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Instream-Flow Analysis for the Luquillo Experimental Forest, Puerto Rico: Methods and Analysis

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Cover	Water intake on the Rio Espiritu Santo, Puerto Rico.

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	This study develops two habitat-based approaches for evaluating instream-flow require- ments within the Luquillo Experimental Forest in northeastern Puerto Rico. The analysis is restricted to instream-flow requirements in upland streams dominated by the common communities of freshwater decapods.			
	In headwater streams, pool volume was the most consistent factor in predicting the abundance of common freshwater shrimp. In second- and third-order tributaries, both water depth and velocity can be used to define their habitats. The most common species of shrimp are reclusive during the day; at night they prefer areas of low velocity (<0.09 m/s) and areas shallower than 0.4 m. In headwater streams, total usable shrimp habitat declines rapidly when water depth in the deepest pools is less than 0.5 m. In second- and third-order tributaries, the amount of habitat declines rapidly when discharge is within one standard deviation of the average annual 7-day minimum flow. These discharges are typically exceeded between 95 and 99 percent of the time.			
	Analysis of habitat loss associated with different instream-flow constraints showed that habitat loss increases greatly when water extraction is equal to or greater than Q98. Among-reach differences in the amount of usable habitat resulting from differences in channel morphology can be as high as 35 percent. Therefore, site-specific studies should be conducted when using habitat-preference relations in a particular area.			
	Keywords: Instream flow, aquatic ecology, water supply, tropical rivers, Luquillo Experi- mental Forest.			
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Introduction

Diverting stream water and building dams can change the amount and frequency of stream flow, water quality, recreational opportunities, channel geomorphology, and the abundance and diversity of aquatic organisms. Determining how much stream water can be removed from a system while sustaining aquatic resources has been a major water management issue for decades (Lamb and Doerksem 1987). With the rapid increase in water demand in the humid tropics, better methods for determining appropriate schedules for water withdrawal are needed (Dudgeon et al. 1994, Griesinger and Gladwell 1993, Pringle and Scatena 1999). This need is especially true in the Caribbean National Forest of Puerto Rico, which also is known as the Luquillo Experimental Forest (fig. 1). More than 30 water intakes exist on streams originating within the forest. These intakes typically consist of small (<3-m high) dams that supply gravity-driven waterdistribution systems (Nauman 1994). About 30 percent of the stream water draining from the Luquillo Experimental Forest is appropriated annually for municipal use (fig. 2). However, because most water leaves the forest during short-duration, high-flow events, on an average day, more than 50 percent of the stream water draining the forest is removed before it reaches the ocean. These withdrawals alter the abundance and diversity of the aquatic community (Benstead et al. 1999, March et al. 1998) and are expected to increase in the future (CNF Forest Management Plan 1995). Managing these intakes while maintaining the ecological integrity of the national forest is a major challenge to resource managers (Gonzalez-Caban and Loomis 1997). This paper presents and compares methods for determining instream-flow requirements for water diversions within the Luquillo Experimental Forest. The analysis is restricted to instream-flow needs of resident decapods within the humid life zones of the forest. Issues involving fishdominated communities, urban or coastal-plain streams, water pollution (Hunter and Arbona 1995), or the biologic effects of large dams (Holmquist et al. 1998) are not discussed.

The Instream-Flow Problem

Extracting stream water can result in many interrelated, cumulative effects throughout a watershed (fig. 3). Developing withdrawal schedules to minimize these effects is a complex problem influenced by ecological, engineering, social, and economic factors. In general, withdrawal schedules are defined by the amount of water that is withdrawn from the river (W), and the instream-flow, or the amount of water left in the stream to maintain a desired attribute of the ecosystem (fig. 4). The amount of instream-flow can vary with many factors including season, natural characteristics of stream flow, and the attribute that is to be maintained. Attributes commonly considered when these flows are being determined include prior appropriations, water quality, habitat and channel morphology, and recreational and commercial activities like fishing, swimming, boating, and scenic beauty. The need to maintain the morphology and function of channel features, riparian areas, and stream valleys also has been recognized (Hill et al. 1991).

The ultimate goal of a water-withdrawal schedule is to meet the needs of the users while minimizing both operating costs and adverse environmental effects. If water is extracted without considering instream requirements, stream channels can be completely dewatered and result in many negative effects. Adjacent to and downstream of a diversion, dewatering can cause changes in channel morphology, riparian vegetation, and the abundance and quality of aquatic habitat. Effects at the watershed scale can include reducing downstream water quality, creating barriers to migrating aquatic organisms, and changes in estuarine habitats. Social and economic factors also influence withdrawal schedules because capital, administrative, and operating costs can increase when variable withdrawal schedules are implemented. Finally, both withdrawals and instream-needs can be constrained by seasonal variations in the supply and demand of water.



Figure 1—Location map of water intakes in around the Luquillo Experimental Forest, Puerto Rico.



Figure 2—Average annual water-use budget for the Luquillo Experimental Forest in the early 1990s. (Based on Nauman 1994 and Garcia-Martino et al. 1996.)



Figure 3—Conceptual model of potential cumulative impacts associated with water withdrawals from streams draining the Luquillo Mountains of Puerto Rico.



Figure 4—Conceptual model of factors influencing instream-flow analysis and water extraction schedules in headwater streams.

The earliest formal legislation design to protect instream water in the United States was in 1915 when Oregon prohibited diverting water that supplied the falls of the Columbia River Gorge (Lamb and Doerksem 1987). Since the early 1970s, stream flows for maintaining fisheries, aesthetics, recreation, and downstream estuaries have been widely recognized as legitimate uses of water. Although the need for instream flows is widely recognized, people disagree about what these flows actually are and how they should be determined (for reviews see Armour and Taylor 1991, Hill et al. 1991, Petts and Maddock 1994, Reiser et al. 1989). In the past two decades, many methods have been developed for examining and estimating instream-flow requirements. These methods typically use some combination of historical low flows, channel geomorphology, and or aquatic ecology to define instream flows.

Historical low-flow approaches to instream flow are primarily used for planning water supplies and abating pollution. This approach is based on the premise that to maintain an aquatic ecosystem, regulated flow should not fall below some commonly occurring natural low flow. These methods typically define instream flow as a proportion of the average annual flow (Mathews and Bao 1991, Tennant 1976) and are generally based on low-flows with recurrence intervals of 10 years or more (that is, the 7-day, 10-year low flow). Although these methods are relatively simple to use, they have been criticized for not explicitly considering aquatic organisms or recognizing the role of high-flow events in maintaining aquatic habitat or life cycles of aquatic organisms (Stalnaker 1981). Furthermore, if stream flow is maintained at a historical low-flow for prolonged periods, the aquatic biota can be more severely affected than during infrequent, short-duration naturally occurring low-flow.

Instream-flow requirements based on geomorphic criteria are typically based on discharges or water levels needed either to maintain water at a definable geomorphic surface or to maintain geomorphic processes associated with channel maintenance, like sediment transport. These methods usually define minimum allowable flows by a water depth or channel width considered sufficient to maintain channel morphology, aquatic habitat, navigation, swimming, or any other channel-related attributes. Like the historical low-flow approach, the geomorphic approach has been criticized for not explicitly considering aquatic organisms or their habitat requirements.

Ecological approaches that use habitat requirements and life cycles of target species to define instream-flows are the most complex. The best known model of this type is the Physical Habitat Simulation System (PHABSIM), developed by the U.S. Fish and Wildlife Service (Bovee 1982, Bovee and Milhous 1978, Milhous et al. 1989). This model uses species-specific habitat-abundance relations and open-channel hydraulic simulations to estimate the amount of available habitat as a function of discharge. The most common variables linking species abundance or preference to channel hydraulics are water depth and velocity. These habitat-discharge models assume relatively stable relations between species abundance and the physical features of the channel. Although habitat-abundance relations are widely acknowledged, characterizing them involves several assumptions and procedural conventions (Orth and Maughan 1982, 1983, 1986; Mathur et al. 1984: Scott and Shirvell 1987). The most common assumption is that the habitat and physical features being measured (like depth or velocity) are the major influences on species abundance and that other factors like competition, predation, food supply, and downstream conditions are less important. These models often assume that all available habitats have been sampled. Model results also have been shown to differ considerably depending on the habitat variables used (Gan and McMahon 1990). Regardless of their potential shortcomings, a survey of instream-flow legislation and

practices indicated that habitat-discharge based methods are the most common in North America (Reiser et al. 1989). The users of this approach, however, indicated the need for more species-specific habitat information and methods designed for small watersheds and steep gradient mountain streams (Nestler 1993). In contrast to the biologically based methods in North America, most withdrawal schedules in tropical and subtropical streams have been based on historical low flows (table 1). Because little is known about the effects of regulating tropical warm-water streams, however, it cannot be assumed that the effects are similar to those in temperate, cold-water streams (Ward and Stanford 1993). Nor can methods derived in other environments be transferred directly without calibration or modification. The Luquillo Approach This study builds on Luguillo's long history of ecological and hydrological research to develop two habitat-based approaches for evaluating instream-flow requirements: the PHABSIM model approach and a "whole-pool" abundance-habitat approach based on relations developed from long-term monitoring of aquatic populations. Three tasks were part of both approaches (fig. 5). First, relations between channel habitat and the abundance of selected aquatic species were determined. These relations were then used with either the hydraulic models of the PHABSIM model (fig. 6) or measured channel-geometry relations to develop reach-scale relations between the habitat abundance and stream discharge or stage. Using these relations, temporal variations in the relative abundance of aquatic habitat given different operating rules were then modeled using a 15-year record of daily discharge. Because the number of instream-flow studies in the Loquillo and, similar tropical environments are expected to increase in the near future, the methods used are discussed in detail as a guide for future studies and management activities. Of the common organisms in Luquillo streams (discussed below), we selected the freshwater-shrimp community to be the focus group for determining withdrawal schedules. First, these shrimp are the most abundant aquatic species in headwater streams within the forest and have a dominant role in the ecology of these streams (Covich and McDowell 1996). Secondly, because these shrimp travel from the headwaters to the estuary and back during their life, their abundance and size distributions are excellent long-term indicators of the health of the entire river system. Catching freshwater shrimp is also important to recreation, nutrition, and commerce throughout the Caribbean. These species are distributed throughout much of the Caribbean (Chace and Hobbs 1969, Harrison and Rankin 1976, Hart 1961, Hobbs and Hart 1982, Hunte 1977, 1978), and are related to genera that live in continental rivers (Abele and Blum 1977, Darnell 1956) and on various Pacific islands (Ford and Kinzie 1982, Kinzie 1998). Furthermore, macroinvertebrates have been shown to be sensitive to river regulation in Puerto Rico (Benstead et al. 1999, Holmquist et al. 1998) and elsewhere (Armitage et al. 1987). Study Area Like those on other high-elevation Caribbean islands, the Luquillo Mountains have a central igneous core that is surrounded by an apron of sedimentary rocks. In the **Physical Environment** Luquillo Mountains, the headwaters are forested and under the protection of the USDA Forest Service. The lower foothills and coastal plain are dominated by urban, suburban, industrial, and agricultural land uses (Scatena 1989). The area has a subtropical, humid, maritime climate influenced by both orographic and global-scale synoptic weather systems. Unlike areas with monsoonal tropical climates that receive most of their annual rainfall during a well-defined rainy season, rainfall in the Luquillo Mountains is evenly distributed throughout the year. Mean annual rainfall increases from 1000 mm/yr in the lowlands to nearly 5000 mm/yr at the highest elevations (Garcia-Martino et al. 1996).

Table 1—Examples of instream-flow studies in the humid tropics, with ISF denoting instream flow, and	Q
exceedence frequency of stream discharge	

Location (reference)	Environment drainage area	Method	Operating rules
Caribbean National Forest, Puerto Rico (Hansen et al. 1985)	Mountainous, Subtropical moist to rain lifezones Drainage area = 1.3 km ² -8 km ²	Duration of historical streamflows	ISF = base flow minimum + 20% of all flows above baseflow minimum. Baseflow minimum for ecosystem maintenance = Q90; swimming = Q70-Q80; scenic = Q50-Q60; research = Q100
Rio Icacos, CNF, Puerto Rico (ENSR Consulting 1991)	Mountainous, Subtropical moist to rain lifezones Drainage area = 3.3-7.3 km ²	PHABSIM and historical streamflows	Average lowest daily flow during the dry season as estimated from a 10-year discharge record
Rio Culebrinas, Puerto Rico (internal Dept. of Natural Resources, Puerto Rico report)	Subtropical moist to wet lifezone 184-251 km ²	Historical low flows	ISF requirement recommended as historical daily low flow from 30-year record.
Rio Mameyes at Palmer, Puerto Rico (internal Dept. of Natural Resources, Puerto Rico report)	Coastal plain site draining 30 km ² of subtropical moist to rain lifezones	Duration of historical low flows	Extraction limited to Q99 with a minimum flow constraint of Q99
Rio Grande de Arecibo, Puerto Rico (PRASA 1995)	Coastal plain reach draining 520 km ² of subtropical moist to wet lifezones	Historical flows and hydrologic Budget	Minimum flow = water required to maintain recharge from river to ground water + freshwater inflow needed to maintain the "ecological integrity" of the estuary.
Miyama Hills Reservoir, Guam (Payne and Associates 1990)	Coastal plain, low gradient (1%) stream	PHABSIM	Flows between 0.4-0.7 cfs needed to maintain highest level of usable area. Recommended flow release of 0.5 cfs was recommended
Wailuaiki hydroelectric project, Maui, Hawaii (Payne and Associates 1987)	Montane, slope of volcanic crater	PHABSIM	ISF of 20 to 36% mean annual flows (28-113 l/s) was recommended to maintain aquatic resources.
Lumahai River, Kauai, Hawaii (Payne and Associates 1987)	Mid-elevation and coastal plain streams	Habitat utilization criteria	<i>Atya</i> bisculcata utilizes depths of 0.25-1.5 ft, velocities <0.5 cfs

Methods used to analyze instream-flow relations and operating rules for water intakes

- A. Shrimp-habitat characterization
 - 1. Visual point measurements
 - a. Daytime and nighttime
 - b. First- and third-order streams
 - 2. Analysis of long-term trapping data
 - a. First-order streams
- B. Reach-level shrimp abundance-discharge relations
 - 1. PHABSIM model
 - a. First-order streams
 - b. Third-order streams
- C. Whole-pool geometry model
 - 1. First-order streams
- D. Temporal variation in shrimp abundance under different operating rules
 - 1. 15-year time series of daily discharge on a third-order reach

Figure 5—Outline of methods used to analyze instream-flow relations and operating rules for water intakes within the Luquillo Experimental Forest, Puerto Rico.

A. Channel cross sections surveys: Cross sections were established at every major geomorphic feature, and at least three cross- sections were established per reach. Horizontal distances and vertical elevations were measured every meter in each cross section. B. Water surface level modeling: Channel conveyance method C. Hydraulic simulations: Manning equation D. Velocity adjustment factors: None E. Combined suitability factor: Lowest limit method F. Velocity cell scan method: None G. Criteria values for attributes: Zero H. Habitat curve set construction: By visual observation of species in day and night Ι. Habitat variables:

Figure 6—Options used in PHABSIM model simulations in the Luquillo Experimental Forest, Puerto Rico.

Corresponding to this climatic gradient are changes in life-zone designation, forest composition and structure (Ewel and Whitmore 1973, Lugo and Lowe 1995). Land use (Thomlinson et al. 1996), stream morphology (Ahmad et al. 1993, Clark 1997), instream metabolism (Ortiz-Zayas 1998), and the abundance and diversity of aquatic and terrestrial organisms (Bhajan et al. 1978, Covich and McDowell 1996) also change along this elevation gradient.

Water temperature in headwater streams is relatively consistent throughout the year and ranges between 18 and 24 °C (Covich et al. 1996). The average pH of stream water is 7.2. Stream discharge is highly variable and high flows can occur at any time of the year (fig. 7). Tenfold increases in discharge have been recorded within an hour. The frequency of daily discharges is highly skewed: peak discharges are several hundred times average discharge, and flows that are exceeded 99 percent of the time (Q99) are typically 20 to 30 percent of Q50 (fig. 8). Because high flows are considerably greater than the storage capacities of the dams within and around the forest, the high discharge events necessary for maintaining channel, riparian, and valley features (sensu Hill et al. 1991) are still common downstream from water intakes. Therefore, the need to maintain periodic high flows has not been considered in defining operating rules for these lowhead dams.

The morphologies of stream channels in the Luquillo Experimental Forest and in other Caribbean montane environments reflect the interactions of tectonic movements, periodic high-magnitude floods, and a plentiful supply of coarse bedload (Ahmad et al. 1993). At lower elevations, stream channels often have high-flow channels, multiple depositional surfaces, and relatively wide valleys (Clark 1997). In the Luquillo Experimental Forest, streams typically flow through steep, bedrock and boulder-lined channels with narrow, rectilinear valleys. Waterfalls and bedrock-constrained glides are common features of the landscape. Median pool size varies from about 1 m³ in first-order channels to more than 100 m³ in third-order channels. First-order channels typically are shaded and have pools maximum depths less than 0.75 m (fig. 9). Second- and third-order tributaries have relatively open canopies and pool depths that are usually less than 1.5 m (fig. 10). Although individual pools do experience fill and scour events that influence local populations (Covich et al. 1991, 1998) channel cross-section morphology and reach morphology are relatively stable. Moreover, because channel morphology is relatively stable at the reach scale, transient changes in stream-bed morphology were not considered in this analysis.

Biological Environment Luquillo streams in particular, and Caribbean streams in general, exhibit strong relations between elevation, stream water temperature, and aquatic diversity. The adults of several aquatic species are segregated by elevation and natural barriers like waterfalls (Abele and Blum 1977, Bhajan et al. 1978, Boon et al. 1986, Covich et al. 1996, Villamil and Clements 1976). Species richness typically increases downstream and with the presence of top-level carnivores (Covich et al. 1996, 1998). At the reach scale, species abundance and community composition also are influenced by riparian vegetation and seasonal variations in life cycles, habitat stability, and the amount of time that has lapsed since the last disturbance event.



Figure 7—Daily discharge for the Rio Mameyes at Puente Roto by water extraction schedule.



Figure 8—Flow duration curves and ecological characteristics of flows for selected streams draining the Luquillo Mountains of Puerto Rico. (Quinones et al. 1984).



Figure 9—Number of individual shrimp observed by water depth for freshwater shrimp in streams of the Luquillo Experimental Forest, Puerto Rico.



Figure 10—Number of individual shrimp observed by water velocity for freshwater shrimp in streams of the Luquillo Experimental Forest, Puerto Rico.

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	Common freshwater shrimp of the Luquillo Experimental Forest		
	Phylum Arthropoda		
	Class Crustacea		
	Order Decapoda		
	Family Atyidae		
	Atya scabra		
	Atya lanipes		
	Atya innocous		
	Family Xiphocariscaridae		
	Xiphocaris elongata		
	Family Palaemonidae		
	Macrobrachium carinus		
	Macrobrachium crenulatum		
	Macrobrachium faustinum		
	Macrobrachium heterochirus		
	Macrobrachium acanthurus		

Figure 11—Common freshwater shrimp of the Luquillo Experimental Forest, Puerto Rico (Adapted from Covich and McDowell 1996).

The headwater streams of the Luquillo Experimental Forest have relatively few aquatic species compared to many mainland streams. Nevertheless, predaceous eels, omnivorous mullets, 4 species of gobiid-like fish, 2 species of grazing gastropods, more than 60 species of aquatic insects, and more than 11 species of decapod crustaceans are present (fig. 11, Covich and McDowell 1996). In lower elevation stream reaches, eight fish species and one eel live in these streams. Above major waterfalls, the only fish is the grazing goby (*Sicydium plumieri*), other vertebrate predators are rarely found, and shrimps and crabs play major trophic roles in the aquatic and riparian environment.

In low-elevation reaches, the densities of adult shrimp are relatively low (Bhajan et al. 1980; Johnson pers. observ.) and identifying juveniles to species is difficult. In middle and upper elevation streams, shrimp of the Atyidae and Xiphocariscaridae families are the most abundant and have average densities between 0.8 and 1.7 shrimp per m² (Covich 1988). Nevertheless, densities exceeding 20 shrimp per m² of pool substrate are not uncommon. These shrimp play major roles in detrital processing, instream productivity, and in determining the distribution and abundance of benthic insects and algae (Covich 1988, Covich et al. 1991, Pringle et al. 1993, Pringle and Blake 1994). The most common species are *Atya lanipes* (Holthius) and *Xiphocaris elongata* (fig. 12).



Figure 12—Pool volume versus abundance and biomass of freshwater shrimp trapped in the Quebrada Prieta during 1994.



Figure 13—The abundance and biomass of freshwater shrimp in 100 adjacent pools versus the average depth of the deepest of the 100 adjacent pools for two first-order streams within the Luquillo Experimental Forest, Puerto Rico.

Less common are *A. scabra* (Leach), *A. innocous* (Herbst), and *Micratya poeyi* (Guerin-Meneville). At low stream flow velocities, *Atya* scrape algae and particles from substrate (Covich 1988). At water velocities above 5 cm sec⁻¹ they use modified chelae to filter detrital particles from the water column and often line up perpendicular to flow (fig. 13). *Xiphocaris* are also detritus feeders but lack the modified chelae of the *Atya* species and collect and shred individual particles with small pinchers.

Predatory palaemonidae shrimp also live in most Luquillo streams and are represented by five *Macrobrachium* species. *Macrobrachium carcinus* are found in the upper portions of rivers where currents are rapid and dissolved oxygen concentrations are generally above 6 mg/l (Covich and McDowell 1996). They are typically the largest shrimp in the headwaters and the ones most often targeted by commercial and sport fishermen. *Macrobrachium acanthuris* live in coastal plain and estuarine reaches with lower velocities, dissolved oxygen above 4 mg/l, and water temperatures between 23 and 26 °C (Villalobos-Figueroa 1992). All *Macrobrachium* species are active predators and use large claws for grasping prey (Crowl and Covich 1994).

Atya, Macrobrachium, and *Xiphocaris* are amphidromous; that is, they spend most of their life cycle in freshwater but temporarily reside in coastal areas during larval stages (Chace and Hobbs 1969, Choudhury 1969, Hunte 1978). Unlike some fish species where the adults migrate to the estuaries to release their larvae, ovigerous female shrimp remain in the headwater streams and release their planktonic larvae into fresh water where they are washed downstream to the estuaries (Abele and Blum 1977, Benstead et al. 1999, Ford and Kinzie 1982, March et al. 1998). These larvae remain planktonic for about 10 to 14 weeks at which time they metamorphose into benthic-dwelling juveniles, which migrate upstream. As the juveniles grow, they must periodically shed their rigid exoskeltons. While in this soft molting phase, they are highly vulnerable to predation and cannibalism. Thus their survival during this molting and migrating period is highly dependent on refugia like tight-fitting crevices or burrows. Birds, eel, mullet, and sleepers are known shrimp predators. Mullet have been observed to consume shrimp up to three quarters of their own body length (Johnson pers. obs.).

Reports conflict on the seasonality of freshwater shrimp reproduction. Some have noted the presence of gravid females primarily during the wet season (Chace and Hobbs 1969, Lewis and Ward 1966), whereas others have observed gravid individuals throughout the year (Darnell 1956, Kinzie 1998). Four years of trapping in one of the headwater streams studied here indicates that though there are some gravid individuals at all times of the year, there are fewer gravid *Atya* and *Xiphocaris* during the drier winter months (Johnson et al. 1998). In morphologically stable pools, most *Atya* and *Xiphocaris* are gravid between March and November. In unstable pools that have large changes in sediment storage, gravid individuals of *Atya* and *Xiphocaris* can occur any time of the year. Other studies have indicated that *M. carcinus* and *M. crenulatum* are typically gravid in natural and captive breeding situations between May and September (Bhajan et al. 1978, Lewis and Ward 1966). Other *Macrobrachium* species, such as *M. faustinum*, can be gravid at other times of the year (Johnson et al. 1998).

Considerable anecdotal evidence exists about the upstream migration of shrimp, but little is actually known about factors that influence the initiation, timing, and rate of upstream migration. Common speculations and hypotheses include:

- Storm flows and resulting changes in estuary salinity help shrimp to find the mouths of rivers and trigger migrations.
- Storm flows facilitate upstream migration through predator-rich reaches.

- Most migrations occur during the waning lunar phase.
- Shrimp migrate in the shallow water at the margins of the stream channel.
- Chemical scents released by predators encourage continued movement upstream of the smaller prey (Crowl and Covich 1994).
- Migration and larvae release are most common in the early evening, and that low head dams do not act as complete barriers to the upstream or downstream migration of shrimp (Benstead et al. 1999, March et al. 1998). These low head dams, however, do increase predation on postlarval shrimp and can entrain large amounts of the larvae before it reaches the estuary.

On reaching headwater pools, and presumably throughout their upstream migration, predation can be important in structuring stream communities (Crowl and Covich 1994). In headwater streams, negative relations between *Atya* abundance and the presence of large predatory *Macrobrachium* have been related to avoidance responses by *Atya*. In these streams, predation rates range between 0.08 and 0.42 *Atya* per *Macrobrachium* per day (Crowl and Covich 1994). Generally, smaller *Atya* are more vulnerable than adults and have a stronger movement response to chemical and tactile cues. Although these shrimp are very mobile and can quickly change positions in a pool, mark-recapture studies have found that adult individuals tend to reside within a single pool for long periods. The most common movement among pools is typically in a downstream direction and occurs after storm flows. The greatest storm-related movement of a marked shrimp is 75 m downstream of their resident pool (Covich, unpublished data).

Study ReachesThe two first-order streams used in this study, the Quebrada Prieta and Bisley 3, are
currently being studied as part of the Luquillo Long-Term Ecological Research Program
(fig. 1). Both stream reaches are perennial, steeply sloping, and have continuous ripari-
an cover (fig. 2). Furthermore, they are lined with large (2 m) boulders that form pools
with many crevices and have substrates that range from shallow sands and silts to hard
rock. Available habitats in these streams are typical of headwater streams in the Luquillo
Experimental Forest and range from sandy runs with low complexity to highly complex
habitats of boulder crevices and accumulations of organic detritus.

Location	Elevation	Reach length	Wetted perimeter	Wetted width	Average depth
	т	т	т	т	т
Prieta	390	50	3.3 (0.92)	2.9 (0.9)	0.17 (0.07)
Bisley 3	254	67	2.52 (.79)	2.15 (.67)	0.14 (.06)
Rio Mameyes near Puente Roto	86	98	15.2 (.56)	14.1 (.96)	0.37 (.21)

Table 2—Geometry of stream reaches studied in the Luquillo Experimental Forest, Puerto Rico ^{*ab*}

^a Elevations were estimated from 1:24,000 USGS topographic maps.

^b Standard error in parentheses.

Two mid-elevation, third-order streams—the Rio Mameyes at Puente Roto (fig. 10) and the Espiritu Santo above the town of El Verde, also were used to develop discharge-habitat relations (fig. 5). The mode and average daily discharge at Puente Roto are 0.57 m³s⁻¹ and 1.33 m³s⁻¹, respectively. The channel morphology in both reaches consists of large bedrock pools and boulder-lined riffles, but the Espiritu Santo site also contained a large waterfall-pool complex in the middle of the study reach. Both reaches have riparian vegetation along their banks. Because of the wide width of the channels, however, only part of the channel is completely shaded at any given time.

Habitat Characterization

Methods

The habitat-abundance relations for Luquillo shrimp were determined by using two independent methods: visual observations and measurements at the location of individual shrimp and long-term shrimp abundance data from baited wire funnel traps. The areas chosen for these habitat characterizations were selected because they had consistently high densities of shrimp and contained multiple examples of the full range of microhabitats that occur within Luquillo Experimental Forest streams.

Visual counts are probably the most common method for defining habitat preference in instream-flow studies (Milhous et al. 1989). Visual counts, however, can be biased by the ability of an individual to blend in with the background, water depth, turbulence, suspended sediment, and other factors that influence transparency of the water column. Recording visual observations of nocturnal behavior also can be a logistical problem. Fortunately, observing shrimp in Luquillo streams is generally not a problem because they reside in clear, shallow pools and at night, their eyes reflect the light of a flashlight.

Visual point measurements were made on the two first-order study reaches and one third-order stream. In the third-order reach of the Espiritu Santo, habitat preferences were made from the river bank by day and by snorkeling at night. Because juvenile *Macrobrachium* closely resemble *Xiphocaris*, individuals were collected to verify identification. In the first-order streams, visual point measurements were made at baseflow conditions during both day and night. During the day, the location and species of each shrimp was recorded and marked by a numbered marker. After the entire reach was observed, water depth, water velocity, and size of substrate material were recorded for each marker. Night observations (after 9 p.m.) were made several days later in the same reach. Shrimp were observed by shining a flashlight into the water and noting the species before they swam for cover. A numbered marker was then placed where the shrimp were first observed to reduce any potential bias from startle response. Microhabitat measurements of water depth, velocity, and substrate at each marker were made the next morning. Because shrimp generally seek cover if disturbed or startled, multiple observations of the same individual were unlikely.

Abundance estimates were restricted to two first-order streams where long-term data trapping data existed. Shrimp have been trapped with baited wire funnel traps in these streams since 1988 (Covich et al. 1991). In the Quebrada Prieta, pools have been sampled every two months from 1988 to 1996. Pools in Quebrada Bisley were sampled several times a year from 1988 to 1991 and again in 1994. Following established procedures, baited traps were placed in the stream in the late afternoon and captured individuals were identified to species, counted, and released the next morning (Covich et al. 1991). The number of traps per pool was adjusted for pool area to equalize sampling effort and allow direct comparisons of relative shrimp densities over a range of pool sizes. If large stormflows occurred during the trapping, shrimp abundance was not recorded and trapping was repeated several days later. During each sampling, the maximum depth of the pool and the depth of the trap were recorded.

Habitat-abundance relations were based on the average number of shrimp trapped per pool during 1994, a drought year selected to represent habitat preferences during natural low-flow conditions. The geometry of the pools—average length, width, depth, and wetted perimeter and the percentage of each substrate type in the pools—were determined during baseflow conditions and regressed against the annual average shrimp densities. An advantage of this method is that it incorporates the habitat conditions of the entire pool over time. A disadvantage is the amount of time and effort needed to collect the data before valid relations can be developed.

Results

The observed densities of shrimp varied by species, technique, and time of day (table 3). Point observations made during the late afternoon had many fewer shrimp than either visual estimates made at night or densities estimated by trapping. Because *Xiphocaris* have transparent bodies and are more difficult to observe, they were not counted during the day. At night, however, light reflects from their eyes and species identification is possible. Likewise, due to the low abundance and reclusive nature of *Macrobrachium*, adequate day or nighttime habitat relations could not be developed by using the visual technique.

	Atya	Xiphocaris
	(per 50)	m of channel)
Visual-daytime	47	0
Visual-night	353	310
Trap averages	1335	655

Table 3—Number of individuals observed and trapped in a 50-m, first order reach of the Quebrada Prieta, Luquillo Experimental Forest, Puerto Rico, 1996

The first-order stream habitat utilization curves developed here for *A. lanipes* (fig. 9 and 10) are similar to those created for a Hawaiian species of *Atya* (*A. bisulcata*) using daytime observations (Kinzie et al. 1998, Payne and Assoc. 1987). Our daytime *Atya* habitat utilization curves for *Atya* are based on much fewer individuals than those based on night sampling. Nevertheless, they indicate that *Atya* prefer shallow water and higher velocities during daytime and are distributed over a much wider range of depths and are more abundant in low velocity areas at night (Johnson and Covich 2000).

Analysis of trapping data from headwater streams and measures of pool geometry (that is, average and maximum water depth, pool area, and pool volume) indicated that pool volume was the most consistent factor in predicting the abundance of shrimp during 1994 (fig. 12). In the Prieta sampling reach, *Atya* densities were 200 times those of *Macrobrachium*, and pool volume was correlated significantly with the abundance of all shrimp species. Pool area was also significantly correlated with the abundances of *Atya* and *Xiphocaris*, but not *Macrobrachium*. Maximum pool depth was related to *Marobrachium* abundance but not to Atyid abundance. In Quebrada Bisley, all types of shrimp were much less abundant than in the Prieta. Atyids were only twice as abundant as *Macrobrachium* abundance. Fish and eels, present in this reach and not in the Prieta, may play an important role in determining the community structure and abundance.

At the mid-elevation Rio Espiritu Santo sampling study site, no adult *Atya* were observed during either day or night. At night, however, very small juvenile *Atya* (total body length of 10 mm) were seen moving upstream along the margins of fast-moving water. These juveniles were not visible in pools or other areas of slow-moving water. On one night, 120 *Xiphocaris* were observed clustered on vertical portions of various boulders and rock outcrops. Water depths associated with these *Xiphocaris* ranged from 0.05 to 1.2 m. Water velocities were less than 0.05 ms⁻¹. During the day, only 10 *Xiphocaris* were observed at night in low-velocity habitats near crevices. A few *M. faustinum* also were observed in the downstream portions of the fast glides that the *Atya* were climbing. During the day, gobies, mountain mullet, and eels also were observed in these pools.

- Summary of Habitat Characterization
- Field observations in first-order pools suggested that all but a few Atya hide under cover during the day. At night, most occupy areas of low velocity (< 0.09 m/s) and depths less than 0.4 m. *Xiphocaris* also were reclusive during the day and prefer low-velocity areas at night. During baseflow conditions, *Macrobrachium* were more abundant in pools with maximum depths greater than 0.35 m, and in pools with volumes greater than 2 m².
- In mid-elevation, third-order streams, most shrimp were observed migrating upstream in either low-velocity habitats near crevices or along the edges of fast-moving water. Differences in habitat preference between first- and third-order channels suggested different habitat preferences for resident and migratory populations. Furthermore, the abundance of shrimp in crevices and in the margins of fast-moving water suggested the importance of maintaining refugia and flow in channel margins that are used for upstream migration.
- Predation appeared to be a major influence on behavior of these shrimp. During the day, visual predators are probably the greatest threat so the shrimp stay in high-velocity areas that can obscure visibility and reduce risk. At night, when the effectiveness of visual predators is relatively low, many shrimp were found in low-velocity habitats along the edges of pools. These differences indicate the importance of sampling at night when developing habitat relations for these organisms. Moreover, daytime sampling can underestimate the size of the population and the preferred water depth and overestimate the preferred velocity.
- Our field observations showed large differences in the abundance and structure of aquatic communities and in the amount of usable habitat between streams of the same order. These differences can be influenced by the local habitat conditions as well as the rate of upstream migration, the presence or absence of predators, and differences in the behavior of resident and migratory individuals. The observed differences indicate the importance of conducting site-specific surveys when doing instream flow analysis.

Stream-Reach
ModelingThe abundance of shrimp in a stream depends not only on the density of shrimp in a
habitat type but also on the abundance of habitat in a reach. To determine the relations
between discharge and shrimp abundance at the reach scale, habitat-abundance rela-
tions were applied to surveyed reaches within the Luquillo Experimental Forest. Two
independent approaches were used: reach-scale relations of pool volume to stage and
relations of shrimp abundance to pool volume derived from the long-term shrimp trap-
ping data; and the hydraulic module of the PHABSIM model and the habitat preference
curves. Both approaches model the amount of preferred habitat at different water levels
and indicate potential, but not necessarily actual habitat. Neither approach considered
the effects of migration, predators, food supply, or other measures of habitat quality that
may influence shrimp abundance in a particular area.

Pool-volume and water-level relations were developed by measuring the geometry of 100 adjacent pools in different headwater streams. All of these pools were large enough to hold a standard shrimp trap at base flow and had a length of at least 0.5 m in at least one direction. Given the normal density of this type of pool, a 100-pool segment is typically more than 500 m long and contains various channel habitat features and morphologies (like riffles, runs, coarse woody debris dams, etc.). The average depth of each pool was estimated as the average of five randomly selected water depths. Maximum potential pool depth was defined as the distance from the top of the pool outlet to the deepest part of the pool and is a measure of the maximum depth a pool can attain while remaining an distinct geomorphic unit. The plane-view shape of each pool was also categorized as circular, triangular, or rectangular. Pool volume for a given water depth was determined by treating each pool as a cylinder with the cross-sectional shape and dimension corresponding to those measured in the field. In the analysis, the volume of any pool was considered constant when water depth was equal to or greater than the maximum potential depth of the pool. For each water level and corresponding pool volume, the number of shrimp in each pool was estimated by using the abundance to pool volume relations that were calculated from the long-term trapping data (fig. 12). The total abundance of shrimp in the reach at each water depth was then calculated as the sum of shrimp in the 100 individual pools and graphed on the basis of the average depth of water in the deepest pool in the 100-pool reach (fig. 13).

Habitat abundance estimated by using the PHABSIM model were based on hydraulic simulations that modeled the depth and velocity in a surveyed area as a function of discharge. The Manning equation calibrated to one set of field-measured water surface elevations was used to simulate water surface elevations at different discharges (Milhous et al. 1989). Each study reach was surveyed by using an automatic level-type transit. At least three cross sections were surveyed at each reach, with the most downstream section being located at a riffle or other hydraulic control. Elevations in each cross section were surveyed at least once every 1 m for uniform sections, and more frequently in areas with irregular substrates or where the stream width was less than 10 m. At each point, elevation, water depth, water velocity, and substrate type were recorded. If either depth or velocity were unsuitable, then the model considered that microhabitat section to be unsuitable to the shrimp. At the mid-elevation study site on the Espiritu Santo, Xiphocaris were only observed clustered on boulders in slow-moving water and exhibited no preference for specific water depth. Therefore, the site was considered to be sub-optimal habitat for resident shrimp and was not used in simulations of usable area.

The hydraulic simulations of the PHABSIM model produced consistent discharge-usable habitat relations in the higher order mid-elevation streams (fig. 14). The PHABSIM model, however, produced more irregular discharge-usable habitat relations in the steep and more complex headwater reaches (fig. 15). Apparently because of the boulders in these channels, considerable heterogeneity of velocities, depths, and energy losses is found between cross sections. This heterogeneity can result in more variable and less accurate discharge-usable area relations.

The percentage of channel area modeled as "usable" can vary considerably between reaches of the same and different orders. Between the headwater reaches of Bisley and Prieta, differences in the estimated abundance of individuals or usable habitat resulting from differences in channel morphology alone can be as high as 35 percent (figs. 14 and 15). The maximum amount of usable habitat for *Xiphocaris* accounts for about 45 percent of the wetted channel in the headwater reaches of Bisley and Prieta.

Results



Figure 14—Usable habitat for freshwater shrimp by discharge for the Rio Mameyes at Puente Roto, Luquillo Experimental Forest, Puerto Rico.



Figure 15—Usable habitat for freshwater shrimp by discharge for headwater streams within the Luquillo Experimental Forest, Puerto Rico.

	In contrast, only 11 percent of the mid-elevation reach at Puente Roto is considered "usable" for the same species. Most of the usable habitat at Puente Roto is in shallow pools in the boulder-lined margins of the channel. Velocities, water depth, and increased predation by fish make large parts of the thalweg unsuitable in this particular reach.
Summary of Stream- Reach Modeling	 When the average depth of water in the deepest of 100 adjacent pools in a first- order reach was less than 0.5 to 0.4 m, the abundance of shrimp in a 100-pool reach declined rapidly (fig. 13).
	 The amount of usable habitat begins to decline rapidly at discharges below Q90 in mid-elevation reaches (fig. 14). At discharges above Q50, there is little increase in habitat with increases in discharge.
	• When discharge fell between 0.06 and 0.03 m ³ /s in headwater streams and between 0.75 and 0.5 m ³ /s in mid-elevation reaches, the amount of available habitat declined rapidly for all species. These discharges typically correspond to between 0.35 and 0.20 liters/sec/ha and are usually within one standard deviation of the average annual 7-day minimum flow. The exceedence frequencies of these discharges are typically between Q99 and Q96 (fig. 8).
	• Differences in channel morphology alone can result in considerable variation in the abundance of individuals or usable habitat among reaches of similar stream order. Similarity in the shapes of the habitat-abundance curves suggests that regardless of the absolute abundance of shrimp within a reach, similar velocities and water depths will be necessary to maintain resident populations. Because of differences in channel morphology, however, different discharges will be needed to maintain the desired velocities and water depths in different reaches. Therefore, reach-specific surveys should be conducted when habitat preference relations are used to define instreamflow levels for a particular area.
Temporal Modeling	Luquillo streams are subject to wide variations in daily stream discharge, which in turn
Methods	can result in large variations in the abundance of available habitat. To account for these temporal variations, 15 years of daily discharges in the Rio Mameyes at Puente Roto (fig. 7) and the usable area-discharge relations for the reach (fig. 14) were combined to simulate the long-term abundance of habitat under various water-withdrawal schemes (figs. 16, 17, 18). The relative merits of various operating rules were then evaluated by comparing the estimated amount of usable habitat under the operating rule to the estimated habitat-discharge relation for <i>Atya</i> at Puente Roto and the discharge record at Puente Roto (fig. 14). Similar results were obtained from simulations that used usable habitat-discharge relation for <i>Xiphocaris</i> . Results are graphed and reported in relation to the 7-day average and 7-day minimum flows to allow direct comparisons with published low-flow records (Garcia-Martino et al. 1996).
Results	In simulations without water extraction, neither stream discharge nor the amount of usable <i>Atya</i> habitat reached zero during the 15-year period (fig. 16). In contrast, when withdrawals are allowed without instream-flow constraints, the temporal variability in usable habitat increases dramatically and there are extended periods without usable habitat. Nevertheless, when some minimum level of instream-flow is maintained, the temporal variation in usable habitat is reduced and the stream channels are never completely dewatered.
	Without minimum flow constraints, the average annual 7-day minimum level of usable habitat decreases rapidly with increases in the amount of water extracted (fig. 17). Even when water extraction is limited to Q99, without instream-flow constraints, the average



Figure 16—Seven-day running average usable habitat for *Atya* spp. under different operating rules at the Rio Mameyes at Puente Roto, Luquillo Experimental Forest, Puerto Rico.

annual 7-day minimum is about 40 percent less than in the undisturbed condition, and there can be several days per year when usable habitat is zero. When extractions are limited to Q99 and instream-flows are maintained at Q99, the average annual 7-day minimum is about 95 percent of the undisturbed condition. In contrast, with a minimum instream-flow constrained at 50 percent of Q99, the annual daily minimum and annual 7-day minimum is below historical minimums every year.



Figure 17—Average annual 7-day minimum usable habitat for *Atya* spp. by extraction rate for the Rio Mameyes at Puente Roto, Luquillo Experimental Forest, Puerto Rico.



Figure 18—Percentage of time the 7-day average usable habitat for *Atya* spp. is equaled or exceeded for different extraction schedules at for the Rio Mameyes at Puente Roto, Luquillo Experimental Forest, Puerto Rico.

	These simulations suggest that by maintaining a minimum instream-flow of Q99 or great- er, the amount of usable habitat will not be reduced below the naturally occurring levels (figs. 16 and 17). If large quantities of water are continuously withdrawn from a stream, however, the amount of usable habitat will remain at drought levels for extended periods (fig. 18). For example, with an instream-flow constraint of Q99 and a water extraction of Q98, 20 to 30 percent of the time, the amount of usable habitat will be equal to that which normally occurs during drought conditions. These results reflect that minimum instream-flows maintain minimum levels of habitat. Additional changes in the abundance, structure, and composition of the populations may occur as a result of being confined to these minimum habitats for extended periods each year. Moreover, though the range of minimum instream-flows considered here can maintain minimum conditions for abun- dant species, they may not be appropriate for maintaining rare species or even com- mon species needed for recreational or commercial shrimping.
Summary of Temporal Modeling	• Without minimum instream-flow requirements, water intakes occasionally will be dewatered and commonly experience severe reductions in the amount of usable habitat. Maintaining instream-flow equal to or greater than Q99, however, will increase the average annual minimum level of usable habitat to levels within the historical, undisturbed minimum levels. With a minimum instream-flow of 50 percent of Q99, every year the 7-day minimum will be below the historical, undisturbed 7-year minimum.
	• Because of naturally occurring variations in discharge, neither the average daily or average annual 7-day minimum level of usable habitat increases considerably when instream-flows are greater than Q98. Even with minimum instream-flows the amount of time usable habitat is at or near historical minimums increases rapidly when extractions are greater than Q98.
Conclusions	Our results indicate that habitat models based on local conditions can be useful in defin- ing instream-flow requirements and withdrawal schedules that reduce adverse impacts to aquatic communities. The items listed below were designed to help develop water extraction schedules for Luquillo streams. Nevertheless, reach-specific field verifications should be done before intake-specific management strategies are adopted.
	In resident headwaters areas, the most common shrimp prefer moderate to low veloci- ties (<0.35 m/s), well oxygenated (DO > 6 mg/l) water, and depths less than 0.4 m. In mid-elevation reaches where predation is common, shrimp migrate headward in low- velocity habitats near crevices in bedrock or boulders, along the edges of fast-moving water, and along channel margins. Therefore, instream-flow and riparian management strategies should be designed to maintain resident pool habitat in headwater streams and channel margins habitats in migratory reaches. Providing habitat structure (boul- ders, course woody debris etc.) that will reduce predation below low head dams and other "bottle-necks" also can help sustain populations (Benstead et al. 1999).
	In headwater streams, the amount of usable habitat declines rapidly for common shrimp species when the average depth of water in the deepest of 100 adjacent boulder pools is less than 0.5 m and when discharges fall below 0.02 to 0.06 m ³ /s. At velocities below 0.05 m/s, the common atyid shrimp switch their feeding behavior from the efficient filtering of detrital particles to less efficient scrapping (Covich 1988). In mid-elevation reaches, available habitat declines rapidly when discharge falls below the annual 7-day minimum and the shallow pools along the boulder-lined channel margins are dewatered. Because of among-stream variation in available habitat and population structure, site-specific surveys must be made when operating rules for specific intakes are defined. Moreover, channel habitat should be surveyed for each specific case before the habitat-abundance relations developed here should be applied.

	Diurnal and seasonal variations in life cycles also should be considered when rules are developed for operating water intakes (Benstead et al. 1999, Johnson et al. 1998, March et al. 1999). Because juvenile shrimp tend to migrate at night and adults release their larvae at night, maintaining water levels during peak periods of night-time activity and during peak breeding seasons can be an effective way to maintain populations (Benstead et al. 1999). Therefore, in addition to providing a day-time minimum instream- flow, water extractions in middle and lower elevation reaches should be reduced or elimi- nated during night-time periods of peak larval release and migration.
	Without minimum instream-flows constraints equal to or above Q99, the amount of usable habitat will be below historical levels for extended periods each year if extractions are more than Q99. At discharges greater than Q50, there is little increase in habitat with increasing discharge. Therefore, extractions at these discharges should have little affect on usable shrimp habitat.
	Future research needs include a greater understanding of the headwater migration of freshwater shrimp and the effects of prolonged periods of minimum instream-flows on the abundance and structure of aquatic populations. In addition, habitat requirements for common fish and other aquatic organisms must be developed before minimum instream-flow requirements can be developed for lower elevation or coastal plain streams that surround the Luquillo Experimental Forest.
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