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Longitudinal variation in macroinvertebrate assemblages below a large-scale hydroelectric dam

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Abstract Worldwide, dams have had pervasive impacts on their associated river systems. In this study, we examined the effects of a large-scale dam on the downstream macroinvertebrate assemblages of a 65-km stretch of the Chattahoochee River (Georgia, USA) over an 11-year period. We quantified differences among six sites within the study reach using NMS, ANOSIM, invertebrate metrics (Shannon–Weiner diversity, number of EPT taxa, and number of sensitive taxa), and indicator analysis. We compared results from this study to the nearby unregulated

Middle Oconee River. There were significant differences among all sites and increases in all macroinvertebrate metrics as distance from the dam increased (and diel flow variation decreased). Indicator analysis supported this pattern: no EPT indicator taxa existed directly below the dam, whereas 17 were indicators at the final site. Similarity between the Middle Oconee and the Chattahoochee was moderate (52%). Our results suggest that impacts of the dam are far-reaching and long-term, and that the macroinvertebrate assemblage does not return to a fully representative state even 65 km downstream. This study contributes to the small but growing field of research on effects of dams over long temporal and spatial scales.

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Introduction

Dams have had a pervasive impact on the majority of the world's river systems, ranging from altered temperature regimes and sedimentation patterns (Poff et al., 1997; Vinson, 2001) to substantial changes in biological communities (Poff et al., 1997; Vinson, 2001; Haxton & Findlay, 2008; Holt et al., 2014). Many researchers consider flow regime as the most important variable shaping biotic communities and

abiotic factors in lotic systems (Poff et al., 1997; Gibson et al., 2005; Kennard et al., 2007; Konrad et al., 2008; Poff & Zimmerman, 2010; Holt et al., 2014). This concept holds for dam-impacted streams as well and may in fact play an even larger role depending on the dam management regime. Large-scale hydropower dams, in particular, create highly variable stream flows based on energy demands at different times of the day (Richter & Thomas, 2007). In general, this involves a rapidly changing hydrologic cycle, with discharge peaks that may be much higher than in a natural system followed by very low water releases aimed at recharging the reservoir (Richter & Thomas, 2007). These extreme alterations in hydrologic amplitude can occur over short periods of time (24 h) and may result in heavy scouring of the river channel, altered temperature regimes, displacement of riverine organisms, and stranding of slow-moving aquatic organisms (Andrews, 1986; McKinney et al., 1999; Topping et al., 2000; Richter & Thomas, 2007).

On the other hand, artificially cold tailwater habitat below dams has created productive coldwater fisheries that otherwise would not have been present based on geographical and ecological constraints. From a recreational standpoint, these fisheries provide excellent angling opportunities and generate a significant source of revenue for local natural resources agencies. However, while dams create these man-made habitats, they can have differing degrees of impact on the macroinvertebrate communities based on their operations, in turn impacting the primary food source for fish. Therefore, it is of primary importance to investigate the effects of dam operations on the macroinvertebrate community in order to gain a bottom-up perspective on the overall health of the ecosystem.

Recent studies have characterized macroinvertebrate communities below dams (Haxton & Findlay, 2008; Poff & Zimmerman, 2010). Overall, these studies show severe impacts on the communities with decreased species richness and abundance as well as a shift to more disturbance-tolerant assemblages (Vinson, 2001). Few studies have examined changes over large spatial scales, however (Stevens et al., 1997; Marchetti et al., 2011; Cross et al., 2013; Minshall et al., 2014). The majority of the research has focused on relatively small sections of rivers (from 150 m to 27 km) immediately below dams. Our study adds to the small but growing field of research on large-scale impacts of dams on macroinvertebrate communities.

The goal of our study was to investigate assemblage patterns along a 65-km stretch of river below a major dam over an 11-year study period. This study took place on the Chattahoochee River near Atlanta, Georgia (USA). This river is highly impacted by humans, primarily in the form of Buford Dam, a large-scale hydroelectric dam. The primary objectives of this study were to (1) characterize the macroinvertebrate assemblages within the 65-km tailwater section of the Chattahoochee below Buford Dam, (2) assess spatial variation in the macroinvertebrate assemblages along this 65-km section, and (3) compare the macroinvertebrate assemblage in this section of the Chattahoochee with a historically published assemblage from the nearby unregulated Middle Oconee River.

Materials and methods

Study sites

The Chattahoochee River begins in the Appalachian Mountains of north Georgia and flows south to the Gulf of Mexico after joining the Flint River in southern Georgia to form the Apalachicola River. The drainage area of this river system is approximately 50,760 km². The current study focuses on a 65-km stretch of the Chattahoochee River just below Buford Dam, located within the Chattahoochee River National Recreation Area in the Piedmont region of Georgia (Fig. 1). Buford Dam is a major hydroelectric dam that provides service to a large portion of the Atlanta population. The dam was completed in 1956 and has exerted exclusive control over this section of the river since its construction. Based on demand for electricity, water flow through this dam can be highly variable. Buford Dam is managed to maintain a base flow of 21.2 m³ s⁻¹ at Peachtree Creek (approximately 76 km downstream from the dam) to guarantee downstream communities receive sufficient water. However, the amount of variation that can occur within a single day can be quite extreme, with fluctuations of up to 280 m³ s⁻¹, creating a very unnatural flow regime within the river below Buford Dam. The most extreme diel amplitude fluctuations occur in the section directly downstream of the dam (Fig. 2). Average daily amplitude just below Buford Dam is 133.53 m³ s⁻¹. As distance from the dam

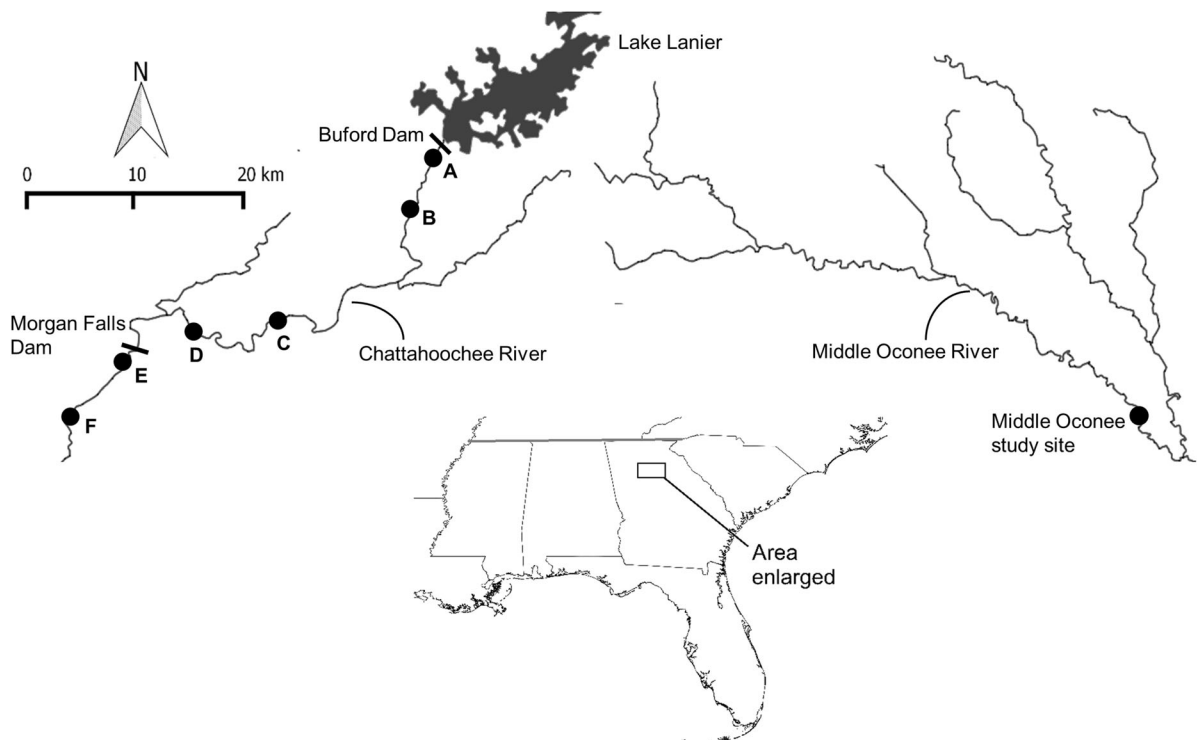


Fig. 1 Location maps of the Chattahoochee River study area and Middle Oconee River study area (Grubaugh and Wallace, 1995) in Georgia, USA. Study site locations within each river system are noted

increases, diel amplitude fluctuations decrease (average diel amplitude 73 km downstream from Buford Dam = $40.38 \text{ m}^3 \text{ s}^{-1}$) (Fig. 2). Releases from the dam are hypolimnetic, creating a fluctuating temperature regime in addition to the fluctuating amplitude. Water temperatures directly below the dam range from 6.2 to 17.6°C, creating (at times) an abnormally cold stretch of river for this region. As a result, a productive recreational trout fishery has developed and is managed by the Georgia Department of Natural Resources (DNR). Until recently, few biological studies have focused on this section of the river (O'Rourke, 2014; Holt et al. 2014), but the National Park Service (NPS) is interested in quantifying the ecological effects of the current dam management regime regarding spatial variation in the macroinvertebrate communities and how these communities compare to an unregulated river in the Georgia Piedmont.

In addition to Buford Dam, a second smaller hydroelectric dam (Morgan Falls Dam) 56 river km downstream from Buford Dam (Fig. 1) exerts

influence over the final section of the study area (15 km). Minimum flow from this dam is maintained at $21.2 \text{ m}^3 \text{ s}^{-1}$, and the river below this dam experiences far less diel amplitude variation (Fig. 2), which may help moderate some of the extreme differences in flow from Buford Dam.

Within the study reach, six sites were chosen for macroinvertebrate sampling ranging from just below Buford Dam (site A) to Cochran Shoals (site F) (Fig. 1). These specific sites were chosen based on their proximity to the two dams controlling water flow in the study reach: two sites just below Buford Dam (A and B), two sites part-way between Buford and Morgan Falls Dams (C and D), and two sites below Morgan Falls Dam (E and F). See Fig. 1 for specific locations of sites within the study area. The substrate throughout the study area is characterized by bedrock, loose gravel, and sand. Specific substrate data are not available for each individual sampling site. Large woody debris occurs sporadically but is limited by peaks of discharge associated with power production. The two sites closest to Buford Dam (A and B)

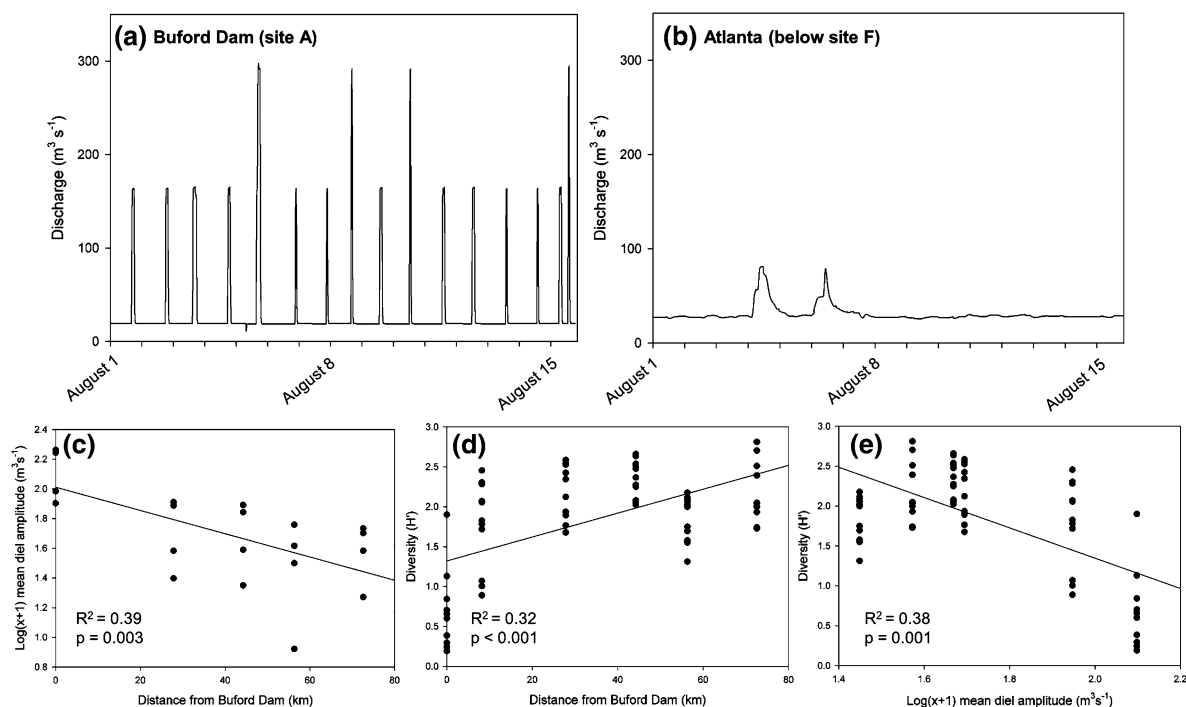


Fig. 2 Patterns in hydrology and macroinvertebrate responses to hydrology in the Chattahoochee River study area. **a**, **b** Hydrographs depicting the difference in diel discharge over a 15-day period (2011) between **a** a USGS gage just below Buford Dam (site A—gage 02334430) and **b** a USGS gage 73 km below Buford Dam (~ 8 km below site F—gage

02336000). **c** Linear regression showing a significant negative relationship between diel amplitude and distance from Buford Dam. **d**, **e** Linear regressions (HD data only) showing significant impacts of **d** distance from Buford Dam and **e** diel amplitude variation on macroinvertebrate assemblages within the study area

experience more severe scouring of the substrate than the remainder of the study area. Site E (below Morgan Falls Dam) is significantly deeper than the remaining sites with increased scour as well (though to a lesser degree than sites directly below Buford Dam). The land bordering the river throughout the study area is composed primarily of bottomland hardwood forest (Zomlefer et al., 2012). Regarding fish populations in the study area, the primary consumers of macroinvertebrates include stocked rainbow trout (*Oncorhynchus mykiss*) and naturally reproducing brown trout (*Salmo trutta*). Population numbers of these species are fairly similar throughout the study reach, with the exception of site B, which tends to have slightly lower numbers of each (O'Rourke, 2014). Sites below Morgan Falls Dam were not sampled for fish by O'Rourke (2014).

In addition to the primary Chattahoochee River study area, we also incorporated a study from the nearby unregulated Middle Oconee River (Grubaugh & Wallace, 1995) as a means for comparison to the

regulated Chattahoochee. The Middle Oconee study site is located approximately 68 km east of the Chattahoochee study area in the Piedmont region of Georgia (Fig. 1). While the Chattahoochee is in a highly urbanized area, the Middle Oconee watershed remains rural. We do not consider this a “reference site,” however, due to the impact of animal agriculture in the Middle Oconee watershed (see below). In addition, the Middle Oconee drainage area (at the sampling site) is smaller than the Chattahoochee drainage area (at the head of the study reach) (1030.8 km² vs. 2693.6 km², respectively). The differences between these two watersheds impose limitations on the comparison between these two systems. Unfortunately, published taxa lists from Piedmont rivers of a similar size in Georgia are lacking. Thus, this study was our only opportunity for comparison with a river of approximately similar size in the Piedmont region of Georgia. Despite these limitations, we believe that a comparison between the regulated

Chattahoochee and unregulated Middle Oconee can still provide useful insights into the effects of river regulation. They are both in the Piedmont physiographic region and have been influenced historically by intensive row crop agriculture prior to the early twentieth century (Grubaugh & Wallace, 1995). Since then, row crop agriculture has significantly decreased in both systems. Urbanization has increased significantly in the Chattahoochee watershed, whereas the Middle Oconee has experienced an increase in animal agriculture (e.g., poultry, dairy, and cattle farms).

Macroinvertebrate sampling

Both Hester–Dendy (HD) multi-plate samplers (Hester & Dendy, 1962) and a Surber sampler (Surber, 1937) were used to collect macroinvertebrates over an 11-year period (2001–2011). HD multi-plate samplers contained nine 76-mm² masonite plates attached to a wire cable anchored on or near the river bank to a permanent structure. The plates were deployed in a free-flowing section of the river at each of the six sites and remained in place for a period of 3 months during each of the sampling periods. Surber samplers consisted of a 500- μ m net (with an opening of 22.9 cm in diameter) and a 30.5-cm² open base. Surber samples were taken at only five of the six sites (A–D and F) due to excessive depth at site E. Sampling locations at each site were determined based on accessibility and were stratified to target available habitats in which macroinvertebrates are likely to occur: sand, small gravel, bedrock covered with algae, and/or vegetation. Quarterly for 11 years, three replicate samples were collected using each sampling device.

All macroinvertebrates collected in the field were preserved in 70% isopropyl alcohol, enumerated, and identified to the lowest possible taxonomic level (genus in most cases) using keys in Klemm (1995), Wiggins (1996), Kathman & Brinkhurst (1999), Needham et al. (2000), Epler (2001), Stewart & Stark (2002), Adler et al. (2004), Dillon et al. (2003), Westfall & May (2006), Mackie (2007), Merritt et al. (2008), and Thorp & Covich (2010). The caddisfly genus *Ceratopsyche* was treated as a separate genus in this study, although it is now considered a sub-group within *Hydropsyche* (Geraci et al., 2010).

The specific sampling methodology for the Middle Oconee study can be found in Grubaugh & Wallace (1995). In summary, the authors sampled one site on

the Middle Oconee River on a monthly basis over a period of 1 year. The authors used a modified T-sampler (Merritt et al., 2008) (similar to a Surber sampler) to collect macroinvertebrates on the substrate, which was composed of bedrock and large boulders. Macroinvertebrates were preserved in the field in 5–10% formalin and identified in the laboratory to the lowest taxonomic level possible (typically genus or species).

Assemblage analyses

Differences in overall macroinvertebrate assemblages among the six study sites (A–F) within the Chattahoochee were analyzed to determine changes along the length of the study area. Abundance data from HD plates and Surber samplers were kept separate for all analyses due to differences in sampler catch efficiencies. Each replicate sample (each site, season, and year) was kept separate for all analyses unless otherwise noted. All abundance data were $\log(x + 1)$ transformed due to lack of normality and relativized by sample. Nonmetric multidimensional scaling (NMDS, Bray–Curtis Similarity, Kruskal fit scheme 1, 25 restarts) was used to visualize patterns in assemblages among sites. Analysis of Similarities (ANOSIM, Bray–Curtis similarity, 999 permutations, one-way layout, factor = site) was used to test for statistical significance among macroinvertebrate assemblages at each site. *R*-values from ANOSIM indicated whether the between- or within-site dissimilarity was greater in each pairwise comparison between sites, where $0 \leq R \leq 1$. Larger *R*-values indicated greater dissimilarity in the macroinvertebrate assemblages between the two sites versus within each site individually. Indicator analysis (Dufrene & Legendre, 1997) was used to identify taxa that represented each site, followed by randomization (Monte Carlo) tests (4999 permutations) to determine significance. Indicator taxa are those that are both abundant and consistently found at a specific site relative to the remaining taxa. Based only on the indicator taxa for each site, average tolerance values were calculated (see following for tolerance value explanation). In addition to indicator analysis, three macroinvertebrate metrics were used to help characterize the overall assemblages at each site: Shannon–Weiner diversity (*H'*), mean number of EPT (Ephemeroptera, Plecoptera, and Trichoptera) taxa, and

mean number of sensitive taxa. Sensitive taxa were based on tolerance values from the North Carolina Biotic Index (NCBI) (Lenat, 1993) and Grubaugh & Wallace (1995). For this study, sensitive taxa were considered those with a tolerance value ≤ 3 (GADNR, 2007). We used ANOVA (one-way, factor = site) and post hoc Tukey tests to determine significance among these metrics. Seasons within years were pooled for these analyses (years and sites remained independent).

We investigated assemblage change over the length of the river in response to (1) distance from Buford Dam and (2) diel hydrologic amplitude using USGS flow data from gaging stations at sites A (gage 02334430), C (gage 02335000), D (02335450), E (gage 02335815), and F (gage 02336000). Average diel amplitude was calculated at each of these sites over four years (2008–2011) (USGS, 2013). Site B was not included due to absence of a nearby USGS gage. Amplitude was $\log(x + 1)$ transformed due to lack of normality. To determine if a pattern existed between distance from Buford Dam and diel amplitude variation, we performed a linear regression using 4 years of flow data (2008–2011) from each of the gages listed above and the distance of each gage from Buford Dam. Based on this regression, we determined average diel amplitude at site B as well. Regression analysis also was used to determine difference in H' , mean number of EPT taxa, and mean number of sensitive taxa over the length of the study area (km from dam) as well as over the range of diel amplitudes within the study reach. Sites and years were treated independently for these analyses; seasons within each year were combined.

The taxa list for the Chattahoochee River below Buford Dam was then compared to the macroinvertebrate data set from a comparable site on the Middle Oconee River (Grubaugh & Wallace, 1995). Sorenson's Index was calculated to determine similarity between the two river assemblages using the equation: $\beta = 2c / (S_1 + S_2)$, where c is the number of taxa in common, S_1 is the number of taxa in the Chattahoochee River, S_2 is the number of taxa in the Middle Oconee River, and $0 \leq \beta \leq 1$ ($\beta = 0$ indicates no similarity between the two rivers, and $\beta = 1$ indicates 100% similarity). Because the Middle Oconee was sampled using only a modified T-sampler, only Surber data from the Chattahoochee River were used for a more direct comparison. Due to changes in taxonomy and differences in level of identification for some

groups, we used a conservative approach when calculating the similarity index between these two assemblages. To determine whether the macroinvertebrate community of the Chattahoochee differed from that of the Middle Oconee, Sorenson's Index was calculated using (a) the entire Chattahoochee study area (versus the Middle Oconee) and (b) only the site furthest downstream from Buford Dam (site F) (versus the Middle Oconee). The latter was used to determine whether the macroinvertebrate assemblage 65 km from the dam returned to a more representative Piedmont river condition. Percent EPT and percent sensitive taxa were also calculated for the Chattahoochee River (overall), site F only, and the Middle Oconee River to determine whether differences were being generated by indicators of high water quality.

NMDS, ANOSIM, and H' analyses were performed using Primer v6 software (Primer-E Ltd, Devon, UK). Indicator analysis was performed using PC-ORD (version 6; MjM Software, Gleneden Beach, OR, USA). All other statistical analyses were performed using SAS software (version 9.3; SAS Institute, Inc., Cary, NC, USA). All significance testing used $\alpha = 0.05$.

Results

All taxa collected during the study along with tolerance value designations are listed in Online Resource 1. Overall, 159 taxa were collected comprising 145 genera, 60 families, and 22 orders. Site-specific analysis among the six study sites (A–F) on the Chattahoochee River shows that the macroinvertebrate assemblage at each site was significantly different from all other sites (Table 1). There was also a general community progression from site A through site F (Fig. 3), indicating a successive change in assemblages from one site to the next. Sites furthest from each other exhibited the greatest difference in macroinvertebrate assemblages. A temporal effect was detected as well based on the NMDS plot. However, in this study, the focus was on spatial variation. For temporal effects, see Holt et al. (2014). Numerous indicator taxa were identified for each of the six study sites (Table 2). While compositions of indicator taxa differed, there was no difference among sites in average tolerance values of these indicator taxa. H' (HD samples only) was significantly lower at

Table 1 R-statistic values from ANOSIM for the Chattahoochee River study sites

	A	B	C	D	E
B	0.323	–	–	–	–
C	0.711	0.326	–	–	–
D	0.629	0.405	0.142	–	–
E	0.906	0.641	0.480	0.491	–
F	0.902	0.713	0.425	0.468	0.417

All R-statistics are significant ($P < 0.05$), indicating significant differences in macroinvertebrate communities at each site. Only results from analysis of Hester–Dendy data are shown here; Surber data support these results

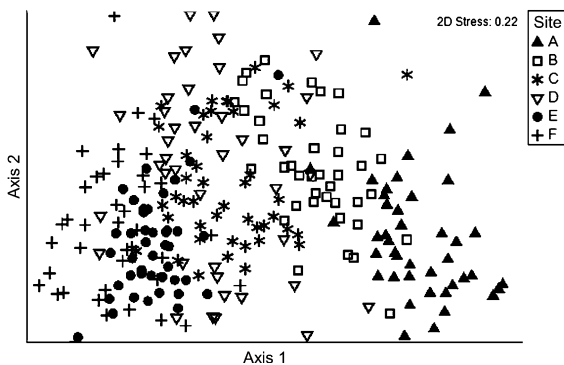


Fig. 3 Nonmetric multidimensional scaling (NMDS) (Bray–Curtis similarity) results showing differences in macroinvertebrate communities among the six study sites in the Chattahoochee River study area. Only Hester–Dendy samples are shown here; Surber data support this same pattern

site A compared to the other five sites (Table 3). Based on Surber samples, A and B had significantly lower H' than C, D, and F (Table 3). Number of EPT taxa and sensitive taxa generally increased from site A to site F (Table 3) with sites closest to each other being most similar. However, the number of sensitive taxa in HD samples did not differ between sites A, B, and C.

Significant patterns emerged in relation to linear distance from Buford Dam as well. Average diel amplitude decreased significantly with increasing distance from Buford Dam ($R^2 = 0.39$, $P = 0.003$) (Fig. 2c). Annual amplitude variation did not change in response to distance from the dam ($R^2 = 0.04$, $P = 0.38$). There was a significant positive relationship between H' and distance from Buford Dam for both HD and Surber samples (HD: $R^2 = 0.32$, $P < 0.001$; Surber: $R^2 = 0.52$, $P < 0.001$) (Fig. 2d). Number of EPT taxa vs. distance from the dam

exhibited a similar relationship (HD: $R^2 = 0.63$, $P < 0.001$; Surber: $R^2 = 0.47$, $P < 0.001$). Although slightly weaker, the relationship between number of sensitive taxa and distance from Buford Dam was also positive (HD: $R^2 = 0.25$, $P < 0.001$; Surber: $R^2 = 0.26$, $P < 0.001$).

From a hydrological perspective, there were many similar patterns to those mentioned previously. Because of the relationship between diel amplitude and distance from Buford Dam, it is not surprising that H' showed a significant increase as diel amplitude decreased (HD: $R^2 = 0.38$, $P < 0.001$; Surber: $R^2 = 0.58$, $P < 0.001$) (Fig. 2e). Number of EPT taxa and (to a weaker extent) number of sensitive taxa follow the same trend [EPT (HD): $R^2 = 0.55$, $P < 0.001$; EPT (Surber): $R^2 = 0.53$, $P < 0.001$; sensitive taxa (HD): $R^2 = 0.13$, $P = 0.001$; sensitive taxa (Surber): $R^2 = 0.27$, $P < 0.001$].

Comparison between the Chattahoochee and Middle Oconee Rivers showed moderate assemblage similarity, with the Middle Oconee exhibiting a stronger tendency towards sensitive taxa (Table 4). Despite the fact that the total number of EPT taxa was greater in the Chattahoochee than in the Middle Oconee (36 vs. 26 EPT taxa, respectively), percent EPT was similar between the two rivers (Table 4). Focusing only on site F, the two rivers appear less similar with respect to EPT taxa: the Chattahoochee at site F has fewer total EPT taxa than the Middle Oconee (23 vs. 26 EPT taxa, respectively) and a lower percentage of EPT to total taxa (Table 4). This dissimilarity was also apparent when comparing taxa unique to each system as well as those that are common to both (Table 5). The Middle Oconee contained a greater number of unique EPT and sensitive taxa than did the Chattahoochee. No Plecoptera were unique to the Chattahoochee, while the Middle Oconee contained five unique plecopterans (all of which are sensitive taxa). On the other hand, the Chattahoochee contained four macrocrustaceans that are unique to that system (*Caecidotea*, *Crangonyx*, *Hyalella*, and *Lirceus*), whereas the Middle Oconee contained none.

Discussion

The distinct assemblages that developed at each of the six Chattahoochee sites indicate considerable

Table 2 Indicator taxa by site in the Chattahoochee River study area (Hester–Dendy and Surber data combined)

Site	Order	Family	Genus	Mean TV
A	Diptera	Chironomidae	<i>Cricotopus</i>	4.4
			<i>Cricotopus/Orthocladius</i>	
			<i>Eukiefferiella</i>	
			<i>Orthocladius</i>	
B	Lumbriculida Gastropoda Amphipoda Trombidiformes Ephemeroptera Plecoptera Diptera	Simuliidae	<i>Simulium</i>	6.34
		Lumbriculidae	<i>Lumbriculus</i>	
		Physidae	<i>Physa</i>	
		Hyalellidae	<i>Hyalella</i>	
		Lebertiidae	<i>Lebertia</i>	
		Ephemerellidae	<i>Ephemerella</i>	
		Taeniopterygidae	<i>Taeniopteryx</i>	
		Chironomidae	<i>Cricotopus</i>	
			<i>Cricotopus/Orthocladius</i>	
			<i>Eukiefferiella</i>	
			<i>Parametriocnemus</i>	
			<i>Stictochironomus</i>	
			<i>Thienemannimyia</i> group	
			cf. <i>Limnophora</i>	
		Muscidae		
		Simuliidae	<i>Simulium</i>	
C	Tricladida	–	–	4.63
	Lumbriculida	Lumbriculidae	–	
	Amphipoda	Crangonyctidae	<i>Crangonyx</i>	
	Isopoda	Asellidae	<i>Caecidotea</i>	
	Ephemeroptera	Baetidae	<i>Iswaeon</i>	
		Ephemerellidae	<i>Dannella</i>	
		Brachycentridae	<i>Brachycentrus</i>	
	Diptera	Lepidostomatidae	<i>Lepidostoma</i>	
		Chironomidae	<i>Parametriocnemus</i>	
			<i>Tvetenia</i>	
D	Tricladida	–	–	5.9
	Lumbriculida	Lumbriculidae	–	
	Bivalvia	Cyrenidae	<i>Corbicula</i>	
	Amphipoda	Crangonyctidae	<i>Crangonyx</i>	
	Isopoda	Asellidae	<i>Lirceus</i>	
	Trombidiformes	Lebertiidae	<i>Lebertia</i>	
	Ephemeroptera	Baetidae	<i>Iswaeon</i>	
	Plecoptera	Capniidae	<i>Allocapnia</i>	
			<i>Nemocapnia</i>	
			<i>Pteronarcys</i>	
	Trichoptera	Brachycentridae	<i>Micrasema</i>	
		Hydropsychidae	<i>Ceratopsyche</i>	
		Chironmidae		
	Diptera		<i>Dicrotendipes</i>	

Table 2 continued

Site	Order	Family	Genus	Mean TV
E	Isopoda	Asellidae	<i>Caecidotea</i>	5.91
	Ephemeroptera	Heptageniidae	<i>Maccaffertium</i>	
	Odonata	Coenagrionidae	<i>Argia</i>	
	Trichoptera	Brachycentridae	<i>Brachycentrus</i>	
		Hydropsychidae	<i>Cheumatopsyche</i>	
		Hydroptilidae	<i>Hydroptila</i>	
		Leptoceridae	<i>Oecetis</i>	
		Polycentropodidae	<i>Neureclipsis</i>	
		Psychomyiidae	<i>Lype</i>	
	Coleoptera	Elmidae	<i>Macronychus</i>	
	Diptera	Chironomidae	<i>Corynoneura</i>	
			<i>Nanocladius</i>	
			<i>Rheotanytarsus</i>	
			<i>Stenochironomus</i>	
			<i>Synorthocladius</i>	
		Empididae	<i>Hemerodromia</i>	
		Limoniidae	<i>Antocha</i>	
	Gastropoda	Pleuroceridae	<i>Pleurocera</i>	
	Bivalvia	Cyrenidae	<i>Corbicula</i>	
	Isopoda	Asellidae	<i>Lirceus</i>	
F	Ephemeroptera	Baetidae	<i>Acentrella</i>	2.84
			<i>Baetis</i>	
			<i>Heterocloeon</i>	
			<i>Serratella</i>	
			<i>Teloganopsis</i>	
		Heptageniidae	<i>Heptagenia</i>	
			<i>Maccaffertium</i>	
			<i>Stenacron</i>	
			<i>Agnetina</i>	
			<i>Perlesta</i>	
	Plecoptera	Perlidae	<i>Glossosoma</i>	
	Trichoptera	Hydropsychidae	<i>Cheumatopsyche</i>	
			<i>Hydropsyche</i>	
		Lepidostomatidae	<i>Lepidostoma</i>	
		Philopotamidae	<i>Chimarra</i>	
			<i>Forcipomyia</i>	
	Diptera	Ceratopogonidae	<i>Forcipomyia</i>	
		Chironomidae	<i>Polypedilum</i>	

Average tolerance value (TV) for each site was calculated using data from Lenat (1993) and Grubaugh and Wallace (1995)

variation exists within tailwater systems. Many of the *R*-statistics from ANOSIM (Table 1) indicate strong differences among the six study sites, emphasizing significant variation in macroinvertebrate assemblages from site to site. We documented a general

progression in various assemblage metrics as the distance from the dam increased and diel variation in amplitude decreased. In general, the macroinvertebrate compositions improved (i.e., *H'*, numbers of EPT taxa, and numbers of sensitive taxa) with increasing

Table 3 Shannon–Weiner diversity (H'); mean number of EPT¹ taxa; and mean number of sensitive taxa² in the Chattahoochee River study area (separated by sampling device)

Site	Hester–Dendy			Surber		
	H'	# EPT taxa	# Sensitive taxa	H'	# EPT taxa	# Sensitive taxa
A	0.67 ^a	2.64 ^a	0.55 ^a	0.95 ^a	1.09 ^a	0.09 ^a
B	1.77 ^b	5.18 ^{a,b}	0.91 ^a	0.85 ^a	4.27 ^{a,b}	0.55 ^{a,b}
C	2.22 ^{b,c}	8.18 ^{b,c}	1.00 ^a	1.87 ^b	7.09 ^{b,c}	1.45 ^{b,c}
D	2.35 ^c	8.46 ^c	1.73 ^{a,b}	2.12 ^b	6.73 ^{b,c}	1.09 ^{a,b,c}
E	1.85 ^b	10.09 ^{c,d}	1.55 ^{a,b}	—	—	—
F	2.21 ^{b,c}	12.91 ^d	3.00 ^b	2.19 ^b	9.46 ^c	2.18 ^c

¹ Ephemeroptera, Plecoptera, Trichoptera. Significant differences are indicated by different superscript letters (Tukey post hoc test, $P \leq 0.05$). ²Tolerance value ≤ 3 [see Lenat (1993) and Grubaugh and Wallace (1995)]

Table 4 Comparison between macroinvertebrate communities of the Chattahoochee River study area (overall and site F) (Surber data only) and the Middle Oconee River [from Grubaugh and Wallace (1995)]

	Sorenson's Index	% EPT taxa ^a	% Sensitive taxa ^b
Chattahoochee	0.52	52.17	15.9
Chattahoochee—Site F only	0.36	38.33	10.0
Middle Oconee	—	50.98	27.5

Sorenson's Index compares the Middle Oconee to each of the respective sections of the Chattahoochee. Hester–Dendy and Surber data were used for these calculations

^a Ephemeroptera, Plecoptera, Trichoptera

^b Tolerance value ≤ 3 [see Lenat (1993) and Grubaugh and Wallace (1995)]

distance from the dam. This result is logical considering the non-natural conditions directly below any large-scale hydroelectric dam (Graf, 2006; Richter & Thomas, 2007; de Oliveira Naliato et al., 2009). Linear relationships between invertebrate metrics and increasing distance from the dam were most likely in response to changes in diel hydrological amplitude. Extreme variation in amplitude over short time periods (e.g., within a single 24-h period) creates a challenging environment for invertebrates. Water releases from hydroelectric dams increase turbidity and scour, leading to decreased nutrient levels (Baxter & Glaude, 1980; Liu & Yu, 1992; Zhong & Power, 1996). Filter-feeders that require significant water flow for food delivery can still thrive (i.e., *Simulium*) (Merritt et al., 2008), but organisms that are either inefficient at attaching to substrates or use different functional feeding strategies (e.g., grazers, predators) would have a more difficult time. As distance from the dam increases, the amplitude becomes more muted and effects on the hydrologic regime are lessened, allowing for survival of a wider variety of macroinvertebrates.

Linear patterns were consistent despite the presence of a second smaller dam (Morgan Falls Dam) above site E (Fig. 1). Multivariate analyses of the communities at each site showed that all sites were different from each other with no clear distinction between sites above versus below Morgan Falls Dam. In general, H' , numbers of EPT taxa, and numbers of sensitive taxa (Table 3) did not change markedly between areas above and below the small dam with one exception: HD diversity decreased between sites D and E, indicating a potential effect of Morgan Falls Dam. In general, though, this system exhibited a continuum consisting of less sensitive, less diverse assemblages upstream to more sensitive, more diverse assemblages downstream. This lack of distinction is likely due to the fact that daily flow amplitude below Morgan Falls Dam is less variable than that below Buford Dam (Fig. 2), providing further evidence for the impact of severe variation in daily flow amplitude on the macroinvertebrate community of the Chattahoochee.

In addition to changes in H' , EPT, and sensitive taxa, assemblages of indicator taxa also illustrate a

Table 5 List of taxa unique to the Chattahoochee River (site F only) (Surber data only), taxa unique to the Middle Oconee River (Grubaugh and Wallace 1995), and taxa in common between the two rivers

Chattahoochee (Site F)	Common Taxa	Middle Oconee
Non-insects		
<i>Prostoma</i>	Turbellaria	Nematoda
<i>Physa</i>	Oligochaeta	Hirudinea
<i>Lirceus</i>	<i>Pleurocera</i>	<i>Ferrissia</i>
<i>Caecidotea</i>	<i>Corbicula</i>	<i>Somatogyrus</i>
<i>Crangonyx</i>	Hydracarina	Sphaeriidae
<i>Hyalella</i>		Cladocera
Collembola		
EPT		
<i>Acentrella</i>	<i>Baetis</i>	<i>Ameletus</i> ^a
<i>Isaewon</i>	<i>Heterocloeon</i>	<i>Caenis</i>
<i>Dannella</i>	<i>Ephemerella</i>	<i>Serratella</i>
<i>Ephemerella</i>	<i>Maccaffertium/Stenonema</i> ^{a,b}	<i>Epeorus</i> ^a
<i>Teloganopsis</i>	<i>Agnetina</i>	<i>Isonychia</i>
<i>Heptagenia</i> ^a	<i>Paragnetina</i> ^a	<i>Amphinemura</i>
<i>Brachycentrus</i> ^a	<i>Perlesta</i> ^a	<i>Shipsa</i> ^a
<i>Micrasema</i> ^a	<i>Taeniopteryx</i>	<i>Neoperla</i> ^a
<i>Ceratopsyche</i>	<i>Hydropsyche</i>	<i>Pteronarcys</i> ^a
<i>Ceraclea</i>	<i>Lepidostoma</i> ^a	<i>Strophopteryx</i> ^a
<i>Chimarra</i> *	Glossosomatidae*	<i>Ochrotrichia</i>
	<i>Cheumatopsyche</i>	<i>Nectopsyche</i>
		<i>Lype</i>
		<i>Rhyacophila</i>
Miscellaneous insects		
<i>Argia</i>	<i>Nigronia</i>	<i>Corydalus</i>
<i>Progomphus</i>	<i>Optioservus</i> ^a	<i>Promoresia</i>
	Chironomidae (Tanypodinae)	<i>Stenelmis</i>
	Chironomidae (non-Tanypodinae)	<i>Chelifera</i>
	Simuliidae	<i>Hemerodromia</i>
	<i>Antocha</i>	
	<i>Tipula</i>	

^a Sensitive taxa (tolerance value ≤ 3) [see Lenat (1993) and Grubaugh and Wallace (1995)]

^b *Maccaffertium* and *Stenonema* are considered the same taxon for this comparison due to taxonomic changes between the two studies

similar pattern. From a qualitative point of view, it is useful to point out the types of taxa indicative of each study site from the beginning of the study reach to the end (see Table 2). Taxonomic diversity of indicators was relatively low at site A compared to sites further downstream, and the taxa at site A directly below the dam consisted of only Diptera; no EPT or sensitive taxa were characteristic of this site. However, a greater variety of taxa became indicators at each successive site downstream, and the number of EPT indicators climbed steadily, culminating at site F with 17 EPT indicators. In contrast, Cross et al. (2011) found a complete absence of EPT taxa over a 25-km study area

below Glen Canyon Dam (Colorado River) prior to and following an experimental flood release. The fact that there were numerous EPT indicator taxa in the Chattahoochee suggests that the flow management regime and water quality here support survival of these more-sensitive organisms. Average tolerance values at each of the Chattahoochee study sites based on these indicator taxa did not exhibit a significant pattern (albeit several taxa do not have a tolerance value associated with them).

The expansive impacts of Buford Dam on macroinvertebrate assemblages are made even more apparent when comparing the Chattahoochee study area to an

unregulated section of the Middle Oconee River. Based on the moderate degree of assemblage similarity between the rivers (overall), the low assemblage similarity between site F and the Middle Oconee, and the lower percentages of sensitive taxa in the Chattahoochee River (overall and at site F), our study suggests that even after 65 km, macroinvertebrate assemblages did not return to a more representative Piedmont river condition.

Looking at the taxa that are unique to each system supports this idea as well, with fewer unique EPT and sensitive taxa being found at site F in the Chattahoochee versus the Middle Oconee (Table 5). The Middle Oconee contains five plecopterans (stoneflies) that were not found at site F in the Chattahoochee (which contained no unique stoneflies). In addition, the Chattahoochee seems to favor macrocrustaceans (absent from the Middle Oconee), which are typically disturbance-tolerant organisms. This provides further evidence that the Chattahoochee River 65 km from Buford Dam is still ecologically functioning differently from a comparably more naturally flowing Piedmont river.

Several reasons may explain this discrepancy. (1) Low assemblage similarities between the rivers could be due to the 1-year versus 11-year sampling periods for each study (Middle Oconee and Chattahoochee, respectively), and the Middle Oconee study sampled only a single site. However, despite much less sampling, more total taxa were collected from the single Middle Oconee site than over 11 years at site F on the Chattahoochee. (2) Differences in flow variation could explain the patterns (Belmar et al., 2013), with the Chattahoochee experiencing unnatural alterations of flow due to Buford Dam and the Middle Oconee experiencing a more natural flow regime. Significant changes in Chattahoochee macroinvertebrate assemblages have indeed been documented between years with exceptionally high vs. low flows (Holt et al., 2014). (3) Differences in water quality as a result of differing land use in the watershed of each river may cause altered macroinvertebrate assemblages. The Chattahoochee is located in the metropolitan Atlanta area, which has a population of over six million people. The study site, however, is located in a protected corridor managed by the NPS and the water cycles through a large reservoir (Lake Lanier) prior to release down the river. The Middle Oconee is located in a largely rural area, with Athens (whose 1995

population was approximately 88,760) being the primary center of urbanization in the area. However, as one of the primary poultry production areas of Georgia, the Middle Oconee basin is impacted via nutrient enrichment, which has been shown to significantly affect stream macroinvertebrate assemblages (Justus et al., 2010). Thus, while water qualities between the two rivers likely differ, both are anthropogenically impacted. Urbanization and agriculture have both been shown to significantly affect stream macroinvertebrates (Bruno et al., 2014). It is possible that urbanization at the scale of the metropolitan Atlanta area is having a greater impact on the macroinvertebrate fauna of the Chattahoochee River as compared to the agricultural inputs in the Middle Oconee watershed. (4) The abnormally cold temperatures in the tailwater section of the Chattahoochee could be favoring a macroinvertebrate assemblage that is more characteristic of streams further north in the Ridge and Valley and Blue Ridge regions rather than the Piedmont (Hynes, 1970; Johnson & Harp, 2005). Colonization of the Chattahoochee study area by these coldwater organisms, however, may be difficult as nearby local source populations may be lacking. Thus, many may be in low abundance or absent unless they have strong flight capabilities (e.g., Diptera) (Johnson & Harp, 2005).

Because of some of the limitations listed above (e.g., different sampling periods and land use practices), we cannot say with certainty that alteration to the flow of the Chattahoochee River is the sole driver of the differences in the macroinvertebrate assemblages between these two river systems. In addition, we cannot rule out the River Continuum Concept (RCC) (Vannote et al., 1980) as contributing to the linear change in macroinvertebrate assemblages within the Chattahoochee River. However, RCC effects are unlikely due to the fact that stream order remains the same throughout the study area, and the RCC typically applies to much longer stretches of river than the 68 km investigated here.

In conclusion, this study provides evidence for the influence of hydroelectric dams via diel amplitude alterations on riverine macroinvertebrate communities and is one of only a few studies to analyze these effects over long temporal and spatial scales. We have shown that macroinvertebrate assemblages change continuously over a 65-km tailwater section and that these changes appear to be in response to altered diel

flow variation. Using several invertebrate metrics, we documented increasing diversity and presence of sensitive macroinvertebrates as distance from the dam increased (and diel variation decreased). Finally, we provided evidence that the macroinvertebrate assemblages in the Chattahoochee River are still different from a typical Piedmont assemblage even 65 km below the dam. The conclusions from our study suggest that there are likely long-term, far-reaching impacts of many other large-scale dams around the world on aquatic macroinvertebrate assemblages well removed from dams, and that assemblages may vary dramatically within individual impacted areas.

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