gauge number 50063800, Espiritu Santo near Río Grande), ~1.5 km upstream of the dam.

The field data were used to calculate three regression equations used for simulation modeling. First, total stream discharges measured on each occasion at the dam were regressed against simultaneously measured discharges at the USGS gauge station, in order to construct a relationship between discharges at the two points on the river (Fig. 2):

$$\ln(y) = 0.875 \ln(x) + 0.535 \quad (1)$$

where y = discharge (m³/s) at the dam site, and x = discharge (m³/s) at the USGS gauge. Second, a regression was used to estimate the abstraction rate at the intake from the discharge at the dam (Fig. 3):

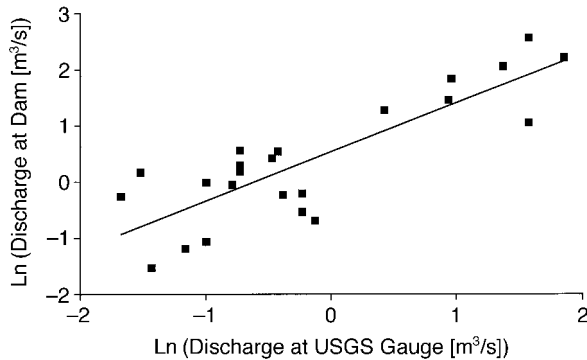


FIG. 2. Relationship between discharge at dam (m^3/s) and discharge at the gauge station (m^3/s), during the study period. The fitted regression line is given by Eq. 1, where $r^2 = 0.70$ and $P < 0.0001$.

$$\ln(y) = 0.210 \ln(x^2) + 0.292 \ln(x) - 0.800 \quad (2)$$

where y = water abstraction rate (m^3/s), and x = discharge (m^3/s) at the dam site. Third, the density of larval shrimps measured at 1955 during each sampling visit was regressed against instantaneous total discharge at the dam (Fig. 4). This regression was bootstrapped (1000 iterations) to obtain parameter means ± 1 SD:

$$\ln(y) = -0.849 \pm 0.224 \ln(x) + 10.487 \pm 0.183 \quad (3)$$

where y = larval drift density (no. larvae/ 100 m^3), and x = discharge (m^3/s) at the dam.

The model (referred to as Model I) randomly picked a mean daily discharge (at the USGS gauge) from the 30-yr record and calculated discharge (m^3/s) at the dam site based on regression Eq. 1. This estimate was then used by the model to calculate water abstraction rate and larval density (at 1955) based on Eqs. 2 and 3, respectively. To incorporate variable biological processes (e.g., larval release by females) in the relationship between discharge and larval drift density, at each iteration the slope and intercept constants of regression Eq. 3 were randomly picked from a normal distribution, with means and standard deviations obtained from the bootstrap. Resampling Stats software (Version 4.09; Resampling Stats 1995) was used for all bootstrapping and simulation modeling.

Our field measurements of abstraction rate may have underestimated actual values, because of complex flow fields inside the water intake. For this reason, we modified Model I to include recent estimates of the long-term mean abstraction rate at the Espiritu Santo Dam ($0.91 \text{ m}^3/\text{s}$; Naumann 1994). In this version of the model (Model II), all the river flow was abstracted at discharges $< 0.91 \text{ m}^3/\text{s}$. Above this discharge value, a fixed rate of $0.91 \text{ m}^3/\text{s}$ was abstracted.

The resulting estimates of discharge, abstraction rate, and larval drift density were used to calculate entrainment rate (number of shrimps entrained per unit of time at 1955) and survival rate (number of shrimps passing

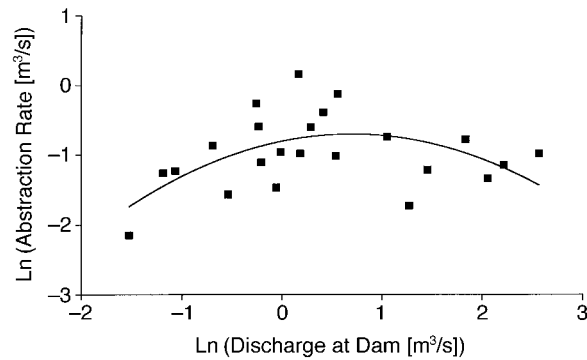


FIG. 3. Relationship between abstraction rate (m^3/s) and discharge at dam (m^3/s), during the study period. The fitted regression curve is given by Eq. 2 ($r^2 = 0.29$, $P = 0.03$). Abstraction rates decline at high water velocities, because the water intake is parallel with stream flow; the abstraction rate is also determined by control of flow at the receiving water plant.

over the dam without being entrained per unit of time at 1955). In our estimates of survival rate, we assumed that larvae were homogeneously distributed in the water column (i.e., the fraction of discharge flowing into the intake equaled the proportion of larvae lost from downstream transport). Although patterns in bulk flow may change with discharge and possibly affect within-channel drift density, we do not believe our estimates of entrainment were affected. If bulk flow patterns are important in determining within-channel larval density (i.e., larval densities are higher in bulk flow), during periods of low discharge, bulk flow will be into the intake and lead to high entrainment densities, relative to the drift densities of surviving larvae. In contrast, during periods of high discharge (when survival rates are high), turbulent flows will give rise to a well-mixed larval distribution; the proportion of larvae entrained at these times would consequently be a function of abstraction rate relative to discharge only. Our esti-

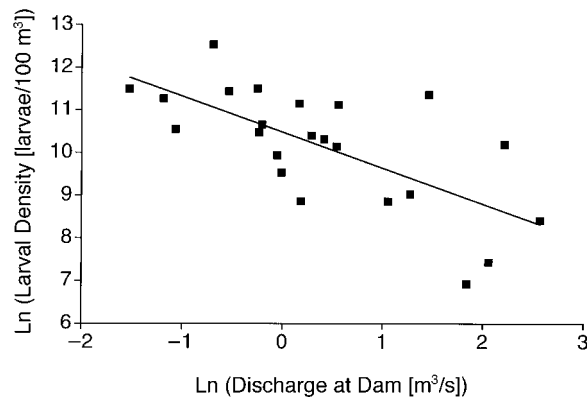


FIG. 4. Relationship between drift density of larval shrimps (no. larvae/ 100 m^3) and discharge at the dam (m^3/s), during the study period. Fitted regression line: $\ln(y) = -0.849 \ln(x) + 10.479$, where x = discharge at the dam and y = larval drift density ($r^2 = 0.46$, $P = 0.0004$).

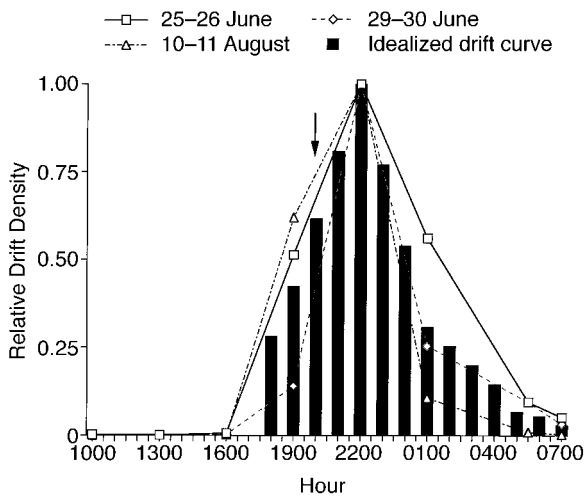


FIG. 5. Relative drift density of larval shrimps over three diel periods at a site 750 m above the dam. The idealized curve of nocturnal drift density was obtained from the means of these three diel curves. The arrow indicates the time of sampling at the dam on each sampling date (1955).

mates of entrainment are therefore likely to be conservative, if discharge is an important factor in determining the spatial variation in larval drift density.

In order to estimate daily entrainment and survival of larval shrimps, we constructed an idealized daily drift curve using data from a concurrent study on the diel patterns of larval drift (March et al. 1998). We used data from three diel (i.e., 24-h) drift studies, conducted ~750 m upstream of the dam site (Fig. 5). Drift densities of larval shrimps (measured every 3 h) were standardized relative to the peak in each diel (all diels showed a peak in larval drift density at 2200). Standardized values for each diel were then averaged to obtain the drift curve. Hourly nocturnal values (i.e., those during 1800–0700), that fell between the 3-h sampling points, were obtained from regressions between sampling points.

Total nocturnal larval drift at the dam site was calculated from the idealized daily drift curve (Fig. 5). Entrainment drift samples for the present study were collected at 1955 (i.e., at ~2000); hourly data on the idealized drift curve consequently were standardized relative to this datum (i.e., drift at 1955 = 1). The model multiplied the estimated drift rate (no. larvae/ $\text{m}^3 \times \text{discharge}$ [in m^3/s] \times 3600 s/h = no. larvae/h) at 1955 by the resulting factor for each nocturnal hour and summed these values in order to obtain total daily entrainment and survival values. (Note that the drift density at any hour was assumed to remain constant for the following hour). The model followed this sequence (random choice of discharge, regression calculations, multiplication by nocturnal hourly factors, and summing) for a total of 10 000 iterations (“days”) each time it was run. Means \pm 1 SE were then calculated for daily entrainment and survival of larval shrimps.

Random sampling of daily discharge values does not incorporate temporal autocorrelation in the time series. However, the log-normal distribution of values in the discharge record suggested that temporal autocorrelation was not of significant concern; random sampling therefore was considered legitimate.

The minimum and maximum instantaneous discharges measured at the discharge gauge during sampling were $0.16 \text{ m}^3/\text{s}$ and $4.8 \text{ m}^3/\text{s}$, respectively. Discharge values picked at random from the discharge record that were $<0.16 \text{ m}^3/\text{s}$ or $>4.8 \text{ m}^3/\text{s}$ were constrained at those values, in order to avoid extrapolation beyond the range of our field data, while still incorporating some of the effects of these extreme values. Mean daily discharge values of $<0.16 \text{ m}^3/\text{s}$ and $>4.8 \text{ m}^3/\text{s}$ represented 1% and 6.6% of the values in the 30-yr record, respectively.

The 30-yr discharge record and model were used in two different ways. First, long-term entrainment and the effects of mitigation options (temporary stoppages in abstraction during peak drift) were investigated by calculating mean daily larval entrainment in two cases: (1) in the absence of mitigation measures; and (2) if abstraction was halted during 2200–2300 (1 h), during 2100–0000 (3 h), and during 2000–0100 (5 h). We chose these three time intervals because they represent three relatively conservative management options. This version of the model randomly picked daily mean discharge values from the whole discharge record and was run for 10 000 iterations. Second, we investigated differences in entrainment mortality caused by seasonal changes in river discharge, by separating the 30-yr discharge record into months (848–961 mean daily discharge values per month) and running the model for each month (10 000 iterations).

Sensitivity analyses

We used sensitivity analyses to investigate the effects of the three parameters that varied in the models (i.e., discharge at the USGS gauge, and the intercept and slope of the regression used to estimate larval drift density from discharge at the dam) on estimates of larval entrainment and survival. The sensitivity of the model to changes in discharge was performed over the range of discharges experienced during sampling ($0.16 \text{ m}^3/\text{s}$ – $4.8 \text{ m}^3/\text{s}$). For this analysis, the slope and intercept constants of the regression equation used to estimate larval drift density from discharge at the dam were set at their mean values.

The sensitivity of the models to changes in the slope and intercept constants of the drift density regression was evaluated over the range $+2 \text{ SD}$ to -2 SD from the mean, for each parameter. The other parameter in the regression was set at its mean value for each analysis, respectively, and discharge at the gauge was set at its mean daily value for the 30-yr discharge record ($1.62 \text{ m}^3/\text{s}$; Note that at this discharge, survival exceeds entrainment).

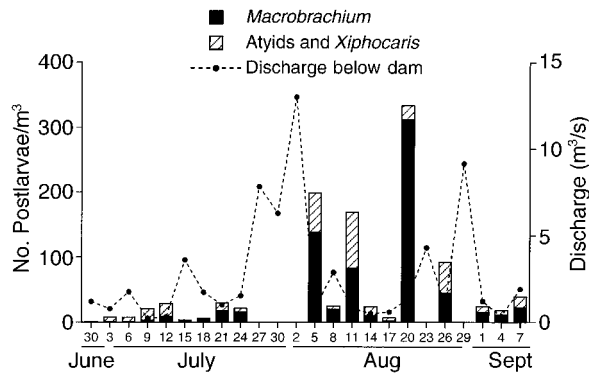


FIG. 6. Density of postlarvae directly below the dam during the study period (left axis) and discharge as measured at the dam (right axis), on each sampling date.

RESULTS

Effects of damming on upstream migration of postlarvae

The average density of postlarval shrimp swimming below the dam was 42 individuals/m³ (Fig. 6). The maximum observed density was 334 postlarvae/m³, and four sharp peaks in postlarval density occurred during the latter half of the study. The average density of these peaks was 199 individuals/m³. Excluding these peaks, the average postlarval density was 12.1 individuals/m³. The density of *Macrobrachium* (Palaemonidae) postlarvae was consistently higher than that of *Xiphocaris* (Xiphocarididae), and *Atya* and *Micratya* (Atyidae) postlarvae. The ratio of *Macrobrachium* postlarvae to atyid and xiphocaridid postlarvae averaged 2.1:1 during the study period.

Postlarvae were observed to move upstream over the dam on almost every visit. However, the numbers of migrating individuals scaling the dam varied greatly between visits. Typically, postlarvae were found traveling up cracks in the defunct fish ladder, seepages along the dam face, and the wetted margins of the dam structure. However, the favored route seemed to depend on discharge. Postlarvae scaling the dam avoided areas of high flow.

We observed postlarvae scaling the wetted margins of both the dam and natural geomorphic obstacles. When postlarvae were observed crawling up the dam face along areas wetted by water *not* originating from the top of the dam face (e.g., water leaking from very small rusted holes in the fish ladder) they became disoriented upon reaching the source of the water and did not continue upward into unwetted areas. This suggested that water flow is a crucial cue to upstream crawling movement and that the flow rate of water required to sustain a cue to migration could be extremely low.

Entrainment of larval shrimps

The mean \pm 1 SE rate of water abstraction measured during the 24 samplings was 0.45 ± 0.05 m³/s. En-

trainment mortality of larvae was highly dependent on stream discharge (Fig. 7a). The mean mortality measured in the 24 samplings was $41.8 \pm 6.9\%$. The mean entrainment rate was 233 ± 64 larvae/s, and the highest measured was 1167 larvae/s (Fig. 7b). Excluding this peak, the entrainment rate averaged 190 ± 49 larvae/s.

Modeling results

Simulations indicated that the mean mortality associated with a fixed abstraction of 0.91 m³/s (Model II) over a 10 000-d period is 62% (7.9×10^6 larvae/d; Fig. 8). Model I estimated the long-term mortality rate at 34% ($4.32 \pm 0.02 \times 10^6$ larvae/d; Fig. 8). Comparisons of different intake management scenarios indicated that long-term entrainment mortality could be reduced by eliminating water withdrawals during evening periods of peak drift (Fig. 8). Specifically, at withdrawal (abstraction) rates based on field measurements (Model I), a 1-h stoppage (2200–2300) would reduce long-term entrainment to 27%, a 3-h stoppage (2100–0000) to 18%, and a 5-h stoppage (2000–0100) to 11% (Fig. 8a). Entrainment estimates for Model II were 50%, 32%, and 20%, respectively, for these stoppage times (Fig. 8b). Moreover, intake operating schedules, based on diel variations in drift, could reduce entrainment mortality with relatively small losses in the amount of water withdrawn. Assuming a constant abstraction rate throughout a day, water intake stoppages of 1, 3, and 5 h would result in water yield losses of 4.2%, 12.5%, and 21%, respectively.

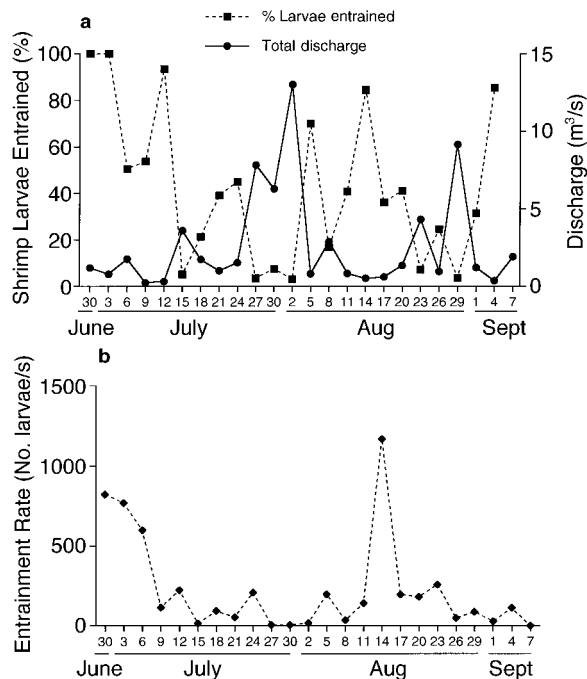


FIG. 7. (a) Percentage of larval entrainment at the water intake (left axis) and discharge at the dam (right axis), and (b) entrainment rate of larval shrimps at the intake, during the study period.

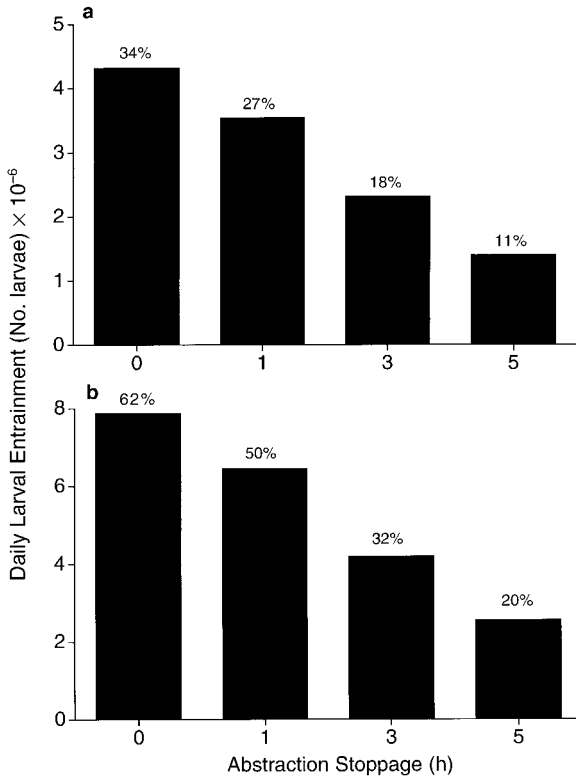


FIG. 8. Model estimates of mean larval entrainment under simulated mitigation scenarios (no stoppage, and stoppages of 1, 3, and 5 h during peak evening drift), based on the 30-yr discharge record for (a) the model based on field measurements of abstraction rate (Model I), and (b) the model based on a fixed abstraction rate (Model II). Numbers above bars indicate percent larvae entrained. Standard errors were too small to report.

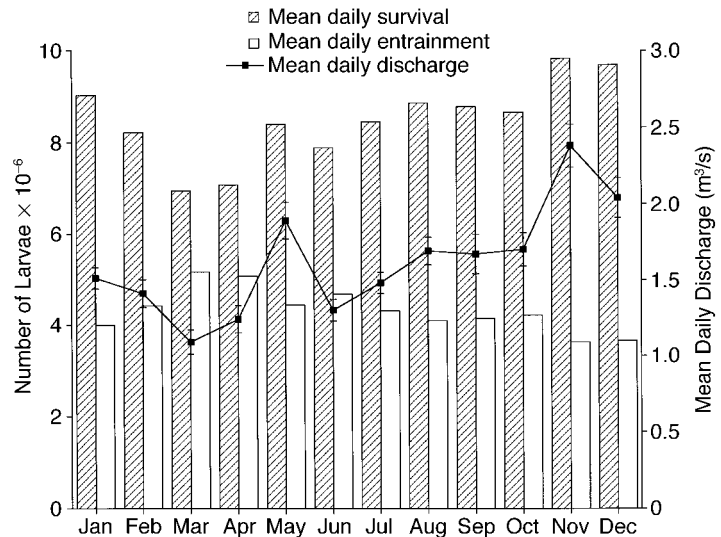
Modeling indicated that survival and entrainment of larval shrimps vary on a seasonal basis, as a function of monthly variation in stream discharge. On a monthly basis, the mean proportion of larvae entrained through continuous water abstraction of $0.91 \text{ m}^3/\text{s}$ (Model II) varied between 50% (November and December) and 76% (March), over the 30-yr simulation period. When the mean abstraction rate was based on field measurements (Model I), mean monthly mortality varied between 27% (November and December) and 43% (March) (Fig. 9; monthly trends were similar for Model II).

Sensitivity analyses

Discharge was the primary determinant of larval survival and entrainment. Analysis of the sensitivity of Model I to stream discharge revealed that entrainment declined curvilinearly with discharge (Fig. 10a). Survival increased rapidly with discharge, exceeding entrainment mortality at $\sim 0.45 \text{ m}^3/\text{s}$. Sensitivity to discharge in Model II followed a slightly different pattern (Fig. 10b). Entrainment increased (and survival was zero) when discharge was $< 0.48 \text{ m}^3/\text{s}$ at the gauge (i.e., $0.91 \text{ m}^3/\text{s}$ at the dam). Beyond this point, survival increased curvilinearly and entrainment declined curvilinearly.

Increases in the slope and intercept constants, used to estimate larval drift density from stream discharge, increased estimates of larval survival and entrainment curvilinearly and linearly, respectively (Fig. 11 for Model I; analysis results were very similar for Model II). Rates of increase differed between the two model outputs, however. Estimates of larval survival were more sensitive than those of entrainment to variations in the constants of the regression. Responses of the model to variation in the slope and intercept constants were dependent on the discharge variable. At the discharge used in the sensitivity analysis ($1.62 \text{ m}^3/\text{s}$), sur-

FIG. 9. Model estimates of mean monthly larval survival and entrainment based on the 30-yr discharge record (left axis) and mean daily discharge ($\pm 1 \text{ SE}$) (right axis), for each month in the 30-yr discharge record.



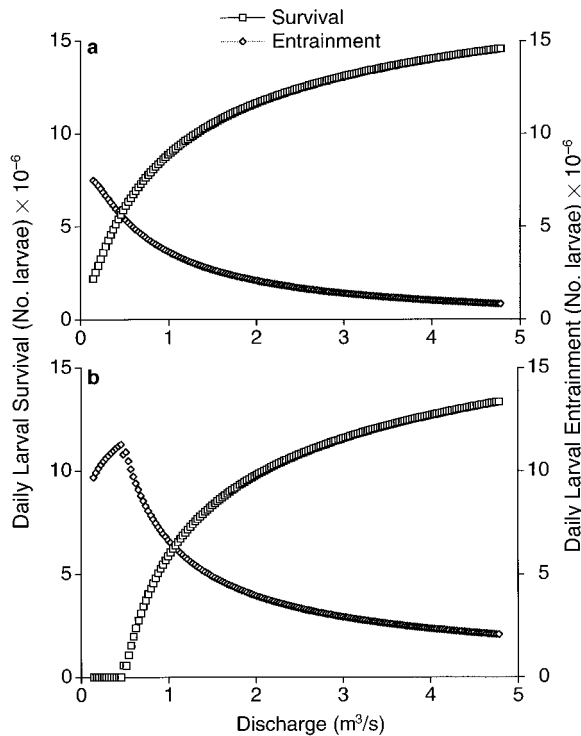


FIG. 10. Sensitivity analysis showing model output (larval survival, left axis; entrainment, right axis) in response to variation in discharge (range 0.16–4.8 m³/s) for (a) the model based on field measurements of abstraction rate, and (b) the model based on a fixed abstraction rate. Regression slope and intercept constants for the relationship between discharge and larval density were set at their mean values (-0.849 and 10.487, respectively).

vival was higher than entrainment, and increases in both slope and intercept increased estimates of survival, relative to estimates of entrainment.

DISCUSSION

Current water resource issues in Puerto Rico provide a window into the future of many tropical areas (Pringle and Scatena 1998a). Population growth and increased urbanization likely will accelerate in developing countries. Demands for municipal water supplies will increasingly conflict with in-stream flow requirements for maintenance of aquatic ecosystem integrity. Our study is representative of water intake structures throughout Puerto Rico and revealed impacts of water abstraction on a key ecological component of tropical stream communities. Such impacts are likely to be widespread because of the pantropical distribution of ecologically similar organisms and the increasing construction of small, low-head dams for water abstraction in these areas.

Effects on upstream migration of postlarvae

Our observations of postlarvae climbing up the dam indicated that, unlike many high dams on the island (Holmquist et al. 1998), this 1.2 m high structure did

not act as a complete barrier to the upstream migration of juvenile shrimps. Observed climbing ability is expected in species that are adapted to migrate over natural geomorphic barriers in steep boulder-lined montane streams where waterfalls are often >10 m in height. However, our data indicate that this dam is a temporary obstacle to upstream migration, particularly when water flow over the dam was low or nonexistent. During low-flow periods, the dam created a "bottleneck" by restricting the number of routes over the dam.

One potential consequence of the dam-induced bottleneck is increased predation of postlarvae. Increased predation (especially by the mountain mullet, *Agonostomus monticola*) could result, not only from the increased density of postlarval shrimps immediately below the dam, but also as a consequence of the bottleneck effect that the dam has on the upstream migration of these predatory fishes as they return from marine spawning habitat. We observed large numbers of mountain mullet, unsuccessfully trying to scale the dam, and they were frequently observed in the dam tail waters. Potential for increased predation rates, as a consequence of elevated predator and prey densities below dams, clearly is a subject for future research.

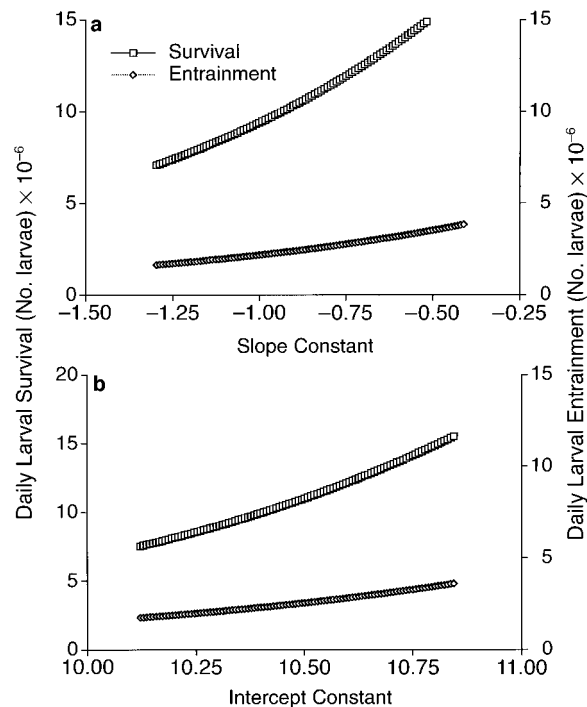


FIG. 11. Sensitivity analyses showing model output (daily larval survival, left axis; entrainment, right axis) in response to variation in (a) slope and (b) intercept constants in the regression used to calculate larval density from discharge at the dam site. The other constant (intercept or slope) in the regression was set at its mean value for each analysis, and discharge was set at the 30-yr mean daily value (1.62 m³/s), as measured at the USGS gauge. The ranges used in the analyses were (a) mean slope \pm 2 SD (-0.849 \pm 0.448) and (b) mean intercept \pm 2 SD (10.487 \pm 0.366).

Entrainment effects on shrimp populations

Our field data and modeling results show that first-stage larvae of freshwater shrimps are extremely vulnerable to entrainment into water intakes during their downstream drift to estuarine habitat. Entrainment mortality during the study period was particularly marked during prolonged periods of relatively low flow when all, or nearly all, of the stream water was diverted into the water intake. Indeed, our field studies and modeling analysis indicate that stream discharge and the amount of water withdrawn from the river determine larval survival. At this particular site, larval survival is high when storms cause relatively high discharges. When abstraction rates, relative to total stream flow, are as high as those commonly used by PRASA and other water authorities, long-term larval mortality may be >60% of undisturbed conditions.

The consequences of entrainment-induced larval mortality for eventual adult densities in upstream populations depend on the relative importance of density-dependent and -independent mortality factors during larval growth in the estuarine habitat. For example, if eventual adult density in upstream populations is determined by density-dependent factors (e.g., competition), entrainment of larvae may not have an adverse effect, because increases in mean survival will compensate for entrainment mortality. Conversely, if adult densities upstream are determined more by density-independent factors (e.g., abiotic variables), increases in larval mortality through entrainment will have an adverse effect on eventual recruitment into adult populations. Unfortunately, the ecology of marine and estuarine invertebrate larval stages is poorly understood, due to the practical difficulties of following cohorts through time (Rumrill 1990, Morgan 1995). However, in situations in which larvae are sparsely distributed in the estuarine habitat, density-independent mortality factors may be more important than density-dependent factors. Sampling of the plankton in the Espiritu Santo estuary and that of an adjacent, undammed river (Río Mameyes) indicated that larval shrimps occur at very low densities (0–80 larvae/m³; J. P. Benstead, *unpublished data*), suggesting that density-independent mortality factors may be more important in determining survival. Entrainment of larval shrimps during migratory drift toward the estuary may therefore have a significant impact on subsequent recruitment to upstream adult populations.

While the cumulative impacts of high levels of entrainment mortality have yet to be quantified, they likely have important implications for the size and structure of adult populations, and for stream and estuarine food webs. Reductions in adult populations could influence upstream ecosystems in a number of ways. Freshwater shrimps are the dominant component of headwater stream communities in Puerto Rico as well as many other areas of the tropics. They are the most common

consumers in the streams draining the LEF, and they drive important ecosystem processes such as nutrient cycling and leaf litter processing (Covich and McDowell 1996, Pringle 1996). Therefore, reductions in populations of shrimps upstream of dams and water intakes could have ecosystem level effects (Pringle 1997). In addition, freshwater shrimps are important prey for top predators such as the mountain mullet *Agonostomus monticola* and American eel *Anguilla rostrata* (Cruz 1987, Phillip 1993, Covich and McDowell 1996). Finally, larval crustaceans comprise a significant component in the diet of many estuarine and juvenile oceanic fishes and are important prey for estuarine invertebrate predators (Morgan 1992). In a survey of the fishes in the Espiritu Santo estuary that was conducted before the dam was built, Corujo (1980) found that 66% of the 58 species fed on decapod larvae, shrimps, and other small crustaceans. In four of the species, decapod larvae comprised $\geq 50\%$ of the gut contents. Large-scale reductions of inputs of freshwater shrimp larvae into estuaries are therefore expected to affect estuarine food webs.

It is important to note that population-level responses of migratory biota to damming and water abstraction may be characterized by a significant time lag. For example, in our study system the impacted species are relatively long lived (>6 yr) invertebrates that are being impacted by a dam and water intake constructed in 1984. If the dam is having a negative impact on recruitment into adult populations upstream, effects may remain to be seen. Analysis of shrimp abundance and size class data being collected as part of the Luquillo Long Term Ecological Research program (Covich et al. 1996) may detect such impacts on recruitment if they exist.

RECOMMENDED MITIGATION STRATEGIES

Water intakes and low-head dams have a number of effects on the ecology of tropical rivers. Our results indicate that mitigation of their deleterious effects on the migration of biota is feasible. While low-head dams apparently represent an obstacle to the upstream migration of postlarvae, our observation of shrimps scaling the dam during most flow conditions indicate that “bottlenecking” impacts can be lessened. Postlarval shrimps are adapted to negotiating natural geomorphic barriers. They are also capable of passing low-head dams, provided that flow over the dam exists to maintain migration cues and routes. Installation and regular maintenance of functional fish ladders and provision of flows over dams will facilitate migration.

Mitigation of entrainment effects is technically more difficult. Larvae are <2 mm in length, and they drift passively in the current. Their small size and fragility compromise utility of screens or other deflection devices. In some areas, the water abstraction may be reduced through water conservation and the efficient use of existing water supplies, thereby possibly reducing

impacts. For example, the Puerto Rican water authority suffers large losses within its distribution system and cannot account for >40% of its daily production (Morris 1994). The adoption of water-efficient technologies and price incentives can also reduce consumption and, therefore, the water withdrawn from aquatic ecosystems (Frederick 1993).

An additional and complementary measure is to use ecological knowledge to develop water intake management practices that mitigate impacts without significant losses of water for human use. We suggest that the periodicity of larval release by adult shrimps provides such an opportunity. Modeling results show that by eliminating water withdrawals during 3–5 h, post-dusk periods of peak larval drift, entrainment mortality can be reduced to 11–20%, without large losses in water yield. Improved understanding of the factors that influence the timing of larval release (e.g., seasonality in reproduction) would result in further decreases in entrainment mortality with minimal losses of available water. Losses in abstracted water could be further minimized by increasing water withdrawal (abstraction) during daylight hours, when larval drift and postlarval migration is low or nonexistent. We believe that carefully timed stoppages in water abstraction offer a new and cost-effective approach to offsetting entrainment effects on many migratory organisms. However, mitigation measures can only be researched and implemented if tropical water resource managers appreciate the threat to populations of amphidromous organisms. The widespread occurrence of amphidromy makes it imperative that environmental impact assessments of proposed damming projects consider this easily overlooked mode of migration. Towards this end, appropriately designed field measurements must be incorporated into such assessments (e.g., diel sampling of drifting organisms that will detect the presence of larval migration).

Our study shows the importance of developing and implementing management practices that have been tailored specifically for tropical aquatic ecosystems. Poorly planned, “crisis” management, that involves little consideration of ecological impacts, has dominated tropical water resource management in the past (Pringle and Scatena 1998*a, b*). For example, Vaux and Goldman (1990) list institutional, methodological, and ecological constraints to the integration of applied ecology with water resources development in the tropics. Our study illustrates that, although we have a great deal to learn about tropical freshwater ecosystems, appropriate management strategies can be developed using easily gathered ecological data. For example, the migratory drift of amphidromous larval shrimps is a relatively recently studied phenomenon (Füreder 1994, Pringle and Ramírez 1998, March et al. 1998). Nevertheless, because of the now-established nocturnal migratory behavior of these organisms, appropriate management of dam/water intake structures (e.g., reductions in noc-

turnal water abstraction) can decrease the impacts of damming on downstream migration. However, the effects of damming and water abstraction will depend on dam/intake design, abstraction rate, discharge regime, and life histories of local species. These factors underscore the importance of developing mitigation measures that are tailored to individual sites.

In the absence of mitigation measures, damming and water abstraction will continue to disrupt the functional linkages between headwaters and estuaries that are created by migratory species in the tropics and elsewhere. This study demonstrates how ecological information can be applied to mitigate the inevitable impacts of water resource development facing large areas of the tropics. Simple models that are parameterized with locally gathered ecological data are powerful tools in the development of such mitigation measures.

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