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Factors affecting fish assemblage structure during seasonal stream drying

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Abstract – We evaluated fish assemblage structure during stream drying in north west Arkansas in 2002 and 2003. We sampled fish with a seine and backpack electrofisher and measured habitat variables along transects. Linear regression models were selected *a priori* and ranked according to Akaike's Information Criterion. In 2002, total fish density was negatively related to pool area and maximum depth, and positively related to canopy openness and substrate diversity. Similarly, central stoneroller (*Campostoma anomalum*, Rafinesque) and creek chub (*Semotilus atromaculatus*, Mitchill) densities were negatively related to maximum pool depth. In 2003, fish species richness was positively related to pool area whereas total fish, central stoneroller, and creek chub densities were negatively related to maximum pool depth. In addition, total fish density was negatively related to substrate diversity. Results indicated that physical factors are important predictors of fish assemblage structure during stream drying. However, differences among response variables between years indicated that the magnitude of stream drying might be critical in intermittent streams.

Introduction

Although flooding is a well-studied and important phenomenon, less is known concerning the role of drought in stream dynamics (Lake 2000; but see Matthews & Marsh-Matthews 2003). In many regions around the world, seasonal drying reduces streams to intermittent pools that often persist and provide refuge to biota. During isolation, aquatic organisms in stream pools can be exposed to harsh abiotic and biotic factors because of drying, lack of flow and increased vulnerability to predation (Larimore et al. 1959; Magoulick & Kobza 2003). However, the importance of these factors in drying streams is not clearly understood. In particular, relatively little is known about the effects of drought on fish at larger spatial and temporal scales (Matthews & Marsh-Matthews 2003).

Even though stream drying is a harsh event, organisms in intermittent streams have adapted to, and are tolerant of, these conditions (Resh et al. 1988; Magoulick & Kobza 2003). Resh et al. (1988) defined disturbance as an event characterised by a frequency, intensity and severity outside of the normal range. By this definition, stream drying should not be considered a disturbance unless drought conditions persist for longer than average periods of time. Consequently, predictable stream drying may not directly kill tolerant fish species.

Previous research in intermittent stream systems has emphasised the role of abiotic factors in structuring fish assemblages. Capone & Kushlan (1991) reported relationships between physical habitat variables and species richness, species composition, fish size and fish density in dry-season stream pools in north east Texas. Three fish assemblage groups in pools were best discriminated using the variables days wet, average depth, maximum depth, pool area and bank height. Similarly, Magoulick (2000) demonstrated a relationship between local abiotic factors and fish assemblage structure in dry-season stream pools in north west Arkansas. Total density of large (≥80 mm total length, TL) fish, density of large central

stonerollers and density of small (<80 mm TL) sunfish (*Lepomis cyanellus*, Rafinesque; *Lepomis megalotis*, Rafinesque and *Micropterus dolomieu*, Lacépède) each was consistently and positively related to pool depth. These findings support the hypothesis that physical factors are important in structuring fish assemblages in variable or harsh environments (Grossman et al. 1998).

We hypothesised that physical habitat variables would be important predictors of fish assemblage structure during stream drying. Therefore, we used abiotic variables to build predictive models for species richness and fish density in drying stream pools. Unlike many studies investigating assemblage structure during a single sampling occasion per year, our study investigated changes in assemblage structure associated with stream drying in a repeated measures design. Understanding these relationships will provide insight into the importance of abiotic factors in streams with intermittent flow as well as evaluate the recolonisation potential for individual pools in seasonally drying streams.

Study area

We conducted the study on Haw (93°17′07″W, 35°39′22′N), Hurricane (93°09′33″W, 35°46′12″N) and Indian (93°08′11″W, 35°40′19″N) creeks located in the Boston Mountains Ecoregion of north west Arkansas, USA. The streams were moderate-gradient tributaries of Big Piney Creek in the Arkansas River Drainage Basin. Streams were characterised by riffle-pool morphology dominated by bedrock and gravel substrates (Shackleford 1987). Pool volume ranged from 9.2 to 226.3 m^3 and maximum depth ranged from 0.32 to 1.75 m during the sampling period in 2002 and 2003. Conductivity ranged from 45 to 145 μS·cm^{-1} and stream temperatures were variable during the sampling period in 2003 (Haw Creek mean = 22.1 °C and range = 13.8–31.0 °C, Hurricane Creek mean = 20.5 °C and range = 14.6–28.3 °C, Indian Creek mean = 22.5 °C and range = 10.6–32.0 °C).

Methods

We sampled at monthly intervals during periods of stream drying on 12–16 August, 10–15 September and 20–29 October in 2002. Because of an earlier drying period in 2003, we sampled on 20–24 July, 18–21 August and 18–22 September. The study reaches were selected based on access to areas with similar watershed size that exhibited stream drying and pool isolation. Seventeen pools were sampled during 2002, including two pools in each of Haw and Hurricane creeks and 13 pools in Indian Creek. To increase sample size, we sampled the same pools in 2003, and added three pools in Haw Creek, and two pools in Hurricane Creek.

A three-person team conducted removal sampling in pools with two downstream seine passes (6-mm mesh), followed by one upstream backpack electrofisher pass in 2002, and two upstream electrofisher passes in 2003. The additional backpack electrofisher pass during 2003 was necessary to increase sampling efficiency and improve abundance estimation (described below). We used a Smith-Root model 12-B electrofisher operated at a frequency of 60 Hz, with direct pulse duration of 8 ms, and ranging in voltage from 300 to 500 V. Although some pools had minimal flow across drying riffles, block nets were used to prohibit movements of fish during sampling. We held fish in separate buckets for each pass prior to processing. Fish were identified to species and placed in 10-mm (TL) size categories.

We calculated the following assemblage response variables for every pool: species richness, total fish density, central stoneroller density and creek chub density. These species were selected because of their abundance and representation of different feeding guilds. To reduce the frequency of zero values in our data, no attempt was made to divide the fish assemblage data into size categories. We used program SPECRICH (Hines et al. 1999) to estimate species richness for every pool using total catch data from two seine passes and either the single electrofisher pass in 2002, or the two electrofisher passes in 2003. This method calculates species richness from species count data using a jackknife estimator (Burnham & Overton 1979), which accounts for heterogeneity in detection probabilities among species. Fish densities were calculated by dividing abundance estimates by the corresponding pool volumes. Fish abundance was calculated as the total catch for the single electrofisher pass and the two seine passes in 2002. In 2003, we estimated fish abundance by the Zippin (1956) removal method for the two electrofisher passes in program MARK (White & Burnham 1999). All response variables, excluding species richness, were inverse-square-root transformed to satisfy normality and equal variance assumptions (Sokal & Rohlf 1995). All results, including model selection and parameter estimates, are presented in terms of transformed data. However, the direction of the relationship is presented after back transforming the data because of the reversing effect of reciprocal transformations. For example, positive coefficients derived from transformed data indicate negative associations among raw data.

Habitat variables were collected systematically along cross-stream transects placed at 3-m intervals, and with a minimum of five transects per pool. We

recorded pool depth and substrate categories at three equidistant points along each transect. Substrate categories followed a modified Wentworth scale (Cummins 1962), but we added a bedrock category and merged silt with sand (0.0039–2 mm), gravel (>2–16 mm), pebble with cobble (>16–256 mm) and boulders (>256 mm). The degree of canopy openness was calculated by summing the two angles measured using a clinometer from the centre point of each transect to the top of the canopy on each bank and subtracting from 180°. In addition, pool length, width and maximum depth were recorded. We measured the following abiotic predictor variables for each pool: area, maximum depth, mean canopy openness, per cent undercut bank, the relative percentages of pool substrate and the Simpson's diversity index for pool substrate composition (Magoulick 2000). Temperature loggers (Onset Corp. StowAway Loggers Pocasset, MA, USA) were deployed at the uppermost and lowermost pools on each stream for the duration of the study in 2003 to estimate the range and mean stream temperature from recordings made twice hourly. Finally, discharge data were obtained from a gauging station (USGS gauge 07257006, USGS 2007) downstream on Big Piney Creek.

Relationships between fish assemblage response variables and predictor variables over the three sampling occasions were evaluated by simple- and multiple-linear regression in a repeated measures design (Littell et al. 1996). Prior to this analysis, we defined a set of seven candidate models for each assemblage variable. The models represented *a priori* hypotheses and biologically important relationships. In general, we selected pool dimension variables to represent pool persistence, and canopy openness as a potential index of primary productivity. Finally, we selected habitat substrates and per cent undercut bank as potential cover variables, and substrate diversity for pool complexity. We limited the models to combinations of four variables because of low sample size. In addition, the candidate model set included a global model that incorporated all possible variables and selected interactions. After we determined that the global models fitted the data, based on analysis of the residuals, we selected the best models using Akaike's Information Criterion adjusted for small sample size (AIC$_c$, Burnham & Anderson 2002). All statistical analyses were performed by maximum likelihood in SAS PROC MIXED (SAS Institute 1999).

With this approach, models were ranked by the difference between the lowest AIC$_c$ value and each remaining AIC$_c$ value (ΔAIC$_c$). In addition, we calculated the relative likelihood of each model, or Akaike weight (w_i), and the relative likelihood of a model over the best model using the evidence ratio (w_1/w_i, Burnham & Anderson 2002). The best model

has an evidence ratio of one and increasing ratio values indicate decreasing likelihood. For example, a model with a ratio of 10 is 10 times less likely than the best model and is not well supported. In general, ratios <8 show strong relative support for the models (Royall 1997). After selecting the best models, we examined the 95% confidence intervals (CI) around the partial coefficient (PC) estimates to determine the direction and magnitude of the relationship between the predictor and response variables.

In addition to model selection, we used AIC$_c$ values to select the appropriate covariance structures for the global models (Littell et al. 1996). We made no attempt to group the 2002 and 2003 data because of the variation in sampling regimes. We selected a first-order factor analysis structure for species richness in 2002, and a compound symmetry structure for species richness in 2003. The first-order factor analysis has six parameters modelling specific variances. The compound symmetry structure has two parameters that model a homogeneous variance and a constant correlation (Littell et al. 1996). In terms of total fish density, we selected a compound symmetry structure in 2002, and a first-order autoregressive structure in 2003. The autoregressive structure has two parameters that model a homogeneous variance with an exponentially declining correlation (Littell et al. 1996). Similarly, central stoneroller density incorporated a compound symmetry structure in 2002, and a first-order autoregressive structure in 2003. In terms of creek chub density, we selected a first-order autoregressive structure in both 2002 and 2003. After the covariance structures were selected, they were applied to all models embedded within the global models.

Results

Environmental variables differed among streams and between years (Table 1). In 2002, daily discharge was >51-year average in July and August, and then dropped below average in September and October, whereas discharge was consistently less than average during 2003 (Fig. 1). At the pool scale, volumes varied and were lowest during the middle sampling occasion in 82% and 68% of the pools in 2002 and 2003, respectively (Fig. 2). In contrast, abundance estimates varied with no pattern among monthly sampling occasions (Fig. 2). The volume and abundance results produced density estimates that were highest during the middle sampling occasion in 47% and 55% of the pools in 2002 and 2003, respectively (Fig. 2). A total of 14,135 fish was collected during the study representing 22 fish species.

Species richness varied among monthly sampling occasions and between years (Fig. 3). Model selection results for species richness were inconclusive in 2002

Table 1. Means (standard error) of abiotic predictor variables used in the 2002 ($N = 51$) and 2003 ($N = 66$) fish assemblage regression analyses. Measurements are in metres, except for canopy openness is in degrees. Substrate categories are in decimal fractions relative to the total substrate counts.

| Variable	Haw		Hurricane		Indian	
	2002	2003	2002	2003	2002	2003
Mean width	6.78 (0.60)	5.39 (0.49)	8.28 (1.14)	8.23 (0.58)	6.40 (0.27)	6.13 (0.28)
Mean depth	0.31 (0.05)	0.26 (0.04)	0.22 (0.03)	0.20 (0.02)	0.37 (0.02)	0.33 (0.02)
Maximum depth	0.58 (0.04)	0.72 (0.11)	0.53 (0.09)	0.56 (0.04)	0.88 (0.05)	0.85 (0.04)
Area	300.48 (53.65)	185.75 (25.61)	321.24 (56.60)	356.05 (28.93)	232.70 (19.76)	221.53 (18.72)
Volume	101.22 (27.36)	46.97 (7.56)	79.01 (21.99)	75.96 (11.85)	85.49 (8.54)	75.34 (8.31)
Canopy openness	17.04 (5.37)	18.68 (2.97)	59.96 (5.46)	45.56 (3.74)	24.81 (1.39)	28.12 (1.24)
Undercut bank	0.01 (0.01)	0.02 (0.01)	0.00 (0.00)	0.02 (0.01)	0.16 (0.03)	0.12 (0.03)
Silt and sand	0.13 (0.05)	0.07 (0.02)	0.00 (0.00)	0.01 (<0.01)	0.02 (0.01)	0.03 (<0.01)
Gravel	0.18 (0.04)	0.22 (0.04)	0.07 (0.03)	0.12 (0.02)	0.23 (0.02)	0.26 (0.02)
Pebble and cobble	0.06 (0.01)	0.10 (0.02)	0.05 (0.02)	0.09 (0.03)	0.29 (0.03)	0.28 (0.02)
Boulder	0.06 (0.02)	0.08 (0.02)	0.03 (<0.01)	0.11 (0.02)	0.28 (0.03)	0.28 (0.02)
Bedrock	0.56 (0.02)	0.53 (0.05)	0.84 (0.06)	0.67 (0.05)	0.17 (0.04)	0.16 (0.03)
Substrate diversity	2.55 (0.14)	2.54 (0.20)	1.48 (0.19)	2.18 (0.23)	2.97 (0.11)	3.04 (0.09)
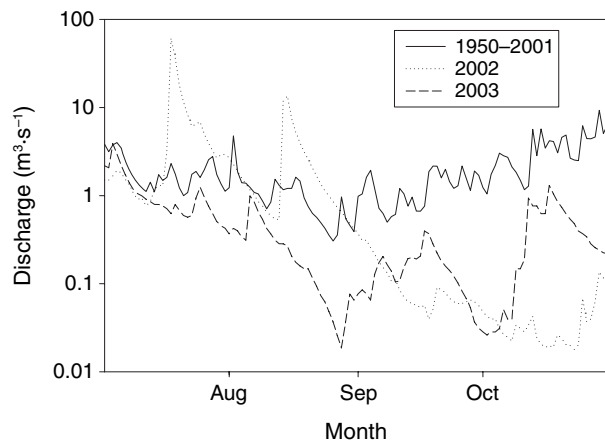
Fig. 1. Daily discharge in Big Piney Creek downstream from the study area in 2002, 2003 and 1950 to 2001 mean. Months were selected to represent the stream drying and sampling periods.

(Table 2). There were six plausible models with evidence ratios <8. In addition, the parameter estimates for the six plausible models were too imprecise to be conclusive. In 2003, the regression model containing area as a predictor was the only strongly supported model; it was approximately 86 times more likely than the next best-fitting model. The area model demonstrated a significant positive relationship with species richness (PC = 0.02 and CI: 0.01–0.03).

Similar to species richness, results were inconclusive for total fish density in 2002 (Table 3). There were five plausible models with evidence ratios <8 including the canopy, maximum depth and global models. In addition, there was support for the canopy and area models, including and excluding the interaction term. The maximum depth and global models demonstrated a negative relationship between back transformed total fish density and maximum depth

with PC estimates of 0.69 (CI = 0.19–1.19) and 0.62 (CI = 0.14–1.10), respectively. In addition, the global model demonstrated a positive relationship between total fish density and canopy openness (PC = −0.02 and CI = −0.03–0.00) and a positive relationship with substrate diversity (PC = −0.18 and CI = −0.35–0.00). Finally, the canopy and area model with no interaction demonstrated a weak negative relationship with back transformed total fish density and area (PC = 0.001 and CI = 0.000–0.002) and a positive relationship with canopy (PC = −0.01 and CI = −0.02–0.00). In 2003, the best regression model for total fish density was that containing maximum depth as the predictor variable and the global model. The depth model demonstrated a negative relationship between maximum depth and back transformed total density (PC = 0.91 and CI = 0.67–1.14). Similarly, the global model demonstrated a negative relationship between depth and density (PC = 0.85 and CI = 0.65–1.05) and a negative relationship between density and substrate diversity (PC = 0.15 and CI = 0.06–0.25).

In 2002, plausible models for predicting central stoneroller density included the canopy and maximum depth model with no interaction and the individual canopy and maximum depth models (Table 4). However, only the depth estimates were significant indicating a negative relationship between back transformed central stoneroller density and maximum depth. PC estimates for maximum depth were 1.38 (CI = 0.04–2.72) for the two-predictor model and 1.59 (CI = 0.22–2.95) for the maximum depth model. In 2003, the maximum depth model and the canopy and maximum depth model excluding the interaction best predicted central stoneroller density. Parameter estimates demonstrated a negative relationship between density and maximum depth for both the two-parameter model (PC = 1.79 and CI = 0.98–2.59) and the
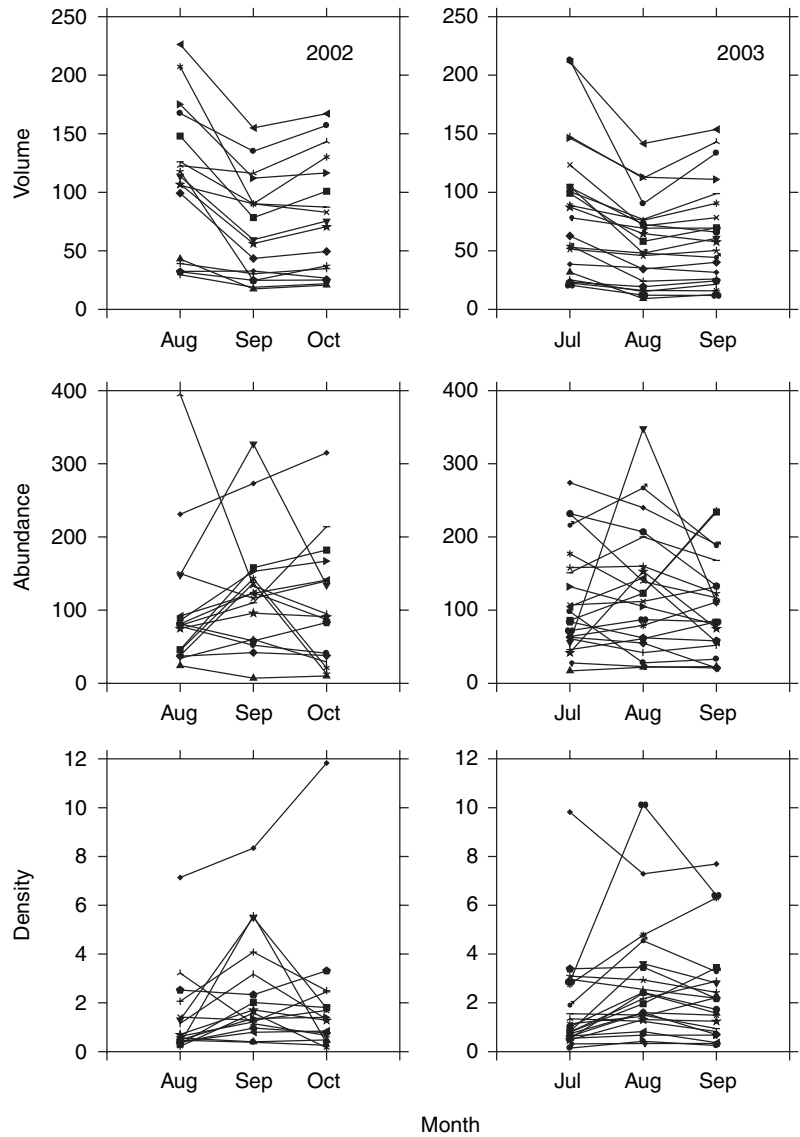
Fig. 2. Repeated measures of pool volume (m^3), total fish abundance (number of individuals) and density (abundance·*volume*$^{-1}$) in 2002 and 2003 (symbols represent individual pools).
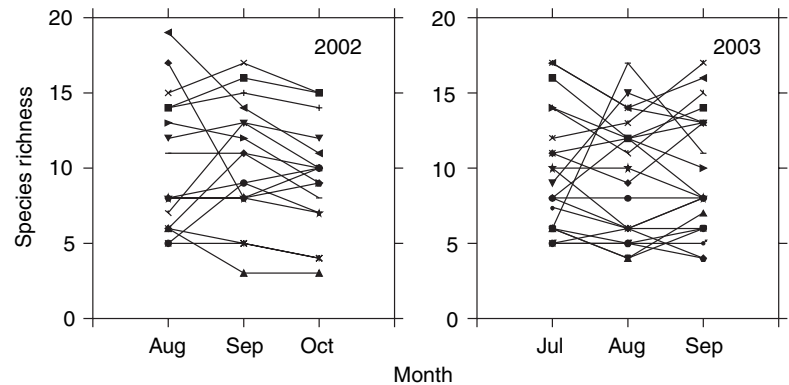

Fig. 3. Repeated measures of species richness in 2002 and 2003 (symbols represent individual pools).

maximum depth model (PC = 1.77 and CI = 0.98–2.56).

Similar to the previous fish assemblage variables, creek chub density showed a consistent relationship between years. The model incorporating maximum depth best predicted creek chub density in both 2002 and 2003 (Table 5). In addition, the relationships between back transformed creek chub density and

Table 2. Model selection in a repeated measures linear regression of habitat variables against species richness in 2002 ($N = 51$) and 2003 ($N = 66$). The global model incorporates all variables and the single interaction.

Model	$-2 \log(L)$	No. of parameters	Δi†	Akaike weight (w_i)	Evidence ratio (w_1/w_i)
2002					
Area	238.4	10	0	0.28	1.00
Simpson	238.9	10	0.5	0.22	1.28
Boulder	239.5	10	1.1	0.16	1.73
MaxDepth	239.7	10	1.3	0.15	1.92
MaxDepth* Simpson	236.6	12	1.5	0.13	2.12
MaxDepth, Simpson	238.8	11	3.6	0.05	6.05
Global	234.2	14	6.1	0.01	21.12
2003					
Area	311.3	6	0	0.99	1.00
Global	309.6	10	8.9	0.01	85.63
Simpson	328.4	6	17.1	0.00	>1000
MaxDepth	328.8	6	17.5	0.00	>1000
Boulder	329.0	6	17.8	0.00	>1000
MaxDepth, Simpson	328.3	7	19.5	0.00	>1000
MaxDepth* Simpson	328.0	8	21.9	0.00	>1000

†2002 minimum $AIC_c = 263.9$; 2003 minimum $AIC_c = 324.7$.
AIC, Akaike's Information Criterion.

Table 3. Model selection in a repeated measures linear regression of habitat variables against inverse-square-root total fish density in 2002 ($N = 51$) and 2003 ($N = 66$). The global model incorporates all variables and the single interaction.

Model	$-2 \log(L)$	No. of parameters	Δi†	Akaike weight (w_i)	Evidence ratio (w_1/w_i)
2002					
MaxDepth	35.8	6	0.0	0.44	1.00
Canopy, Area	34.4	7	1.3	0.23	1.92
Global	26.3	10	2.1	0.15	2.86
Canopy* Area	34.1	8	3.9	0.06	7.03
Canopy	39.7	6	3.9	0.06	7.03
Area	40.4	6	4.6	0.04	9.97
Simpson	42.9	6	7.2	0.01	36.60
2003					
MaxDepth	−14.5	6	0.0	0.52	1.00
Global	−24.9	10	0.2	0.48	1.11
Simpson	12.2	6	26.7	0.00	>1000
Area	13.3	6	27.8	0.00	>1000
Canopy	14.8	6	29.3	0.00	>1000
Canopy, Area	13.1	7	30.1	0.00	>1000
Canopy* Area	13.1	8	32.7	0.00	>1000

†2002 minimum $AIC_c = 49.7$; 2003 minimum $AIC_c = -1.1$.
AIC, Akaike's Information Criterion.

Table 4. Model selection in a repeated measures linear regression of habitat variables against inverse-square-root central stoneroller density in 2002 ($N = 51$) and 2003 ($N = 66$). The global model incorporates all variables and the single interaction.

Model	$-2 \log(L)$	No. of parameters	Δi†	Akaike weight (w_i)	Evidence ratio (w_1/w_i)
2002					
MaxDepth	133.4	6	0.0	0.53	1.00
Canopy, MaxDepth	132.4	7	1.7	0.23	2.34
Canopy	136.7	6	3.3	0.10	5.21
Canopy* MaxDepth	132.4	8	4.5	0.06	9.49
Undercut	138.5	6	5.1	0.04	12.81
Boulder	138.6	6	5.2	0.04	13.46
Global	131.9	10	10.1	0.00	156.02
2003					
MaxDepth	119.2	6	0.0	0.72	1.00
Canopy, MaxDepth	119.2	7	2.4	0.22	3.32
Canopy* MaxDepth	119.2	8	5.0	0.06	12.18
Global	117.2	10	8.5	0.01	70.11
Boulder	134.8	6	15.5	0.00	>1000
Canopy	136.5	6	17.2	0.00	>1000
Undercut	136.5	6	17.2	0.00	>1000

†2002 minimum $AIC_c = 147.3$; 2003 minimum $AIC_c = 132.7$.
AIC, Akaike's Information Criterion.

Table 5. Model selection in a repeated measures linear regression of habitat variables against inverse-square-root creek chub density in 2002 ($N = 51$) and 2003 ($N = 66$). The global model incorporates all variables and the single interaction.

Model	$-2 \log(L)$	No. of parameters	Δi†	Akaike weight (w_i)	Evidence ratio (w_1/w_i)
2002					
MaxDepth	130.8	6	0	0.80	1.00
Global	123.4	10	4.2	0.10	8.17
Boulder	136.9	6	6.2	0.04	22.20
Canopy	137.5	6	6.8	0.03	29.96
Undercut	137.5	6	6.8	0.03	29.96
Boulder, Undercut	136.9	7	8.8	0.01	81.45
Boulder* Undercut	134.8	8	9.6	0.01	121.51
2003					
MaxDepth	139.7	6	0	0.98	1.00
Global	136.9	10	7.8	0.02	49.40
Undercut	157.0	6	17.3	0.00	>1000
Boulder	157.0	6	17.4	0.00	>1000
Canopy	157.1	6	17.4	0.00	>1000
Boulder* Undercut	154.0	8	19.4	0.00	>1000
Boulder, Undercut	156.9	7	19.8	0.00	>1000

†2002 minimum $AIC_c = 144.7$; 2003 minimum $AIC_c = 153.1$.
AIC, Akaike's Information Criterion.

maximum depth were negative in both years (2002: PC = 1.63 and CI = 0.50–2.76; 2003: PC = 2.13 and CI = 1.31–2.95).

Discussion

Fish assemblage structure in Haw, Hurricane and Indian creeks was related to physical factors. Important abiotic factors were pool area, maximum depth, canopy openness and substrate diversity. However, the relative importance of these factors varied among species and between years. Species richness was positively related to pool area in 2003, but this was not the case in 2002. The importance of area in 2003 may indicate that the drier conditions in that year increased the importance of abiotic factors in drying streams. In a previous study at the same sites, Magoulick (2000) demonstrated a greater relationship between local abiotic variables and fish assemblage

structure during a drought year. In the present study, we found maximum depth was a consistently good predictor of central stoneroller and creek chub densities in both 2002 and 2003.

In addition, the positive relationship between species richness and area in 2003 supports the hypothesis proposed by Schlosser (1987) that species richness should increase with increasing depth, habitat heterogeneity and temporal stability. Similarly, Capone & Kushlan (1991) reported increasing species richness with increasing pool depth, pool persistence and channel size in north east Texas streams. In contrast to the predictions regarding habitat complexity, our results provided no support for a relationship between species richness and substrate diversity. Similarly, total fish density was positively related to substrate diversity and canopy openness in 2002, but negatively related to substrate diversity in 2003. Therefore, substrate diversity may not be an adequate measure of habitat complexity as diversity does not account for the quality of different substrate types.

Biotic interactions are also important factors regulating habitat selection among species. For example, the negative relationships between fish densities and maximum depth in 2002 and 2003 may reflect avoidance of larger predatory fish. Increasing maximum depth can result in greater predation risk from larger aquatic predators (Power 1987). For example, brassy minnows (*Hybognathus hankinsoni*, Hubbs 1929) were displaced from pools into riffles in the presence of smallmouth bass in an artificial stream (Schlosser 1988). Similar predator avoidance responses have been noted in studies with central stonerollers (Power et al. 1985; Gelwick et al. 1997). In contrast, Magoulick (2000) noted that large central stonerollers were positively related to pool depth. Therefore, it is likely that smaller individuals are driving the negative relationship between central stonerollers and maximum depth in the present study. However, these results may simply indicate that fish are being congregated as pool area decreases. More research is needed to investigate the relative importance of habitat size and abundance in determining fish densities in drying pools.

Studies investigating assemblage structure also must consider sampling error. Peterson et al. (2004) reported that multipass electrofishing removal methods produced underestimates of salmonid abundance by an average of 88% in central Idaho and southwest Montana. The authors suggested that unless the first pass capture efficiency is high and successive reduction in capture efficiency is low, abundance will be seriously underestimated. Therefore, density model results in this study should be viewed with caution. Future work must incorporate variables that affect sampling efficiency, including fish size and habitat, into models that adjust abundance estimates.

This study demonstrated the dynamic relationship between fish biota and their drying stream pool refugia. In Haw, Hurricane and Indian creeks, a longer drying period in 2003 may have increased the importance of abiotic factors in stream pools. Larger pools acted as refugia for more species compared with smaller pools that were less likely to persist. Further development of models that explain variation in fish assemblage structure will be essential to the conservation of stream communities. Specifically, understanding the role of refugia in drying streams will give insight into the recolonisation potential of streams impacted by natural and anthropogenic disturbances.

Acknowledgements

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