Effects of small impoundments on downstream crayfish assemblages

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Abstract. Dams and impoundments, both large and small, affect downstream physicochemical characteristics and up- and downstream biotic communities. I tested whether small dams and their impoundments altered downstream crayfish assemblages in northern Mississippi. I sampled crayfish and measured physicochemical variables at 4 sites downstream of impoundments (outlet sites) and 4 sites not influenced by impoundments (undammed sites) in August, September, and November 2004. In November 2010, I sampled 7 undammed, 6 outlet, and 3 intermediate sites (influenced by beaver activity or ~1 km downstream of an impoundment). Crayfish assemblages differed between undammed and outlet sites. Catch-per-unit-effort (CPUE) of *Orconectes* (*Trisellescens*) sp. was higher in undammed than outlet sites in both years. *Procambarus* (*Pennides*) spp. CPUE was lower in undammed than outlet sites in November 2010 and nearly so in November 2004. In 2004, *Procambarus* (*Ortmannicus*) *hayi* was common in autumn at outlet sites but virtually absent from undammed sites, but in 2010, *P. hayi* CPUE did not differ between categories. *Cambarus striatus* CPUE, which was low overall, did not differ between categories in 2004 but was higher in undammed sites in 2010. Seasonal differences among taxa in reproductive timing were important to understanding impoundment effects. The most consistent difference in habitat was that undammed sites had significantly higher width:depth ratios than did outlet sites. Based on the number of mapped small impoundments and a conservative estimate that each impoundment influenced crayfish assemblages over 2 km, I estimated that impoundments probably affect crayfish assemblages in >284 km of stream in the upper Little Tallahatchie River subbasin. Extrapolated to the entire Gulf Coastal Plain, impoundments may influence crayfish assemblages over thousands of stream kilometers.

Key words: dams, impoundments, crayfish, streams, assemblage structure, habitat, Mississippi, seasonality.

Influences of reservoirs on streams vary depending on impoundment size, physiographic and climatic setting, location in the drainage, condition of water flowing into the reservoir, and season. Regardless of the variation, nearly every study has shown some downstream effects of impoundments on biota, and some have shown upstream effects. Downstream effects include both physicochemical and biological changes and occur below small ponds (Mackay and Waters 1986, Smith et al. 2002) and large reservoirs (Palmer and O'Keeffe 1990b, Graf 2006). Downstream physicochemical effects commonly include changes in hydrology, including increased incidence of stream drying, thermal regime, conductivity, nutrients, turbidity, and pollutants (Palmer and O'Keeffe 1990a, b, Camargo et al. 2005, Arnwine et al. 2006, Gangloff et al. 2011). Biotic changes often include increases in

chlorophyll *a* and invertebrate biomass (Mackay and Waters 1986) and decreases in invertebrate diversity or shifts in assemblage composition (Vaughn and Taylor 1999, Lessard and Hayes 2003, Arnwine et al. 2006). Increases in densities of freshwater mollusks (Gangloff et al. 2011) and numerous changes in fish communities occur below dams in the southeastern USA (Helms et al. 2011). Impoundments also influence upstream communities, including fish (Ruhr 1956, Winston et al. 1991, Pringle 1997, Porto et al. 1999, Helms et al. 2011), atyid shrimps, and other organisms (Pringle 1997).

Given the observed effects of impoundments and dams on other faunal groups, one may also expect to find impacts on crayfishes. However, no published studies have focused on the effects of impoundments on downstream crayfish assemblages. During a study of recolonization by fishes and crayfishes after drought in northern Mississippi streams (Adams
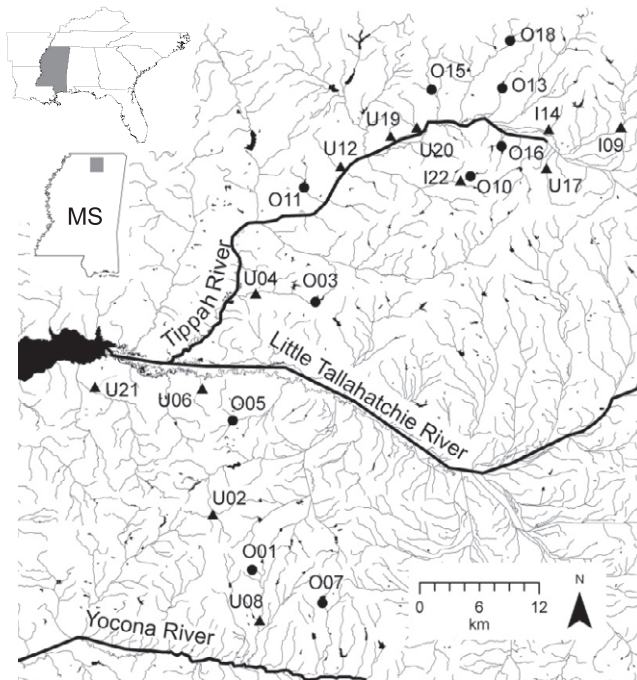
FIG. 1.   Study area in northern Mississippi, USA. Letters in study site labels indicate outlet (O; circles), undammed (U; triangles), or intermediate (I; triangles) sites.

and Warren 2005), I noticed that seasonal changes in crayfish densities trended in opposite directions at sites downstream of small impoundments vs at sites not near impoundments. These patterns could have been caused by impoundment effects on all crayfish species or by differences in assemblage composition combined with seasonal life-history or behavior patterns that varied among species.

Timing of life-history events differs among crayfish genera or subgenera, so the differences in seasonal patterns of abundance among sites could have resulted from differences in the prevalence of the 3 dominant genera among sites. The 3 most common stream crayfish genera in the Coastal Plain ecoregion (Chapman et al. 2004) portion of the upper Yazoo River basin, Mississippi, are *Procambarus*, *Orconectes*, and *Cambarus* (SBA, unpublished data). Common *Procambarus* species in the streams include *P. (Ortmannicus) hayi*, *P. (Pennides) vioscai*, and *P. (Pennides) ouachitae*. In northern Mississippi streams, *Procambarus* spp. usually are captured only in low densities in mid-summer. *Procambarus hayi* release young in late summer to early winter with peak recruitment from mid-October to mid-December (Payne 1972). *Procambarus (Pennides)* species can have reproductive peaks in spring and autumn (Walls 2009). Crayfish belonging to the *Trisellescens* subgenus of *Orconectes* in the Yazoo River basin have never been assigned to a

species. Because *O. (Trisellescens)* specimens from the basin share characteristics of both *O. etnieri* and *O. chickasawae*, their specific identity is unclear, and I will refer to the taxon as *O. (Trisellescens)* sp. This taxon is most abundant in stream samples from late winter to mid-summer, and females of the subgenus release young primarily from late-spring to early-summer in Mississippi (Adams 2008). The common stream *Cambarus* species is *C. striatus*, which is least abundant in open water during summer and releases young primarily from autumn through early spring (SBA, personal observation). Abundance of *Cambarus* species in samples from perennial streams is usually much lower than that of the other 2 genera.

My goals were to quantify differences in crayfish assemblages in sites influenced vs uninfluenced by upstream impoundments and to explore habitat correlates of the observed assemblage patterns. My specific research questions were: 1) how does crayfish assemblage structure differ between undammed vs impoundment-outlet streams, 2) does crayfish population size structure differ between the 2 categories of sites, and 3) are differences in crayfish assemblages related to physicochemical characteristics of sites.

Methods

Study area and impoundments

The study area included streams in the upper Little Tallahatchie and Yocona subbasins upstream of Sardis and Enid reservoirs, respectively, in the Yazoo River basin, Mississippi, USA (Fig. 1). The Yazoo River drains a large portion of northern Mississippi and flows into the Mississippi River. The study area, in the Northern Hilly Gulf Coastal Plain ecoregion (65e), is marked by dissected hills, gentle to steep side slopes, and low-gradient streams underlain predominantly by sand, sandy clay, and silt (Chapman et al. 2004). Bedrock control features are lacking, and dominant stream substrate is sand. Streams typically are deeply incised, with flashy hydrographs and little habitat diversity. Channel incision has created base-flow conditions marked by an absence of deep pools and organic debris (e.g., wood and leaf mats) (Shields et al. 1994).

Numerous flood-control, earthen dams were constructed on small streams throughout the region between 1959 and 1975, and small impoundments continue to be built on private property. Dams included in my study were in 1st- through 3rd-order streams and created impoundments ranging from ~6 to 20 ha (Appendix S1; available online from: http://dx.doi.org/10.1899/12-161.1.s1). The impoundments were relatively small, but I estimated the average dam

height to be ~14 to 18 m, and most impoundments had large standpipe outlets that released surface water through a culvert. In most cases, outlet culverts were perched high above the outlet stream. Discharge from most of the impoundments was no longer actively managed, but discharge patterns differed between streams not influenced by impoundments (undammed streams) and those downstream of impoundments (outlet streams). In outlet streams, peak discharges were reduced, and in study-area streams that dried during a severe drought, flow continued longer into summer and resumed later in the autumn in outlet than in undammed streams (Adams and Warren 2005). Most impoundments in the Holly Springs National Forest (HSNF) were managed by the US Forest Service for recreational fishing and were periodically fertilized, limed, and stocked with centrarchid fishes. Personnel at the HSNF are engaged in an ongoing effort to rehabilitate aging dams and improve fish habitat in the reservoirs.

Sampling methods

I selected sites based on stream order, proximity to upstream impoundments, and accessibility. Undammed sites either had no upstream impoundments (3 sites) or were ≥1.6 km downstream of a dam (range 1.6–5.9 km, median 2.7; Appendix S1). For 2 of the undammed sites, the nearest upstream impoundment was on a small tributary. I found no indication of relict dams upstream of any site, but some sites may have had nearby beaver dams that I did not document. With 1 exception, outlet sites were 0.02 to 0.18 km downstream of a dam (measured in a geographical information system [GIS]; Appendix S1). Jones Creek (site O07) was 0.38 km downstream of a dam, but beaver dams occurred between the sampling site and the dam.

In 2010, 3 sites considered undammed before sampling were potentially influenced by either recent beaver activity (small beaver ponds within the stream channel; sites I09 and I14) or by an impoundment 0.9 to 1.1 km upstream (sites I09 and I22). I categorized these sites as intermediate and treated them as a distinct group. I did not include these sites in most analyses, but I retained them to examine possible effects of beaver ponds and to explore how far impoundment effects extended downstream.

I conducted sampling in 2 phases. In 2004, I sampled in late July to early August, September, and November to compare seasonal patterns in crayfish assemblages between 4 undammed and 4 outlet sites. In autumn 2010, I sampled 16 sites (7 undammed [including 2 sampled in 2004], 6 outlet,

and 3 intermediate) to assess whether the differences observed between stream categories in autumn 2004 reappeared in another year over a larger number of sites. In 2010, sites were sampled between 29 October and 18 November, except for 1 site that was sampled on 3 December (Appendix S2; available online from: http://dx.doi.org/10.1899/12-161.1.s2). Reach lengths sampled were 40× the mean wetted stream width measured on the 1st sampling date, with minimum and maximum lengths of 160 and 220 m, respectively (adapted from Warren et al. 2002). Sampled reach lengths remained constant across visits at each site unless dry sections necessitated shortening the reach (Appendix S2). I subdivided reaches into 4 subreaches of equal lengths with equal sampling effort applied to each subreach. One outlet and 1 undammed site were almost completely dry in September 2004 and could not be sampled, so sample sizes were lower for September than for other months.

In 2004, I sampled crayfish first with single-pass, backpack electrofishing without block nets and then with a seine. In 2010, I used only electrofishing. I electrofished with a 3-person crew and seined with 2 people. Electrofishing effort was proportional to the wetted stream area to be sampled at each visit, so effort varied among visits. The target electrofishing effort of 1.7 s/m^2 of reach area was based on previous experience with the time required to electrofish all available habitat in small streams in the study area. Actual electrofishing time was recorded for every subreach. Electrofishing was followed by 4 seine samples per subreach. One seine sample consisted of either a sustained seine drag through a habitat type or a set-and-kick seine sample, in which the substrate and any cover were thoroughly disturbed. Immediately after sampling, I identified crayfishes, recorded sex and reproductive form, measured post-orbital carapace length (POCL), and released them in the subreach where they were captured. I collected voucher specimens for each species. These specimens are currently housed in SBA's collection but will be deposited with the Mississippi Museum of Natural Science.

Habitat sampling included measures of channel characteristics, water quality, and stream discharge. I measured wetted width (m) and thalweg depth (cm) at 4 equidistant locations in each subreach. At most sites, I used the transect method (Harrelson et al. 1994) with a Marsh–McBirney Flowmate 2000 and topsetting rod (Marsh–McBirney, Frederick, Maryland) at 1 location per site to calculate stream discharge (m^3/s). In some instances, I calculated discharge from the time required for water from a culvert to fill a bucket to a known volume. I measured

water-quality variables, including dissolved O_2 (mg/L and % saturation), conductivity (µS/cm), pH, and temperature (°C) at the time of crayfish sampling with a Hydrolab Minisonde in 2004 and a Hydrolab Quanta in 2010 (HACH–Hydrolab, Loveland, Colorado). At outlet sites, I measured water quality near the upstream ends of the sites. I calibrated Hydrolabs daily for dissolved O_2 and weekly for other measures. In 2004, I recorded water temperature continuously from the first to the last sampling date at each site except U06 with Water Temp Pro loggers (Onset Corporation, Bourne, Massachusetts). I described the amount of leaf litter at each site on each visit based on a visual survey and the amount of leaves in the seine hauls. On each site visit, I calculated mean wetted stream width, thalweg depth, and width:depth ratio.

Data analyses

I analyzed crayfish data at the species level for *P. hayi* and *C. striatus* and at the subgenus level for *O. (Trisellescens)* sp. (probably a single species). I combined *P. vioscai* and *P. ouachitae* into a subgeneric group, *P. (Pennides)* spp., before analyses because: 1) very small juveniles could not be distinguished, 2) the species were sometimes syntopic, and 3) data on small individuals were important to the analyses but could only be retained by combining the species. For quantitative analyses of crayfish densities, I used only data from electrofishing because seining effort was difficult to quantify precisely. Electrofishing data were converted to catch-per-unit-effort (CPUE) as number of crayfish per second of electrofishing. Data were analyzed with a combination of multivariate and univariate analyses.

Assemblage structure

I used several approaches to test whether assemblage structure differed between undammed and outlet sites. First, I used multiresponse permutation procedure (MRPP; in PC-ORD, version 6.12; MjM Software, Gleneden Beach, Oregon) with Sørenson distance to compare matrices of taxa by CPUE between stream categories. I analyzed data for each month–year combination separately. I then used univariate Kruskal–Wallis tests (SPSS, version 18.0.0; IBM, Armonk, New York) to test whether CPUE of each taxon varied between categories.

For data from November 2010, when the sample size was larger, I used indicator species analysis (McCune and Grace 2002) as an independent analysis of whether any taxa were strong indicators of site membership in the undammed or outlet groups (intermediate sites were excluded). Indicator values

are the percentages of perfect indication calculated from the relative frequency and relative abundance values for each taxon in each stream category. Indicator values can range from 0 to 100, with 100 representing a perfect indicator of group membership. The relative difference in indicator values between groups is more important than the actual indicator value (Peck 2010). The reported *p*-values are the proportions of 5000 randomized trials that had an indicator value greater than or equal to the maximum observed indicator value for the taxon. The analysis was conducted in PC-ORD.

I examined changes in CPUE over time to test whether seasonal trends differed among taxa. I used the related-samples Wilcoxon signed ranks test (SPSS) to compare CPUE between August and November 2004 for each taxon and assessed the direction of change visually.

Crayfish sizes

I compared crayfish size-frequency distributions across stream categories and months for each taxon that was represented by sufficient data. I used Kolmogorov–Smirnov (K–S) tests of the null hypothesis of no difference in size-frequency distributions between groups (SPSS). To compare between stream categories, I compared size-frequency distributions in undammed vs outlet sites within each time period. I made temporal comparisons by testing each pair of months in 2004 within undammed and outlet sites separately. For analyses of size-frequencies in 2004, I used the data from both electrofishing and seining.

Habitat

I compared habitat data between undammed and outlet sites for each month–year combination using MRPP with a Sørenson distance measure followed by Kruskal–Wallis tests on individual habitat variables. Before conducting MRPP, I relativized habitat data by columns to compensate for differing scales of measurement (McCune and Grace 2002). I analyzed temperature data from 2004 as mean temperatures and mean daily temperature ranges by month and compared between groups with *t*-tests (SPSS). I summarized August temperatures from 6 to 31 August and used mean October temperatures to represent the early November samples. I did not include temperature in the multivariate analyses of habitat, because data for 1 site were missing.

To associate habitat variables with CPUE in November 2010 data, I used nonmetric multidimensional scaling (NMDS). I ordinated sites by the CPUE of each taxon and graphed the ordination with a joint-plot

overlay showing habitat vectors (McCune and Grace 2002). I used a relative Sørenson distance measure, so the ordination emphasized the relative abundance of taxa at each site. The analysis followed the steps outlined by Peck (2010). To identify the optimal number of axes and the best starting configuration, I used the Autopilot feature in PC-ORD. Autopilot performed 40 runs on the real data, stepping down the dimensionality from 6 to 1 axes, 50 runs on randomized data, and a maximum of 400 iterations/run. Each run had a random starting configuration, and the best starting configuration was saved for each dimensionality. The optimal dimensionality was selected based on minimizing stress and dimensionality (McCune and Grace 2002). I then ran NMDS one time on real data using the starting configuration saved from the Autopilot run for the appropriate dimensionality and with a maximum of 250 iterations on randomized data to calculate the probability of obtaining a lower stress value at random. I graphed the ordination with axes rotated to orthogonal principal axes, which tends to maximize the variance explained by axis 1 (Peck 2010). The joint-plot overlay displays habitat variables most strongly related to the ordination axes and indicates the relative association of the variables with each axis and the relative magnitude of the association (Peck 2010).

Extrapolation of impoundment effects

I estimated the cumulative effects of impoundments on small streams by extrapolating effects across the study area. I used the HSNF map and a 1:182,000-scale statewide topographic map (DeLorme 1998) and counted the impoundments connected to streams in the Little Tallahatchie River subbasin upstream of Sardis Reservoir. According to the maps, most of the dams I studied impounded ~600–900 m of stream, not accounting for stream sinuosity. I estimated that each small impoundment influenced crayfish assemblages for ≥ 2 km, on average, including inundated, upstream, and downstream segments. I multiplied the number of impoundments by 2 km to obtain a rough estimate of the total stream length over which crayfish populations might be influenced by dams and impoundments in the subbasin.

Results

Crayfish CPUE

In 2004, crayfish assemblage structure differed significantly between undammed and outlet sites in August (MRPP, $A = 0.28$, $p = 0.026$, $n = 8$), but not in September or November (September: $A = 0.145$, $p =$ 0.079, $n = 6$; November: $A = 0.13$, $p = 0.062$, $n = 8$; Appendix S3; available online from: http://dx.doi.org/10.1899/12-161.1.s3). Single-taxon Kruskal–Wallis tests on 2004 data indicated that CPUE of $O.$ (Trisellescens) sp. was higher at undammed than outlet sites during August and September (Fig. 2A). Procambarus hayi CPUE was significantly higher at outlet sites than undammed sites in September and November (Fig. 2B). Procambarus (Pennides) spp. and C. striatus did not differ significantly between stream categories in any month (Fig. 2C, D). Although comparisons of CPUE between categories in November 2004 for $O.$ (Trisellescens) sp. and $P.$ (Pennides) spp. were not significant, the small sample sizes provided low statistical power to detect differences. Therefore, the p-values ($p = 0.083$) from Kruskal–Wallis tests on November 2004 data suggested possible differences in CPUE between stream categories that warranted further investigation with larger sample sizes.

In November 2010, with a larger sample size, assemblage CPUE differed overall among 3 stream categories (undammed, $n = 7$; intermediate, $n = 3$; outlet, $n = 6$; MRPP, $A = 0.16$, $p = 0.016$; Appendix S3). Pairwise comparisons of categories revealed significant differences between undammed and outlet sites (MRPP, $A = 0.214$, $p = 0.010$) but not between intermediate and either undammed or outlet sites ($A \leq 0.09$, $p \geq 0.100$). Single-taxon comparisons of CPUE from 2010, comparing only undammed vs outlet sites, differed from the 2004 results (Fig. 3). In 2010, $P.$ $hayi$ CPUE did not differ between stream categories (Kruskal–Wallis, $p = 0.485$), but all other taxa differed significantly. Orconectes (Trisellescens) sp. and $C.$ $striatus$ ($p = 0.007$ and 0.025, respectively) had higher CPUE in undammed sites, whereas $P.$ (Pennides) spp. had higher CPUE in outlet sites ($p = 0.020$). No taxon differed in CPUE between intermediate and either dammed or outlet sites. In 2010, the highest $P.$ (Pennides) spp. and $C.$ $striatus$ CPUEs were from site I22, 1.1 km downstream of an impoundment, and the highest $P.$ $hayi$ CPUE was from site I14, influenced by a beaver pond (Appendix S3). Cambarus striatus was absent from both sites influenced by beaver ponds.

Based on the November 2010 data, $O.$ (Trisellescens) sp. was the strongest indicator species and was representative of undammed sites. Procambarus (Pennides) spp. was a highly significant indicator of outlet sites (Table 1). Cambarus striatus was a significant indicator of undammed sites in the 2010 data. Relative abundance was more important than relative frequency in driving the indicator values of all 3 taxa (Table 1).

Seasonal variation in occurrence and abundance of taxa was substantial in 2004. From August to November, CPUE of $O.$ (Trisellescens) sp. decreased
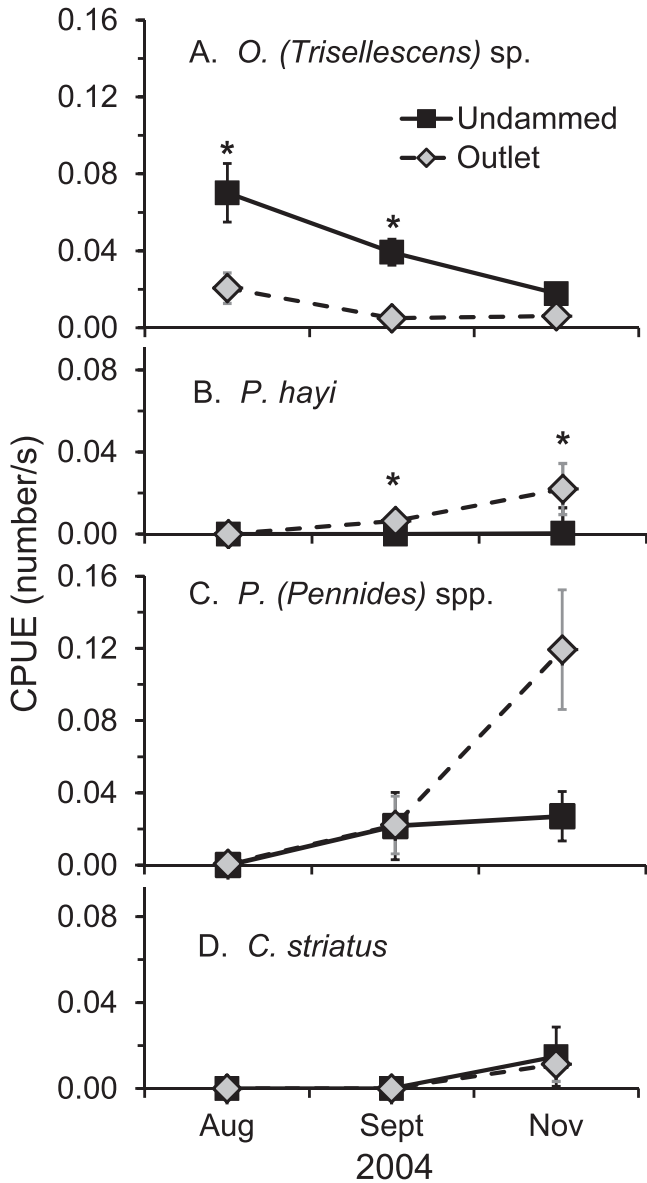
FIG. 2. Mean (±1 SE) catch-per-unit-effort (CPUE) of *Orconectes (Trisellescens)* sp. (A), *Procambarus (Ortmannicus) hayi* (B), *Procambarus (Pennides)* spp. (C), and *Cambarus (Depressicambarus) striatus* (D) from August to November 2004 in northern Mississippi stream sites with or without an upstream impoundment. Asterisks indicate month–genus combinations for which CPUE differed significantly between undammed and outlet sites (Kruskal–Wallis, α = 0.05).

significantly, whereas that of *C. striatus*, *P. hayi*, and *P. (Pennides)* spp. increased over the same period (Fig. 2A–D; related-samples Wilcoxon signed ranks tests, all *p* < 0.03). *Orconectes (Trisellescens)* sp. occurred in the most site × month combinations and was absent from the catch at only 1 outlet site in September (Appendix S3). *Cambarus striatus* was captured at all but 1 site (U04) in November, but at
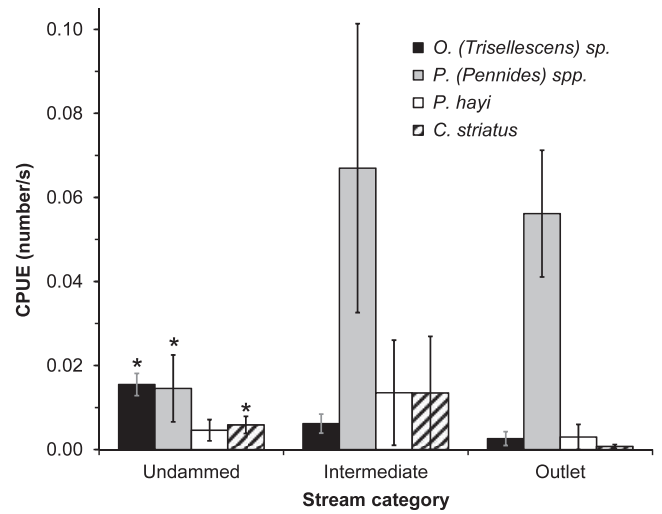

FIG. 3. Mean (±1 SE) catch-per-unit-effort (CPUE) of *Orconectes (Trisellescens)* sp., *Procambarus (Pennides)* spp., *Procambarus (Ortmannicus) hayi*, and *Cambarus (Depressicambarus) striatus* in undammed, intermediate, and outlet sites in November 2010. The intermediate category included 3 sites in which fauna may have been influenced by an impoundment or beaver pond (see Methods). Asterisks indicate taxa for which CPUE differed significantly between undammed and outlet sites.

no sites in August or September. *Procambarus hayi* was not caught in August and was nearly absent from undammed sites in all samples, with 1 specimen caught in each of 2 undammed sites in November and none in other months. *Procambarus (Pennides)* spp. was found at 2 outlet sites in August, 2 sites in each category in September, and all sites in November 2004.

Crayfish sizes

Seasonal changes in CPUE were driven largely by changes in abundances of small, age-0 individuals, but also included changes in older age classes. Adults and large juveniles of *Procambarus* taxa began appearing in small numbers in September (Figs 4A, B, 5A), but the large increases in CPUE resulted primarily from the appearance of age-0 *Procambarus* in September and November. Size distributions changed significantly from September to November 2004 at dammed and outlet sites for *P. (Pennides)* spp. (Fig. 4A–D; K–S tests, *p* < 0.001) and at outlet sites for *P. hayi* (Fig. 5A, B; *p* = 0.009). Most age-0 recruitment of *O. (Trisellescens)* sp. was completed by August, and very few individuals <10-mm POCL appeared in the November catch (Fig. 6A–D). In all sites, size distributions of *O. (Trisellescens)* sp. differed between each pair of months (*p* < 0.03) except September–November at

TABLE 1. Indicator species analysis results for November 2010 catch-per-unit-effort data. Relative frequency indicates the percentage of sites in each group where the taxon was present. Relative abundance indicates the percentage of a taxon's total abundance represented by the mean abundance in the group. Higher indicator values represent stronger indicators of group membership. Bold numbers are the maximum indicator values for each taxon.

Taxon	Relative frequency		Relative abundance		Indicator values		
	Undammed	Outlet	Undammed	Outlet	Undammed	Outlet	p
Orconectes (*Trisellescens*) sp.	100	67	86	14	**86**	10	0.003
Procambarus (*Pennides*) spp.	43	100	21	79	9	**79**	0.014
Cambarus striatus	86	50	89	11	**76**	6	0.032
Procambarus hayi	43	17	61	39	**26**	7	0.542

outlet sites (Fig. 6B, D; $p = 0.344$). In both undammed and outlet sites, 96% of *C. striatus* were <10 mm POCL, so all seasonal patterns of CPUE in this species were caused by small juveniles.

POCL-frequency distributions differed between stream categories within months for some taxa, but results were not entirely consistent between years. Size distributions of *O.* (*Trisellescens*) sp. differed between undammed and outlet sites in every sampling period (Fig. 6A–D; $p < 0.05$). POCL-frequency distributions of *P.* (*Pennides*) spp. differed between stream categories in September and November 2004 ($p < 0.001$), and November densities of age-0 individuals were much greater in outlet than undammed sites (Fig. 4A–D). However, results were inconsistent between years for *P.* (*Pennides*) sp. and *C. striatus*, both of which had POCL-frequency distributions that differed between undammed and outlet sites in November 2004 ($p < 0.001$) but not in 2010 ($p > 0.07$). POCL-frequency distributions of *P. hayi* did not differ between undammed and outlet sites in November 2010 ($p = 0.344$) and could not be compared in 2004 because of small sample sizes in undammed sites.

Habitat

In 2004, physical-habitat variables differed between outlet and undammed sites in August and November (MRPP, $A = 0.08$ and 0.10, $p = 0.048$ and 0.036, respectively, $n = 8$), but not in September ($A = 0.05$, $p = 0.244$, $n = 6$). In univariate analyses of physical-habitat variables, only dissolved O_2 and width:depth ratios differed significantly between outlet and undammed sites (Table 2). Width:depth ratios were higher at undammed than outlet sites in November and August, indicating that channels of undammed sites tended to be wider and shallower than those of outlet sites (Table 2). Dissolved O_2 was lower in outlet than undammed sites during all 2004 samples (Table 2). Stream discharge during sampling did not differ between stream categories, but in September

2004, 3 of 4 outlet sites stopped flowing vs 1 of 4 undammed sites. Two outlet sites that ceased flowing retained water, but 1 site in each category dried almost completely in September. Outlet channels tended to have more hard clay and less sand substrate and to accumulate much more leaf biomass in autumn than undammed sites (SBA, personal observation). Mean temperature and mean daily temperature range did not differ between outlet and undammed sites in any month.

Habitat comparisons among stream categories in November 2010 had both similarities to and differences from habitat comparisons in 2004. In 2010, habitat differed among stream categories (MRPP, $A = 0.134$, $p = 0.019$, $n = 16$), but only undammed and outlet sites differed in pairwise comparisons ($A = 0.159$, $p = 0.013$, $n = 13$). In 2010, as in 2004, width:depth ratios were higher in undammed than outlet sites (Table 2). However, in 2010, dissolved O_2 did not differ between stream categories, and mean thalweg depth was shallower and pH was slightly higher in undammed than in outlet sites (Table 2).

NMDS results on 2010 data were consistent with previous analyses. The 1st axis separated undammed from outlet sites primarily by differences in CPUEs of *O.* (*Trisellescens*) sp. and *P.* (*Pennides*) spp. (Fig. 7). The 1st axis represented 80% of the variation in the data. One undammed site (U17) was an outlier along axis 1. Intermediate sites plotted between the outlet sites and most of the undammed sites along axis 1. Variation in CPUE of *P. hayi* was primarily responsible for axis 2. The joint-plot overlay indicated that 3 habitat variables were strongly associated with the 1st ordination axis. Higher width:depth ratios and pH values and lower thalweg depths were associated with undammed sites and *O.* (*Trisellescens*) sp. (Fig. 7). No habitat variables were strongly associated with axis 2. The NMDS autopilot analysis indicated that 1 or 2 axes were optimal, but the 2-dimensional solution had substantially lower stress
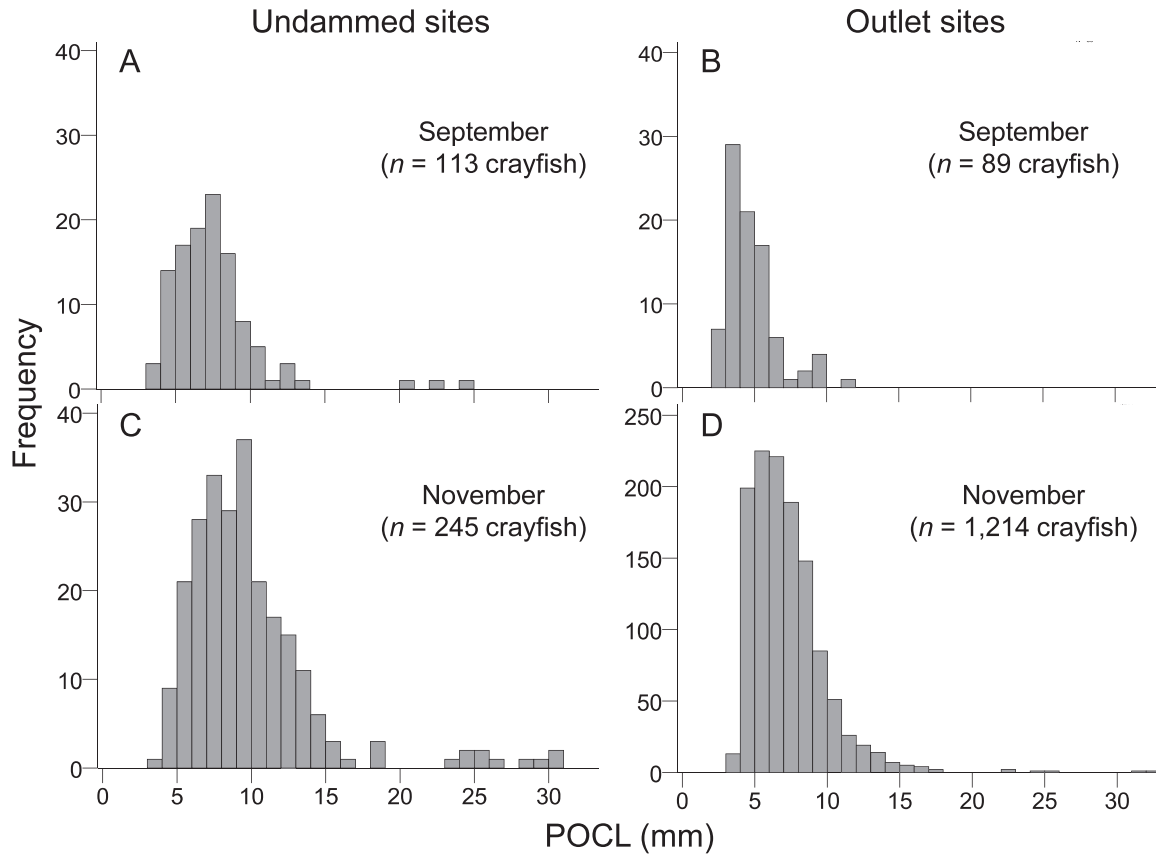
FIG. 4. Post-orbital carapace length (POCL) frequencies of *Procambarus* (*Pennides*) spp. captured by electrofishing and seining in September (*n* = 3 sites/category) (A, B) and November (*n* = 4 sites/category) (C, D) 2004 from undammed (A, C) and outlet (B, D) stream sites. Note different *y*-axis scale in panel D.

(stress = 2.6, p = 0.036), so I chose 2 dimensions for the final run on real data.

Extrapolation of effects

I counted 142 impoundments connected to streams in the Little Tallahatchie River subbasin upstream of Sardis Reservoir. Many more small impoundments that appeared on aerial photographs were not indicated on the maps I used. Based on the impoundment count and a conservative estimate of 2 km of stream influenced by each impoundment, crayfish assemblages were potentially influenced by small reservoirs in ≥ 284 km of stream in this 3228-km^2 portion of the Little Tallahatchie subbasin.

Discussion

Impoundment effects on crayfish densities and extrapolation of effects

Crayfishes were influenced by upstream dams and impoundments in Mississippi. Small dams and their impoundments altered the structure of downstream crayfish assemblages, and generally favored *Procambarus* over *Orconectes* species. The most consistent result across sampling periods and analyses was that *O.* (*Trisellescens*) sp. reached higher abundances in and was most indicative of undammed sites. In an unpublished study in Alabama, Hartfield (2010) found lower summer CPUE of crayfish below intact and breached low-head dams than upstream of the impoundments, but the data were not analyzed by genus or species. Because *O.* (*Trisellescens*) sp. constituted almost my entire crayfish catch in August 2004, my finding of lower *O.* (*Trisellescens*) sp. CPUE downstream of impoundments is essentially the same as the pattern for total crayfish CPUE. Therefore, my results are consistent with those from Alabama in that crayfish densities were reduced below impoundments in summer. In contrast, *Procambarus* taxa tended to be more abundant in outlet than undammed sites in autumn, but results at the subgenus level were somewhat inconsistent between years. I attributed the fact that *P.* (*Pennides*) spp. differed
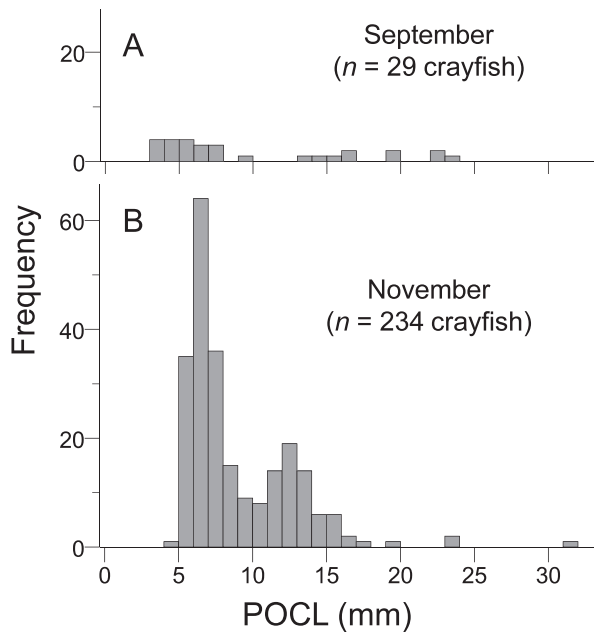
FIG. 5.   Post-orbital carapace length (POCL) frequencies of *Procambarus* (*Ortmannicus*) *hayi* captured by electrofishing and seining in September (*n* = 3 sites) (A) and November (*n* = 4 sites) (B) 2004 from outlet stream sites.

significantly between stream categories in 2010 but not in 2004 to the smaller sample size and ensuing lower statistical power in 2004. The contrasting results for CPUE of *P. hayi* and *C. striatus* between years may reflect high spatial variability relative to their low overall densities or may indicate that they were responding to factors other than impoundment.

The streams and reservoirs considered in my study were small, but the near ubiquity of headwater impoundments across the local landscape makes the results applicable to a large extent of stream habitat. In addition to downstream effects, impoundments also influence crayfish assemblages in the inundated stream segment (e.g., see distribution of *P. vioscai* in Walls 2009). I also have observed differences in assemblages upstream of impoundments. During my 13 y of crayfish sampling in the Little Tallahatchie River drainage, the highest *P. hayi* populations I have encountered were in 1st- or 2nd-order streams within several hundred meters upstream of impoundments (SBA, unpublished data). My estimate that impoundments influence crayfish assemblages in >284 km of stream in the upper Little Tallahatchie River drainage can be further extrapolated over a much larger area. Smith et al. (2002) estimated that when impoundments as small as <0.1 ha are considered with the more typically documented very large impoundments, densities of 1 to 3 impoundments/km² exist over

much of the Eastern Great Plains and Lower Mississippi Valley and densities of 0.3 to 1 impoundment/ km² exist in most states along the Atlantic coast. Therefore, impoundments may be influencing crayfish assemblages in thousands of stream kilometers across the Gulf Coastal Plain, which is a global hotspot of crayfish diversity (Taylor et al. 2007).

Because crayfishes often have strong direct and indirect trophic interactions and can modify habitat through bioturbation (Nyström 2002), alterations to crayfish assemblage structure have great potential to ripple throughout ecosystems. Crayfishes can have top-down or more-complex effects on multiple trophic levels in aquatic ecosystems (Weber and Lodge 1990, Creed 1994, Parkyn et al. 1997, Usio 2000, Dorn and Wojdak 2004), and their influence on food webs extends to terrestrial ecosystems (Englund and Krupa 2000, Ernst and Ernst 2003, Tablado et al. 2009, Dekar et al. 2010). Crayfishes are important prey for many fishes, and they influence behavior, reproduction, and biomass of some fish species (Guan and Wiles 1997, Dorn and Mittelbach 2004). They can alter stream and floodplain habitats by burrowing, changing stream sediment-transport dynamics, and foraging on macrophytes (Statzner et al. 2000, Nyström 2002, Dorn and Wojdak 2004, Johnson et al. 2011). Therefore, alteration of crayfish assemblages has potentially far-reaching, complex, ecosystem effects.

Many of the impoundments counted by Smith et al. (2002) were an order of magnitude smaller than those in my study, and research on how impoundments on the scale of farm ponds influence crayfish assemblages would be useful. In addition, comparisons of the effects of small anthropogenic impoundments vs beaver ponds on crayfish assemblages would be informative. Crayfish assemblages in my intermediate sites were intermediate between those at undammed and outlet streams, but the small sample size limited my ability to make inferences about these sites. The relatively high mean CPUE of *Procambarus* species in intermediate sites (Fig. 3) suggests that beaver activity may benefit these species. In contrast, *C. striatus* was absent from beaver-influenced sites. Its relatively high CPUE in the intermediate category was attributable solely to 1 site that was 1.1 km downstream of a reservoir. I predict that with a larger sample size, crayfish assemblages at beaver-influenced sites would be more similar to outlet than to undammed sites.

Though not conclusive, my results suggest that relatively small beaver ponds may influence crayfish assemblages. If so, then impoundments on the scale of farm ponds also would be likely to influence assemblages. Beaver ponds can shift invertebrate communities from those typical of small streams to
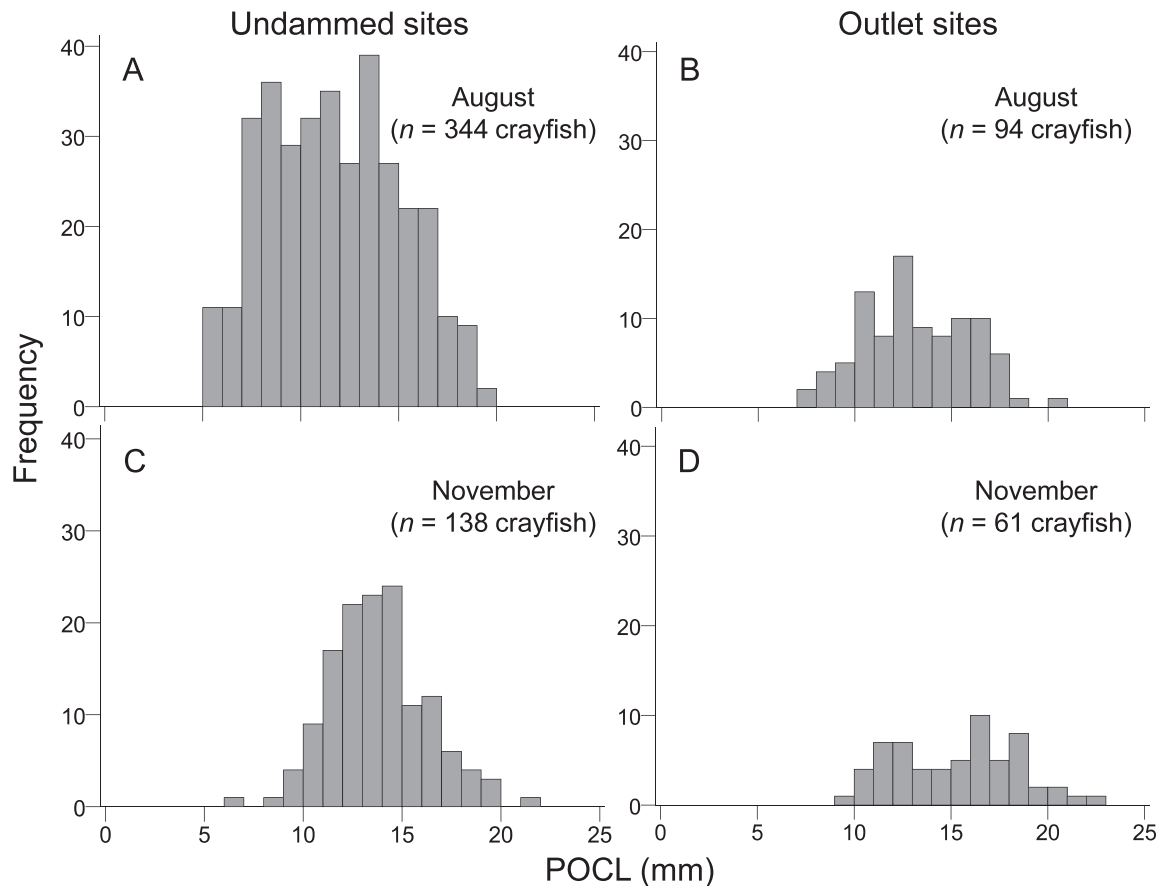
FIG. 6.   Post-orbital carapace length (POCL) frequencies of *Orconectes* (*Trisellescens*) sp. captured by electrofishing and seining in August (*n* = 4 sites/category) (A, B) and November (*n* = 4 sites/category) (C, D) 2004 from undammed (A, C) and outlet (B, D) stream sites.

ones more typical of ponds (Naiman et al. 1988). Thus, beaver ponds may influence crayfish assemblages in ways similar to those of artificial impoundments. Other work has shown that beaver ponds can influence stream temperature, dissolved O_2, and hydrographs (Collen and Gibson 2000), although not necessarily to the same degree or even in the same direction as reservoir influences. For example, small reservoirs often cause outlet streams to dry seasonally (Arnwine et al. 2006), but beaver ponds may cause intermittent streams to become perennial and can reduce hydrograph variation (Collen and Gibson 2000). In my study, outlet sites typically had sparse woody debris, whereas beaver ponds may tend to increase woody debris. However, beaver effects on streams are complex, depend on local and regional conditions, and are difficult to predict (Collen and Gibson 2000).

One question of interest is how crayfish assemblages in impoundment-influenced stream sites compared to historical assemblages in these streams. However, because of pervasive and extreme channel incision,

even undammed streams in the study area do not represent historical conditions. Historically, streams in the study area were less incised (Simon and Darby 1997), probably had much more abundant large wood (Shields et al. 1994), and were influenced to a greater extent by beaver ponds (Naiman et al. 1994). So, if crayfish assemblages in reservoir outlets tend to be more typical of assemblages in stream reaches downstream of beaver ponds, are the reservoirs moving assemblages closer to or farther from historical conditions? This question would be useful to address in a basin with intact reference sites.

Habitat

The mechanisms by which upstream impoundments favored *Procambarus* taxa over *O.* (*Trisellescens*) sp. at outlet sites are speculative despite physical differences between outlet and undammed streams. The most consistent difference in measured habitat variables between stream categories across years was

TABLE 2. Mean (SD) values for habitat variables summarized by stream category and sampling month. Sample sizes (sites/stream category) are given in parentheses in column headings. Sample sizes for water temperatures from undammed sites were 1 less than indicated. p-values are from Kruskal–Wallis tests comparing physical-habitat variables in outlet and undammed sites by sampling month. Water temperatures are monthly means of continuously recorded water temperatures. DO = dissolved O_2, n/a = not available.

Parameter	August 2004			September 2004			November 2004			November 2010		
	Undammed (4)	Outlet (4)	p	Undammed (3)	Outlet (3)	p	Undammed (4)	Outlet (4)	p	Undammed (7)	Outlet (6)	p
Q (m³/s)	0.013 (0.006)	0.015 (0.014)	0.56	0.005 (0.002)	0.006 (0.010)	0.51	0.033 (0.015)	0.031 (0.028)	0.56	0.013 (0.017)	0.058 (0.064)	0.12
Wetted width (m)	3.11 (0.625)	2.31 (1.008)	0.23	2.38 (0.191)	1.79 (0.907)	0.51	3.58 (0.727)	2.72 (0.852)	0.15	3.03 (1.178)	4.15 (1.951)	0.20
Thalweg depth (cm)	11.3 (5.089)	17.7 (6.899)	0.15	14.4 (7.931)	10.9 (5.777)	0.51	13.7 (4.677)	21.3 (5.298)	0.08	11.6 (5.231)	30.4 (12.893)	0.03
Width:depth ratio	32.5 (16.063)	13.4 (3.594)	0.02	20.0 (9.522)	16.7 (0.679)	0.51	27.5 (6.141)	13.1 (3.765)	0.02	26.9 (2.917)	14.2 (3.616)	0.00
DO (mg/L)	7.37 (0.837)	5.96 (0.668)	0.04	7.40 (0.762)	3.90 (1.700)	0.05	8.79 (0.318)	7.46 (1.261)	0.02	10.03 (1.134)	9.29 (1.873)	0.67
Conductivity (µS/cm)	49.10 (16.761)	34.90 (9.603)	0.15	60.97 (13.755)	65.70 (19.040)	0.83	40.60 (10.892)	40.38 (11.075)	0.77	38.29 (18.509)	36.17 (7.731)	0.47
pH	7.57 (0.106)	7.68 (0.380)	0.66	7.56 (0.310)	7.71 (0.183)	0.51	6.54 (0.085)	6.40 (0.105)	0.11	6.87 (0.202)	6.41 (0.186)	0.00
Temperature (°C)	21.6[a] (0.645)	22.9[a] (2.003)	0.16	20.7 (0.595)	22.1 (1.822)	0.48	18.0[b] (0.581)	18.8[b] (0.856)	0.29	n/a	n/a	n/a

[a] Mean water temperatures for 6–31 August 2004
[b] Mean water temperatures for October 2004

that outlet streams had narrower, deeper channels (smaller width:depth ratios) than undammed streams. Differences in channel morphology between stream categories could contribute to differences in crayfish assemblages or may simply be correlated with other, more important effects of upstream impoundments. In contrast to the other habitat variables measured, channel morphology is expected to remain relatively constant across a span of several years. Qualitative observations indicated that outlet sites had finer substrate, less large wood, more leaf accumulation in autumn, and altered hydrographs compared to undammed streams. Small outlet streams in the same ecoregion in Tennessee also had narrower, more entrenched channels, finer substrate (silt/clay), and lower dissolved O_2 relative to reference streams (Arnwine et al. 2006). Outlet streams in Tennessee also had other water-quality alterations, especially higher levels of Mn and NH_3, and altered temperature and hydrologic regimes (Arnwine et al. 2006). In my study, dissolved O_2, pH, and thalweg depth comparisons across stream categories were inconsistent across years, but these variables were affected by short-term weather and flow conditions in the weeks just before sampling. Ideally, habitat and water-quality variables would be measured continuously over a long period to ascertain their effects on crayfish assemblages, because measuring at the time of sampling is likely to miss conditions most stressful to crayfishes. For example, the timing and magnitude of extremely low stream discharges or the lowest dissolved O_2 levels in mid-summer are more likely to influence assemblage structure than are the same variables in November. Gore and Bryant (1990) showed that *O. neglectus* used varying flow conditions over the course of a year and over its life cycle and that females with eggs used faster water in riffles than did males and females without eggs. They cautioned that changes in flow regimes during critical phases of the life cycle may be detrimental to the species.

During my study and a post-drought recolonization study (Adams and Warren 2005), large amounts of leaf litter accumulated in the streams below impoundments because autumn storms, which occurred when impoundment levels were low, did not produce high flows downstream of impoundments. At undammed sites, leaf packs increased in autumn, but many leaves were flushed out of the headwaters during high storm flows leaving little organic debris behind (Shields et al. 1994). The leaf accumulations below impoundments provided abundant cover, and probably food, for crayfishes and may have been particularly advantageous for the very small, age-0 *Procambarus* individuals released into the stream
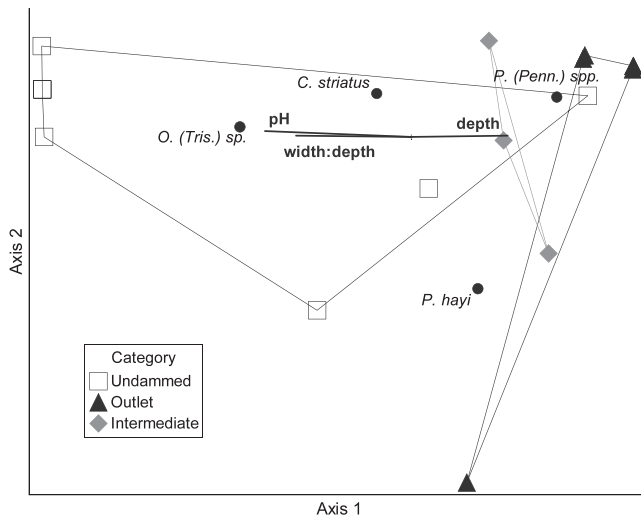
FIG. 7. Nonmetric multidimensional scaling (NMDS) ordination of 2010 data using the relative Sørenson distance measure (ordination reflects proportions of species in each site). Sites (large symbols) were ordinated by taxon catch-per-unit-effort (CPUE) and plotted with a joint-plot overlay of the habitat variables most strongly correlated with the site × taxon ordination. Note that some symbols overlap. The habitat vectors show the relative association and magnitude of habitat variables with the axes (see Methods). Black circles represent the weighted-average scores on the 2 axes for each taxon. Polygons enclose all points from a given stream category. *O. (Tris.)* sp. = *Orconectes* (*Trisellescens*) sp., *P. (Penn.)* spp. = *Procambarus* (*Pennides*) spp., *P. hayi* = *Procambarus* (*Ortmannicus*) *hayi*, *C. striatus* = *Cambarus* (*Depressicambarus*) *striatus*.

during the time of leaf accumulation. Possible reasons for lower CPUE of *Orconectes* in the outlet sites include low dissolved O_2 during some periods, less sand substrate, and possibly greater risk of predation from centrarchid fishes during summer when *Orconectes* are most active. The best growth of *P. clarkii* occurred at dissolved O_2 levels >3 mg/L, whereas that for several *Cambarus* species occurred at levels >5 or 7 mg/L (Nyström 2002), considerably higher than the mean of 3.9 mg/L that I observed in outlet sites in September 2004. O_2 requirements are unknown for the species in my study. We did not quantify fish during sampling, but abundance and diversity of *Lepomis* spp. appeared to be higher at outlet and beaver pond sites than at undammed sites (SBA, personal observation). Many of the impoundments were stocked periodically with predatory fishes, including *Micropterus salmoides* and *Lepomis* spp. (B. Oswalt and K. Lee, US Forest Service, HSNF, personal communication). Hartfield (2010) also suggested, based on correlative evidence, that concentrations of predatory fishes at outlets of

low-head dams might have reduced summer crayfish abundances in Alabama streams.

Seasonal differences

Characterizations of ecological effects on southeastern stream crayfish assemblages should be made during multiple seasons to incorporate contrasting seasonal patterns in life history among taxa. The apparent effects of impoundments on total crayfish abundance appeared very different in August than in November. The opposite seasonal trends in CPUE of *O.* (*Trisellescens*) sp. and CPUE of other taxa from August to November probably were the result of differences in recruitment timing, behavior, and perhaps mortality. POCL-frequency histograms from my study confirmed that recruitment of age-0 *Orconectes* had waned by the August sampling date. Decreasing CPUE of *O.* (*Trisellescens*) sp. in autumn may have been the result of a combination of mortality, increased sheltering behavior as water temperatures dropped (and, thus, avoidance of sampling gear), and possibly emigration. However, other work indicates that *O.* (*Trisellescens*) sp. is most abundant in headwater streams (SBA, unpublished data), so large-scale emigration away from headwater sites seems unlikely.

Recruitment of age-0 crayfishes explained most of the increase in CPUE of *Procambarus* taxa in autumn, and outlet sites typically had much higher levels of recruitment than undammed sites. The first appearance of large juvenile and adult *Procambarus* taxa in autumn had to be a result of either behavioral changes or immigration. Presumably, adult *P. hayi* burrowed during the summer, and thus, were absent from August samples. Extensive summer burrowing has been documented for *P. hayi* (Payne 1972), but not for *P.* (*Pennides*) spp. Penn (1956a) noted that *P. ouachitae* was strongly nocturnal in Arkansas, so perhaps some *P.* (*Pennides*) spp. emerged at night during summer and were well sheltered, if not burrowing, by day. *Procambarus hayi* could have immigrated to outlet sites from upstream impoundments because, unlike the other species encountered, *P. hayi* commonly inhabit impoundments and ponds (Payne 1972). Conversely, most members of the *Procambarus* subgenus *Pennides* occur almost exclusively in flowing streams (Penn 1956b, Walls 2009). Because *P.* (*Pennides*) spp. were not likely to inhabit the impoundments and because small numbers of *P.* (*Pennides*) spp. adults began to appear in both undammed and outlet sites in autumn, any immigrants to outlet sites probably originated downstream.

A more complete understanding of how impoundment effects interact with the contrasting seasonality

in reproduction of *Procambarus* taxa vs *O.* (*Triselles-cens*) sp. would require spring sampling. However, undammed sites can have much higher flows than outlet sites in spring, and the differences in flow would create differences in sampling efficiency among stream categories. In studying crayfish population recovery after droughts, I observed that total crayfish CPUE increased in outlet and undammed sites from January to June, but subsequently declined only in undammed sites (unpublished analyses of data from Adams and Warren 2005). This observation suggests that the spring reproductive pulse may have been less affected by upstream impoundments than the autumn pulse of *Procambarus* reproduction. However, those results may have been confounded by drought effects.

Conclusion

Small dams and their impoundments on 1st- to 3rd-order streams altered downstream crayfish assemblages relative to undammed streams. CPUE of *O.* (*Trisellescens*) sp. tended to be lower and that of *Procambarus* species higher downstream of impoundments. Much of the difference in *Procambarus* CPUE between outlet and undammed streams in autumn was the result of high recruitment of age-0 *Procambarus* downstream of impoundments in autumn. Results from intermediate sites suggest that similar effects may be seen near beaver ponds and as far as 1 km downstream of impoundments. When extrapolated across the Gulf Coastal Plain, my results indicate that impoundments may alter crayfish assemblages over thousands of stream kilometers. Because crayfishes have strong trophic interactions and can modify habitats, alterations of crayfish assemblage structures by impoundments may produce detectable changes in both aquatic and terrestrial ecosystem structure and function.

Acknowledgements

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