Effects of impoundments on stream crayfish assemblages

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Abstract: Life-history timing, trophic interactions, and colonization potential of stream benthos are linked to a stream's flow regime. Modifications to flow regimes often alter the composition of benthic assemblages. We assessed the impacts of relatively large storage dams (>15 m in height, >400-ha impoundments) on crayfish assemblages in southern Appalachian Mountain streams, Alabama, USA. We sampled crayfishes at multiple sites in flowing sections upstream and downstream of dams in 3 impounded streams and along similar lengths of 2 unimpounded streams in the Bear Creek and Cahaba River drainages. We analyzed at 2 scales: within and between drainages. This multi-scale approach allowed us to assess the effects of impoundments on crayfish assemblages in 1 drainage and then assess whether impoundment effects could be generalized across drainages. We compared crayfish assemblages between impounded and unimpounded streams and examined changes in crayfish assemblages with distance from impoundments, considering land-use history as a potential confounding factor. Adult densities averaged 45% higher, and sizes 10% smaller, in downstream sections of unimpounded streams compared with impounded streams. Densities and sizes of adults in upstream sections did not differ between unimpounded and impounded streams. In both drainages, unimpounded stream crayfish assemblage structure gradually shifted along the stream length, with species present upstream differing from those present downstream. Conversely, in all impounded streams, species assemblages did not differ between upstream and downstream sections, illustrating that dams diminish crayfish diversity. Nonetheless, finer-scale assessments showed that crayfish density and richness increased with distance downstream of impoundments. This suggests that assemblage recovery is possible with increasing distance downstream of impoundments. Additionally, we detected fewer crayfish assemblage differences between impounded and unimpounded streams in the Cahaba River drainage than the Bear Creek drainage. In the Cahaba River drainage, urbanization and the presence of an invasive crayfish species in both streams may have hindered our ability to distinguish impoundment effects on crayfishes. Our results show that large dams negatively affect crayfishes and may affect hundreds of crayfish species in thousands of stream km, possibly altering stream systems by interfering with the numerous ecosystem functions influenced by crayfishes.

Key words: crayfish, dams, impoundments, assemblage structure, land-use changes, assemblage recovery, anthropogenic disturbance

A stream's flow regime is a major determinant of aquatic species' distributions and life histories (Vannote et al. 1980, Ward and Stanford 1983, Poff et al. 1997, Lytle and Poff 2004), with many life events (e.g., spawning, larval survival, growth patterns, recruitment) synchronized with the historical flow regime. As such, modification of the flow regime, such as water impoundment by dams, alters the composition of stream communities. Documented effects on stream biota resulting from dams and their associated impoundments include decreases in species diversity, as well as changes in biomass, dominant species, and dispersal of fishes, invertebrates, and mussels (Mbaka and Mwaniki 2015, Wu et al. 2019, Barnett and Adams 2021). These biological responses are often dampened with distance from dams (Ward and Stanford 1983). For example, fish and mussel species assemblages and biomass often become increasingly similar to pre-dam assemblages with increasing distance from dams, in both upstream and downstream directions (Penczak et al. 1984, McGregor and Garner 2003, Phillips and Johnston 2004).

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Alabama, USA, is a freshwater biodiversity hotspot, supporting 60% of North America's native mussel species, 43% of native freshwater snails, 38% of native fishes, and 24% of native crayfishes, many of which are endemic to the southeastern USA (Lydeard and Mayden 1995). In addition, northern Alabama is in the southern Appalachian Mountains (ARC 2009), the global center of crayfish diversity (Crandall and Buhay 2008). Although Alabama supports rich freshwater ecosystems, it contains >100 large dams (>15 m in height, impoundment area >400 ha; NID 2009), and declines in aquatic species richness and diversity are occurring at an alarming rate (Lydeard and Mayden 1995).

Crayfishes play an important role in stream ecosystems by processing detritus, altering the composition of macrophytes and substrate, and transferring energy to predators, including fishes, birds, and other crayfishes (Chambers et al. 1990, Hanson et al. 1990, Momot 1995, Rabeni et al. 1995, Statzner et al. 2003, Stenroth and Nyström 2003). Despite their importance, crayfish populations are declining worldwide, with 48% of North American crayfish species considered threatened (Taylor et al. 2007) and endangerment rates rapidly increasing (Richman et al. 2015). Dams are one of many threats to crayfishes that can disturb habitat, alter flow regimes, and impede migration (Richman et al. 2015, Barnett et al. 2020, Barnett and Adams 2021).

Small dams and impoundments (<15 m in height, impoundment area <400 ha; NID 2009) alter crayfish assemblages (species composition, density, and size distribution) relative to unimpounded streams, with assemblages differing upstream and downstream of impoundments (Joy and Death 2001, Adams 2013) and lower densities of some crayfish genera downstream of impoundments compared with unimpounded streams (Adams 2013). Relative to small dams, larger dams and impoundments presumably pose greater barriers to migration and flow of organic matter (Barnett et al. 2020) and, thus, may have larger effects on crayfishes (Barnett and Adams 2021). No study has yet assessed the effects of large dams and impoundments on crayfish assemblage structures.

Unlike for other stream organisms (e.g., mussels [McGregor and Garner 2003], aquatic insects [Armitage 1978], fishes [Phillips and Johnston 2004]), pre-dam crayfish data are not available for most streams, precluding temporal longitudinal analyses of the impacts of damming on crayfish populations. Instead, to assess how habitat modifications affect crayfish populations, studies often compare streams that have modified vs unmodified habitats (Joy and Death 2001, Adams 2013, Barnett et al. 2020). However, to attribute differences in stream communities to dam effects, it is important to consider other possible differences among the streams that are unrelated to dams. For example, land use is a key driver of stream habitat complexity and species diversity (Harding et al. 1998, Wang et al. 2001, Gragson and Bolstad 2006, Stendera et al. 2012). Thus, if watershed land uses are not comparable historically or contemporarily among comparison streams, this may confound determination of the effects of dams on stream communities.

We assessed the effects of large dams on crayfish assemblages in Alabama streams. To do this, we compared crayfish assemblages in impounded and unimpounded streams within and between 2 Hydrologic Unit Code (HUC) level 8 drainages. We also assessed recent and historical land uses within and among 5 HUC level 11 watersheds to assess this potential confounding factor. We addressed 3 questions (Table 1): 1) do crayfish species distributions, densities, or size composition differ between impounded and unimpounded streams within a drainage, and if so, are differences consistent between drainages; 2) do impounded streams' crayfish assemblages change with distance from impoundment; and 3) do recent and historical land uses, which could potentially confound inference about the relationship between dams and crayfish assemblages, differ within or among watersheds?

METHODS

To assess the effects of large dams on crayfish assemblages, we conducted a 2-scaled field survey of crayfishes in 2 impounded and 3 unimpounded streams in the Bear Creek drainage (BCD; 24 sites) and Cahaba River drainage (CRD; 14 sites), Alabama, USA. We sampled streams in the BCD for 2 y to assess differences between crayfishes in impounded and unimpounded streams within a drainage. During the 2nd sampling y, we also sampled streams in the CRD to assess if differences between crayfish assemblages in impounded and unimpounded streams were consistent between drainages. We summarized crayfish assemblages in 3 ways: assemblage structure (species × site matrices of densities), density (crayfish/100 m^2), and adult sizes. We used both univariate and multivariate split-plot designs to test our predictions that 1) the dominant crayfish species will differ between impounded and unimpounded streams, 2) densities will be lower in impounded than unimpounded streams, and 3) crayfishes will be larger downstream in impounded than unimpounded streams (Table 1). We also used multivariate analyses to test our prediction that crayfish assemblage structure in impounded streams will become more similar to that in unimpounded streams with distance from impoundments. We characterized recent and historical land use within each drainage and used multivariate analyses to test our prediction that land uses do not differ within and between watersheds and, thus, is not a confounding factor.

Study area

The study area included flowing sections of impounded and unimpounded streams in the BCD (Tennessee River Basin) and CRD (Mobile River Basin) (Fig. 1). Both drainages

Table 1. Research questions, statistical analyses, and expected results or alternative explanations about the relationships between crayfish assemblages and stream impoundments in the Bear Creek drainage (BCD) and Cahaba River drainage (CRD), Alabama, USA. PERMANOVA = permutational analysis of variance, LME = linear mixed-effects repeated-measures model, ANOVA = analysis of variance.

Research topic	Research question	Statistical analyses	Expected results if impoundments affected crayfish assemblages (Questions 1 and 2) or alternative explanations of crayfish assemblage differences (Question 3)
Impoundment effects on crayfish assemblages	Do crayfish species distributions, densities, or size composition differ between impounded and unimpounded streams within a drainage, and if so, are differences consistent between drainages?	PERMANOVA	Differences in dominant species in impounded vs unimpounded streams.
		LME	Greater crayfish densities in unimpounded than impounded streams.
		ANOVA	Larger crayfishes and fewer juveniles in downstream sections of impounded streams compared with downstream sections of unimpounded streams.
	Do impounded streams' crayfish assemblages change with distance from impoundments?	PERMANOVA	Impounded streams' crayfish density and species richness increase with distance upstream and downstream from impoundments, becoming similar to unimpounded stream assemblages.
Land-use effects	Do recent and historical land uses differ within or among watersheds?	PERMANOVA	If recent and historical land uses differ within or between watersheds, we infer that land use may also influence crayfish assemblages in study streams.
			If recent and historical land uses do not differ within or between watersheds, we infer that land use was not a major influence on crayfish assemblages.

have diverse aquatic faunal assemblages, including numerous imperiled species (e.g., BCD: Cumberlandian Combshell, Snail Darter, Blueface Darter; CRD: Frecklebelly Madtom, Goldline Darter, Cahaba Shiner) (Cahaba River National Wildlife Refuge Establishment Act 2000, McGregor and Garner 2003, Phillips and Johnston 2004). Within each drainage, impounded and unimpounded streams were in the same ecoregion and had comparable widths and distinct riffle–run–pool complexes. We studied 3 streams in the BCD (2 impounded: Little Bear Creek and Cedar Creek, 1 unimpounded: Rock Creek) and 2 streams in the CRD (1 impounded: Little Cahaba River, 1 unimpounded: Shades Creek). The BCD streams were in the Southeastern Plains ecoregion in Franklin and Colbert counties, and the CRD streams were in the Ridge and Valley ecoregion in St. Clair, Shelby, and Jefferson counties (United States Environmental Protection Agency level III ecoregions; Griffith et al. 2001). Impounded streams each had 1 earthen storage dam. Dams were 17 to 29 m high, creating impoundments with surface areas of 425, 631, and 1700 ha in Little Cahaba River, Little Bear Creek, and Cedar Creek, respectively (Table S1). Little Bear Creek and Cedar Creek dams were built in 1975 and 1979, respectively, and used for flood control. Little Cahaba River dam was built in 1911, raised to its current height in 1929, and impounded Lake Purdy for municipal water storage. Annually, from November until February and during heavy rain events, water is released from water intake valves 19.5 and 23.2 m below full-pool levels in Little Bear and Cedar creek impoundments, respectively. In Little Cahaba River, when water flow in the river is too low to meet municipal water usage demands, water is released from 2 valves 11.0 and 15.5 m below Lake Purdy's full-pool level.

Stream sampling

In impounded streams, we selected 10 sites at set intervals based on stream distance upstream and downstream of impoundments. We mimicked these selections in unimpounded streams, using distance from headwaters to

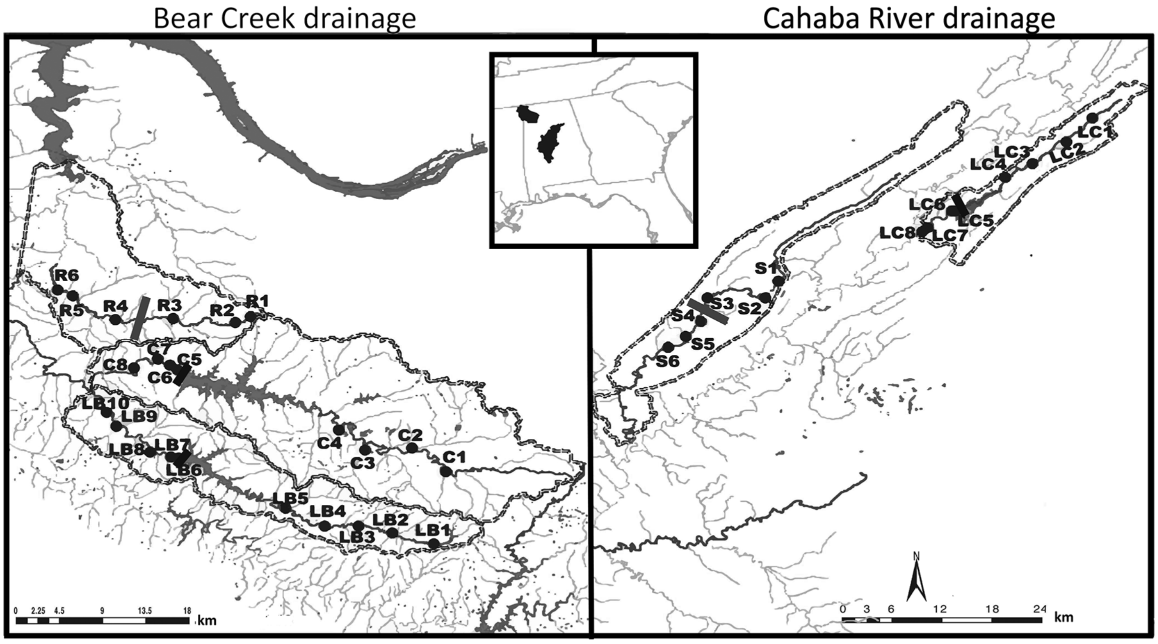

Figure 1. Map of Bear Creek and Cahaba River drainages, Alabama, USA, with collection sites represented by labeled circles. Sites are numbered in ascending order from upstream to downstream, with letters representing stream names (R = Rock Creek, C = Cedar Creek, LB = Little Bear Creek, S = Shades Creek, and LC = Little Cahaba River). Dashed lines delineate each stream's watershed. Gray bars crossing Rock and Shades creeks delineate the midpoint between each unimpounded stream's upstream and downstream sections. Black bars crossing Cedar Creek, Little Bear Creek, and Little Cahaba River represent each stream's dam, with shaded polygons behind the black bars representing impoundments. Inset shows drainage locations within the southeastern USA, with the Bear Creek drainage in the northwest corner and the Cahaba River drainage in the center of Alabama.

mouth to identify the midpoint. If a predetermined site was inaccessible, or if water levels were too deep to sample, we sampled the closest accessible site. If there was no accessible site near the predetermined site, no site was sampled. Because Rock Creek was the only unimpounded stream in the BCD, we selected sample sites in Rock Creek based on average distances sampled upstream and downstream in Little Bear and Cedar creeks, beginning with the furthest accessible Rock Creek upstream site. These site-selection criteria led to sampling 3 to 5 sites upstream and downstream of impoundments and upstream and downstream of the midpoint in the unimpounded stream (hereafter, upstream and downstream sections). We had a total of 38 sites. BCD had 24 stream sites: 6 in Rock Creek (unimpounded), 8 in Cedar Creek (impounded), and 10 in Little Bear Creek (impounded). CRD had 14 stream sites: 6 in Shades Creek (unimpounded) and 8 in Little Cahaba River (impounded) (Table S1, Fig. 1).

We conducted sampling over 2 y (2015–2017) and at 2 spatial scales (within and between drainages). Because stream crayfishes in the southeastern USA normally mate and are most active during the spring or autumn, we sampled in the spring/summer (May–July, hereafter spring) and autumn/winter (September–December, hereafter autumn). We visited sites once/seasonal sampling round (1st y [BCD]: spring and autumn of 2015, 2nd y [portion of BCD and CRD]: autumn 2016 and spring 2017).

During the 1st y, we sampled streams within the BCD for within-drainage comparisons, and during the 2nd y we assessed streams in both the BCD and CRD for between-drainage comparisons. This sampling scheme allowed us to assess the effects of impoundments on crayfish assemblages in one drainage and then assess whether impoundment effects could be generalized across drainages. For the within-drainage comparisons, we sampled all 24 sites in the BCD. For the between-drainage comparisons, we sampled 2 streams (1 impounded and 1 unimpounded) each in the BCD ($n = 16$ sites) and CRD ($n = 14$). In the BCD, we re-sampled Rock and Little Bear creeks, selecting the latter to represent the drainage's impounded streams because its dam and impoundment were most similar in size to those in the Little Cahaba River.

At each site, we sampled 1 linear reach with a length 30× the wetted stream width or a minimum or maximum length of 200 or 500 m, respectively (Simon 2004). Reach lengths remained constant across seasons unless dry sections shortened a reach (Adams 2013). We divided each reach into 2 subreaches with equal lengths. Using 2 crews, we simultaneously electrofished upstream subreaches and kick seined downstream subreaches (see Barnett et al. 2021). Because the effectiveness of electrofishing depends on water clarity, we always used that method upstream to avoid the turbidity created by kick seining, whose effectiveness does not depend on water clarity. Within each subreach we sampled riffle and run macrohabitats (Bisson et al. 1982). We only sampled riffles and runs with maximum depths ≤1 m (≥85% of each reach) because of the ineffectiveness of our sampling methods in pools and deeper waters. Sampling efforts in each subreach were partitioned between macrohabitats in proportion to the % stream length of each macrohabitat. To standardize efforts, we calculated the total number of kick seines and the electrofishing duration, based on the area sampled within each stream, before sampling began, and once the target sampling effort was reached we stopped sampling (Barnett et al. 2021).

In upstream subreaches, we conducted single-pass electrofishing using a backpack electrofisher (programmable output wave, battery-powered electrofisher set at 50–60 Hz, 4–5 ms pulse width 300–500 V; model 12-A, Smith-Root, Vancouver, Washington) with a circular anode covered with 3-mm mesh and 2 dipnet operators (3-mm mesh nets). We recorded the area (m^2) sampled and electrofishing times, which ranged from 250 to 2000 s/subreach (3–8 s/m; mean 5 s/m ± 1.2 SD).

In downstream subreaches, we kick seined 20 plots (2 m long × 1.5 m wide) every 100 m (Simon 2004). We used a 2.6-m long × 1.6-m high seine with 3-mm mesh, polyester, knotless netting. In each subreach, 2 to 3 people alternated kicking. One person lifted large rocks and kicked to disturb the substrate immediately upstream of the seine. Each kick-seine plot was at least 2 m away from any previously sampled plot, and plots were randomly spaced throughout the subreach.

For all crayfishes captured, we recorded species, sex, life stage (i.e., adult, juvenile), and postorbital carapace length (POCL; mm). We used expert knowledge to identify crayfishes in the field. We preserved voucher specimens for each species in ≥70% ethanol, and we referred to Hobbs (1981) to confirm species identifications in the lab. We used the POCL of the smallest Form-I male (reproductive) to demarcate both male and female juveniles from adults (Barnett et al. 2017).

Quantifying drainage land use

To address our 3rd research question (Table 1), we classified recent and historical land uses for both drainages. To quantify recent land use for each stream's watershed, we used imagery from Landsat 8 Operational Land Imager (https://landsat.gsfc.nasa.gov/satellites/landsat-8/). We downloaded satellite imagery from United States Geological Survey Earth Explorer online remote sensing database (https://earthexplorer.usgs.gov) for the BCD (path/row: 21/36, accessed 27 August 2015) and CRD (path/row: 22/37, accessed 20 August 2015). Cloud-free images were downloaded to ensure proper classifications of agricultural lands. We classified land uses within each drainage as forest, water, agriculture (including grasses), barren, or developed, using supervised classifications in Earth Resources Data Analysis System Imagine (version 16; Hexagon Geospatial, Madison, Alabama). We merged 10 to 20 training classes for each land-use classification and used maximum likelihood calculations (Foody et al. 1992, Jia et al. 2011) to classify images. To assess classification accuracy, we overlaid 120 randomly selected stratified points on the original Landsat images and visually verified assigned land-use categories. The overall classification accuracy (mean = 90%) and Kappa statistics (mean = 0.81; Table S2) showed that supervised classifications were suitable for this assessment (Congalton and Green 1999, Tso and Mather 2001).

To quantify historical land uses for each watershed, we used 1:20,000 aerial photography (400 dpi) from the University of Alabama's cartographic research laboratory. BCD photographs were from 31 October 1970 (Rock Creek), 12 November 1971 (Little Bear Creek), and 16 November 1971 (Cedar Creek). CRD photographs were from 29 October 1960 (Little Cahaba River) and 15 November 1960 (Shades Creek). Photographs covered ≥94% of watersheds. We visually defined land uses using ArcGIS (version 10.5.1; Esri™, Redlands, California). We used 11-digit HUCs of each watershed (USGS 2009) to extract watersheds from each classified image and used attribute tables from extracted images to quantify the percentage of each land use within a watershed.

Historical land-use change To assess whether land-use changes over time might confound our interpretation of dam effects on crayfish assemblages, we examined whether any major land-use changes occurred within watersheds and whether recent (2015) or historical (1960–1971) land uses differed among watersheds (Table 1: Question 3). Each watershed's recent and historic land-use percentages were calculated and $\log_e$ (variable + 1) transformed to meet normality assumptions for maximum likelihood tests. Separately for each drainage, we calculated Euclidean distance matrices comparing land uses (recent and historical) between each pair of watersheds. We then used permutational analysis of variance (PERMANOVA), separately for each drainage, to test responses of land uses to 2 fixed effects: watershed and time (recent and historical). We tested for differences between recent and historical land uses within each watershed, as well as for differences in both recent and historical land uses among watersheds (BCD: $n = 3$, CRD: $n = 2$). All analyses were performed in the PRIMER software (version 7.0; Auckland, New Zealand) and the PERMANOVA add-on (Anderson et al. 2008) with 9999 permutations of residuals for the multivariate analysis.

Effects of dams on crayfish assemblages

Our research questions addressed the effects of impoundments on crayfish assemblages (Table 1: Questions 1 and 2). To test for differences in crayfish assemblages between impounded and unimpounded streams, we used both univariate and multivariate split-plot designs. Streams were whole-plot factors, and stream sections upstream or downstream of dams and midpoints were split-plot factors. Electrofishing and kick-seining data were characterized as number of crayfishes collected/100 m^2 and were summed for each reach for analyses. For univariate models, histograms of model residuals did not depart from normality, and for multivariate models, dispersion did not vary among groups. We did not find land-use differences among watersheds or over time (see Results), so we did not consider land use to be a potential confounding factor in the remaining analyses.

Assemblage comparisons To compare assemblages between impounded and unimpounded streams, we summarized crayfish assemblages in 3 ways: assemblage structure, density, and adult sizes. We combined all crayfish species collected at a site to calculate density and summarize adult sizes.

Assemblage structure comparisons To test if assemblage structures differed between impounded and unimpounded streams, we used PERMANOVA (Table 1: Question 1). We constructed separate models for each scaled comparison and square-root transformed densities to reduce the contribution of highly abundant species in relation to less abundant species in the analyses (Anderson et al. 2008). We calculated Bray–Curtis similarity matrices comparing assemblage structures between each pair of sites. We used PERMANOVAs to test responses of assemblage structures (response variable) to fixed effects. For within-drainage comparisons we used 3 fixed effects (stream, stream section [upstream/downstream], and season [spring/autumn]). For between-drainage comparisons we used 4 fixed effects (stream type [impounded/unimpounded], drainage [BCD/CRD], stream section, and season). Because sampling was unbalanced for within-drainage comparisons (BCD: 1 unimpounded vs 2 impounded streams), we assessed if there were differences among streams and used post-hoc pairwise comparisons to assess which streams differed. Sampling was balanced for between-drainage comparisons (2 unimpounded vs 2 impounded streams); therefore, stream type was used to assess differences between impounded and unimpounded streams.

PERMANOVA models included 2-way interactions of stream or stream type with stream section, season, and drainage (for between-drainage comparisons), as well as 3- and 4-way interactions (for between-drainage comparisons) with all fixed effects. Because we were only interested in assemblage structure differences between stream types, we did not interpret main effects of stream section, season, or drainage. We selected site as a random effect to account for repeated samples at each site, allowing intercepts to vary among sites. We used pairwise PERMANOVA to obtain p-values for interactive effects between pairs of sites. We also conducted 2-dimensional non-metric multidimensional scaling (NMDS; Clarke 1993) to visualize differences in assemblage structures identified by PERMANOVA. We used the PERMANOVA add-on (Anderson et al. 2008) in PRIMER to conduct NMDS and analyze data, with 9999 permutations of residuals in both the main tests and post-hoc pairwise comparisons.

Density comparisons To test for differences in crayfish density between impounded and unimpounded streams, we compared $\log_e$ density (+0.001) of all species combined using linear mixed-effect repeated-measures models in separate analyses for adult and juvenile crayfishes (Table 1: Question 1). We constructed separate models for each scaled comparison and log transformed the data to meet normality assumptions for maximum likelihood tests. We used the same fixed and random effects described above in PERMANOVA models to assess densities in linear mixed-effect models and used Tukey's honestly significant difference post-hoc tests for comparing means. Analyses were performed with the lmer function of the *lmerTest* package (version 2.0; Kuznetsova et al. 2015) in R software (version 3.4.2; R Project for Statistical Computing, Vienna, Austria).

Adult size comparisons To test for differences in adult crayfish sizes between impounded and unimpounded streams, we compared crayfish POCLs using 1-way (within-drainage) and 2-way (between-drainage) analysis of variance (ANOVA) models in separate analyses for small and large adults (Table 1: Question 1). We calculated the 25th and 75th percentiles of POCLs for each site (combined across seasons) to represent the size of small and large crayfishes, respectively, of all species at each site. Using the 25th and 75th percentiles of POCLs allowed us to assess differences in adults of species with smaller (e.g., carapace length [CL]: 50 mm) and larger (CL: 100 mm) maximum sizes between stream types (Taylor and Schuster 2004). Because adults of species with smaller and larger maximum sizes were present during spring and autumn sampling, we did not assess seasonal differences between size classes.

For within-drainage comparisons, we investigated if adult sizes differed among streams, and used Tukey's honestly significant difference post-hoc tests to assess differences between impounded and unimpounded streams. We included an interaction of stream with stream section to test if adult size differences among streams were consistent between stream sections. For between-drainage comparisons, we investigated if adult sizes differed between stream types. We included 2-way interactions of stream type with drainage and stream section to test if adult size differences between stream types were consistent between drainages and stream sections. ANOVA was performed with the aov function of the *stats* package in R.

Assemblage changes with distance from impoundments

We compared assemblage structure among sites within each upstream and downstream section, separately for each stream, to test if crayfish assemblage structure changed with distance away from the impoundment—or from the stream midpoint in unimpounded streams (Table 1: Question 2, Table S1). We calculated Bray–Curtis similarity matrices, comparing assemblage structures (square-root transformed densities) between each pair of sites within each stream for within- and between-drainage comparisons separately, and assessed differences by PERMANOVA. Because only categorical variables can be used in PERMANOVA, we used dummy variables to categorize distance, with numbers increasing with distance from impoundments or midpoints. Sites directly upstream or downstream of impoundments and midpoints were labeled as 1, and each sequential site was labeled with the next higher number, with stream upstream and downstream sections having 3 to 5 dummy variables each. To distinguish between assemblage structure changes upstream vs downstream of impoundments, interactions of distance and stream section were included in models. Site was a random effect to account for repeated sampling of sites. Only distance and its interactions were interpreted. Data were analyzed in PRIMER, with Monte Carlo simulations used to estimate distribution under the null hypothesis (i.e., no difference in crayfish assemblage structure with distance from impoundment) for overall tests and pairwise PERMANOVA comparisons (Anderson et al. 2008).

RESULTS

Assessment of land-use differences among drainages and years

Forest and agriculture were the dominant land uses in BCD watersheds recently (mean: 80 and 12%, respectively) and historically (mean: 75 and 20%, respectively; Table 2, Fig. S1A, B). Recent and historical land uses did not

Table 2. Recent and historical land-use percentages for each watershed in the Bear Creek drainage (BCD) and Cahaba River drainage (CRD), Alabama, USA. Recent land-use data are from 2015 for both drainages. Historical data are from 1960 (CRD) and 1970 to 1971 (BCD).

Drainage	Watershed	Land use	Historical %	Current %	Difference
BCD	Little Bear	Agriculture	23.0	12.8	−10.2
		Water	0.1	3.0	2.9
		Barren	0.8	2.3	1.5
		Forest	75.1	79.9	4.8
		Developed	1.1	2.0	0.9
	Cedar	Agriculture	23.1	14.5	−8.6
		Water	0.4	3.8	3.4
		Barren	1.6	2.4	0.8
		Forest	71.4	74.3	2.9
		Developed	3.6	5.0	1.4
	Rock	Agriculture	13.4	8.2	−5.2
		Water	0.8	1.0	0.2
		Barren	6.6	2.6	−4.0
		Forest	77.6	86.2	8.6
		Developed	1.7	1.9	0.2
CRD	Little Cahaba	Agriculture	19.2	1.7	−17.5
		Water	2.4	2.5	0.1
		Barren	3.2	5.2	2.0
		Forest	69.1	76.0	6.9
		Developed	6.0	14.6	8.6
	Shades	Agriculture	12.1	4.2	−7.9
		Water	0.1	0.6	0.5
		Barren	7.3	4.3	−3.0
		Forest	74.1	62.6	–11.5
		Developed	6.3	28.3	22.0

differ statistically within any watershed in the drainage (PERMANOVA $F_{1,5} = 3.40$, $p = 0.16$) or among watersheds during either time period (recent: $F_{1,5} = 1.71$, $p = 0.24$; historical: $F_{1,5} = 2.51$, $p = 0.11$). The largest changes from historical (1970–1971) to recent (2015) land uses were conversions of agricultural lands to forests (mean absolute difference = 8.0%) and water (mean absolute difference = 3.2%; Table 2). Agricultural lands were converted to forests in all watersheds but to surface waters only in watersheds with impounded streams.

In the CRD, forest and developed lands dominated land uses during the study (2015 mean = 69 and 21%, respectively), and forest and agriculture dominated historically (1960 mean = 72 and 16%, respectively; Table 2, Fig. S1C, D). Nonetheless, recent and historical land uses did not differ in the drainage (PERMANOVA $F_{1,3} = 5.62$, $p = 0.26$). Similarly, neither recent ($F_{1,3} = 1.83$, $p = 0.26$) nor historical ($F_{1,3} = 3.96$, $p = 0.33$) land uses differed between watersheds in the drainage. The largest changes from historical to recent land uses were conversions of forest and agriculture to developed lands (mean absolute difference = 15%). Because aerial photographs pre-dating the Little Cahaba River dam were not available, we could not assess land-use changes since the pre-dam era.

Assemblage comparisons

We collected 13 crayfish species, with 7 and 8 species in the BCD and CRD, respectively (Fig. 2A–C). Crayfishes were collected in 97% of sites during the study, with densities ranging from 0 to 20 crayfish/100 m^2. *Faxonius validus* (Faxon, 1914) and *Faxonius erichsonianus* (Faxon, 1898) were the most abundant (≥30% of individuals collected) and widespread (present in >90% of sites) species in the BCD. The most abundant and widespread species in the CRD was *Faxonius virilis* (Hagen, 1870), an introduced species native to the Upper Mississippi River and Great Lakes drainages (Hobbs 1959, Schwartz et al. 1963, Hamr 2002). *Faxonius erichsonianus* and *Cambarus striatus* Hay, 1902 were collected in both drainages.

Assemblage structure comparisons Assemblage structures differed between impounded and unimpounded streams only in the BCD (Tables S3, S4, Fig. 3A, B). Species density and richness were higher in unimpounded compared with impounded BCD streams, whereas species density and richness were similar between impounded and unimpounded streams in the CRD. Assemblage structures differed between upstream and downstream sections of unimpounded streams in both drainages, but not of impounded streams in either drainage (Tables S3, S4, Fig. 3A, B). Two species dominated all sites in impounded streams, whereas the dominant species differed between upstream and downstream sections of unimpounded streams (Fig. 2A–C). The NMDS ordinations of species assemblages at each site reflect the

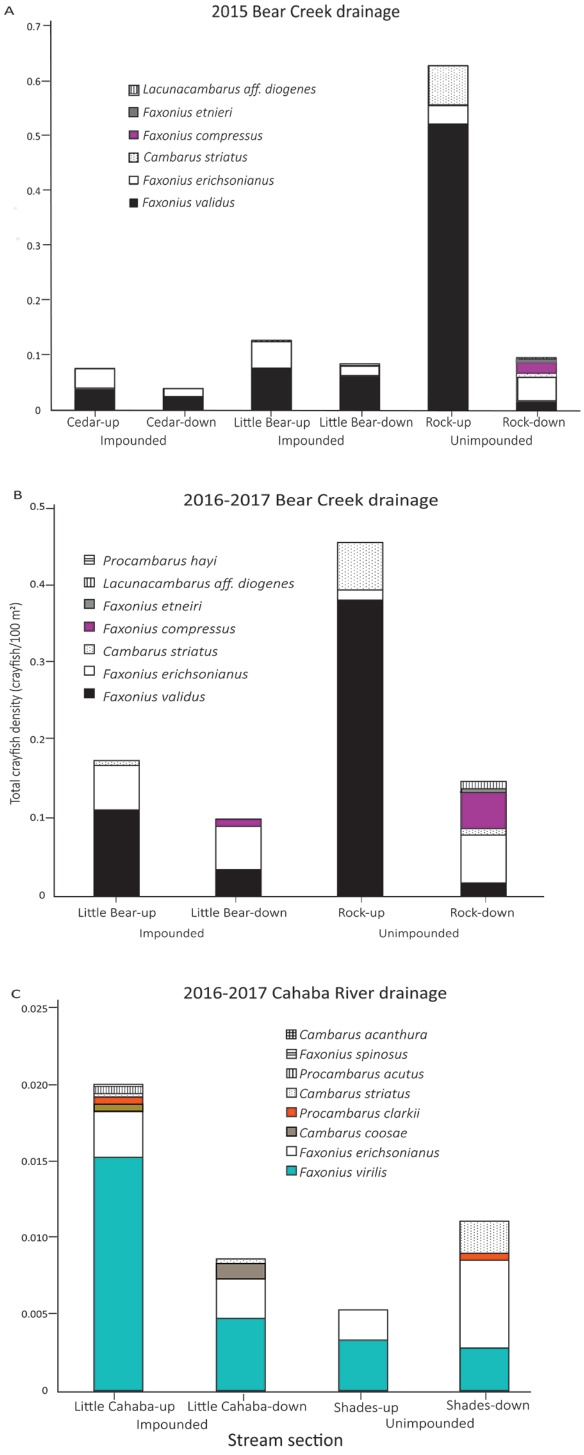

Figure 2. Total crayfish density (crayfish/100 m^2) in upstream and downstream sections of impounded and unimpounded streams for within- (A) and between-drainage (B, C) comparisons in the Bear Creek and Cahaba River drainages, Alabama, USA. Bear Creek drainage sampling was done in spring and autumn of 2015 (Cedar, Little Bear, and Rock creeks) (A) and autumn 2016 and spring 2017 (Little Bear and Rock creeks) (B). Cahaba River drainage sampling was done in autumn 2016 and spring 2017 (Shades Creek and Little Cahaba River) (C). Up = upstream, Down = downstream.

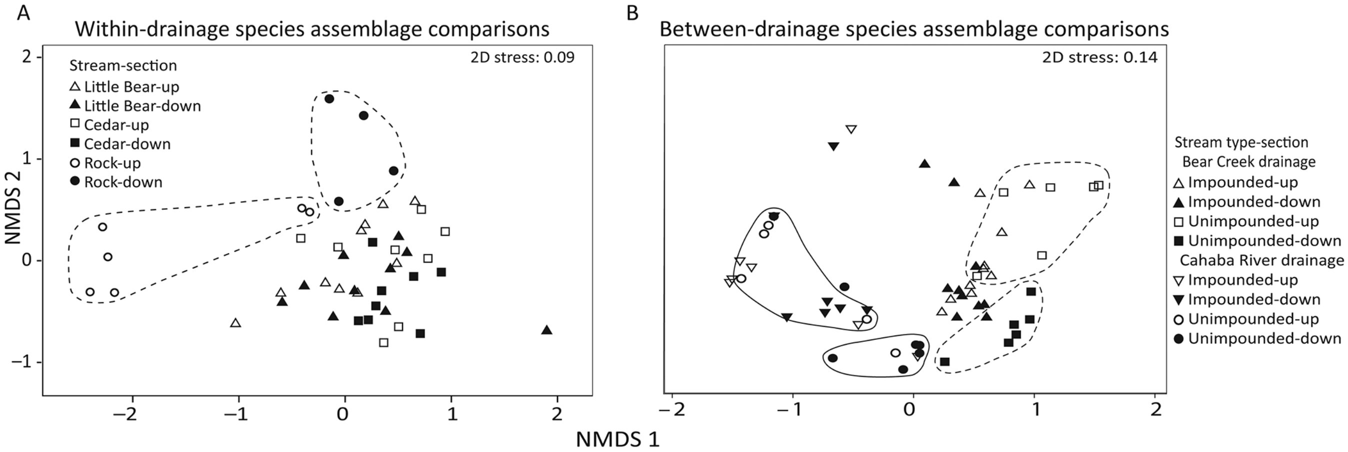

Figure 3. Assemblage structure nonmetric multidimensional scaling (NMDS) ordinations of within- (A) and between-drainage (B) comparisons in the Bear Creek and Cahaba River drainages, Alabama, USA. Symbols represent sites from each stream (A) or stream type (B) and sections within streams (upstream or downstream). Distance between symbols reflect their Bray–Curtis dissimilarities based on species densities in 2-dimensional ordination space. Some symbols overlap. Upstream and downstream sections of unimpounded streams are enclosed by hand-drawn dashed (Bear Creek drainage) or solid (Cahaba River drainage) polygons to highlight differences in assemblage structures (permutational analysis of variance, $p < 0.05$ for unimpounded stream sections, see assemblage structure comparison results). Up = upstream, Down = downstream.

relationships identified by PERMANOVA for species assemblages within unimpounded and impounded streams (NMDS, within drainage: $k = 2$, stress = 0.09, $p = 0.001$, Fig. 3A, S2A, B, S3A, B; between drainage: $k = 2$, stress = 0.14, $p = 0.006$, Fig. 3B, S2A, B, S3A, B).

Density comparisons Adult and juvenile densities averaged 0.4 (range = 0.0–2.3) and 0.7 crayfish/100 m^2 (range = 0–11.6), respectively, across all streams and seasons. Adult densities were 69% higher in both upstream and downstream sections of unimpounded than impounded streams in the BCD (Tables 3 S3, S4). In the CRD, adult densities were 37% higher in downstream sections of unimpounded than impounded streams. Juvenile densities were higher in unimpounded than impounded streams only in the BCD (Tables 3, S3, S4). For within-drainage comparisons, juvenile densities were 94% higher in upstream sections of the unimpounded stream than any other stream sections (Fig. 4A). For between-drainage comparisons, juvenile densities were 83% higher in both upstream and downstream sections of unimpounded than impounded BCD streams (Fig. 4B).

Adult size comparisons Sizes of small (25th percentile) and large (75th percentile) adults averaged 14.1 (range = 9.7–24.9) and 19.7 mm (range = 12.5–34.4) POCL, respectively, across all streams and seasons. Sizes of large adults did not differ between impounded and unimpounded streams in either drainage (Tables 3, S3). However, sizes of small adults differed between sections of impounded and unimpounded streams in both drainages (Tables 3, S3, S4). Small adults were smaller downstream in unimpounded than impounded streams (within-drainage: Fig. 5A; between-drainage: Fig. 5B), and smaller downstream than upstream within unimpounded streams (within-drainage: Fig. 5A; between-drainage: Fig. 5B). Sizes of small adults did not differ between upstream and downstream sections of impounded streams.

Assemblage changes with distance from impoundments

For within-drainage comparisons, assemblage structure changed with distance upstream in impounded and unimpounded streams (PERMANOVA $F_{14,45} = 2.95$, $p < 0.01$). Assemblage structure did not differ with distance downstream of dams in any stream. Sites directly upstream of the Cedar Creek impoundment were dominated (>70% of individuals collected) by *F. erichsonianus*, but *F. validus* became dominant with distance upstream (site C4 compared with sites C1 [$p = 0.04$] and C2 [$p = 0.01$]; site C3 compared with sites C2 [$p = 0.04$]). In Rock Creek, *F. validus* and *F. erichsonianus* dominated assemblages near the midpoint, whereas *F. validus* and *C. striatus* dominated sites farther upstream (site R1 compared with sites R2 [$p < 0.01$] and R3 [$p = 0.02$]).

Conversely, for between-drainage comparisons, assemblage structure changed with distance downstream only in impounded streams ($F_{18,59} = 3.10$, $p < 0.01$). In Little Cahaba River, *F. erichsonianus* and *F. virilis* were the only species collected directly downstream of impoundments, but *C. striatus* and *Cambarus coosae* (Hobbs, 1981) became abundant (>40% of individuals collected) with distance downstream (site LC5 compared with sites LC7 [$p = 0.01$] and LC8 [$p < 0.01$]). In Little Bear Creek, *F. erichsonianus*

Table 3. Means and magnitude of change for crayfish densities (crayfish/100 m^2) and sizes (postorbital carapace length, mm) between impounded and unimpounded streams for within- and between-drainage efforts in the Bear Creek drainage (BCD) and Cahaba River drainage (CRD), Alabama, USA. Within-drainage analyses assess the differences between each stream ($n = 3$) in the BCD. Between-drainage analyses assess the differences between impounded and unimpounded streams across both the BCD and CRD. Only interactions with p-values <0.05 are listed (Table S3). W-D = within-drainage, B-D = between-drainage, LB = Little Bear Creek, C = Cedar Creek, R = Rock Creek, I = impounded, U = unimpounded, × = interaction between fixed effects.

Effort	Assemblage measure	Fixed effects	Levels	Mean	Magnitude of change
W-D	Adult density	Stream	LB	0.36	LB–C: 0.38
			C	0.22	LB–R: −1.58
			R	0.93	C–R: −3.23
		Section × Stream	Upstream		
			LB	0.52	LB–C: 0.40
			C	0.31	LB–R: −1.06
			R	1.07	C–R: −2.45
			Downstream		
			LB	0.20	LB–C: 0.38
			C	0.13	LB–R: −1.58
			R	0.72	C–R: −3.23
B-D		Stream type	I	0.30	I–U: −0.77
			U	0.53	
		Drainage × stream type	BCD		
			I	0.41	I–U: −1.07
			U	0.85	
			CRD		
			I	0.17	I–U: −0.29
			U	0.22	
		Section × stream type	Upstream		
			I	0.37	I–U: −0.49
			U	0.55	
			Downstream		
			I	0.23	I–U: −1.22
			U	0.51	
W-D	Juvenile density	Stream	LB	0.22	LB–C: 0.32
			C	0.15	LB–R: −13.14
			R	3.11	C–R: −19.73
		Section × stream	Upstream		
			LB	0.18	LB–C: 0.06
			C	0.17	LB–R: −24.89
			R	4.66	C–R: −26.41
			Downstream		
			LB	0.26	LB–C: 0.50
			C	0.13	LB–R: −2.00
			R	0.78	C–R: −5.00
B-D		Stream type	I	0.25	I–U: −3.00
			U	1.00	
		Drainage × stream type	BCD		
			I	0.31	I–U: −4.97
			U	1.85	

Table 3. (*Continued*)

Effort	Assemblage measure	Fixed effects	Levels	Mean	Magnitude of change
			CRD		
			I	0.16	I–U: 0.00
			U	0.16	
W-D	Sizes of small adults	Stream	LB	13.89	LB–C: 0.00
			C	13.89	LB–R: 0.09
			R	12.70	C–R: 0.09
		Section × stream	Upstream		
			LB	14.62	LB–C: 0.01
			C	14.48	LB–R: 0.01
			R	14.49	C–R: 0.00
			Downstream		
			LB	13.16	LB–C: –0.01
			C	13.28	LB–R: 0.17
			R	10.91	C–R: 0.18
B-D		Stream type	I	14.57	I–U: 0.02
			U	14.37	
		Section × stream type	Upstream		
			I	14.06	I–U: –0.20
			U	16.90	
			Downstream		
			I	15.15	I–U: 0.22
			U	11.84	
W-D	Sizes of large adults	Stream	LB	18.46	LB–C: –0.07
			C	19.79	LB–R: 0.04
			R	17.67	C–R: 0.10
B-D		Stream type	I	21.29	I–U: 0.08
			U	19.67	

and *F. validus* were the only species collected directly downstream of impoundments, but *Faxonius compressus* (Faxon, 1884) became abundant (>20% of individuals collected) with distance downstream (site LB6 compared with sites LB7 [$p = 0.03$], LB8 [$p = 0.01$], LB9 [$p = 0.02$], LB10 [$p = 0.03$]). *Faxonius erichsonianus* and *F. validus* were also the only species collected directly downstream of Little Bear Creek's dam during within-drainage comparisons, but <10% of the collections further downstream were *F. compressus*; therefore, we did not identify differences between sites with distance downstream of the dam in within-drainage comparisons. In unimpounded streams, assemblage structures did not change with distance upstream or downstream from midpoints during between-drainage comparisons. In contrast with within-drainage results, *C. striatus* was collected throughout the entire upstream section in Rock Creek during between-drainage comparisons, creating similar assemblage structures near the midpoint and further upstream.

DISCUSSION

In this study, which is the 1st to assess effects of relatively large dams and associated impoundments on crayfish assemblages, we found differences in assemblage structure and composition downstream of impoundments compared with unimpounded streams. We found lower adult densities and larger small adults downstream from dams relative to reaches in unimpounded streams in both studied drainages. Crayfish assemblages were also homogenized in only impounded streams in both study drainages. Conversely, crayfish assemblage structure differed between impounded and unimpounded streams in only the BCD. Numerous factors influenced by dams, including reduced habitat complexity and increased predators, could be affecting crayfish densities and size composition. Other factors affecting only CRD streams, such as urbanization and an invasive crayfish species, may also affect crayfish assemblages, resulting in inconsistent differences in assemblage structure between drainages.

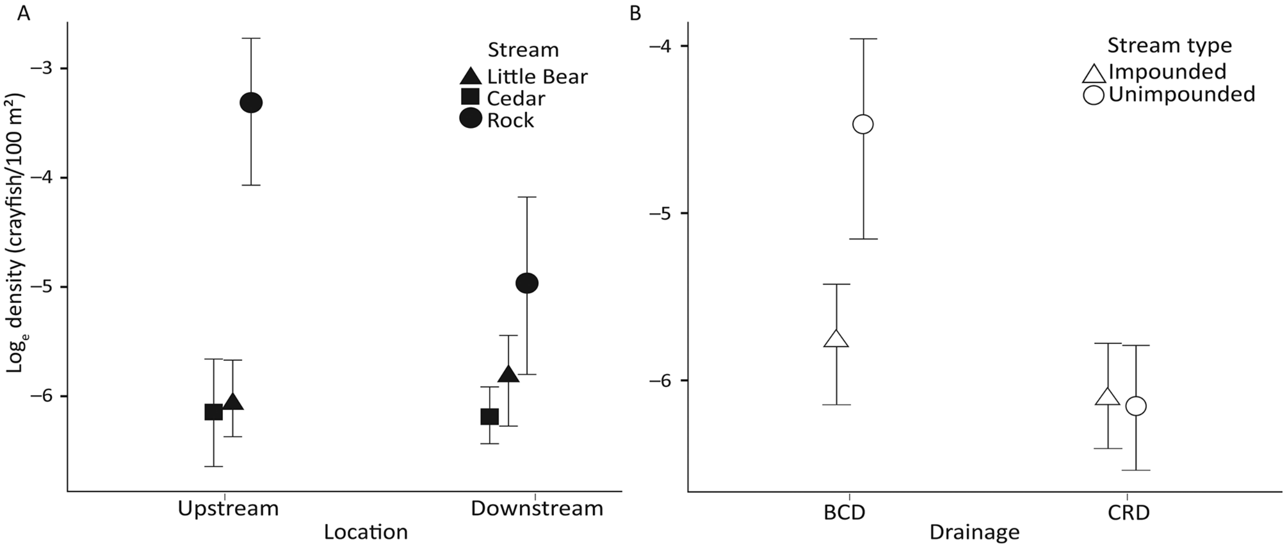

Figure 4. Comparisons of juvenile crayfish density (±95% CI) between upstream vs downstream sites in the Bear Creek drainage (BCD), Alabama, USA, for within-drainage comparisons (A) and between impounded vs unimpounded sites in the BCD and Cahaba River drainage (CRD) for between-drainage comparisons (B). Only relationships where interactions in linear mixed-effect repeated measures analyses had p-values <0.05 are displayed.

Effects of impoundments on crayfish assemblages

Large dams reduced crayfish densities in our study streams; however, small dams can have both positive and negative impacts on crayfish densities (Joy and Death 2001, Adams 2013, Barnett and Adams 2021). In our study streams, adult densities were higher downstream in unimpounded than impounded streams. In New Zealand streams, the density of *Paranephrops planifrons* White, 1842, the only crayfish species collected, was higher upstream of reservoirs than in unimpounded streams (Joy and Death 2001). In Mississippi streams, catch per unit effort (CPUE) of *Faxonius etnieri* spp. complex was lower downstream of small impoundments than in unimpounded streams, whereas CPUE of *Procambarus* spp. was either

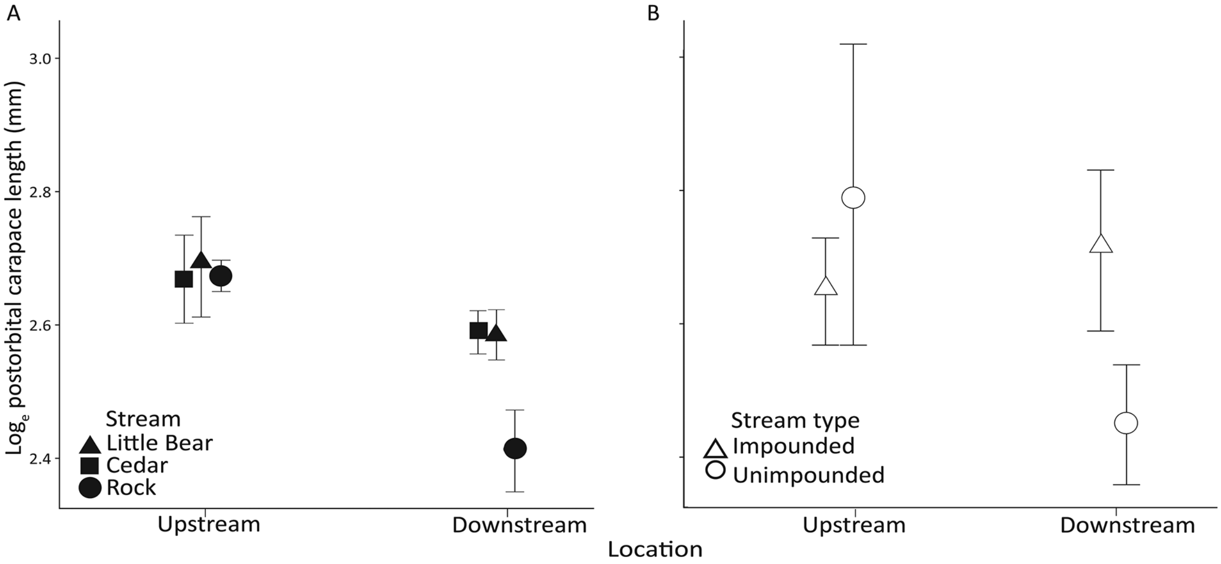

Figure 5. Comparisons of sizes of small adult crayfishes (25th percentile of postorbital carapace lengths ±95% CI) in the Bear Creek and Cahaba River drainages, Alabama, USA, between upstream and downstream sites in within- (A) and between-drainage (B) comparisons. Only relationships where interactions in analysis of variance analyses had p-values <0.05 are displayed.

higher downstream of impoundments or similar among stream types (Adams 2013). Although we did not assess densities by species, *Faxonius* was the most dominant genus collected and, like *F. etnieri* spp. complex in Mississippi, adult densities were higher in unimpounded streams. Given that impoundments can differentially affect crayfish CPUE, depending on the genus (Adams 2013, Barnett and Adams 2021), further study is needed to assess genus and species responses to dams. Our findings of lower adult densities in impounded streams were in line with published research on macroinvertebrate taxa (e.g., Ephemeroptera, Plecoptera, and Trichoptera) sensitive to pollution and anthropogenic changes (e.g., simplified habitats, smaller substrate sizes, flashier hydrographs) but contrasted with findings for less sensitive taxa (Williams and Winget 1979, Holt et al. 2015, Mbaka and Mwaniki 2015, Krajenbrink et al. 2019). Reduced crayfish density can lead to inbreeding and population extirpation (Light et al. 1995, Fetzner and Crandall 2001), as well as to habitat changes, such as increased aquatic vegetation and decreased substrate mobilization (Statzner et al. 2000, Dorn and Wojdak 2004, Johnson et al. 2011). Food-web changes may also occur as crayfish density decreases because crayfishes play important trophic roles within aquatic systems (Hobbs 1993, Parkyn et al. 1997, Englund and Krupa 2000, Usio 2000, Holdich 2002). Because this is the 1st study assessing the impacts of relatively large dams on crayfishes, and only 2 drainages were assessed, more data are needed to determine crayfish responses to dams on a taxon-specific and more general basis.

Dam effects on habitat complexity and crayfish predators (e.g., fishes) can drive changes in aquatic assemblages (Cushman 1985, Wang et al. 2011, Ellis and Jones 2013). In this study, lower adult densities and fewer small species were collected downstream in impounded than unimpounded streams. Habitats that crayfishes use for protection from predators, such as aquatic vegetation, woody debris, and interstitial spaces (Stein 1977, Englund and Krupa 2000, Olsson and Nyström 2009), are often reduced downstream of dams. These habitats are important for crayfish survival, providing heterogeneous sources of food and refuge, which can increase crayfish density (Reynolds et al. 2013). Small crayfishes are more susceptible than larger ones to gape-limited predators (e.g., fishes), and large crayfishes obtain and retain shelter better than small crayfishes (Rabeni 1985, Ranta and Lindström 1993, Alonso and Martínez 2006). Therefore, reducing stream habitat complexity often puts small crayfishes at greater predation risk. Additionally, some predator fishes, especially game fishes, have higher tolerances of altered conditions (Taylor et al. 2001, Phillips and Johnston 2004) and are often more abundant in impounded streams because of fish stocking, which occurs in BCD impoundments (ADCNR 2021a, b). Greater than 40% of the diets of many game fish species (e.g., basses and catfishes) consist of crayfishes (Dorn et al. 1999). Thus, the synergy between increases in game fishes and decreases in habitat complexity potentially greatly increase predation pressure on crayfishes, especially smaller individuals.

Crayfish recover with distance downstream of impoundments

During between-drainage comparisons, crayfish assemblage structures gradually changed with distance downstream of impoundments. Species richness and densities of less-dominant crayfish species increased with distance downstream from impoundments, indicating the potential for species recovery (e.g., assemblages becoming more similar to unimpounded stream assemblages) with sufficient downstream distance from impoundments. Fishes, mussels, and aquatic insects exhibit a similar longitudinal pattern as crayfishes with respect to impoundments (Voelz and Ward 1991, Kinsolving and Bain 1993, McGregor and Garner 2003). Conversely, crayfish assemblage structures did not change with distance downstream of impoundments in within-drainage comparisons. Differing flow conditions between sampling years, which can affect crayfish collections, may have contributed to these contrasting results. Severe-to-exceptional drought conditions occurred throughout the study region during autumn 2016 (between-drainage sampling), with <50% of normal precipitation in study areas (Konrad and Knox 2017). Lower flows and water levels during between-drainage sampling, may have increased sampling efficiency of primarily stream-dwelling crayfishes, increasing the likelihood of collecting rarer species. However, we did not assess if there was a downstream pattern in environmental factors (e.g., flow, DO, pH), so we cannot infer what drove the downstream pattern in crayfish assemblages.

Crayfish assemblage structure changed with distance upstream of the Rock Creek midpoint and Cedar Creek impoundment. However, unlike in Rock Creek where less dominant species (e.g., *C. striatus*) became abundant with distance upstream, this did not occur in the Cedar Creek impoundment. Thus, upstream recovery did not occur in any impounded stream. *Faxonius erichsonianus* and *F. validus* were the most abundant crayfishes collected upstream of BCD impoundments, with very few collections of any other crayfish species. These species were also the most abundant crayfishes found in guts of fishes in BCD impoundments (37 of 42 identified: ZCB, unpublished data), indicating that they were the dominant crayfish prey of predatory fishes. Impoundments often function as hubs for habitat generalist species, with generalists abundant within and upstream of impoundments and no changes in assemblages with distance upstream (Herbert and Gelwick 2003, Light 2003, Falke and Gido 2006, Johnson et al. 2008). Further, impoundments may be serving as hubs in the BCD, facilitating the expansion and spread of crayfishes adapted to both lentic and lotic conditions (Light 2003, Johnson et al. 2008), which may subsequently decrease the abundance of other native crayfishes through competition for resources.

Potential impacts to stream ecosystem function

Crayfish assemblage structure differences were detected between impounded and unimpounded streams in only the BCD, potentially affecting stream ecosystem function because of differences in the functions and life-history traits of the species present. In the CRD, the same species were present in the unimpounded and impounded streams. Conversely, in the BCD, *F. validus* and *F. erichsonianus* were the only species collected at most impounded stream sites, whereas these species, along with *C. striatus* and *F. compressus*, were abundant in unimpounded streams. Decreased richness in impounded BCD streams highlights the potential for impoundments to affect the ecosystem functions influenced by crayfishes. For instance, *F. validus* and *F. erichsonianus* prefer run habitats (we collected >70% of individuals in runs), burrowing only during dry conditions (Bouchard and Bouchard 1976, Cooper and Hobbs 1980). In contrast, *F. compressus* prefers riffles (we collected 81% of individuals in riffles), digging shallow burrows under substrate (Bouchard 1972, Jones and Eversole 2015), and *C. striatus* seasonally occupies streams (we collected equal amounts in riffles and runs), burrowing in stream banks and floodplains during portions of the year (Bouchard 1978, Hobbs 1989, Stoeckel et al. 2011). Because of their differences in preferred habitats and burrowing behaviors, *F.compressus* and *C. striatus* may affect different functions (e.g., altering substrate composition [Statzner et al. 2000]) and occupy different trophic levels than *F. validus* and *F. erichsonianus* (Larson et al. 2017, Stites et al. 2017). Future studies are needed to assess changes in ecosystem functions caused by impoundment effects on crayfishes.

Potential confounding factors

Land use is a key driver of stream habitat complexity (e.g., availability of interstitial space, abundance of aquatic vegetation and woody debris) and species diversity (Paul and Meyer 2001, Wang et al. 2001, Gragson and Bolstad 2006), and changes to land use could cause subsequent changes to stream biota, potentially confounding interpretation of our results. In the BCD, where we assessed land use before dam installations, surface water area was the only land-use category that changed over time, due directly to the construction of impoundments. Thus, we inferred that the installation and operation of dams in the BCD contributed directly to crayfish assemblage differences between impounded and unimpounded streams, but it is unclear if it is the sole contributor. The installation and operation of impoundments were also inferred as the cause of changes in fish assemblages in the BCD (Phillips and Johnston 2004). In the CRD, dam installation and operation, as well as urbanization may have affected crayfish assemblages. The mean percentage of developed lands in the CRD increased from 6.2% in 1960 to 21.5% in 2015. Although no significant differences were detected between historical and recent land uses within the CRD in our analysis, increasing urbanization >10% can drastically decrease stream species richness and abundances (Wang et al. 2000). Changes in land use between historical and recent years may have been difficult to detect in our analyses because of small sample sizes (5 streams), resulting in low statistical power. Thus, we cannot reject the possibility of an urbanization effect, which can affect all streams in a drainage (i.e., impounded and unimpounded streams) in multiple ways (Wolman 1967, Hollis 1975, Booth 1991, Gregory et al. 1992, Paul and Meyer 2001, Walsh et al. 2005, Wheeler et al. 2005, McGrane 2016). Moreover, crayfish assemblage similarities between impounded and unimpounded streams in the CRD may be due, in part, to urbanization.

Invasive species and habitat modification are the leading contributors to population declines of native crayfishes globally (Lodge et al. 2000, Taylor et al. 2007, Richman et al. 2015). *Faxonius virilis*, an introduced species, was abundant throughout both streams in the CRD, whereas only native crayfishes were collected in the BCD. Thus, differences in assemblage responses to impoundments between drainages may be due to the presence of *F. virilis* in the CRD (Schuster et al. 2008, Adams 2020). Invasive species may displace native species by outcompeting natives for food and habitat, preying on native species, and altering turbidity and stream habitat structure (Chambers et al. 1990, Light et al. 1995, Hill and Lodge 1999, Twardochleb et al. 2013). Research assessing synergistic effects of impoundments, invasive crayfishes, and urbanization is needed.

Impoundments were managed differently, with BCD impoundments managed for flood control and CRD impoundment for municipal water use. Although management objectives differed, stabilizing flow in impounded streams should impact stream ecosystems similarly. Flow stabilization may reduce the geomorphic complexity of streams, decreasing habitats such as sand/gravel bars and shallow-water habitats (Poff et al. 1997, Graf 2006) that are essential for habitat specialists (Beschta and Platts 1986, Gilvear et al. 2007), such as *F. compressus* (abundant in only the BCD unimpounded stream). Flow stabilization also reduces peak flows, reducing stream–floodplain interactions (Baxter 1977) that are important for crayfishes (Helms et al. 2013) such as *C. striatus* (abundant in only unimpounded study streams), a secondary burrowing species that uses floodplain and stream habitats seasonally. Although impoundment management objectives were a potential confounding factor in our study, we infer that effects of impoundment on flow stabilization was the principal driver, with timing of water release a contributing factor, of variation in crayfish assemblages.

Overall, we found that dams and their impoundments altered crayfish species assemblages relative to unimpounded streams, with greater assemblage differences in downstream than upstream sections. Impounded stream conditions were less favorable for most crayfishes, decreasing or eliminating habitat-specialist species. With >20,000 large impoundments in the southeastern USA (NID 2009) and >270 crayfish species endemic to the region (Taylor et al. 2007), dams may affect hundreds of crayfish species in thousands of stream km (Smith et al. 2002, Adams 2013), possibly altering stream systems by interfering with the numerous ecosystem functions influenced by crayfishes.

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