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Effects of drought and hurricane disturbances on headwater distributions of palaemonid river shrimp (*Macrobrachium* spp.) in the Luquillo Mountains, Puerto Rico

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Abstract. Extreme events (hurricanes, floods, and droughts) can influence upstream migration of macroinvertebrates and wash out benthic communities, thereby locally altering food webs and species interactions. We sampled palaemonid river shrimp (*Macrobrachium* spp.), dominant consumers in headwaters of the Luquillo Mountains of northeastern Puerto Rico, to determine their distributions along an elevational gradient (274–456 m asl) during a series of disturbances (Hurricane Hugo in 1989, a drought in 1994, and Hurricane Georges in 1998) that occurred over a 15-y period (1988–2002). We measured shrimp abundance 3 to 6 times/y in Quebrada Prieta in the Espiritu Santo drainage as part of the Luquillo Long-Term Ecological Research Program. In general, *Macrobrachium* abundance declined with elevation during most years. The lowest mean abundance of *Macrobrachium* occurred during the 1994 drought, the driest year in 28 y of record in the Espiritu Santo drainage. *Macrobrachium* increased in abundance for 6 y following the 1994 drought. In contrast, hurricanes and storm flows had relatively little effect on *Macrobrachium* abundance.

Key words: dispersal, drainage networks, geomorphology, habitat preference, omnivores, prey refugia.

Flow-based events often modify the important roles played by diverse predators and herbivores in aquatic food webs (Flecker et al. 2002). Effects of floods generally are of short duration, and some stream species either resist wash-out from floods by occupying specific microhabitats (Townsend et al. 1997), or rapidly recolonize pools within the drainage network (Covich et al. 1991, 1996). In contrast, effects of extreme low-flow events on stream food webs can persist for several years (Lake 2003, Fritz and Dodds 2004, Wood and Armitage 2004). Low flows associated with prolonged drought can dry riffles and waterfalls, create narrowly constrained channels, disrupt upstream migrations, decrease rates of reproduction, and restrict flow-related chemical communication (Crowl and Covich 1994, Covich et al. 2003). Thus, drought conditions can greatly reduce habitat quality and availability by decreasing pool volumes and hydrologic connectivity (Covich et al. 2000, Bencala 1993, Pringle 2003). Reduced flows lead to accumulations of organic and inorganic materials that further decrease pool volumes and can lower water quality (e.g., low dissolved O_2 resulting from decomposing organic matter). The ecological significance of this loss of habitat is especially important for decapod species, such as *Macrobrachium*, whose life histories most often require upstream migrations from coastal estuaries (Chase and Hobbs 1969, Bowles et al. 2000, Jayachandran 2001).

Drought-based habitat loss in tropical coastal streams is postulated as a major regulator of abundance of large omnivorous decapods. These freshwater shrimp frequently dominate food webs of upper-elevation, rainforest streams where predatory fish are absent (Covich and McDowell 1996, Holmquist et al. 1998, Townsend et al. 2002, Iwata et al. 2003, March et al. 2003). Extended dry periods are typical of many tropical regions, but the aseasonal rainfall that characterizes other wet tropical regions (such as the Luquillo Mountains) results in perennial streams with very low drought frequency. The effects of variable,

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interannual flow and prolonged drought on natural populations of decapods in aseasonal rainforest streams are generally unknown.

Palaemonid shrimp play important ecological roles within tropical and temperate stream food webs (March and Pringle 2003, Mantel and Dudgeon 2004a, b, c). However, these shrimps are studied primarily because of their importance as major food resources in aquaculture (Bowles et al. 2000, Jayachandran 2001). Their dispersal and evolution are becoming better understood as more research is focused on their colonization and recolonization dynamics (Canals 1979, Carini and Hughes 2004, Murphy and Austin 2004).

We demonstrated previously that prolonged drought concentrated populations of *Atya lanipes* and *Xiphocaris elongata* in headwater pools of Quebrada Prieta and that these shrimp populations were vulnerable to habitat fragmentation, habitat loss, and increased predation (Covich et al. 2000, 2003). Here we examine how the spatial distribution of *Macrobachium* spp. responded to extreme events that occurred over a 15-y period (1988–2002) in a small headwater stream, the Quebrada Prieta. The Prieta is situated above a high (>20 m), steep waterfall in the Rio Espiritu Santo drainage. The stream is fishless (except for herbivorous gobies) and dominated by decapods (Covich and McDowell 1996, Crowl et al. 2001). Our study is the first to report effects of drought on *Macrobrachium* spp. and is part of the Luquillo Long-Term Ecological Research Program, a project designed to determine the effects of different types of disturbances on stream communities in the Luquillo Mountains, Puerto Rico (Johnson et al. 1998, Covich et al. 2000, 2003, Crowl et al. 2000, 2001).

Methods

Study site

The Luquillo Experimental Forest (Caribbean National Forest) in Puerto Rico (lat 18°18′N, long 65°47′W) consists of >11,000 ha of steeply sloped rainforest. It is the only tropical rainforest site within the National Science Foundation's Long-Term Ecological Research (LTER) Program. The site is also a United Nations Biosphere Reserve and has been under intensive ecological study for >50 y. Montane streams in northeastern Puerto Rico are characterized by rapid runoff from steeply sloped forest. Infrequent floods alter shrimp habitat availability over time periods ranging from a few hours to a few days (Scatena and Johnson 2001). Precipitation in the Luquillo Experimental Forest (3600 mm) is slightly seasonal, with peak flows from May through December. Annual discharge in streams draining the forest is highly variable and closely follows rainfall (García-Martino et al. 1996, Schellekens et al. 2004). Recurrence intervals of prolonged droughts range from 5 to 10 y, and recurrence intervals of hurricane-derived floods range from 10 to 30 y (Larsen 2000, Covich et al. 2003). Water temperatures range from 18 to 24°C annually.

Geomorphological studies document the hydraulic geometry and network characteristics of the Rio Espiritu Santo drainage. The Espiritu Santo is structurally complex with a total channel length of 277,091 m and 563 stream confluences (A. S. Pike and F. N. Scatena, University of Pennsylvania, unpublished data). The Prieta drainage extends from 305 to 480 m asl. The drainage network is composed of steeply sloped, boulder-lined channels with closed, broad-leaf, evergreen riparian canopies. These habitats vary in their sources of energy along a compressed altitudinal gradient. The drainage network is composed of 1st- and 2nd-order stream channels that ultimately connect to 3rd- through 5th-order channels of the Espiritu Santo in the coastal plain (Clark and Wilcock 2000, March et al. 2002, Ortiz-Zayas et al. 2005). The drainage has been exposed to hurricanes over many millennia and has experienced various types of landuse practices (e.g., selective cutting, coffee production, and charcoal production) that ended >70 y ago (Garcia-Montiel and Scatena 1994, Thompson et al. 2002).

Macrobrachium *in the Rio Espiritu Santo drainage*

Five species of *Macrobrachium* occur in Puerto Rico, but *M. acanthurus* is the only species restricted to lower elevations (Covich and McDowell 1996). *Macrobrachium carcinus*, *M. crenulatum*, *M. faustinum*, and *M. heterochirus* all migrate considerable distances upstream into headwater tributaries. In our studies, *M. carcinus* has been the most persistent species, whereas adult *M. crenulatum*, *M. faustinum*, and *M. heterochirus* occur intermittently. These 3 species appear to have similar life histories. *Macrobrachium* larvae drift downstream into coastal estuaries. All 4 species require brackish water for full larval development before the benthic post-larvae develop and begin to migrate upstream where juveniles continue to grow into reproductive, ominvorous adults (Jayachandran 2001). Juveniles are difficult to identify to species and, thus, individuals of all species were combined for our analysis.

Sampling

Macrobrachium abundance was measured 3 to 6 times/y over a 15-y period (1988–2002) in Quebrada Prieta using baited wire traps left overnight at base-

TABLE 1. Mean values and coefficients of variation (CV) for morphometric variables in 20 pools along the Quebrada Prieta elevational gradient.

		Mean				CV			
Pool	Elevation (m asl)	Length (m)	Width (m)	Depth (cm)	Max depth (cm)	Length	Width	Depth	Max depth
1	276	4.2	3.9	56.1	83.4	15.8	18.8	19.0	23.6
2	280	4.5	1.5	41.8	58.6	23.1	22.4	25.8	18.5
3	307	3.4	3.2	54.3	64.4	4.8	21.2	13.4	25.9
4	324	3.3	2.5	41.8	57.8	19.8	26.2	39.1	20.8
5	349	2.4	1.9	35.7	47.5	10.7	29.9	21.2	19.5
6	358	3.5	2.3	22.9	39.5	11.2	12.7	31.7	19.1
7	360	20.3	3.7	40.9	59.0	6.5	10.1	16.9	11.4
8	361	6.7	2.8	29.0	43.8	23.9	34.8	36.6	14.4
9	362	5.6	4.0	24.9	38.3	13.8	11.3	20.5	14.6
10	363	5.3	5.2	27.7	39.5	7.2	10.5	30.0	20.6
11	368	4.0	1.5	23.0	42.7	21.4	18.2	27.9	52.7
12	374	4.4	2.3	22.5	35.5	18.9	29.7	52.4	28.3
13	380	6.1	2.6	36.0	35.8	20.9	42.3	7.1	53.9
14	381	4.4	2.3	30.5	44.2	18.4	17.3	18.3	18.8
15	412	5.1	1.6	13.2	20.3	18.5	23.6	32.3	31.3
16	418	2.3	1.3	16.7	26.0	32.0	20.8	16.6	26.1
17	420	2.9	1.7	21.7	31.8	27.7	45.7	26.3	27.2
18	430	2.2	1.2	25.0	37.7	23.0	8.7	22.6	27.3
19	435	7.2	1.7	16.5	25.1	33.8	50.5	34.7	34.7
20	440	3.1	1.8	17.8	27.6	28.8	19.7	23.1	22.5

flow. Wire traps (Gee Minnow traps; Cuba Specialty Manufactory, Fillmore, New York) consisted of inverted funnels with enlarged 4-cm entry openings. This trapping method was used previously to monitor populations of shrimp prey (Covich et al. 2000, 2003). *Macrobrachium* abundance and size distributions were determined in 27 pools that ranged in elevation from 274 to 456 m asl along a 1200-m length of channel in the Quebrada Prieta. Only 20 of these pools remained sufficiently deep (Table 1) to sample over the entire study period because bank erosion and storm-transported sediments filled 7 pools. The number of traps used in each pool was scaled relative to pool size and ranged from 2 to 34 traps/pool so that trapping effort was uniform at 0.5 traps/m^2. Shrimp abundances were not recorded if large storm flows occurred during the night of sampling because leaf litter typically accumulated and blocked the trap entrance. Pool morphometry (depth, area, and volume) and flow were recorded at the time each sample was collected.

Adult shrimps were identified to species, and their reproductive status was recorded. All shrimp were counted, and carapace length (CL; length from rostrum tip to end of carapace) was used to assign individuals to 1 of 2 size classes used for analysis of differences between juvenile and adult responses to disturbance (defined as changes in pool morphometry over time).

Statistical analysis

All data were analyzed using SAS (version 8.0, SAS Institute, Cary, North Carolina). Two types of analysis were used to compare abundances and distributions over time. First, intra- and interannual population dynamics (size distributions and abundances) over the 15-y period were explored using analysis of variance (ANOVA). ANOVAs were used to assess among-year and within-year (seasonal) variation in mean shrimp abundances. Second, *Macrobrachium*–habitat associations were assessed using regression analyses. Regression was used to model the relationship between *Macrobrachium* abundance and elevation, and stepwise multiple regressions were used to model the relationships between *Macrobrachium* abundance and pool morphometry. Two levels of physical variation in pool morphometry were used in the multiple regression models: 1) average pool dimensions for all years and the coefficients of variation (CVs) for morphometric variables within each pool were used to represent the complexity of each pool in terms of pool shape; and 2) CVs of morphometric variables over time were used to provide an estimate of pool stability through time. Multiple regression analysis was done 1st using all *Macrobrachium* as the response variable, and 2nd using *Macrobrachium* in 2 size classes (<34.9 mm CL and >35 mm CL) as the response variables. Response variables (no. *Macrobrachium*/pool) were transformed using

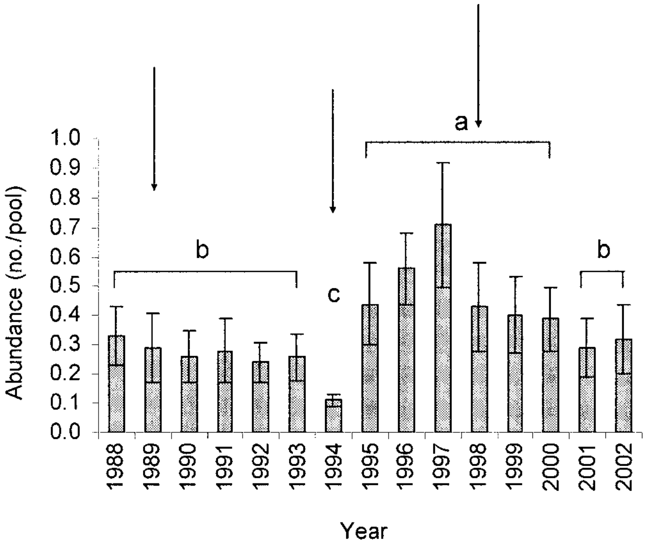

FIG. 1. Mean (±1 SE) total abundance of *Macrobrachium* in 20 pools in Quebrada Prieta from 1988 to 2002. Years with the same letter are not significantly different. The arrows indicate flow-based events: Hurricane Hugo (1989), Hurricane Georges (1998), and the most severe drought in 28 y (1994).

$\log_{10}(y + 1)$ to normalize distributions and standardize variance structure.

Results

Intra- and interannual distributions of shrimp (1988–2002)

Drought effects.—The annual abundance (number of shrimp per pool) of *Macrobrachium* varied significantly among years ($F = 1.91$, $p = 0.0259$; Fig. 1). Mean annual abundance was significantly lower during 1994 relative to any other year between 1988 and 2002 (Ryan–Einot–Gabriel–Welsh Quotient [REGWQ] posthoc comparison), indicating that the 1994 drought affected *Macrobrachium* abundance. 1994 was the driest year among 28 y of record for the Espiritu Santo drainage (Larsen 2000, Covich et al. 2003). Abundance was significantly higher in the 6 y following the drought (1995–2000) than during the years before the drought (1988–1993) and after 2000 (2001–2002). Postdrought abundance peaked in 1997 (Fig. 1). *Macrobrachium* were not observed in any small upper-elevation pools from 1994 to 1997.

Storm-flow effects.—The high storm flows associated with Hurricane Hugo (1989) and Hurricane Georges (1998) had no statistically significant effects on mean annual *Macrobrachium* abundance (Fig. 1). Abundance did not change in response to floods (associated with Hurricane Hugo and other storm events) from 1988 to 1993.

Seasonal patterns of abundance.—Abundance of shrimp was significantly higher in July than in other months ($F = 17.7$, $p = 0.003$) and was consistent throughout the rest of the year (Fig. 2). Abundances tended to be lowest in February, October, and November (Fig. 2).

Influence of elevation.—*Macrobrachium* abundance decreased significantly with elevation ($F = 177.15$, $p < 0.0001$; Fig. 3). Pools generally were shallower at higher elevations, and CVs indicated considerable fluctuations in mean pool depth, mean maximum depth, and overall size in middle- and upper-elevation pools (Table 1). One middle-elevation pool (pool 7 at 360 m asl; Table 1) had relatively high abundances (Fig. 3), apparently because it was consistently among the largest and deepest pools in this small stream (mean pool area = 75.7 m^2, maximum depth = 0.62 m). This pool was unusually long, relatively deep, and less

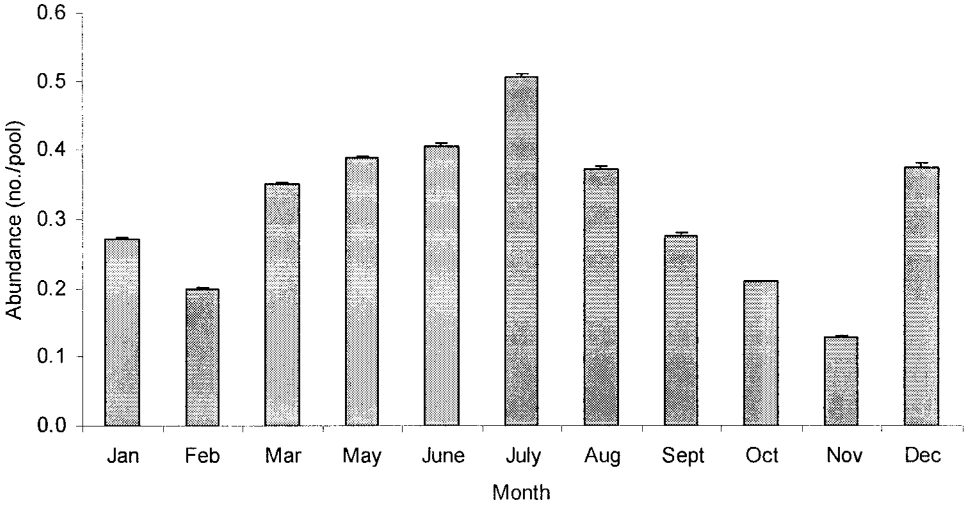

FIG. 2. Mean (+1 SE) monthly total abundance of *Macrobrachium* in 20 pools in Quebrada Prieta from 1988 to 2002.

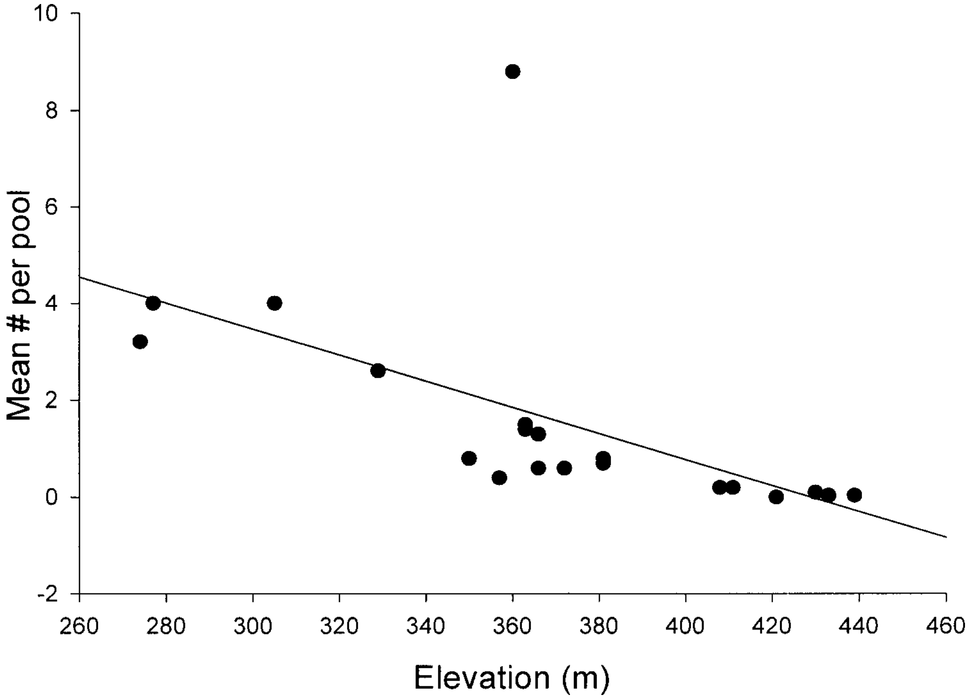

FIG. 3. Relationship between total abundance of *Macrobrachium* (1988–2002) and elevation in Quebrada Prieta.

variable in size relative to other middle-elevation pools because it was on level terrain. The location of this pool in the middle of the elevation gradient affected the strength of the abundance–elevation relationship but not its direction.

Habitat associations.—Macrobrachium was most often associated with deep pools that were narrow and relatively short (Table 2). *Macrobrachium* abundances were predicted best with a multiple regression model that showed a positive association with maximum pool depth and negative associations with average pool width and length ($F = 7.07$, $p = 0.0002$). No other variables were significant at $p = 0.15$. This model explains ~25% of the spatial variation in abundance of shrimp within Quebrada Prieta.

Macrobrachium was most often associated with pools that showed little variation in maximum depth or width:depth ratios ($F = 12.7$, $p = 0.0005$) when total *Macrobrachium* abundances were regressed against physical variables and measures of temporal variation (pool stability). This model explained ~43% of the variation in total abundance among years (Table 2). The model for small (<34.9 mm CL) *Macrobrachium* was almost identical to the model for total *Macrobrachium* (Table 2). The model for large (≥35 mm CL) *Macrobrachium* was not statistically significant, and no morphometric or stability variables could be used to

TABLE 2. Results of 2 stepwise multiple regressions relating total *Macrobrachium* abundance and morphometric variables describing 20 pools along the Quebrada Prieta elevational gradient. The within-pool variability model was based on mean pool dimensions for all years ($n = 15$ y) and the coefficients of variation (CVs) for morphometric variables within each pool. The temporal variability model was based on CVs of morphometric variables over time. See text for further explanation. Only those variables that were statistically significant ($p < 0.15$) in the models are shown.

Morphometric variable	Parameter estimate	Partial R^2	F	p
Within-pool variability model				
Width	−0.03	0.1121	14.2	0.0003
Maximum depth	0.09	0.1301	4.3	0.0401
Length	−0.02	0.0149	3.7	0.0851
Temporal variability model				
CV width:depth ratio	−0.06	0.3175	7.0	0.0185
CV depth	−0.07	0.1148	2.9	0.0847

predict the abundance of large *Macrobrachium*. This inability to model habitat associations for large *Macrobrachium* may have been a consequence of a small sample size. Most (1680/1847) of our captured shrimp were in the small size class. Only 0.1% of the measured individuals were gravid females.

Discussion

Disturbance and habitat

Every stream has individual characteristics at local scales, but stream ecologists have long recognized that disturbance widely affects species' distributions within streams at drainage scales (Resh et al. 1988, Robinson et al. 2004). Dynamic interactions among species' distributions, hydrological variability, and geomorphological constraints are especially important in drainages with complex terrain (Poole 2002, Benda et al. 2004). Over time, the structure of the drainage network responds to variations in stream flow, sediment load, and human intervention. Modifications of natural drainage structures through dam construction, diversions, road building, and channelization change rates of flows and directional attributes. These changes alter upstream migrations and access to headwater pools, especially during periods of extremely low flows. Drainage network analysis is emerging widely as an organizing concept to enable better understanding of the movement of sediments, nutrients, and species within drainages (Power and Dietrich 2002, Benda et al. 2004).

We emphasize that shallow headwater pools are especially vulnerable to habitat loss resulting from a wide range of disturbances within a drainage network, particularly from drought (Covich et al. 2000, 2003, Magoulick 2000, Lake 2003, Stanley et al. 2004). Floods are clearly documented and discrete events, but even extremely high flows usually are short-term relative to persistent low flows during drought (Stanley et al. 1997, Lake 2003). In general, storm flows and erosion within a basin alter many headwater stream communities and ecological processes (Gomi et al. 2002, Woodward and Hildrew 2002), whereas impacts of drought are documented less often (Covich et al. 2003).

Drainage networks

The location of headwater pool habitats relative to steep waterfalls (or other barriers) within a drainage network has long-term significance for sustained persistence of populations in tropical montane catchments, where highly variable rainfall can directly and indirectly alter geomorphology and biological assemblages. The drainage network approach can be used to analyze predator–prey encounters, avoidance strategies, and dynamic responses to changing flow regimes. Over time, geomorphic features such as channel slopes, waterfalls, substrata, and pool depths adjust to the combined hydrologic power of confluent tributaries. These features result from combined geological processes (such as weathering and faulting) that have hierarchical organization.

Storm flows can wash out organisms and detrital food resources. Sediment transport and retention are controlled by variable flows through channel networks that can fill in pools and increase a species' isolation and vulnerability during prolonged droughts. Sediment accumulation eliminates crevices used for refugia from predators, alters substrata used by rooted aquatic plants, covers over periphyton food resources used by grazers, and buries leaf litter used by detritivores. Lack of sediment removal during prolonged low flows results in persistent effects of sediment accumulation and is usually associated with decreased access to pool habitats. Microhabitats such as undercut banks, woody substrata, root mats, and riparian edges are often inaccessible during droughts. These sites serve as refugia for many species of prey so that population densities are altered during disturbances (Covich et al. 2003).

In our study, upstream movements by *Macrobrachium*, other shrimps (used as prey), and predatory fishes, such as mountain mullet (*Agonostomus monticola)* and eels (*Anguilla rostrata*), during their amphidromous life cycles probably are influenced directly by the drainage network structure. Migrations are especially vulnerable when barriers to movement are created by drying out of waterfalls and pools during drought and when constrained channels are subjected to scour during high-flow events. Adult *Macrobrachium* can migrate short distances along dry channels (APC, personal observation), but they generally are found in deep pools where risk of bird and crab predation is minimized. Probable barriers to upstream migration include high waterfalls, shallow reaches, intermediate waterfalls that dry out during droughts, and very steeply sloped channels. *Macrobrachium* also are influenced indirectly by hydrogeomorphic controls on substrata that control pool depths and cover (such as crevices among cobble or under boulders).

However, flow-based events such as prolonged droughts limit access to upper sections of river drainage networks (Covich et al. 2003). These low-water periods that affect stream ecosystems can alter freshwater decapod assemblages by reducing flow velocities required for filter feeding (Covich et al. 2000, Crowl et al. 2001, 2002) and chemical communication among prey regarding the upstream presence of their predators (Crowl and Covich 1994). Floods can either slow upstream movement because of wash-out or enhance upstream migration through inundation of waterfalls, low dams, and various geomorphic barriers. Topologies of lengths of channel within a stream can differ in ways that reflect heterogeneity of terrain, locations of waterfalls, and drainage network development over time. Thus, the locations of barriers within a drainage network influence migratory pathways for all amphidromous species.

Upstream migration

Our observations on *Macrobrachium* distributions clearly are influenced by the size selectivity of our traps. This type of trap is widely used to sample smaller organisms, and our sampling methods were designed initially to monitor the abundant, smaller shrimp species (*Atya lanipes* and *Xiphocaris elongata*) in the stream. Thus, the low numbers of large individuals and the very low % of gravid females (0.1%) is probably a result of our methods rather than a consequence of habitat selection.

However, the distribution of *Macrobrachium* we observed by trapping shrimp in headwater pools may reflect the presence of large numbers of juveniles migrating upstream from the estuary, especially in July. These mostly small, nongravid juveniles may use the headwaters as refugia from predation. As juveniles move upstream and grow, they are subject to predatory fishes at lower elevations. Some fresh- and brackish-water crabs (e.g., *Sarsama* spp.) also are found at lower elevations (APC, personal observation). Small crabs and other predators may feed on *Macrobrachium* post-larvae close to the channel edges during upstream migrations. Once the post-larvae of *Macrobrachium* move upstream and climb above high waterfalls, these small individuals are exposed to invertebrate predation by other freshwater crabs (*Epilobocera sinuatifrons*) and other shrimp (larger *Macrobrachium*) (Zimmerman and Covich 2003).

Many tropical freshwater species (decapods, gastropods, gobiid fishes) have amphidromous life cycles that require upstream migrations over long distances from estuaries (Benstead et al. 2000, Fievet and Eppe 2002, Pyron and Covich 2003, Benbow et al. 2004). Post-larvae and juveniles climb steep slopes and high waterfalls that are barriers to predatory fishes. This migration is often nocturnal, but some individuals move along the channel during the day, especially in shallow, turbid waters. Once above steep waterfalls, post-larvae and juveniles occupy spatial refugia that minimize exposure to fish predators during juvenile growth and adult reproduction.

Macrobrachium diets include a wide range of live and dead plants and animals (Covich and McDowell 1996, Mantel and Dudgeon 2004a, b). This broad feeding niche allows these omnivores to be widely distributed within upper tributaries of coastal drainages even when availability of their primary food resources (invertebrates and microbially conditioned leaf litter) is disrupted by disturbances. *Macrobrachium* abundance might be expected to be greater in large deep pools at low elevations closer to the estuaries because small shallow pools that are vulnerable to desiccation and wash-out of food are often located at high-elevations. However, we cannot distinguish between effects of elevation and effects of pool size because these variables are highly correlated.

We conclude that locations of steep waterfalls within river drainages are a key variable for better understanding of how food webs are assembled and function in complex terrain. Drying out of pools and waterfalls during prolonged drought can create barriers for migratory species. These hydrologic barriers may become more frequent occurrences in tropical rainforest streams if climate changes increase drought frequency (Larsen 2000, Giannini et al. 2001, Covich et al. 2003). Furthermore, human populations have grown, and larger populations already require more access to fresh water, challenging planners to provide sufficient water for both people and riverine species. The future distribution of *Macrobrachium* spp. throughout its biogeographic range is dependent upon continued access to a network of pools above waterfalls that persist during prolonged droughts. These spatial refugia are important components for inclusion in protected riparian corridors and for restoration of impaired stream habitats. If riverine habitats and populations of native freshwater species are to be sustained, future decisions regarding where to locate water diversions, build new dams, or remove old dams must consider drainage network attributes. Protection of key upstream habitats and connectivity with downstream habitats within the context of specific geomorphic features are essential for conservation of these widely distributed decapods (Jayachandran 2001).

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