Invertebrate Assemblage Changes Indicative of Reduced Flow in an Agricultural Watershed

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Abstract. Water extractions for agricultural irrigation have reduced stream baseflows in dry years and likely have increased the number of intermittent stream reaches within the lower Flint River basin. We characterized macroinvertebrate assemblages in stream reaches spanning a gradient of flow permanence to identify key taxa and traits indicative of flow alteration within this basin. We sampled common substrate types (rock and wood) monthly from September to December 2013 in stream reaches exhibiting either perennial stream flow or different degrees of intermittency. We also collected monthly overnight drift samples at each of these sites when flow was present. This information was used to classify taxa as sensitive, tolerant, or resilient with respect to increased intermittency based on their occurrence across this flow gradient. Drift data and published literature were used to link taxa responses to specific functional and life history traits such life cycle, response to drying, and ability to disperse. Taxa indicative of perennial reaches included those that lack desiccation resistance (Hydropsyche, Isonychia) and those with univoltine life cycles (Ancyronyx, Taeniopteryx), while those indicative of intermittent reaches either had adaptations to avoid desiccation (Ostracoda, Copepoda) or were able to recolonize quickly following flow resumption. Linking taxa responses to specific traits will allow for the development of predictive models describing assemblage responses to increased stream intermittency.

INTRODUCTION

Increased consumptive water demand has led to declining stream flows and an increased prevalence of stream intermittency in many watersheds (Caschetto et al. 2014). Within the southeast, this trend is being exacerbated by climate shifts that have reduced average annual precipitation and/or increased drought frequency and

severity (Hopkinson et al. 2013). As a result, emphasis on the effect of hydrologic alteration on aquatic biota has increased in recent years (Poff et al. 2010, Datry et al. 2011). In agricultural areas, this alteration is of growing importance as droughts increase the tenuous balance between the quantity of human water withdrawals and instream flow needs.

Benthic stream invertebrates possess various adaptations and life-history characteristics that affect their response to reduced stream flow and channel drying. Mobile invertebrates can disperse to avoid drying by either drifting downstream (Poff and Ward 1991, James et al. 2008) or flying away (Williams 1996). Some species can tolerate periods of drying by burrowing into wet sediment, moving into the hyporheic zone, or entering diapause (Tronstad et al. 2005, Stubbington and Datry 2013). Once flow resumes, recolonization can occur directly through aerial dispersal and egg oviposition by flying adults and movement of desiccant-resistant taxa from the sediment or other spatial refugia (Williams and Hynes 1976).

This study assessed changes in invertebrate assemblage composition across a gradient of flow permanence within a watershed where flow regimes have been altered by both surface and groundwater extraction for agricultural irrigation. We further examined how these taxonomic shifts were related to specific functional and life history characteristics that might determine sensitivity to stream drying. We hypothesized that those taxa most sensitive to reduced flows would be univoltine (reproduce once a year), have no specific adaptations to persist during drying, and lack dispersal capabilities that would allow them to recolonize quickly following flow resumption.

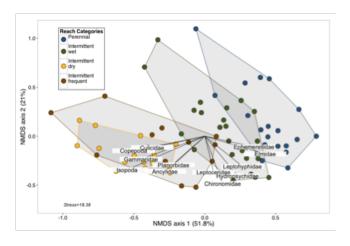


Figure 1: Sampling locations within Ichawaynochaway Creek, southwest GA.

SITE DESCRIPTION

The Ichawaynochaway creek (IC) watershed occupies roughly a third of the drainage area of the lower Flint River Basin in southwestern Georgia. The creek originates in the Fall Line Hills and then flows through the karst geology of the Dougherty Plain that is underlain by the Upper Floridan Aquifer, an important water source to the creek and its tributaries (Hicks et al. 1981, Golladay and Battle 2002). High water demand from center pivot irrigation during recent supraseasonal droughts has greatly reduced growing season stream flow in this watershed (Rugel et al. 2012), resulting in many streams ceasing to flow or drying completely.

METHODS

We sampled 13 stream reaches within the IC basin (Fig. 1) following the end of a supraseasonal drought representing a range of flow permanence based on available hydrologic records and observation during the drought. Reaches were classified as perennial (n=4), intermittent-wet (ceased flowing during drought but maintained pools; n=3), intermittent-dry (dried during drought and tend to seasonally dry; n=3), and intermittent-frequent (tend to dry multiple times a year; n=3).

Invertebrates were sampled monthly from two common stream substrates, rock and wood, in each reach from September through December 2013 with the exception of two reaches that were dry in November and three that were dry in December. Samples were collected by disturbing three haphazardly selected $0.09~\mathrm{m}^2$ areas into a slack sampler (500 ?m mesh size), combining collected material into a single sample for each habitat within each reach (Moulton et al. 2002). Drift samples were

also collected monthly by placing a drift net $(0.46~\mathrm{m}\times0.30~\mathrm{m})$ flush with the bottom of the stream before sunset and retrieving it the next morning for all reaches with measurable flow. Invertebrates for all samples were preserved in the field in 95% ethanol and returned to the lab. In the lab, samples were fractioned into course and fine partitions (using nested 1mm and 500?m sieves) and stained with Rose Bengal for ease of sorting. Samples with a large number of organisms were randomly subsampled volumetrically as necessary to obtain a minimum of 200 individuals per sample (Vinson and Hawkins 1996). Individuals were identified to the lowest feasible taxonomic level. Most insects were identified to genus with the exception of Diptera, which were identified to family (Chironomidae to Tanypodinae and non-Tanypodinae).

Discharge was measured in each reach every other week using the cross-sectional method with a minimum of 30 measurements taken using either a Marsh-McBirney Flo-MateTM 2000 or Acoustic Doppler Current Profiler (ADCP) (RD Instruments, Poway, CA) depending on stream depth. Two of the reaches had previously established U.S. Geological Survey gages that provided discharge.

Multivariate analysis was performed using Non-metric Multi-dimensional Scaling (NMDS) with Bray-Curtis dissimilarity measures on $\log \sqrt{x} + 1$ -transformed abundance data with rare taxa removed (those present in less than 5% of samples) to examine differences in assemblage composition among reach types over the sampling period. Family level (or coarser if not identified to family) were included in a secondary matrix and correlated with NMDS axes to interpret which taxa had a strong influence on these axes. Indicator species analysis was conducted to determine taxa indicative of reach types. Analysis was performed in R version 3.1.2 using vegan and indicspecies (M.D. Caceres and Legendre 2009; Oksanen et al. 2013)

Functional and life history traits that might influence taxon responses to intermittency including, life cycle, adaptations to tolerate or avoid drying, and dispersal abilities, were determined for taxa indicative of different reach types. Voltinism (the number of times a year a taxa reproduces) was determined based on literature specific for the region. Taxa found to persist in sediments after drying in previous studies were categorized as resistant (Larned et al. 2007; Datry 2012; Stubbington and Datry 2013). Propensity to disperse was categorized based on whether the taxa were present in drift at any point during sampling or if they had the ability to fly. General linear mixed models (GLMM) relating the number of individuals with each characteristic to fixed effects of reach type, habitat type, and characteristic type were assessed with a random effect of reach to account for

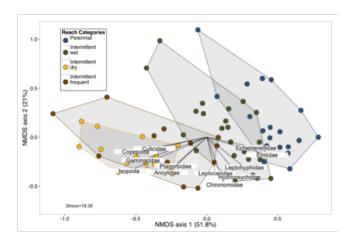


Figure 2: NMDS ordination of rock and wood samples from September to December 2013. Taxa shown represent those significantly correlated with the axes (p<0.01).

repeated measures. Further examinations of combinations of these characteristics were conducted based on results from the initial analysis. Richness was compared using a Poisson distribution with Laplace approximation (lme4) while abundance was analyzed using a negative binomial distribution (glmmADMB) to account for overdispersion (Bates et al. 2012, Fournier et al. 2012). Pairwise comparisons between reach types were adjusted using Bonferonni corrections to detect significant differences for each of the metrics. Analysis was performed in R version 3.1.2.

RESULTS

Non-metric Multi-dimensional scaling (NMDS) generated a convergent two-dimensional ordination (Fig. 2) that represented 72.8% of the variation in the original dissimilarity matrix. The gradient of flow permanence was associated with axis 1; however, intermittent-frequent reaches at the start of sampling were more similar to more perennial reaches than intermittent-dry. Relationships between these axes and the abundance of families revealed that the abundance of multivoltine and/or resistant taxa increased with increasing stream intermittency.

Indicator species analysis revealed several taxa indicative of perennial streams, many of which are univoltine and non-resistant. Intermittent-wet and intermittent-dry reaches had a similar number of indicator taxa; however many of those in intermittent-wet were not desicant resistant as compared with those in intermittent-dry reaches. Finally, intermittent-frequent reaches had the fewest number of indicator taxa (Fig. 3).

Characteristics that differed significantly among reach types included voltinism, resistance to drying and dispersal. Multivoltine taxa (those that reproduce more than once a year) were more abundant and account for

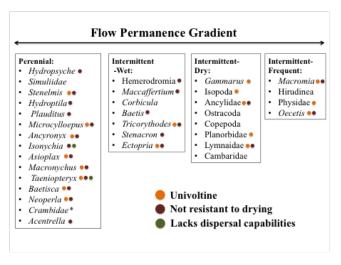


Figure 3: Indicator species analysis across gradient of flow permanence. Dots show characteristics that make taxa more sensitive to flow alteration. *Indicates a lack of information on voltinism.

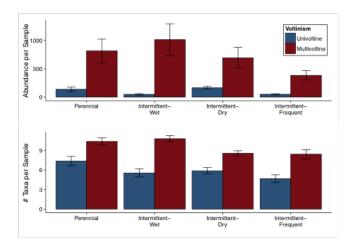


Figure 4: Mean±SE of abundance and richness of different voltinism per sample across reach types.

more taxa than univoltine taxa in all reach types (df=1, χ^2 =144.59,64.58, p<0.001). No differences were detected among reach types for multivoltine taxa abundance or richness (Fig. 4). Univoltine taxa were more abundant in perennial reaches than in intermittent-frequent and intermittent-wet reaches but not intermittent-dry reaches (df=3, χ^2 =19.98, p<0.001). Univoltine taxa richness was similar across reach types.

Abundance and richness of resistant and non-resistant taxa also differed among reach types. Resistant taxa were more abundant in all reach types while more non-resistant taxa were present (df=1, χ^2 =70.00,42.48, p<0.001). Non-resistant taxa were more abundant in perennial reaches compared to intermittent-dry reaches but not other reaches (df=3, χ^2 =14.25, p=0.003) while resistant taxa

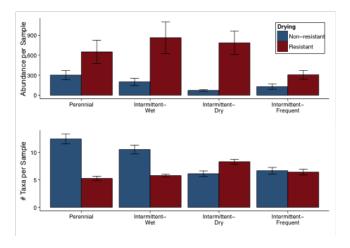


Figure 5: Mean±SE of abundance and richness of resistant to drying per sample across reach types.

abundance was similar across reach types (Fig. 5). Non-resistant taxa richness was greater in both perennial and intermittent-wet reaches compared to intermittent dry reaches but not intermittent-frequent reaches (df=3, χ^2 =25.59, p<0.001). Resistant taxa richness was greater in intermittent-dry and intermittent-frequent reaches than in perennial and intermittent-wet reaches (df=3, χ^2 =14.30, p=0.003).

Most taxa in all reach types were capable of dispersal (df=1, χ^2 =568.66, 490.82, p<0.001). Abundance was similar among reach types for those that disperse and those that do not. Richness was greater in perennial reaches than in intermittent-dry reaches for those that do not disperse (df=3, χ^2 =9.01, p=0.030) but was similar across reach types for those that disperse.

Univoltine abundance and richness did not follow expected patterns; therefore the resistance to drying of these taxa was further investigated. Univoltine taxa that were not resistant to drying were more abundant in perennial reaches than all other reaches (df=3, χ^2 =45.38, p<0.001), comprising 97% of the univoltine abundance, while resistant univoltine taxa were most abundant in intermittent-dry (87%) and intermittent-frequent reaches (54%) (df=3, χ^2 =73.56, p<0.001).

Perennial reaches also had a greater richness of univoltine non-resistant taxa than intermittent-dry and intermittent-frequent (df=3, χ^2 =16.90, p<0.001) with 92% of the univoltine richness being non-resistant taxa. Resistant univoltine taxa richness increased with the degree of stream intermittency and was significantly lower in perennial reaches than in intermittent-dry and intermittent frequent reaches (df=3, χ^2 =40.80, p<0.001).

DISCUSSION

Understanding the ecological effects of reduced stream flows and drying events has become increasingly important as water shortages become increasingly common in the southeastern U.S. (Seager et al. 2009). Our sampling allowed us to examine taxa characteristics across a gradient of flow permanence following the end of a supraseasonal drought. Stream reaches that dried completely during the drought had fewer taxa that were non-resistant though no clear pattern was seen for voltinism or dispersal. Further examination of voltinism and ability to persist during drying did reveal that the majority of univoltine taxa in perennial streams were non-resistant while those more intermittent sites had a greater proportion of resistant taxa. These findings suggest that conversion of streams from perennial to intermittent status can result in the loss of those taxa that are univoltine and cannot persist drying.

Our results showed that a large portion of the taxa within this watershed either drifted or flew at some life stage. While perennial streams had more taxa that did not disperse, our sampling was limited in categorizing a taxas response to reduced flows because perennial streams did not decline in flow during sampling. Other studies have noted an increase in invertebrate drift with reduced flow as a response to avoid drying (James et al. 2008).

Assemblage composition differences were greatest between those reaches that maintained some water during the previous drought as opposed to those that dried completely. This is likely the result of different taxonomic responses to drought because some organisms can persist or recolonize quickly. Indicator species analysis revealed that the most intermittent reaches were largely a subset of more perennial reaches. While few differences were detected among dispersal during this study, drift has been shown to increase with a reduction in flow (James et al. 2008). We created a conceptual model that compiles these characteristics into categories to predict which organisms will be most affected by reduced flow and drying (Fig. 6). Those taxa that are most sensitive are not adapted to tolerate drying and have poor dispersal abilities (Elmidae, some genera of Plecoptera). Here dispersal includes being univoltine as those taxa are less capable of recolonizing a dried reach following flow resumption compared to multivoltine taxa. In comparison, resistant taxa are those taxa that favor extreme condition and can quickly recolonize following flow resumption (Chironomidae, Gammarus). While these categories are broad, they seek to understand at a large scale the changes in assemblage composition that

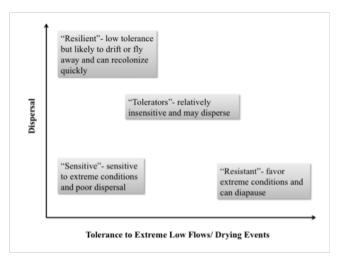


Figure 6: Conceptual diagram of characteristics of organisms that contribute to their ability to persist during low flow and drying events.

may be seen with an increasing frequency of low-flow and no-flow events.

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