Effects of extreme low flows on freshwater shrimps in a perennial tropical stream

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SUMMARY

1. Long-term data on rainfall suggests that perennial rainforest streams rarely are subject to drying of riffles or pools in the wet, non-seasonal Caribbean climate of Puerto Rico. Unusually low rainfall in 1994 caused some headwater riffles to dry out completely, resulting in isolated pools, reduced pool volumes and loss of access to microhabitats by benthic invertebrates.

2. From 1992 to 1998, shrimp populations were sampled bimonthly using baited traps in six pools along 1200 m (from 305 to 480 m in altitude) of Quebrada Prieta, a second-order headwater stream in the Luquillo Experimental Forest (Caribbean National Forest).

3. Following contraction of the smaller and shallower pools in the most upstream section of the stream, mean densities of the dominant shrimp (*Atya lanipes*) increased from 22 to 75 shrimp m^{-2} of pool area during the 1994 drought year. A second common species (*Xiphocaris elongata*) increased from 5 to 14 shrimp m^{-2}. A smaller percentage of adults of both species was gravid during the drought.

4. Following the 1994 drought (1995–1998), densities of both shrimp species and reproductive activity of *Atya* returned to predrought (1990–1993) levels. However, the reproductive activity of *Xiphocaris* remained lower than in the predrought period.

5. It is suggested that prolonged droughts, even in tropical rainforest biomes, may significantly alter aquatic communities through localised crowding effects resulting from habitat contraction, and lead to prolonged decreases in reproductive output. Consequently, major alterations in aquatic populations and communities would be predicted by current climate change scenarios of decreased total rainfall and increased variability.

Keywords: atyidae, drought, habitat contraction, pool morphology, reproduction, tropical streams

Introduction

The relationship between stream flow variability and benthic communities is a major area of study in temperate-zone ecosystems (Stanley, Fisher & Grimm, 1997; Hart & Finelli, 1999). Because the time intervals between both flood and drought events are often highly variable, it is important to know the time since the last extreme event to understand the biotic responses to these disturbances. Although much work has been focused on floods, comparatively little research has examined the importance of relatively infrequent and extremely low flows, in determining benthic community responses (Giller, 1996; Lake, 2000; Magoulick, 2000). In part, this lack of research reflects the difficulty in predicting when and where a drought is likely to occur. Floods are usually discrete and relatively short-term events, while extremely low flows can persist for months or years and are likely to be ramp rather than press or pulse disturbances (Lake, 2000, 2003).

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It is important to consider the duration as well as magnitude and intensity of this type of disturbance (Dracup, Lee & Paulson, 1980; Humphries & Baldwin, 2003). Dry periods often alter species distributions on an annual basis in many Neotropical headwater streams where discharge is usually seasonal (Chapman & Kramer, 1991; Rincon & Cressa, 2000). However, effects of protracted low flows or drought along altitudinal gradients in non-seasonal rainforests are rarely reported. These small headwater streams are critical habitats for species of decapods, gastropods and fishes that migrate upstream from coastal estuaries (Covich & McDowell, 1996; Benstead *et al.*, 1999; Benstead, March & Pringle, 2000). Physical characteristics, such as minimum flows, strongly influence these upstream movements and the biotic distributions within the whole drainage network (Crowl & Covich, 1994; Johnson & Covich, 2000; Scatena & Johnson, 2001). Some immediate effects of high flows on decapod communities (Covich *et al.*, 1991, 1996; Johnson *et al.*, 1998) as well as the short-term effects of low flows on pool habitats and on abundance of freshwater shrimp (Covich *et al.*, 1998; Covich, Crowl & Scatena, 2000) have been documented previously.

This study reports the first long-term data on responses by freshwater shrimps to a prolonged drought and their return to predrought densities along an altitudinal gradient in a Puerto Rican headwater stream. The effects of an extreme low-flow period on the densities, sizes, and reproductive activity of the two species of freshwater shrimps that dominate the benthic community of this headwater stream are described. We tested the hypothesis that the increase in density of the shrimp during the low-flow period would be greatest in upper-altitude pools because of greater loss of pool habitat relative to lower-altitude pools. It was further hypothesised that filter feeding by *Atyid* shrimp would be reduced or eliminated during drought periods as a result of extremely low flows and high shrimp densities, thereby decreasing reproduction.

Methods

Study site

Quebrada Prieta is a second-order tributary that begins at 550 m altitude and flows into Quebrada Sonadora at 310 m altitude, a major tributary of the Rio Espiritu Santo in the Luquillo Experimental Forest (Caribbean National Forest), northeastern Puerto Rico (18°18′N, 65°47′W). This site is a United Nations Biosphere Reserve and under intensive study by the US National Science Foundation's Long Term Ecological Research Program (see Scatena, 1995; Covich & McDowell, 1996 for further descriptions). The steeply sloped stream channel is cobble and boulder-lined with variable amounts of sediments from bank erosion and landslides. Water temperatures range annually between 20 and 26 °C. Mean annual precipitation is 3600 mm year^{-1} with rain generally distributed throughout the year, with peaks in May–June and September–November, although total annual rainfall is highly variable among years (Garcia-Martino *et al.*, 1996; Larsen, 2000). Stream discharge, measured from a nearby gauge (U.S. Geological Survey station 50063440) on the Quebrada Sonadora, is also typically highly variable with short periods of seasonally low-flow (Scatena & Johnson, 2001). The 1994 drought was characterised regionally by several months of record-low flows of the Luquillo Experimental Forest (U.S. Geological Survey, 1995). The Rio Espiritu Santo had the lowest flow in 28 years. Eight species of decapods occur in the stream, although the total number of species varies among years. The decapod community is consistently dominated by two abundant species of shrimp and these species are the focus of the present study.

Sampling

Distributions and abundance of shrimps in six pools along 1200 m of stream channel of Quebrada Prieta (from 305 to 480 m altitude) were sampled bimonthly. The pools were selected to represent: lower- (305–330 m); middle- (390–410 m); and upper- (460–480 m) altitude locations. These pools were monitored at least six times annually since 1988, as part of a Long-Term Ecological Research (LTER) monitoring programme, to determine impacts of hurricane disturbances (Covich *et al.*, 1991, 1996). Shrimps were sampled with baited wire traps that were submerged and left overnight in pools. All shrimps were removed from the traps, identified, counted, carapace length (CL) measured with calipers, reproductive status recorded and then returned to the same pools. Identifications were based on Chace & Hobbs (1969). Measured shrimp were placed into two size classes. *Atya lanipes*

Holthuis >20 mm CL and *Xiphocaris elongata* Guerin-Meneville >13 mm CL were classified as large. These size classes are based on the long-term analysis of size distributions and reproductive behaviour. If storm flows occurred during the sampling, shrimp abundance for that night was not recorded, because leaf litter typically accumulates and blocks the trap entrances during high-flow events. When such events occurred, traps were reset at least 48 h later. The maximum water depth of the sampled pools, three width measurements, a maximum length measurement, and five random depths were recorded at the time of sampling. From these data, pool area, volume and mean depth were derived.

Data analysis

To test the hypothesis that drought affected pool morphology and shrimp abundance, the six bi-monthly samples per year of both physical pool data and shrimp densities were used to compare annual means among three groups of pools. *A priori*, the two low-altitude pools were placed in one category, the two middle-altitude pools in another and the upper two pools in a third. Data from 1990 to 1993 were used as predrought years, 1994 as the drought year, and 1995–1998 as postdrought years. These categories were determined by comparing annual hydrographs across the sampling period. Data from 1988 to 1989 were eliminated from the analyses because of the effects of Hurricane Hugo, and data from 1999 were not used because of influence of Hurricane Georges. Prior to analysis of variance (ANOVA), annual means were calculated for variables representing pool morphology (maximum depth, average depth and volume) and shrimp abundances for each pool for each of the years sampled (1990–1998). In addition, the percentage of shrimp that were gravid (carrying eggs) and the percentage of shrimp that were large (see size-class description above) were calculated. Two-way ANOVAs was performed using the three altitudinal positions (lower, middle and upper) and the three time periods (pre, during and postdrought) as factors, with physical habitat variables and shrimp abundances as the response variables. Because of the unbalanced nature of the data, type-III sums of squares was used to calculate F-statistics. Prior to analyses, physical and shrimp density variables were $\log_{10}$-transformed to ensure normality and stabilise variances. Both percentage gravid and percentage large shrimp were arc-sin, square-root transformed. Following ANOVA, *post hoc* comparisons were performed using the Ryan–Einot–Gabriel–Welsch (REGWQ) test (Day & Quinn, 1989). Statistical analyses were performed using SAS 6.10 for PCs (SAS Institute Inc, 1993).

Results

Physical responses

Mean annual pool depths and volumes varied across the altitudinal gradient, but the largest reductions during the 1994 drought in mean depth and mean volume occurred in the upper-altitude pools (Fig. 1). Mean annual maximum pool depths ranged from 18 to 72 cm during the period of observation, with deeper pools occurring consistently at lower altitudes. Middle-altitude pools (located in relative level, unconfined channel reaches) remained relatively uniform in depth and volume, while lower-altitude pools (larger, deeper pools located in confined channel reaches) and high-altitude pools (smaller, shallow pools in confined channel reaches) were reduced in depth and volume during the drought.

Results from the two-way ANOVAs for the three physical response variables suggested that significant differences existed for both time period (before, during and after the drought) and spatial position along the altitudinal gradient. Pool depth was significantly different among times (df = 2,45; F = 8.2, $P < 0.05$), among altitudes (df = 2,45; F = 22.9, $P < 0.001$), but without interaction between site and time (df = 4,45; F = 0.3, $P \gg 0.05$). *Post-hoc* comparisons showed that pools in the lower and medium altitudes were not significantly different from each other but were deeper than upper-altitude pools. Pool depths were significantly lower than depths before and after the drought. Maximum pool depth was significantly different among times (df = 2,45; F = 6.8, $P = 0.05$) and among altitudes (df = 2,45; F = 39.9, $P = 0.0001$), but without interaction between site and time (df = 4,45; F = 0.4, $P \gg 0.05$). *Post-hoc* comparisons showed that the lower-altitude pools were significantly deeper than the intermediate-altitude pools, with the upper-altitude pools being much shallower. Maximum depths decreased significantly during the drought but were not different before or after the
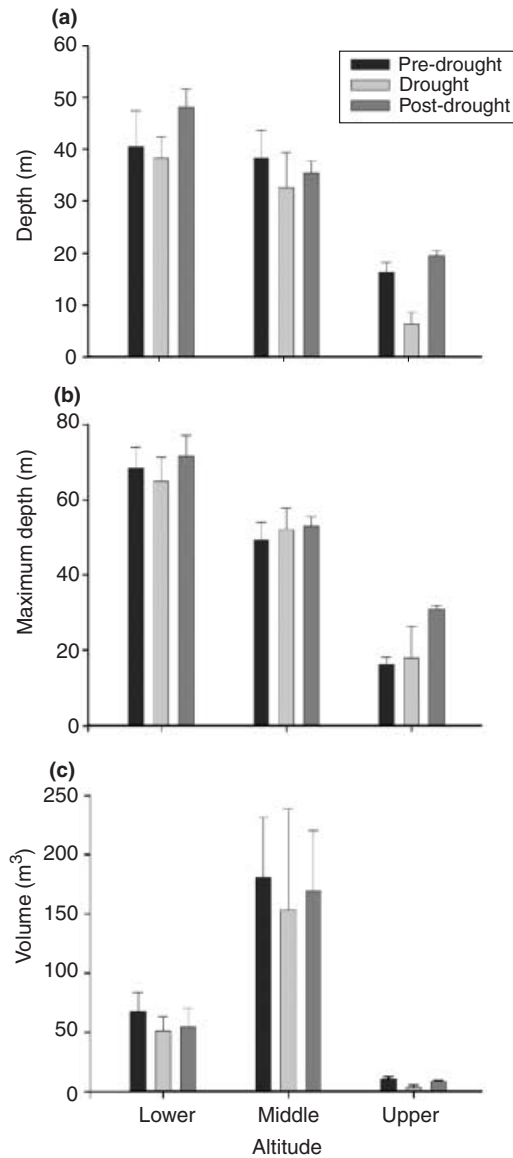
Fig. 1 Changes in (a) mean ± 1 SE depth, (b) maximum depth and (c) volume of pool habitats before, during and after the 1994 drought at lower-, middle- and upper-altitude positions in Quebrada Prieta.

Fig. 2 Changes in mean ± 1 SE densities of (a) *Atya* and (b) *Xiphocaris* in pool habitats before drought, during drought and after drought at lower-, middle- and upper-altitude positions in Quebrada Prieta.

drought. Pool volume was significantly different among times (df = 2,45; F = 3.2, P < 0.05) and among altitudes (df = 2,45; F = 6.7, P < 0.01), but without interaction between altitude and time (df = 4,45; F = 0.1, P ≫ 0.05). *Post-hoc* comparisons for pool volume suggested that pool volumes were different among the altitudes, with the largest pools at the intermediate altitudes and the smallest pools at the most upstream sites. *Post-hoc* comparisons suggested that pool volumes, unlike the other physical variables,
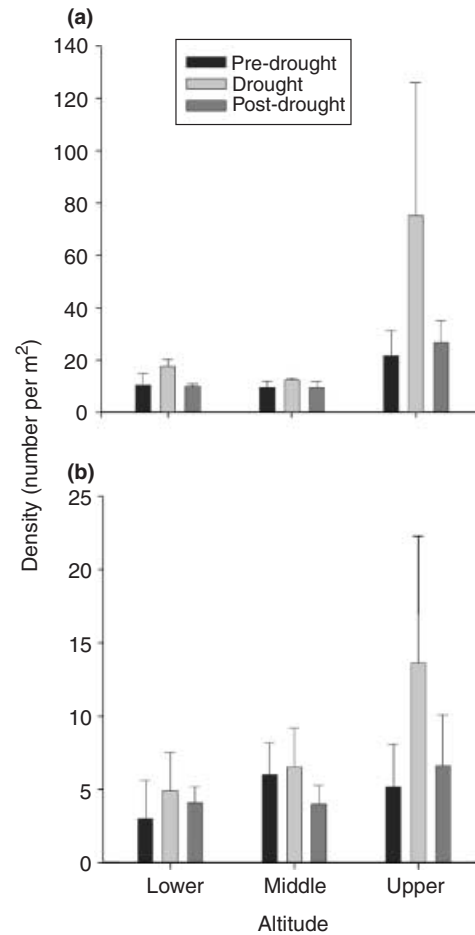
were highest before the flood, and lowest during and after the flood, but not different between these two periods.

Biotic responses

Mean densities were consistently lower for *X. elongata* than for the more abundant shrimp species, *A. lanipes*. The drought had a significant effect on densities in the upper-altitude pools (Fig. 2). Contraction of upper-altitude pool habitats resulted in increased mean densities of both *Atya* and *Xiphocaris*, with mean densities of *Atya* approximately three times higher during the drought in 1994 than before or after the drought (Fig. 2). There was a significant interaction between time and altitude on *Atya* densities
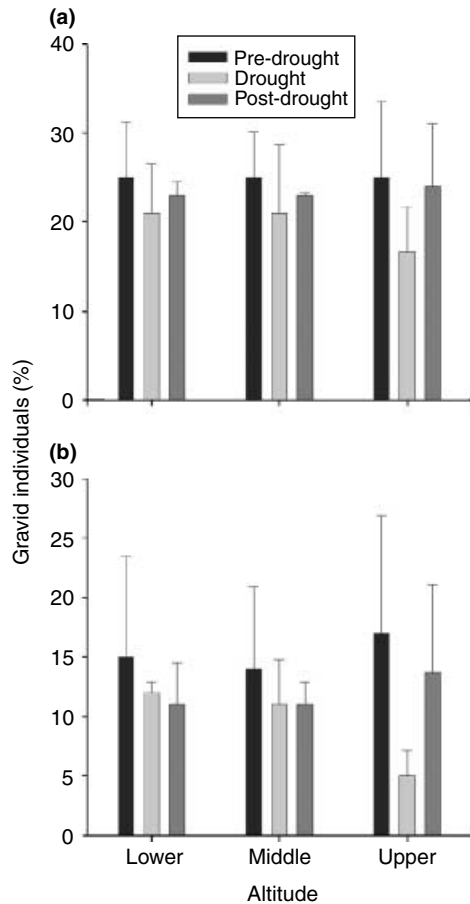
Fig. 3 Changes in mean ± 1 SE percentage of gravid (a) *Atya* and (b) *Xiphocaris* in pool habitats before drought, during drought and after drought at lower-, middle- and higher-altitude positions in Quebrada Prieta.
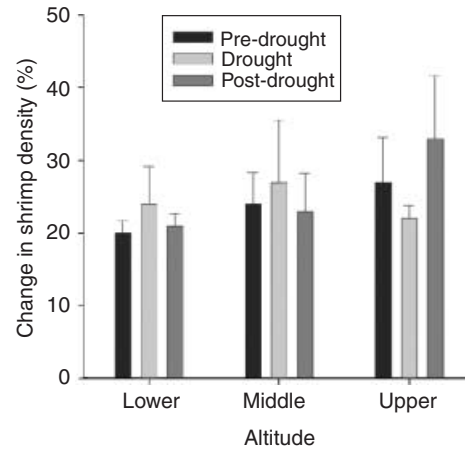

Fig. 4 Changes in mean percentage ± 1 SE of large adult shrimp in pool habitats before, during and after drought at lower-, middle- and upper-altitude positions in Quebrada Prieta.

(df = 4,45; F = 7.3; P = 0.0001). *Post-hoc* comparisons of main effects showed that *Atya* densities were highest during the drought and lowest before and after the drought. *Atya* densities were highest in the upper-altitude pools. *Xiphocaris* densities were affected by time (df = 2,45; F = 8.4; $P < 0.001$) and altitudinal position (df = 2,45; F = 4.2; $P < 0.05$), but the interaction between time and altitude was not significant (df = 4,45; F = 1.9; $P > 0.05$). *Post-hoc* comparisons showed that densities were highest during the drought. Densities were also highest in the upper-altitude pools. The percentage of gravid female *Atya* was only affected significantly by time (df = 2,45; F = 3.5; $P < 0.05$). Neither altitude (df = 2,45; F = 0.2; $P \gg 0.05$) nor the interaction between altitude and time (df = 4,45; F = 0.7; $P \gg 0.05$) affected reproduction of *Atya* (Fig. 3). *Post-hoc* comparisons showed that

the percentage of gravid females was significantly lower during the drought than before or after the drought. There was a significant interaction effect for the percentage of gravid *Xiphocaris* (df = 4,45; F = 3.2; $P < 0.01$). *Post-hoc* comparisons suggested that more females were gravid before the drought than during or after, except for the upper-altitude pools, where the percentage of reproductive females was lowest. There was also a significant time by altitude interaction for the proportion of large shrimp (df = 4,45; F = 4.5; $P < 0.01$). Before and after the 1994 drought, larger *Atya* (>20 mm CL) increased relative to smaller individuals in the upper-altitude pools but not in middle- or lower-altitude pools (Fig. 4). *Post-hoc* comparisons did not reveal any patterns.

Discussion

The hypothesis that shrimp would be most strongly affected by drought in the headwater section of Quebrada Prieta with its smaller and shallower pools, is supported by the two to three-fold increase in mean densities of both shrimp species in the upper-altitude pools. This extreme crowding resulted in decreased reproductive success of shrimps and a significant shift in the size-class distribution. During severe drought, lack of flow eliminates the option for efficient filter feedings by *Atya* as well as any possibilities for facilitation of leaf-litter processing among filter-feeding species and leaf-shredding species such as *Xiphocaris* (Crowl *et al.*, 2001). Despite their differ-

ences in feeding modes (Crowl *et al.*, 2000, 2001), both co-occurring shrimp species responded similarly in 1994, apparently because both species can consume biofilms on hard substrata and leaf detritus. Thus, drought conditions affected these shrimp both through a decrease in habitat volume and subsequent increase in crowding and decreased resource availability resulting from low-flow or ceased-flow. Both of these biotic factors result in increased competition for very limited resources, especially on a per capita basis and ultimately result in reduced reproductive outputs.

During the 1994 drought, the larger *Atya* either moved downstream or were removed by predators. Drought-induced habitat reduction and low-water level elimination of bank-side refugia were probable mechanisms accounting for decreases in abundance of *Xiphocaris*, which are consumed by predatory pala-emonid shrimp (such as *Macrobrachium carcinus* L.) in shallow pools (Crowl & Covich, 1994). Reduced volumes during the drought may have lowered access to rock crevices and undercut banks in some upper-altitude pools. These current data are insufficient for documenting the directional movements or rates of mortality from increased risks of predation that might result from habitat contraction. Documentation and evaluation of predatory effects will require controlled field studies with marked individuals rather than long-term, bimonthly monitoring. However, densities of shrimp returned relatively quickly after the drought, as pool depths increased to similar or greater values measured before the drought. This rapid response suggests either limited mortality or relocation among populations along the altitudinal positions.

Drought impacts on stream decapods will probably vary regionally as a result of different local frequencies and durations of drought occurrences (Larsen, 2000). Recurrence intervals for short-term habitat contraction in the main channels of second- and third-order tropical rainforest streams like the Queb-rada Prieta vary between 5 and 10 years, based on analyses of 30 years of rainfall data from the Luquillo Mountains (Garcia-Martino *et al.*, 1996; Larsen, 2000). The field observations suggest that riffles in main channels begin to dry out after two consecutive weeks without rain. Recurrence intervals for droughts in perennial rainforest streams may provide a basis for evaluating effects of both biotic and abiotic factors that control shrimp population dynamics over annual and decadal time scales.

Although the El Niño-Southern Oscillation (ENSO) phenomenon influences temperature and rainfall variability in the Caribbean, generally (Giannini, Kushnir & Cane, 2001), interannual fluctuations in rainfall in Puerto Rico are thought to be more controlled by the North Atlantic Oscillation (NAO) than by ENSO (Malmgren, Winter & Chen, 1998). These major fluctuations may stress both the natural riverine and human populations. Moreover, rapid growth of human populations may cause stream communities to become even more vulnerable. Diversions and storage of stream waters for increasing human use can exacerbate the natural periods of diminished flows by making low-water periods more persistent and further decreasing migratory populations that have linked estuarine and riverine life histories (Benstead *et al.*, 1999, 2000; Pringle, Freeman & Freeman, 2000). The many connections between biotic interactions and climate-driven variability in discharge are most likely to be increasingly important as human populations continue to grow and demand more fresh water, especially if extreme droughts increase in frequency (Covich, Palmer & Crowl, 1999). These combined effects will decrease minimal levels of discharge needed to maintain populations of many riverine species. Extended periods of extreme low flows will likely result in lower levels of dissolved oxygen and longer residence times of excessive nutrients and toxins.

Acknowledgments

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