

**THE INFLUENCE OF COARSE WOODY DEBRIS, DISTURBANCE, AND
RESTORATION ON BIOLOGICAL COMMUNITIES IN SANDY COASTAL PLAIN
STREAMS**

by

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Abstract

The influence of instream habitat on benthic macroinvertebrates was assessed from multiple descriptive and experimental studies within the Fort Benning Military Installation (FBMI), Georgia and the Tuskegee National Forest, Alabama, USA. Instream habitat, in the form of coarse woody debris (CWD), plays an important role in stabilizing sandy bottom streams in the Coastal Plains of the Southeastern United States.

Chapter 2 describes the results of an instream restoration experiment conducted in 8 streams at FBMI to assess the influence of CWD additions on instream habitat and benthic macroinvertebrate assemblages. Macroinvertebrates were sampled before and after CWD additions in each stream to allow pre- and post-restoration comparisons of assemblages. Results revealed that streams receiving CWD additions dampened the influence of hydrologic disturbance on structural and functional measures of the macroinvertebrate assemblages, whereas non-restored streams showed a general decrease in those same measures.

Chapter 3 describes the results of a multi-stream survey at FBMI designed to examine the influence of catchment disturbance on instream habitat availability and its putative effects on freshwater crayfish populations. Results showed that catchment disturbance was negatively correlated to instream CWD and BPOM habitat and, in turn,

that crayfish density and biomass were strongly related to CWD. These data suggested that catchment disturbance influences crayfish by influence instream habitat availability.

Chapter 4 describes a field experiment designed to quantify the influence of crayfish on benthic food webs in sandy coastal plains streams. The experiment was conducted in a forested section of Choctafaula creek, Macon County, Alabama, with the Tuskegee National Forest. The experimental was an in-situ enclosure-exclosure complete randomized block design. Results showed that crayfish had limited influence on leaf litter (i.e., basal resource), however, they did have a significant influence on other benthic macroinvertebrates. It appears that this influence was due to direct predation, as determined by stable isotope analysis, which showed a trophic position similar to other predators from the study.

Chapter 5 of this dissertation assessed crayfish production and diet from 3 sandy bottom streams at FBMI. The purpose was to equate differences in production and diet to differences in CWD abundance. Results showed crayfish productivity was greatest in the stream with the highest CWD abundance, with the lowest productivity occurring in the stream with the lowest CWD abundance. These results suggest that habitat may play a substantial role on crayfish productivity, and changes to habitat abundance may negatively impact crayfish. Additionally, results showed that crayfish diets were significantly different among streams, with crayfish from the low CWD stream containing a high amount of inorganic matter, suggesting diets are of poor quality compared to crayfish from streams with intermediate to high CWD.

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1. INTRODUCTION

Stream ecosystems are influenced by a wide variety of environmental factors, ranging from anthropogenic disturbance in the uplands to instream habitat availability in the channel. It has been well documented that a streams catchment are tightly connected with stream communities through influence of hydrologic and chemical conditions (Hynes 1975, Junk et al. 1989). Similarly, instream habitat is greatly affected by the surrounding catchment, both with upland and riparian (lateral) regions of the catchment (Harmon et al. 1986, Lenat and Crawford 1994, Wallace et al. 1996, Paul and Meyer 2001, Maloney et al. 2005). Catchment disturbance is an important factor affecting stream communities, often through its influence on instream habitat (Resh et al. 1988, Palmer et al. 1996, Maloney et al. 2008). My dissertation research is separated into 4 primary chapters, with the first data chapter (Chapter 2) describing the influence of hydrologic regime on the efficacy of instream coarse woody debris (CWD) restoration and its influence benthic macroinvertebrates. Chapter 3 focuses on the influence of upland disturbance on both instream habitat and crayfish populations, and how upland disturbance influences crayfish populations indirectly by altering habitat availability. Chapter 4 describes an in situ experiment quantifying the effect of crayfish density on a basal food resource (i.e. leaf litter) and litter-associated benthic macroinvertebrates. The final chapter (5) describes the influence of contrasting CWD abundance on crayfish density, biomass, productivity, and trophic position in the stream food web.

Temporal changes in flow regimes in streams have been shown to greatly influence stream communities and their habitats. Hydrologic impacts can occur from high natural variation (e.g. drought, snow melt), or anthropogenic changes within catchments that alter intensity and duration of instream flow (Resh et al. 1988, Poff and Ward 1989, Paul and Meyer 2001, Rose and Peters 2001, Maloney et al. 2006). These changes can have a strong influence on CWD by decreasing its availability through burial or displacement downstream during flooding events (Shields et al. 2003, Maloney et al. 2005). Restoration efforts to improve instream habitat through the addition of CWD has received only recent attention (Shields et al. 2003, Entekin et al. 2009, Lester and Wright 2009). These efforts attempted to restore woody habitat for stream invertebrates and vertebrates as well as increase streambed stability. However, most of these studies focused only on the influence of CWD additions, and did not consider the influence of the hydrologic regime on CWD restoration efforts. Chapter 2 describes an experimental approach designed to assess the efficacy of CWD restoration during strongly contrasting hydrologic conditions on benthic macroinvertebrate assemblages in sandy coastal plains streams of Western Georgia, USA. During the study, the hydrologic regime showed a substantial change between pre- and post-restoration periods, which likely influenced the efficacy of the restoration effort. The main objectives were to 1) assess if artificial CWD additions altered the benthic macroinvertebrate community assemblage over a 3 y post-restoration period, and 2) characterize differences in macroinvertebrate assemblage response between restored and unrestored streams during extreme wet years with increased hydrologic disturbance.

Land use changes resulting in increased sedimentation of streams through forest practices and soil disturbance can subsequently alter instream habitat and thus impact biotic communities (Lenat et al. 1981, Karr 1991, Wang et al. 2001, Maloney and Feminella 2006, Burcher et al. 2007). Much research has focused on the degradation of faunal composition and diversity associated with sedimentation (Cordone and Kelly 1961, Lenat et al. 1981, Wood and Armitage 1997, Angradi 1999). Sedimentation from upland disturbance can impact benthic macroinvertebrate assemblages by altering behavior (i.e., increasing downstream displacement [drift]) or causing mortality directly by burial (Newcombe and MacDonald 1991, Waters 1995), or indirectly by loss of habitat (Maloney and Feminella 2006). However, there has been considerable work on the general benthic macroinvertebrate assemblage, but comparatively little on the influence of sedimentation on stream crayfish populations. The influence of upland disturbance, through sedimentation, on crayfish could have a substantial influence on stream ecosystems because of their important ecological role in streams (Momot et al. 1978, Huryn and Wallace 1987). The objectives of Chapter 3 were to 1) relate landscape-level land use, specifically catchment scale-disturbance, and instream habitat, 2) investigate the relationships between instream habitat conditions and crayfish population measures, and 3) relate crayfish population measures to catchment-scale disturbance.

The ecological role of crayfish in aquatic ecosystems has long been well known (Momot et al. 1978, Momot 1995). Crayfish have been shown to influence macroinvertebrate assemblages and basal resources (e.g. leaf litter, algae; Creed 1994, Parkyn et al. 1997), sometimes through ecosystem engineering (Creed and Reed

2004), which involves creating or modifying habitats and influencing resource availability for other species (Jones et al. 1994, 1997, Usio and Townsend 2004, Helms and Creed 2005). However, most studies have been done in streams of either high gradient or high latitude, and much of this research has been focused on large, long-lived species. Chapter 4's objectives were to 1) assess the influence of a small, short-lived crayfish species on its basal resource (leaf detritus) and benthic macroinvertebrate prey colonizing leaf litter, and 2) describe crayfish trophic position to assess its potential effect on the benthic food web.

Freshwater crayfish depend on a wide variety of habitats (e.g., gravel, boulders, vegetation, and coarse woody debris) as refuge from predation by fishes and terrestrial vertebrates (Stein 1977). Research has demonstrated the link between habitat availability and crayfish abundance, but few studies have assessed the importance of habitat availability on regulation of intrinsic factors of crayfish populations, including growth and production (Stein 1977, Contreras-Balderas and Lozano-Vilano 1996, Mitchell and Smock 1996). In addition, most stream research on crayfish has been conducted in systems with primary gravel and/or cobble substrate (Momot 1995, Whitley and Rabeni 1997, Evans-White et al. 2003); no studies have been conducted in low-gradient sandy streams. Biota in these systems rely heavily on CWD for available stable habitat, but it is unknown if CWD provides a comparable level of variation in suitable habitat and refuges against predation as structurally diverse upland streams containing gravel-cobble substrates (Huryn and Wallace 1987, Mitchell and Smock 1991). The objective of Chapter 5 was to assess the effect of CWD abundance on crayfish density, biomass and production. In addition, Chapter 5 describes the

influence of variation in CWD and benthic particulate organic matter abundance on crayfish diet and trophic position in the food web.

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2. INFLUENCE OF HYDROLOGIC VARIATION AND INSTREAM HABITAT RESTORATION ON SANDY SOUTHEASTERN PLAINS STREAMS OF WESTERN GEORGIA, USA

2.1 SUMMARY

Hydrologic variation (i.e., floods and droughts) has been shown to greatly influence stream communities, but few studies have assessed varying hydrologic regimes on instream restoration efforts. In small coastal plains streams disturbance from uplands can increase sediment intrusion and reduce abundance of instream coarse woody debris (CWD), in turn reducing habitat availability for benthic macroinvertebrates. This impact can be exacerbated in wet years and thus may limit the effectiveness of restoration efforts. We quantified macroinvertebrates and their habitats in 8 streams for 2 y before and 3 y after artificial addition of CWD (4 restored, 4 unrestored), to assess efficacy of CWD additions as a restoration tool to increase bed stability and increase macroinvertebrate habitat, at the Fort Benning Military Installation, GA. CWD additions had an extremely limited effect on increasing most macroinvertebrate measures. For example, relative to pre-restoration levels, density and % of EPT taxa increased in restored streams during winter, and did not change in unrestored streams; however, these and most other metrics did not differ between restored and unrestored streams in other seasons. We suspect that restoration efficacy was reduced in most streams because of extreme hydrologic conditions during the

post-restoration period the effect of high discharge on burial of CWD additions in these unstable stream beds. While few positive increases were observed in relation to CWD additions, some changes in metrics in unrestored streams compared to restored streams during the post-restoration period. Nonmetric multidimensional scaling ordinations showed shifts in the overall assemblage structure in both restored and unrestored streams in some seasons, with shifts being greater in unrestored streams than restored streams. These data suggest that the CWD additions had a dampening effect on high hydrologic disturbance during the post-restoration period, and that long-term monitoring of instream restoration efforts may be necessary to assess the overall effectiveness of such efforts in streams exposed to highly variable hydrologic conditions.

2.2 INTRODUCTION

The hydrologic regime is a “master variable” exerting a strong governing force on physical, chemical, and biological attributes in streams. Therefore, alterations to these regimes, either by catchment-scale disturbance by humans or natural flooding events can have large ecosystem-level effects (Resh et al. 1988, Poff and Ward 1989, Paul and Meyer 2001, Rose and Peters 2001, Maloney et al. 2006). For example, increased runoff from catchment disturbance increases transport of suspended sediments and solute concentrations, which, in turn, influences stream communities (Paul and Meyer 2001, Swank et al. 2001, Maloney et al. 2006). Additionally, floods can directly affect stream communities by altering instream flow conditions, such as near-bed turbulence regimes, or increase scouring of stream substrates (Carling 1992, Bennison and Davis

1992). Often the above factors act synergistically, and when they occur together, stream community impacts may be even greater.

Instream coarse woody debris (CWD) additions often are used in stream restoration projects to restore instream habitat. Interest in CWD additions as a restoration tool stems from its importance in organic matter storage and stable habitat structure in streams (Bilby and Likens 1985, Harmon et al. 1986, Benke and Wallace 1990, Wallace et al. 1995). It has been suggested that re-establishment of CWD levels in streams may help to restore them to a desired pre-disturbance condition more quickly than that of natural processes (Grippel and White 2000, Hrodeny and Sutton 2008).

Much CWD restoration work has been conducted as 1- or 2-y experiments (Smock et al. 1989, Wallace et al. 1995, Hrodey et al. 2008), yielding little information on long-term success or the influence of varying hydrologic regimes on restoration efforts. Tracking restoration efforts over longer time periods allows for the bracketing of a reasonable amount of hydrologic variation that may influence the restoration efficacy. The purpose of our study was to assess the influence of highly variable hydrologic conditions (i.e., as extreme wet years and high discharge) on the efficacy of instream habitat restoration in low-gradient sandy-bottom streams, in the form of artificial CWD additions. Specifically, we examined 1) if artificial CWD additions altered the benthic macroinvertebrate assemblages and their habitats in restored (vs. unrestored) streams over a 3-y post-restoration period, and 2) the degree to which high hydrological variation in the post-restoration period influence the effectiveness of CWD additions on benthic assemblages and habitats in the restored streams.

2.3 METHODS

2.3.1 Study site

The study was conducted at the Fort Benning Military Installation (FBMI), in west-central Georgia, USA. FBMI occurs in the Southeastern Plains Level-III ecoregion (Ormernik 1987), with a humid and mild climate and year-round precipitation (mean = 105 cm/y), encompassing an area of 735 km². The predominant land use is associated with military training and includes dismounted infantry, tracked vehicle maneuvers (i.e., tanks), heavy weapons usage, and airborne training drop zones (USAIC 2001, Dale et al. 2002). In addition to land use associated with military training activities, forestry practices at FBMI includes selective timber harvesting and controlled burning. Much of the forestry practices are related to restoration of longleaf pine (*Pinus palustris*) forest and red-cockaded woodpecker (*Picoides borealis*) populations (Noss 1989, Dale et al. 2002). Upland vegetation in catchments consists of longleaf pine (*Pinus palustris*) and loblolly pine (*P. taeda*), with some hickories (*Carya* spp.), flowering dogwood (*Cornus florida*), and oaks (*Quercus* spp.), whereas the riparian vegetation was dominated by mesic hardwoods, sweetbay magnolia (*Magnolia virginiana*), water oak (*Q. nigra*), white oak (*Q. alba*), yellow poplar (*Liriodendron tulipifera*), red maple (*Acer rubrum*), black gum (*Nyssa sylvatica*), and sweet gum (*Liquidambar styraciflua*) (Cavalcanti 2004). The study streams have received much attention from previous research, focused mostly on effects of landscape-scale disturbance on instream water quality, benthic community, and ecosystem responses (Houser et al. 2005, 2006, Maloney et al. 2005, 2006, Bhat et al. 2006, Maloney and Feminella 2006). Briefly, these studies have shown a strong linkage between upland disturbance and instream environmental

conditions, including decreased CWD abundance (Houser et al. 2005, Maloney et al. 2006, Maloney and Feminella 2006). Collectively, previous research work has suggested that loss of instream CWD from disturbance may have a significant impact on instream habitat conditions and associated biota, and that the study streams are good candidates for quantifying the influence of in stream restoration (as CWD additions) on benthic communities.

2.3.2 Experimental design

Streams in 8 catchments were selected (Table 2.1); study streams were small (1st or 2nd order) and usually low gradient, with primarily sand, silt, and clay substrates in the active channel. Additionally streams had high riparian shading typical of other small Southeastern Plains streams (Felley 1992). Study streams showed a wide baseline range of CWD abundance, from ~3 to 12% of areal coverage of stream bottom and mean stream gradient from 0.83 to 5.1% (Table 2.1). CWD data was converted to planar area (m² of CWD per m² of stream bed) by multiplying the CWD diameter by length and then dividing by the area of stream bottom sampled for each transect, and then converted to % areal coverage of stream bottom (Maloney et al. 2005).

The study was divided into 2 phases. Phase I (pre-restoration) involved quantifying baseline biotic and abiotic conditions from 8 streams (BC1, BC2, HB, SB2, SB3, SB4, KM1, LPK) spanning a range of upland catchment disturbance level from undisturbed to moderately to highly disturbed, as indicated by the % of the catchment occurring as bare ground and road cover (Table 2.1; Maloney et al. 2005). Phase II (post-restoration) involved a 2-y study of the above 8 streams in which 4 catchments

(SB2, SB3, LPK, KM1) received instream CWD additions (restored streams) and streams in the 4 remaining catchments (BC1, BC2, HB, SB4) were used as controls (unrestored streams). Selected riparian trees were felled (*N. sylvatica* in KM1, SB2, SB3, and *Q. alba* in LPK) and cut into 1-2 m long sections (~10 cm diam) in August 2003, and left on the ground until deployment in the stream. CWD additions involved deploying 10 to 15 woody debris dams (~10 m apart) over a 100- to 150-m reach in November 2003. Individual debris dams consisted of 3 logs placed in a Z-shaped pattern anchored into the streambed by rebar (Roberts et al. 2006). These configurations were done to allow water flow around debris dams during baseflow rather than impounding sections upstream of debris dams. Debris dams traditionally consist of small and large CWD, so we focused on adding larger piece of wood that would accumulate natural smaller wood pieces over time.

During the 1st year of phase-II we observed that much of the CWD additions became buried in 2 of the 4 treatment streams (SB3 and LPK). Thus, we augmented initial CWD addition in these 2 streams in November 2004 to help compensate for these losses. Augmentations consisted adding 10 new debris dams in SB3 and LPK in between debris dams deployed in 2003, such that debris dams occurred every 5 m in these 2 streams.

2.3.3 Benthic microhabitat and organic matter sampling

Stream discharge (velocity-area method, Gore 1996) was estimated seasonally to assess differences in hydrologic conditions over the study. To assess the influence of CWD additions on reach-scale streambed stability, we established cross-stream

transects (4–5 per stream) and measured streambed height at fixed sampling points along each transect. Transects were established ~15 m apart throughout the study reach (see Ray and Megahan 1979, Ziser 1985 for method). Stability was quantified seasonally both 1 y prior to restoration and 3 y after restoration (November 2002 through September 2006). Using this method, small changes in mean bed height over time reflected a stable bed (i.e., low rates of sediment accretion or scour) whereas large changes reflected an unstable bed. A suite of instream physicochemical parameters was sampled seasonally (winter, spring, summer), including 3 current velocity measurements (Marsh-McBirney Flowmeter, Model 2000) at 3 set locations and mean stream channel width and depth (5 measurements per cross-stream transect), to assess the influence of CWD additions on microhabitat conditions.

Natural CWD abundance (woody debris > 2.5 cm in diameter) and benthic particulate organic matter (%BPOM, particles < 2.5 cm in diameter) was quantified during pre- and post-restoration in each stream, to assess effects of instream CWD addition on organic matter retention. CWD was quantified annually, as surface of woody per surface area of stream bed, during spring 2002, 2003, and 2005 along 15 cross-stream transects (~5 m apart) (Maloney et al. 2005), whereas %BPOM was assessed seasonally by taking 6 core (2.5 cm diam) samples from the upper 10 cm of substrate at the same location as current velocity (n = 18 %BPOM samples/stream/date), collected randomly from the center of the channel (n = 3) and the outer 1/3 of the channel (n = 3). In the laboratory, %BPOM from core samples was quantified as ash-free dry mass (AFDM), where samples were dried at 80°C to a

constant mass (48–72 h), desiccated and weighed, combusted at 550°C in a muffle furnace for 3h, and then desiccated and re-weighed for AFDM (Minshall 1996).

2.3.4 Benthic macroinvertebrate sampling

Benthic macroinvertebrates were sampled seasonally (winter, spring, summer) in treatment and control streams both in the pre- and post-restoration period using a combination of 1) quantitative Hester-Dendy (HD) artificial substrate multiplate samplers (Rinella and Feminella 2005), and 2) semiquantitative multi-habitat net samples (Maloney and Feminella 2006). Twelve HDs were used per stream (total area = 1.12 m²) on each sampling date in 4 run microhabitats (3 HDs per run), which were incubated for 6 to 8 wk to allow macroinvertebrate colonization. We used HDs to simulate wood surfaces, and previous research has shown that HDs are a good surrogate for sampling wood habitats in coastal plains streams (Rinella and Feminella 2005). Multi-habitat sampling was conducted using a kick-net (250 µm mesh) with samples collected from general benthic macroinvertebrate habitats (e.g., runs, debris dams, and root wads). We standardized kick-nets to a known area (~1 m²) and time (~1 min) to increase sampling precision, and also to supplement HD samples to better characterize richness and % composition (Maloney and Feminella 2005). Benthic samples were field-preserved with 95% ethanol, returned to the laboratory. There, samples were sieved (125 µm mesh) to remove leaf fragments and small sticks, and the remaining materials sorted for 30 min to remove all large macroinvertebrates (>2mm length); the residue was then poured through graded sieves (2 mm - 125 µm mesh) to remove all large debris. The entire residue material was sorted for HD samples,

whereas we subsampled kick-net residual material (removing at least 200 organisms per subsample, see Vinson and Hawkins 1996) from the elutriate. Macroinvertebrates were identified to the lowest possible taxonomic level, usually genus, using keys in Merritt and Cummins (1996), Wiggins (1996) and Epler (2001).

For each stream we estimated macroinvertebrate density, biomass, Shannon diversity (H'), and species richness for the entire macroinvertebrate assemblage. Biomass was determined by measuring length of animals (nearest mm) and converted length into AFDM using length-mass equations in Benke et al. (1999). Additional macroinvertebrate compositional measures, included Ephemeroptera, Trichoptera, and Plecoptera (EPT) density, Chironomidae richness (Chiro richness), and % of the assemblage as chironomids (%Chiro) and EPT (%EPT). Previous research has suggested that proportions of macroinvertebrate functional feeding groups, such as shredders and scrapers, are greatly influenced by CWD abundance (Wallace et al. 1995). Thus, we also included %Shredders, %Scrapers, %Collectors, %Filterers, and %Predators in our analysis of assemblage composition.

2.3.5 Data analysis

Benthic macroinvertebrate response variables were analyzed by season because previous research in the study streams showed high seasonality in assemblages (Maloney and Feminella 2006). A repeated-measures ANOVA was used to detect the main effects of treatment (restored vs. unrestored streams), period (before vs. after CWD additions), and a treatment-period interaction on macroinvertebrate measures using SAS PROC MIXED (8.0, SAS Institute, 2000 Cary, North Carolina). In this

analysis, treatment and period represented fixed effects and stream was the repeated factor. A significant period effect indicated a difference between pre- and post-restoration, whereas a significant treatment effect indicated response variable differed between treatments. However, both main effects do not discern whether the difference was related to CWD additions or natural differences; rather, a significant treatment-period interaction indicated that CWD additions affected macroinvertebrate measures differently between treatments before and after additions, which was the main contrast of interest. To test the influence of CWD additions we ran a 1-way ANOVA on macroinvertebrate measures that showed significant treatment and period effects. Additionally, we examined the potential effects of hydrologic variation (with precipitation as a surrogate measure for discharge) on macroinvertebrate measures. This procedure was done by performing a 1-way ANOVA on macroinvertebrate measures showing significant period effects. One-way ANOVA was used to determine the effect of CWD additions on habitat and %BPOM for individual streams. To satisfy conditions of normality, count data were square-root transformed, percentage data were arcsine-square-root transformed, and biomass and density were log-transformed (Zar 1999). An α level of 0.05 was used for all significance testing.

We also used nonmetric multidimensional scaling (NMS, McCune and Grace, 2002) to examine yearly macroinvertebrate assemblage similarity by season within and among restored and unrestored streams. NMS is an indirect gradient analysis technique that uses pairwise dissimilarity (Bray-Curtis distance) matrices to estimate stream position in species space (Jongman et al. 1995). Relative abundance of benthic macroinvertebrate data was used for the NMS analysis. Rare taxa were removed to

reduce their influence on ordinations (< 10% of samples) (Cao and Larsen 2001) prior to ordinations, using PC-ORD (MjM Software Design, Gleneden Beach, Oregon). NMS ordination scores were then regressed against independent instream habitat variables to determine which variables were related to macroinvertebrate assemblages in restored and unrestored streams. Additionally, to examine temporal shifts in assemblages attributable to restorations and/or contrasting hydrological regimes we compared mean vector length of faunal shifts in 2-dimensional space between the first year of the study (2001, Summer and Winter; 2002, Spring) and each successive year, by season. We used Pythagorean's theorem to calculate the mean Euclidean distance each assemblage shifted over the study. Finally, we compared among mean vector length of restored vs. unrestored streams using 1-way ANOVA and, if appropriate, Tukey's post-hoc test to determine where differences among means occurred.

2.4 RESULTS

2.4.1 Extent of CWD additions

CWD additions during 2003 increased the areal coverage of instream CWD from 3.79 to 6.90% LPK (82% increase), 3.70 to 8.89% in SB3 (140%), 7.30 to 11.62% in SB2 (59%), and 8.60 to 12.09% in KM1 (40%; Fig. 2.1). Augmentation of CWD during 2004 increased areal coverage of submerged CWD from 3.79 to 10.21% in LPK (169% increase) and 3.70 to 13.46% in SB3 (264%; Fig. 2.1).

2.4.2 Precipitation and Discharge

Precipitation and stream discharge differed greatly over the 5-y study, ranging from below-average to average rainfall leading up to the restoration (1999-2002) to higher than average rainfall post-restoration (2003-2005; Fig. 2.2A). This contrast between periods was greatest during summer with 2003, 2004 and 2005 being the 5th, 4th, and 2nd wettest summers over a 56-y period of record, respectively (Fig. 2.2B). No sampling occurred during summer 2003, so the increase in summer rainfall in 2003 (cf. 1999-2002; Fig. 2.2B) did not influence macroinvertebrate sampling during the pre-restoration period. This large difference in precipitation over the study was evident in high variation discharge between the pre- and post-restoration periods: mean summer discharge was significantly higher in the post- (vs. pre-) restoration period in all streams (Table 2.2, Fig. 2.3). Similar to discharge, mean summer depth showed significant increases in both restored and unrestored streams in the post-restoration period (Table 2.2, Fig. 2.4).

2.4.3 CWD, %BPOM and Streambed Variability

Burial of the debris dams was substantial in the first 2 y following restoration, ranging from ~30% in KM1 to 75% in SB3. The source of sediment in SB2, SB3, LPK likely resulted from a combination of instream and upland sediments.

Overall, %BPOM did not consistently change in either restored or unrestored streams, and little difference occurred between the pre- and post-restoration period. %BPOM showed no increase during winter or spring for either restored or unrestored streams, with increased %BPOM occurring in restored streams only during summer,

and only in 2 of 4 restored streams (SB2: $F = 9.09$, $p < 0.0001$; KM1: $F = 8.43$, $p < 0.0001$). %BPOM significantly decreased in only 2 unrestored streams between pre- vs. post-restoration (BC2 in winter: $F = 7.69$, $p < 0.0001$; HB in spring: $F = 3.39$, $p = 0.029$).

CWD additions appeared to have some effect on mean streambed height following restoration, as bed height either increased (SB2, SB3; $F = 9.90$, $p = 0.009$, $F = 26.16$, $p < 0.0001$, respectively) or decreased (LPK; $F = 62.71$, $p < 0.0001$) during the post-restoration (vs. pre-restoration) period. Only 1 unrestored stream (SB4, $F = 5.50$, $p = 0.037$) showed a significant difference (increase) between pre- and post-restoration. CWD additions appeared to promote accretion in 2 of the 4 restored streams (SB3, SB2) after restoration, which also was evident by the high degree of debris dam burial observed in the first year of post-restoration.

2.4.4 Benthic macroinvertebrates

Increases in precipitation and associated discharge appeared to have their greatest influence on benthic assemblages in summer, the season with the highest number of significant period effects. Macroinvertebrate metrics showing the greatest response to period effects were total biomass, density, richness, and %Filterers (Table 2.3), all of which were lower in both restored and unrestored streams during the post- (vs. pre-) restoration period (Fig. 2.5).

Several macroinvertebrate metrics showed treatment differences between restored and unrestored streams, when comparing before and after restoration. % EPT and EPT density both increased in restored streams during winter, and were significant

for both Period effects and Treatment-Period interactions (Table 3). EPT density significantly increased (by ~3 fold) from pre-restoration levels in restored streams whereas unrestored streams did not change (Fig. 2.6A), as did % EPT (Fig. 2.6B). EPT density and % EPT, % Filterers and % Collectors in spring also showed a significant Treatment-Period interaction (Table 3). However, unlike the EPT and % Collectors metrics, % Filterers decreased in unrestored streams but not in restored streams (Fig. 2.6C). Last, % Scrapers and Chironomidae richness in summer showed a Treatment-Period interaction (Tables 2.3) and, similar to the functional feeding group metrics in spring, % Scrapers and Chironomidae richness significantly decreased in unrestored streams but not in restored streams (Figs. 2.6E and F, respectively).

NMS showed a strong relationship between altered hydrologic conditions and benthic macroinvertebrate assemblages during summer and winter over the study. For summer assemblages, NMS axes 1 and 3 accounted for most of the macroinvertebrate assemblage variation ($R^2 = 0.35$ and 0.25 , respectively; Fig. 2.7A). When axes 1 and 3 were regressed against instream hydrologic and habitat variables, axis 1 was best explained by discharge ($R^2_{\text{adj}} = 0.27$, $p = 0.001$), and axis 3 by depth ($R^2_{\text{adj}} = 0.30$, $p < 0.0001$). For winter assemblages, axes 1 and 3 accounted for most of the variation ($R^2 = 0.32$ and 0.26 , respectively; Fig. 2.7B). When axes 1 and 3 were regressed against instream hydrologic and habitat variables, axis 1 was best explained by discharge and depth ($R^2_{\text{adj}} = 0.25$, $p = 0.002$), and axis 3 was best explained by depth and current velocity ($R^2_{\text{adj}} = 0.13$, $p = 0.042$). For spring assemblages, NMS showed no strong relationships between changing hydrology and benthic assemblages.

The degree of shifts in assemblages in the post-restoration period from 2001 (1st pre-restoration mean vector length) was higher in unrestored streams than restored streams during summer 2005 ($F = 13.10$, $p = 0.011$) and 2006 ($F = 6.78$, $p = 0.040$) (Fig. 2.8A). In contrast, winter mean vector length did not differ from 2002 assemblages in 2005, but did significantly differ in 2006 ($F = 9.89$, $p = 0.02$) (Fig. 2.8B). Spring assemblages in restored or unrestored streams did not significantly shift during the study ($p > 0.05$).

2.5 DISCUSSION

2.5.1 Influence of hydrologic variation on CWD additions

High variable hydrologic regimes may affect instream restoration efforts by increasing sediment inputs and destabilizing instream habitat under varying flow conditions, thus potentially reducing restoration efficacy. Stream and river restoration projects often do little to assess effectiveness of a given project during post-restoration (NRC 1992, Bernhardt et al. 2005); however, by tracking restoration efforts over a longer time period researchers are more likely to gauge overall success of a given project in association with greater variation in hydrologic regimes. The purpose of most restoration projects is to restore the natural range of ecosystem composition, structure, or dynamics (Falk 1990, Allen et al. 2002), but if a project is not monitored long enough to bracket a reasonable magnitude of variation in hydrologic conditions then they may not be able to judge the true outcome of the restoration. Varying hydrology likely will influence instream habitat, such as coarse woody debris (CWD), by displacing it down

stream or by burial (Shields et al. 2003), and efforts to restore such habitats need to be monitored over a long term to assess success.

CWD is an important structural and functional component of sandy bottom streams in the Southeastern US (Benke and Wallace 1990, Benke et al. 2001). Thus, CWD additions within impaired CWD-poor streams have been considered a viable restoration method in prior research (Grippel and White 2000, Webb and Erskine 2003, Lester et al. 2007). However, our results suggest that the efficacy of CWD additions on benthic macroinvertebrates and habitat can be highly variable both temporally and spatially, whose influence may depend on environmental conditions, particularly during hydrologically extreme periods.

Changes to the hydrologic regime appear to have greatly influenced the macroinvertebrate assemblage, especially during the summer. Macroinvertebrate density and biomass was significantly decreased in both restored and control streams, which is counter to that observed by others (Smock et al. 1989, Smock et al. 1992, Wallace et al. 1995). Much research over the last 20 y has demonstrated the importance of flow regime on macroinvertebrate assemblages (Resh et al. 1988, Poff and Ward 1989), often manifested by substantial changes in near-bed hydrology (Bennison and Davis 1992, Townsend et al. 1997, Nelson and Lieberman 2002). Our results showing a strong Period effect for density and biomass suggests a plausible link to changes in hydrologic regime in these streams over the study. Others have found that increased discharge in the form of floods can negatively affect macroinvertebrate density and biomass, as well as overall taxa richness (Suren and Jowett, 2006). Dramatic decreases in density and biomass as well as the shift in macroinvertebrate

assemblages in general would explain why the influence of CWD additions in restored streams was so limited in our experiment.

2.5.2 Hydrologic and CWD addition influence on instream habitat and BPOM

Several studies have shown that following CWD additions, overall or relative (microhabitat) stream depth and volume increase in relation to CWD structures (Wallace et al. 1995, Shields et al. 2003). Wallace et al. (1995) found that the deposition area was associated with an increase in organic matter retention, which, in turn, increased basal resource (detritus) abundance for benthic macroinvertebrates. Our results did not show this pattern as depths in both restored and unrestored streams were higher in the post vs. pre-restoration period during the summer baseflow period. Rather, increases in depth in all streams likely resulted because of increased precipitation and discharge during the post- (vs. pre-) restoration period. In related work from the study streams, Roberts et al. (2007) reported a decrease in reach-scale velocity in restored streams within 1 mo after CWD additions; in contrast, our findings indicated that this difference was not sustained over the longer term, because of possibly changing discharge conditions during the post-restoration period. % BPOM showed no difference between pre- and post-restoration, and likewise there was no difference between restored or unrestored streams. This may have resulted from BPOM being buried at greater depths than our sampling was done, were taken at, suggesting which would suggest our method was inadequate to sample BPOM. Additionally, our BPOM values represent a reach-level %BPOM measure as our samples were not specifically taken at either

natural or artificial debris dams. Thus, it is unclear from our data if CWD additions had a substantial influence of %BPOM.

Instream CWD has been widely associated with increased inorganic and organic matter (Baillie and Davies 2002), and CWD additions have reportedly increased abundance of sediment and particulate matter retention (Wallace et al. 1995, Laitung et al. 2002, Pretty and Dobson 2004), both indicating the importance of CWD in stabilizing stream beds and entraining organic matter. Our results on bed instability did not support this pattern. One reason for the lack of an effect of CWD additions on bed stability was the high degree of burial occurring after CWD additions in 3 of the 4 restored streams (LPK, SB2, SB3). In 2 of these streams where CWD was augmented in 2004 (LPK, SB3) most of these additional logs also became buried by May 2006 sampling (personal observations). Like streambed stability, no differences were observed in %BPOM between restored or unrestored streams. Previous research in the study streams found that upland disturbance had a substantial influence on instream CWD abundance (Maloney et al. 2005). Previous research of the 4 streams that had a significant bed height change in the current study showed that they occur in highly disturbed watersheds (Maloney and Feminella 2005), and this fact along with changing hydrologic conditions between pre- and post-restoration periods may have contributed to these differences. For CWD additions to have a positive influence on streambed stability, increasing %BPOM, and reducing CWD burial under the highly variable hydrologic conditions observed during the study, upstream sediment both in-channel and from disturbed upland sources will likely have to be reduced. Additionally, a relatively small restored reach in larger sediment-disturbed stream appears to have little

positive effect, especially during wet year. A greater restoration effort throughout the reach may help alleviate the influence of hydrologic variability and reduce sediment movement throughout the channel, even in highly disturbed watersheds.

2.5.3 Influence of CWD additions on dampening hydrologic variation

Similar to abiotic factors, most benthic macroinvertebrate metrics showed equivocal response to CWD additions. The transient influence on fishes of CWD additions has been reported elsewhere (Shields et al. 2003) and suggests that the sole use of CWD in restoration practices only may temporarily offset stream impairment. Shields et al. (2003) reported that CWD additions failed because of high discharge events and within 2 y after restoration, with ~ 30% of additions losing wood to downstream displacement. In our study, CWD habitat loss did not occur because of downstream displacement but rather from burial. Winter was the only season in which a positive increase in benthic macroinvertebrate metrics was observed in the restored streams compared to unrestored streams, and this pattern was limited to EPT density and %EPT. Similar increases did not occur in other seasons and may have become dampened from increased precipitation and discharge during the post-restoration period. Even though most metrics did not show an increase in the restored relative to the unrestored streams, many metrics showed a decrease in unrestored relative to restored streams.

NMS showed a strong shift in assemblage structure in both restored and unrestored streams in relation to changing discharge and increasing stream depth; however, restored streams showed a comparatively smaller shift from pre-restoration

conditions compared to the unrestored streams; this result suggested that CWD additions buffered impacts of the altered hydrologic regime. In this context, efficacy of CWD additions in the restored streams was dampened by the high degree of inorganic sediment, but the presence of CWD additions in restored streams, even in a largely buried state, appeared to enhance recovery of benthic macroinvertebrate assemblages. Longer-term studies in these streams are being done to quantify the degree of benthic recovery from hydrologic disturbance and assemblage enhancement to levels consistently exceeding pre-restoration conditions.

2.6 CONCLUSION

A successful restoration project must not only ameliorate impairment in the short term, but also exhibit long-term and self-sustaining effects (Palmer and Allen 2006). Our results suggest that debris dam additions to streams channels, while somewhat effective over the short term, may not be a solution for restoring stream conditions, especially in sand-bottomed channels. Additionally, our results suggest the importance of understanding the influence of background environmental variability, such as strongly contrasting hydrology before, during, and after restoration projects. In addition to the influence of current conditions, an understanding land use legacies in watersheds where restoration efforts will be implemented may help guide the restoration process. Previous work in the current watersheds has shown a significant influence of legacy effects on instream conditions of both biotic and abiotic factors (Maloney et al. 2008). A more productive and self-sustained restoration practice for small headwater streams may be the re-vegetation of riparian zones and ephemeral drains as well as increase the

restoration reach within the stream channel itself. This broader approach to restoration may decrease the movement of new sediment into the perennial channel by both stabilizing upland soils and instream channel conditions, thus reducing the influence of hydrology on benthic communities.

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Table 2.1. Locations and characteristics of study streams. All values measured in this table from Maloney et al. (2005) and Maloney and Feminella (2006).

Stream	Stream code	UTM	Military land use	Drainage area (km ²)	Mean stream slope (%)	Disturbance intensity (% catchment)	Pre-restoration CWD (% areal coverage)
Restored							
Little Pine Knot Tributary	LPK	0719223N 3585421E	Heavy Machinery	0.33	5.10	11.26	3.79
Sally Branch Tributary	SB3	0716673N 3584684E	Infantry/ Ranger	0.72	1.00	10.49	3.70
Sally Branch Tributary	SB2	0716808N 3584787E	Heavy Machinery	1.23	2.31	8.12	7.30
Kings Mill Creek	KM1	0720701N, 3600036E	Infantry/ Ranger	3.69	0.83	4.63	8.60
Control							
Sally Branch Tributary	SB4	0716005N, 3584889E	Heavy Machinery	1.00	1.33	13.65	3.11
Bonham Tributary	BC1	0710893N, 3588286E	Infantry/ Ranger	2.10	1.67	10.46	12.62
Bonham Tributary	BC2	0710627N, 3588976E	Infantry/ Ranger	0.75	2.67	3.15	8.92
Hollis Branch	HB	0717848N 3583123E	Infantry/ Ranger	2.15	2.00	6.62	6.34

Table 2.2. Summary of instream physical variables for restored and unrestored streams, by season.

Variable	Seasonal mean						One-way ANOVA					
	Summer		Winter		Spring		Summer		Winter		Spring	
	Pre-	Post-	Pre-	Post-	Pre-	Post-	<i>F</i>	<i>p</i>	<i>F</i>	<i>p</i>	<i>F</i>	<i>p</i>
Velocity (m/s)												
Restored	0.117	0.210	0.129	0.128	0.125	0.157	***		***		***	
Unrestored	0.074	0.105	0.114	0.114	0.098	0.113	***		***		***	
Depth (m)												
Restored	0.063	0.111	0.125	0.139	0.086	0.115	10.36, 0.005		***		***	
Unrestored	0.083	0.139	0.135	0.169	0.109	0.164	5.67, 0.028		***		***	
Width (m)												
Restored	1.275	1.217	1.535	1.058	1.399	1.028	***		***		***	
Unrestored	1.072	1.218	1.743	0.964	1.290	1.080	***		6.30, 0.022		***	
Discharge (m ³ /s)												
Restored	0.005	0.129	0.010	0.204	0.011	0.215	8.16, 0.010		10.65, 0.004		10.29, 0.005	
Unrestored	0.012	0.088	0.011	0.164	0.006	0.128	16.42, 0.001		26.40, <0.0001		8.27, 0.01	

Table 2.3. F-values (p -values in parentheses) of repeated measures ANOVA ($F_{1,30}$) on compositional macroinvertebrate measures. TRT = restored or control streams, Period = pre- and post-restoration. Boldface indicates values significant at $p = 0.05$.

Metric	Season	Treatment	Period	Treatment*Period
	Winter			
Biomass		2.52 (0.124)	0.38 (0.544)	1.43 (0.242)
Density		18.02 (0.0002)	0.49 (0.488)	0.95 (0.123)
<i>H'</i>		0.98 (0.330)	7.84 (0.009)	1.10 (0.302)
Taxa richness		0.87 (0.359)	0.00 (0.975)	1.52 (0.228)
EPT Density		4.67 (0.039)	4.16 (0.051)	5.47 (0.023)
% EPT		1.38 (0.249)	28.66 (<0.0001)	9.15 (0.005)
% Chiro		0.01 (0.921)	0.00 (0.990)	0.27 (0.645)
Chiro richness		0.57 (0.455)	1.67 (0.206)	1.99 (0.169)
% Predators		3.79 (0.061)	2.31 (0.139)	0.74 (0.395)
% Shredders		0.67 (0.418)	13.41 (0.001)	0.21 (0.648)
% Collectors		0.84 (0.367)	6.65 (0.015)	0.34 (0.565)
% Filterers		0.40 (0.530)	16.65 (0.0003)	0.20 (0.658)
% Scrapers		0.77 (0.389)	0.01 (0.916)	0.08 (0.780)
% Clingers		2.33 (0.138)	1.60 (0.216)	0.22 (0.640)
	Spring			
Biomass		3.26 (0.081)	10.80 (0.003)	2.37 (0.135)
Density		3.65 (0.066)	3.69 (0.065)	1.93 (0.175)
<i>H'</i>		3.08 (0.090)	1.52 (0.228)	0.62 (0.438)
Taxa richness		1.65 (0.209)	12.23 (0.002)	0.04 (0.847)
EPT Density		1.14 (0.294)	1.98 (0.170)	1.13 (0.297)
% EPT		1.95 (0.174)	0.73 (0.399)	0.95 (0.339)
% Chiro		1.11 (0.300)	4.90 (0.034)	2.15 (0.153)
Chiro richness		0.09 (0.767)	12.77 (0.001)	0.04 (0.840)
% Predators		0.07 (0.800)	0.06 (0.810)	1.62 (0.213)
% Shredders		2.37 (0.134)	10.97 (0.002)	1.21 (0.281)
% Collectors		3.15 (0.071)	0.90 (0.352)	13.55 (0.001)
% Filterers		0.05 (0.825)	0.08 (0.775)	7.63 (0.010)
% Scrapers		0.05 (0.819)	37.71 (<0.0001)	0.44 (0.514)
% Clingers		0.64 (0.430)	7.29 (0.011)	0.35 (0.560)
	Summer			
Biomass		0.97 (0.332)	25.70 (<0.0001)	0.07 (0.794)
Density		0.29 (0.596)	5.37 (0.028)	0.00 (0.968)
<i>H'</i>		0.63 (0.434)	2.18 (0.151)	0.34 (0.566)
Taxa richness		2.01 (0.166)	23.34 (<0.0001)	2.13 (0.155)
EPT Density		0.29 (0.596)	5.37 (0.028)	0.00 (0.968)
% EPT		1.19 (0.284)	5.50 (0.026)	0.24 (0.626)
% Chiro		1.55 (0.223)	0.01 (0.923)	6.17 (0.019)
Chiro richness		0.23 (0.636)	7.95 (0.008)	1.51 (0.229)
% Predators		0.40 (0.530)	0.48 (0.494)	1.10 (0.302)
% Shredders		0.58 (0.452)	5.82 (0.004)	0.01 (0.999)
% Collectors		0.65 (0.428)	3.91 (0.058)	0.01 (0.930)
% Filterers		1.30 (0.264)	15.10 (0.001)	0.27 (0.607)
% Scrapers		0.18 (0.677)	12.30 (0.001)	5.98 (0.021)
% Clingers		7.33 (0.011)	0.22 (0.640)	0.23 (0.632)

Figure 2.1. Relative abundance of in-stream coarse woody debris (CWD, as % of total streambed cover), before (pre-restoration, spring 2003) and after debris dam additions (fall 2003 and fall 2004 CWD additions) for the 4 restored streams. Restored streams received debris dam additions in Oct-Nov 2003 and supplemental debris dams (SB3 and LPK) in Nov 2004.

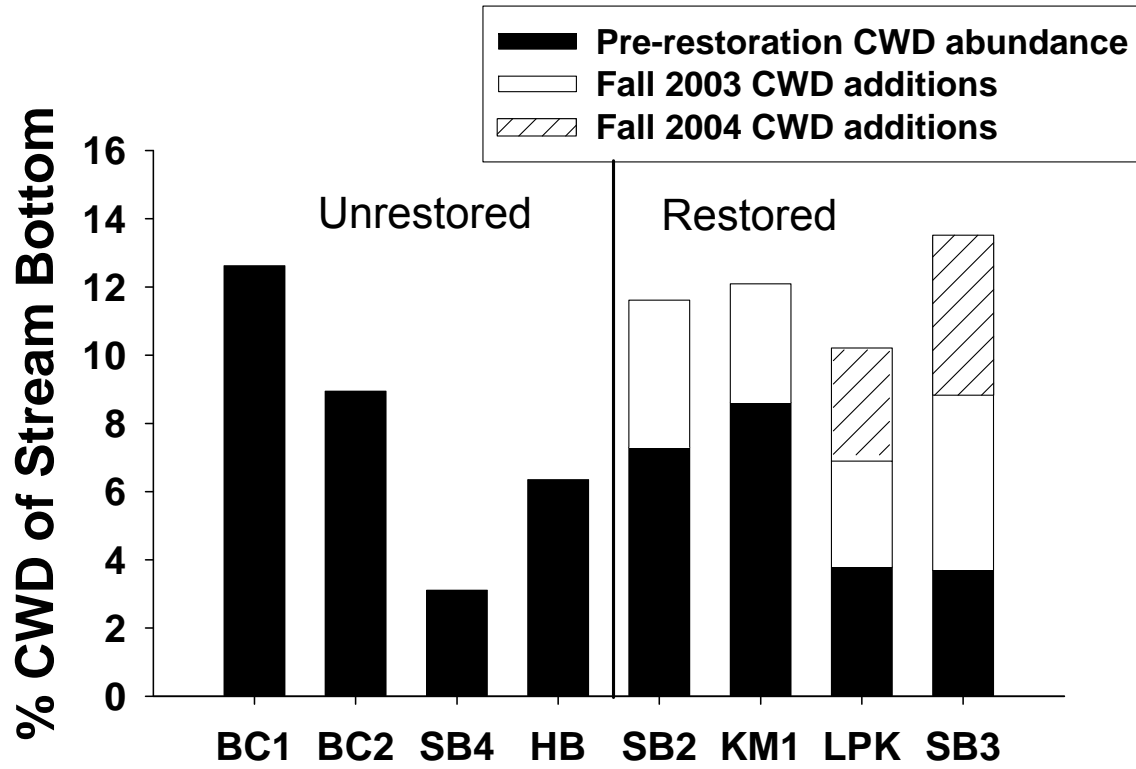


Figure 2.2. Precipitation data from Columbus, Georgia, for the period 1949–2006. Pre-restoration sampling occurred in 2001, 2002, and 2003, whereas post-restoration period occurred in 2004, 2005, and early 2006. Note that much of the post-restoration sampling occurred in years that were among the wettest on record (late 2003, 2004, and 2005). A = annual precipitation, B = summer precipitation.

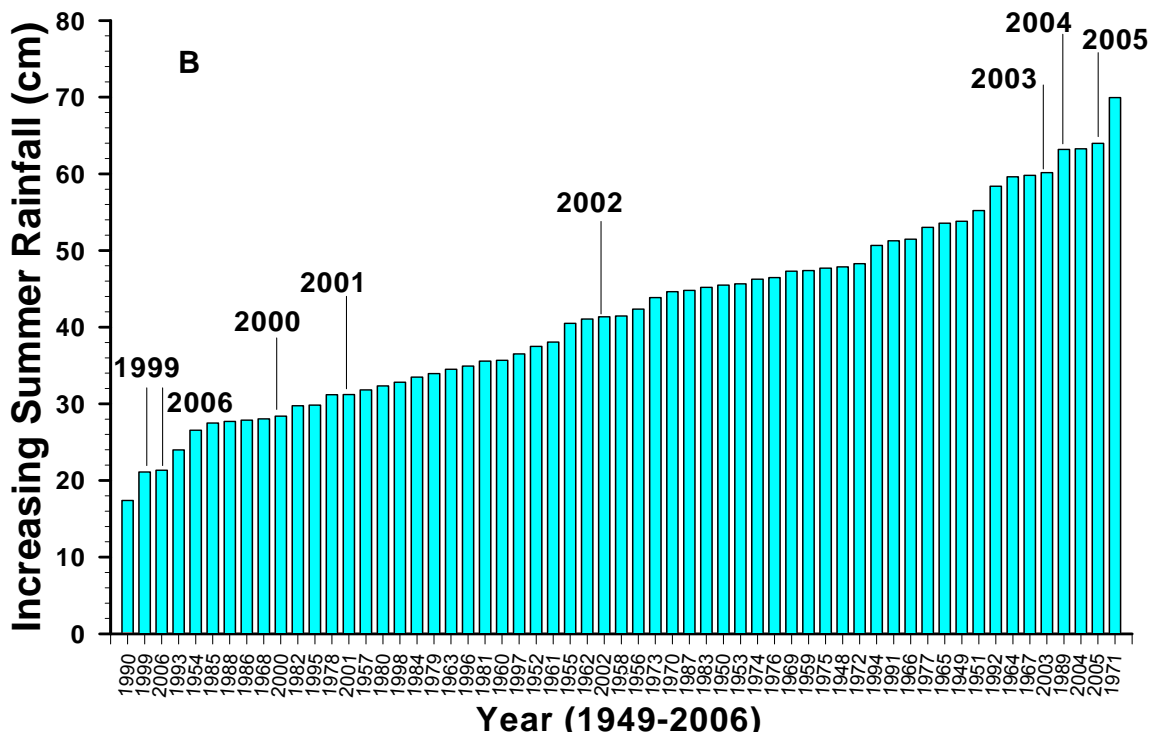
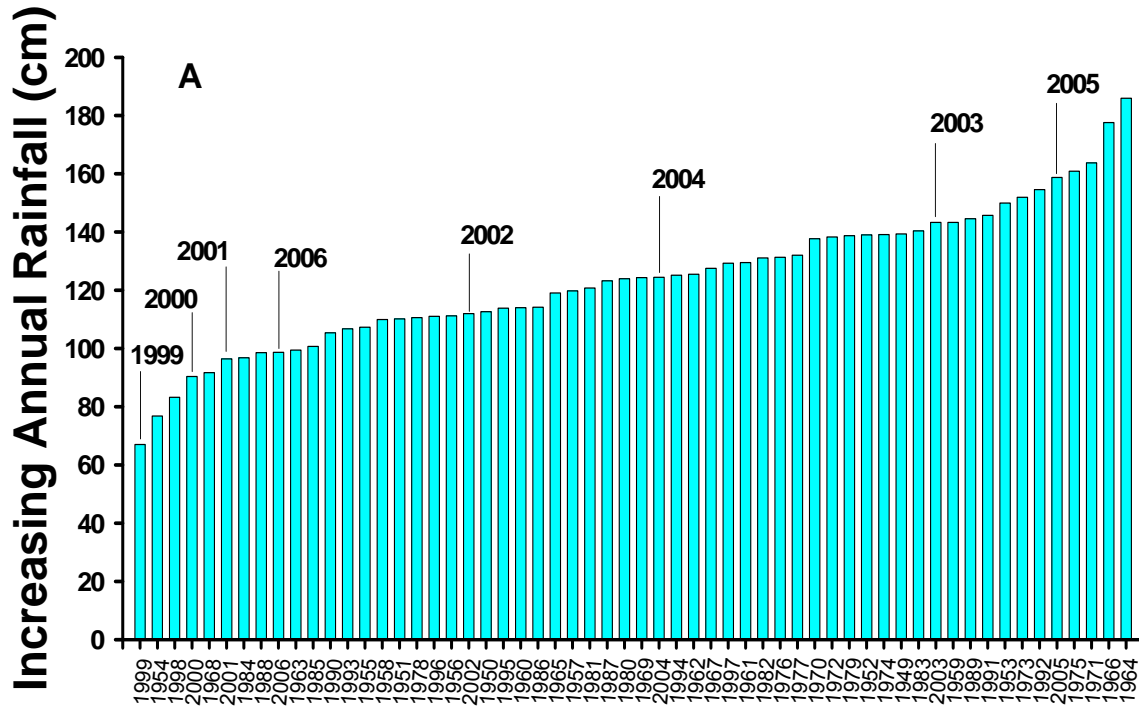


Figure 2.3. Comparison of mean (+1 SE) baseflow discharge in restored (in compartments SB3, SB2, KM1, LPK) (A) and unrestored streams (compartments BC1, BC2, SB3, HB) (B) before (2001- 2003) and after restoration (2004, 2005, 2006). Vertical dashed line on A shows approximate time of debris dam additions (Oct-Nov 2003). Note that much of the post-restoration sampling (2004, 2005) occurred during conditions of substantially higher discharge than pre-restoration sampling ($n = 24$).

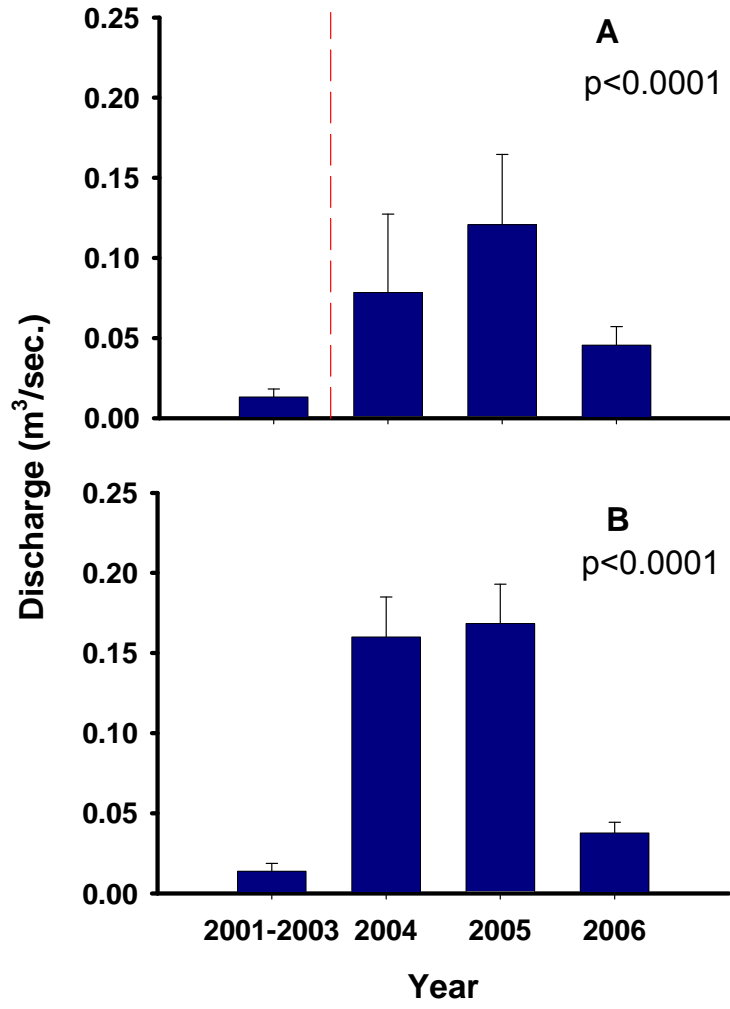


Figure 2.4. Mean (+1 SE) summer depth in restored and unrestored stream during the pre- and post-restoration periods. * = $p < 0.05$.

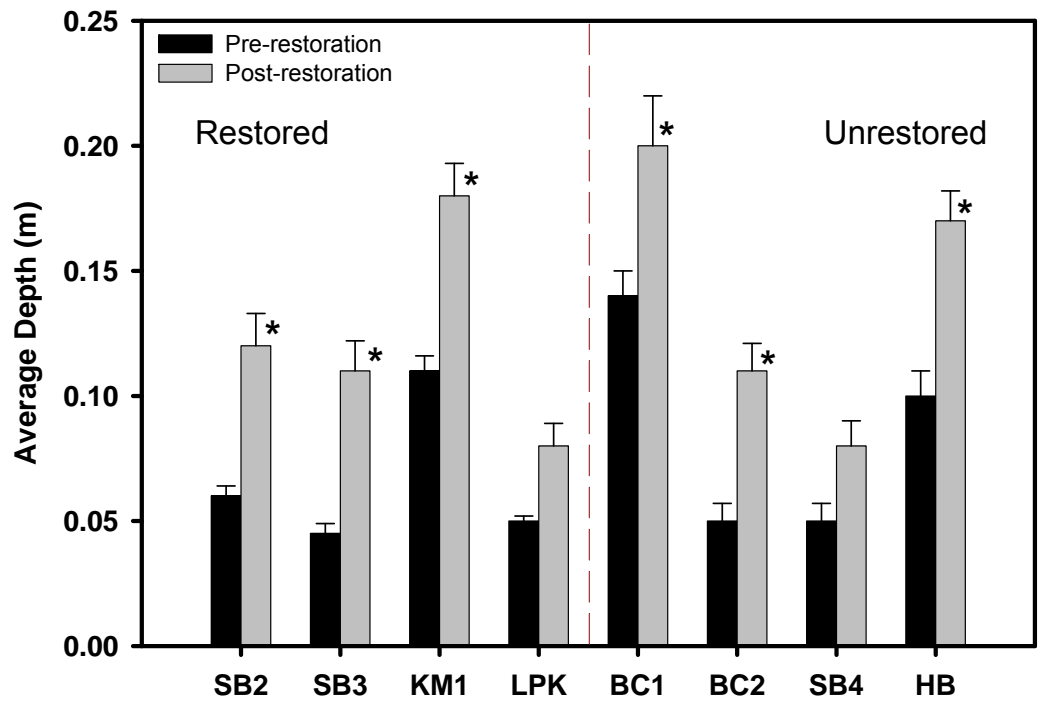


Figure 2.5. Average relative abundance and functional feeding groups of the benthic macroinvertebrate assemblage that showed a significant Period effect during the summer. A = biomass (restored, $F = 14.47$, $p = 0.001$; unrestored, $F = 9.68$, $p = 0.006$), B = density (restored, $F = 12.40$, $p = 0.002$; unrestored, $F = 13.73$, $p = 0.002$), C = species richness (restored, $F = 5.37$, $p = 0.032$; unrestored, $F = 15.26$, $p = 0.001$), D = %Filterers (restored, $F = 4.20$, $p = 0.053$, unrestored, $F = 7.68$, $p = 0.013$) Error bars are standard error. * = $p < 0.05$.

Pre-restoration
Post-restoration

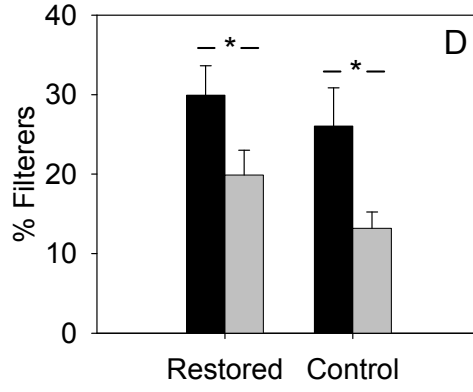
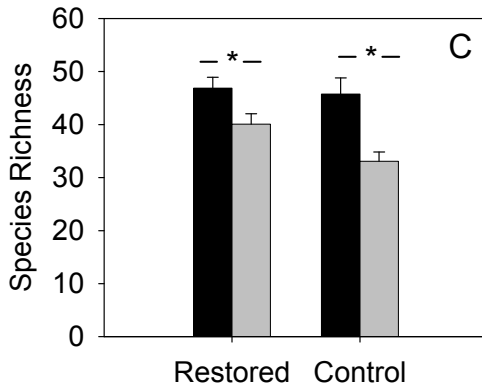
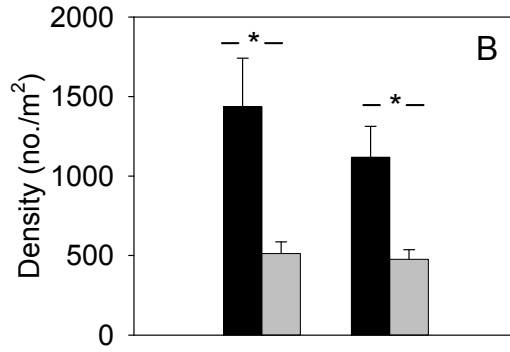
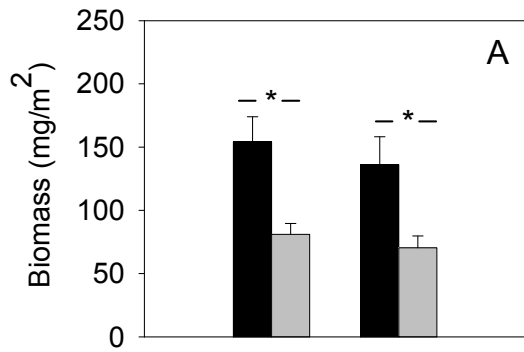


Figure 2.6. Mean (+1 SE) relative abundance and functional feeding groups of the benthic macroinvertebrate assemblage that showed a significant Treatment×Period effect. A = winter EPT density (restored, $F = 10.27$, $p = 0.017$; unrestored, $F = 0.17$, $p = 0.685$), B = winter %EPT (restored, $F = 19.33$, $p < 0.0001$; unrestored, $F = 1.39$, $p = 0.225$), C = spring %Filterers (restored, $F = 1.58$, $p = 0.225$; unrestored, $F = 4.25$, $p = 0.050$), D = spring %Collectors (restored, $F = 1.18$, $p = 0.292$, unrestored, $F = 6.98$, $p = 0.017$), E = summer %Scrapers (restored, $F = 0.59$, $p = 0.45$; unrestored, $F = 7.11$, $p = 0.016$), $F =$ summer Chironomidae richness (restored, $F = 1.08$, $p = 0.312$; unrestored, $F = 12.03$, $p = 0.003$). * = $p < 0.05$.

Pre-restoration
 Post-restoration

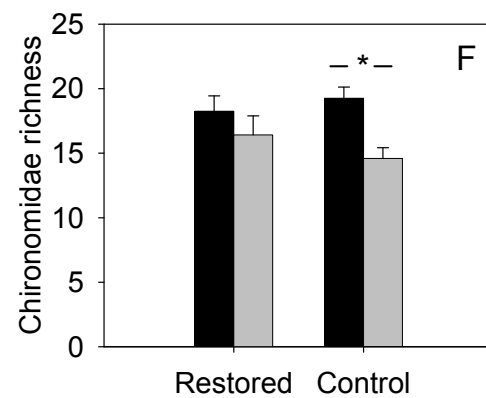
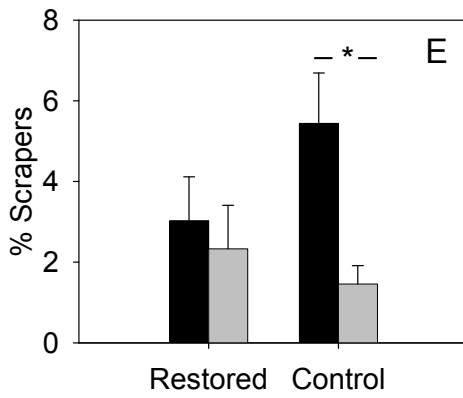
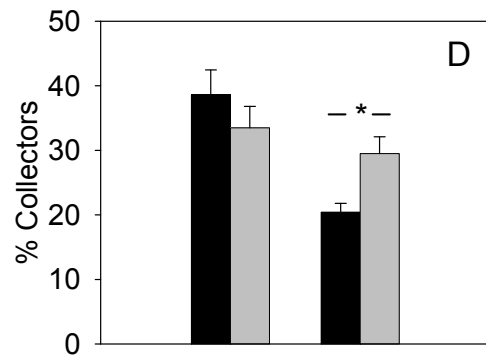
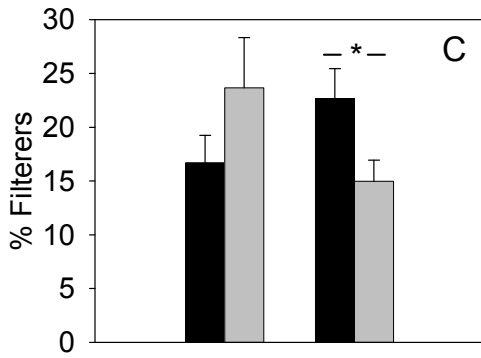
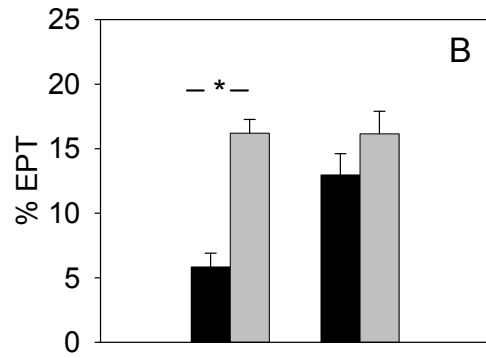
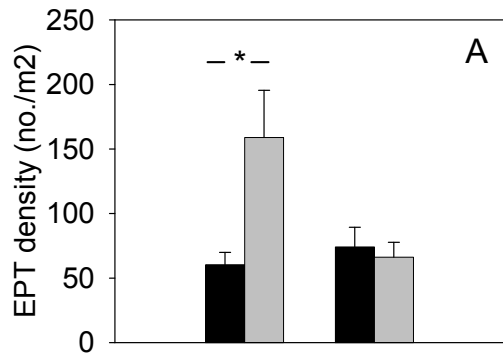


Figure 2.7. Nonmetric multidimensional scaling (NMS) ordination results. Symbols represent stream/year-specific macroinvertebrate scores. A.--- (summer: Circles: 2001, inverted triangle: 2002, square: 2004, diamond: 2005, triangle: 2006). B.--- (winter: Circles: 2002, inverted triangle: 2003, square: 2004, diamond: 2005, triangle: 2006). R^2 values represent the proportion of variation in the macroinvertebrate assemblage similarity accounted for by each axis. Arrows on axes indicate direction of relationships between hydrologic and habitat variables and NMS scores (see text for values). Axis scores are raw values, stress level = 13.01 (summer) and 13.65 (winter), for the three-dimension solution, with a final instability of 0.00001 after 151 iterations for summer, and a final instability of 0.00001 after 67 iterations for winter.

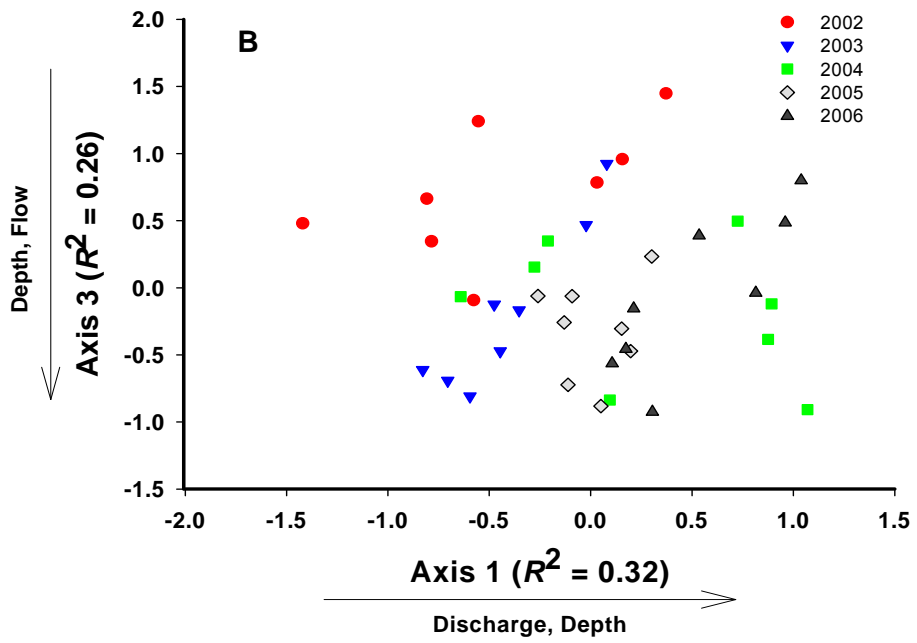
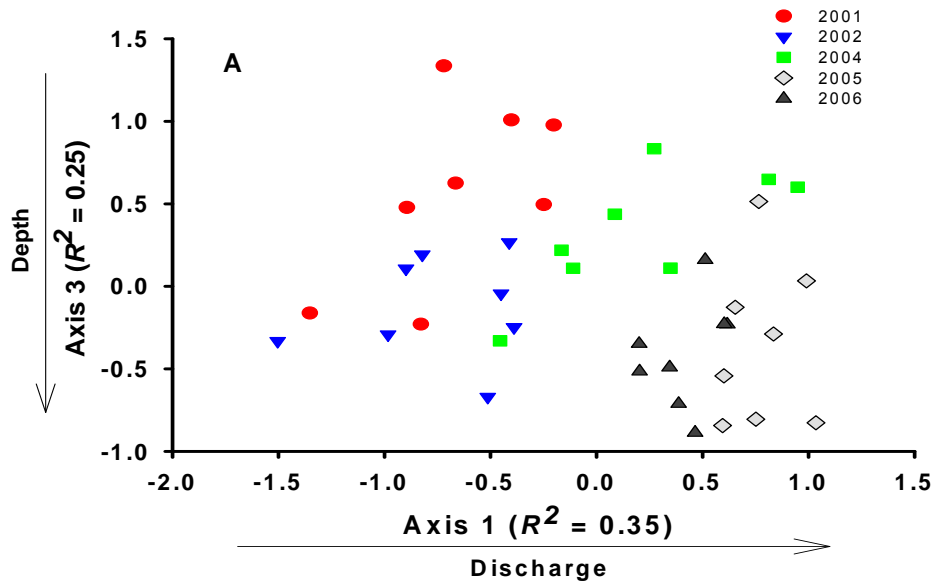
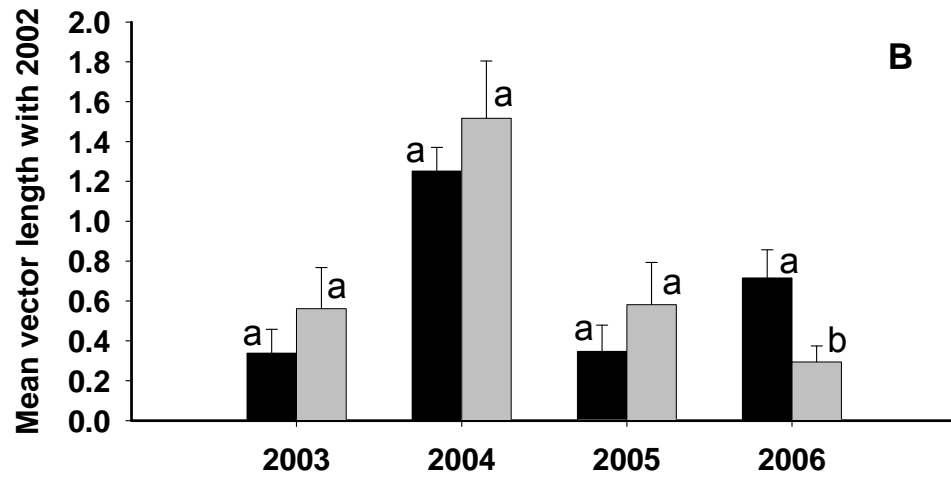
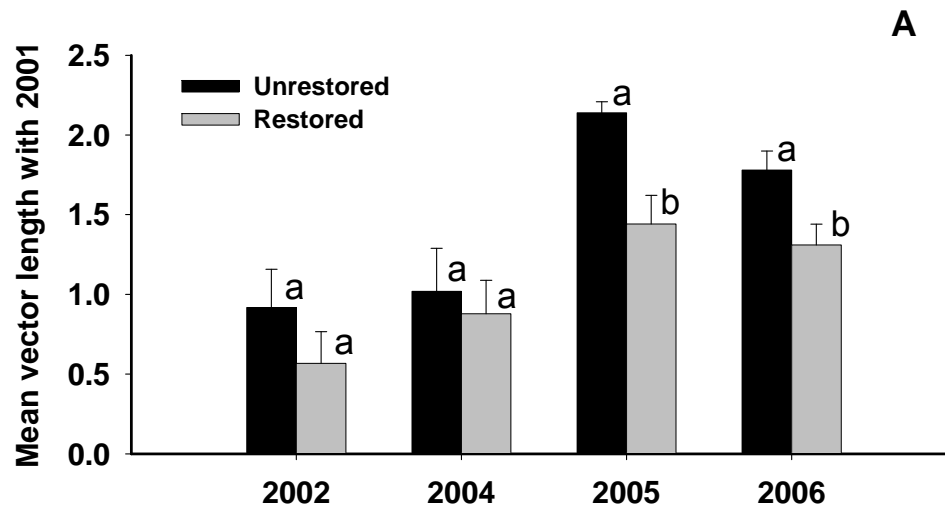


Figure 2.8. Mean (+1 SD) vector length comparison between restored and unrestored streams, with vector length calculated for each stream between the 1st year of pre-restoration sampling (2001: summer, A; 2002: winter, B) and each subsequent year of sampling. Differences between restored and unrestored streams are designated by different letters using Tukey's pairwise comparisons and treatments with the same letter were not significantly different.



**3. MULTI-SCALE CONTROLS ON POPULATIONS OF THE CRAYFISH
PROCAMBARUS VERSUTUS (CAMBARIDAE) IN SANDY STREAMS OF WESTERN
GEORGIA, USA**

3.1 SUMMARY

Landscape disturbance can structure benthic populations principally by altering instream habitat conditions. We evaluated the effects of disturbance on populations of the crayfish *Procambarus versutus*, from small sandy-bottom streams in western Georgia, USA, through the direct influence of catchment disturbance on instream habitat. We quantified crayfish and habitat variables from 8 streams across a gradient of catchment disturbance. Catchment disturbance (as indicated by % of bare ground in the catchment) was negatively correlated with several measures of instream habitat quality, including relative abundance of coarse woody debris (CWD) and percent benthic particulate organic matter (%BPOM) during spring and summer, and mean stream depth. In turn, crayfish density was positively related to CWD and %BPOM across most seasons, whereas crayfish biomass was correlated with CWD, %BPOM, and discharge and depth. Catchment disturbance was a good predictor of crayfish population density and biomass, and appeared to have a greater effect on individuals in runs compared to pools. Pools showed little difference across streams in relation to catchment disturbance; however, crayfish density and biomass decreased across streams in relation to increasing catchment disturbance. These results suggest that

catchment level disturbance influences instream habitat which, in turn, directly influence crayfish populations.

3.2 INTRODUCTION

Disturbance is an important driver of the structure of many stream communities through its direct and indirect effects on instream habitat (Resh et al. 1988, Palmer et al. 1996). Dissimilar disturbance episodes affect communities differently, and these events have been categorized into *pulse*, *press*, and *ramp* disturbance types (Lake 2000). *Pulse* disturbances are intense short-term events, such as floods, which typically have a distinct time frame. *Press* disturbances differs from *pulse* disturbances mainly in the duration of the event, with *press* events (e.g., dams or channelization) arising quickly like *pulses*, but continue influencing the system for a longer time frame. Finally, *Ramp* disturbances arise over a longer time period, such as a drought or the incremental spread of an exotic species, which have a pervasive influence on the system. *Ramp* disturbances are similar to *press* disturbances in having long-term effects, but their impact is more gradual and may not achieve an equilibrium state similar to *presses* disturbance (Lake 2000). Landscape-scale disturbance, such as terrestrial vegetation clearing in a catchment, typically is a *ramp* disturbance because it is usually characterized by a gradual change from one predominant land use condition to another. This change in land use gradually increases disturbance impact on a stream ecosystem, unless a threshold is reached (King et al. 2005, Walsh et al. 2005).

Landuse changes may manifest their influence on streams through land-cover cascades, which couple terrestrial disturbance to instream changes in physicochemical

conditions relevant to stream biota (Burcher et al. 2007). Landscape disturbance often increases sediment entering streams, affecting instream habitat directly through burial and indirectly biota by reducing available habitat for biota (Smock 1997, Maloney and Feminella 2006).

Much research has documented the negative effects of sediment on instream faunal composition and diversity (Cordone and Kelly 1961, Lenat et al. 1981, Wood and Armitage 1997, Angradi 1999). Sedimentation from landscape disturbance can alter benthic macroinvertebrates behavior (i.e., as increased drift), directly causing mortality (Newcombe and MacDonald 1991, Waters 1995). An important component of sediment impacts on stream habitat relates to sedimentation-induced reductions in abundance of submerged coarse woody debris (CWD). In sandy-bottom streams, CWD is a primary source of benthic habitat heterogeneity (Smock et al. 1989, Benke and Wallace 1990, Smock and Gilinsky 1992, Maloney et al. 2005). In this context, through its negative effects on CWD excessive sedimentation can reduce habitat quality and quantity for macroinvertebrates (Schofield et al. 2004).

It has long been known that CWD can greatly influence nutrient retention and cycling and biotic communities in streams (Cummins 1974, Bilby 1981, Bisson et al. 1987). High retention of organic matter as leaf litter by CWD presence can affect structure and function of a full range of benthic organisms from bacteria to fish (Benke et al. 1985, Smock et al. 1989, Hall et al. 2000, Shields et al. 2006). However, compared to other benthic macroinvertebrates, little is known about how landscape disturbance and its effects on CWD affects populations of freshwater crayfish, which are

ubiquitous in many streams and can dominate macroinvertebrate biomass (Momot et al. 1978, Huryn and Wallace 1987).

Crayfish constitute the bulk of benthic macroinvertebrate biomass in many freshwater systems (Mason 1974, Momot and Gowing 1977, Momot et al. 1978, Momot 1995, Rabeni et al. 1995), and play a significant role in many aquatic ecosystems (Webster and Patten 1979, Huryn and Wallace 1987, Hart 1992, Creed 1994). Crayfish have the potential to exert a substantial effect on benthic macroinvertebrates in many freshwater systems, due to their high biomass, polyphagous feeding, and large size relative to other benthic macroinvertebrates (Lodge et al. 1994, Usio and Townsend 2004, Usio et al. 2009). Changes to crayfish populations due to catchment disturbance may influence ecosystem function by reducing a crayfish's influence on basal resources and other benthic macroinvertebrates.

Previous research at the Fort Benning Military Installation (FBMI) in western Georgia demonstrated that catchment disturbance was inversely correlated with instream CWD abundance and substrate particle size, and positively correlated with streambed instability (Maloney et al. 2005). In another study at FBMI, macroinvertebrate richness and overall biotic integrity decreased with increasing catchment disturbance, apparently because of degraded habitat (Maloney and Feminella 2006). Therefore, these streams are excellent systems to determine the effects of catchment-level disturbance on habitat stability and crayfish populations. Because of the multifunctional role that crayfish play in aquatic systems (Helms and Creed 2005), understanding the effects of upland disturbance and instream habitat loss

on crayfish populations can have important implications for the management of stream ecosystems (Parkyn and Collier 2004, Schofield et al. 2004).

Our study was designed to explore the influence of catchment-scale disturbance and instream habitat on the density, biomass, and size frequency of crayfish at FBMI,. The objectives were to 1) relate instream habitat to landscape-scale factors, specifically catchment-scale disturbance 2) investigate the relationships between instream habitat and crayfish population measures, and 3) relate crayfish population measures to catchment-scale disturbance to understand how well disturbance can predict and potentially influence population level variables of crayfish, and 4) determine if crayfish response to catchment-scale disturbance was similar to other benthic macroinvertebrates.

3.3 METHODS

3.3.1 Study area

FBMI is in the Southeastern Plains Level-3 ecoregion (Omernik 1987) (area = 735 km²) has a humid and mild climate and year-round precipitation (mean = 105 cm/y). The primary land use is military training and includes dismounted infantry, tracked-vehicle maneuvers (i.e., tanks), heavy weapons usage, and airborne training drop zones (USAIC 2001, Dale et al. 2002). Undisturbed upland vegetation consists primarily of longleaf pine (*Pinus palustris*) and loblolly pine (*P. taeda*), with some hickories (*Carya* spp.), flowering dogwood (*Cornus florida*), and oaks (*Quercus* spp.). Riparian vegetation is largely intact (canopy cover often >90%, Maloney et al. 2005), and is dominated by mesic hardwoods including sweetbay magnolia (*Magnolia*

virginiana), water oak (*Q. nigra*), yellow poplar (*Liriodendron tulipifera*), red maple (*Acer rubrum*), black gum (*Nyssa sylvatica*) and sweet gum (*Liquidambar styraciflua*) (Cavalcanti 2004).

Much of the landscape disturbance at FBMI is from military training-associated use of heavy tracked vehicles, which disrupts vegetative cover and exposes underlying soils to erosion (Dale et al. 2002). In addition, forestry practices such as thinning, timber harvesting, and controlled burning associated with restoration of the native longleaf pine forest community are prevalent at FBMI (Noss 1989). Previous research has also shown historical land-use, largely from agriculture prior to establishing FBMI as a training facility to be an important factor in contemporary stream conditions (Maloney et al. 2008).

3.3.2 Study sites and landscape-scale measures

Eight 1st- and 2nd-order streams were selected as study sites (Table 3.1), with a ~100-m study reach established per stream. Channels were mostly sand and clay substrate, and consisted of pool and run habitat unit types, with a current velocity range of 0.05 – 0.17m/s, depth of 0.06 – 0.24m, width of 1.0 – 2.1m, and discharge of 0.002 – 0.044m³/s across seasons (Table 3.2). Study streams showed a baseline range of CWD abundance (as m² of CWD per m² of stream bed); from ~12% of stream bottom in LC to ~3% in SB4, and mean stream gradient ranging from 0.83% to 5.1% KM1 and LPK, respectively (Table 3.1) (see also Maloney et al. 2006).

For each catchment, spatial and land-use/land-cover data were quantified with Arcview® 3.2 GIS (Environmental Systems Research Institute, Redlands, CA) using

coverages from the SERDP Ecosystem Management Project (SEMP) data repository (<http://sempdata.wes.army.mil/>). Catchment area (Area) was established from a 1993 digital elevation model (DEM, 10-m resolution); specific grid coordinates of sampling sites were obtained from global positioning system (GPS) units. Disturbance levels were defined as the % of bare ground on slopes > 5% and percent of unpaved road cover within a catchment (%BGRD, Maloney et al. 2005). Previous research showed that this metric was a reliable indicator of upland disturbance influence on multiple measures of stream at FBMI, ranging from abundance of primary and secondary consumer to whole-stream ecosystem metabolism (Houser et al. 2005, 2006; Maloney et al. 2005, 2006, 2008).

3.3.3 Instream habitat measures

We quantified a full range of reach-scale (e.g., CWD, mean velocity and depth) measurements for each study site. Area of each run and pool habitat were estimated using 5 cross-sectional transects to determine average habitat width and 3 longitudinal-transects to determine the length of each habitat unit. Velocity and depth were measured at 5 evenly spaced points along each cross-sectional transect. We estimated discharge seasonally (spring, summer, winter) at the downstream-most sampling point of each site using the incremental method (Gore 1996). In addition, we used a modified transect method to quantify the relative abundance of CWD associated with the stream bed (Wallace and Benke 1984). CWD surveys were conducted annually (spring 2002 and 2003) by measuring all live, dead-submerged, and dead-buried wood pieces >2.5 cm in diameter in 15 cross-stream transects per stream (1-m long per transect). Live

wood was combined with dead wood in surveys because some sites had prominent exposed roots in the stream bed, which could have functioned similarly to dead wood as benthic habitat and/or sources of organic matter retention. In addition, we quantified abundance of benthic particulate organic matter (%BPOM) using sediment cores (PVC pipe, area = 2.01 cm²) taken from the upper 10 cm of the stream bed (n = 3) every 2 mo from March to December 2003; cores were collected from the channel thalweg at 3 points ~25 m apart. In the laboratory, samples were oven-dried to a constant mass at 80°C for 24-48 h, desiccated, and weighed to determine total dry mass, and then ashed in a muffle furnace at 550°C for 3 h. Ashed samples were desiccated and reweighed, and %BPOM was determined as the difference between the dry and ashed masses divided by the total dry mass (Minshall 1996). Previous research at FMBI has shown that CWD and BPOM were strongly related to benthic macroinvertebrate assemblages and whole stream metabolism (Houser et al. 2005, Maloney and Feminella 2006).

3.3.4 Crayfish sampling

The study animal, *Procambarus versutus* (Hagen, subgenus *Pennides*) occurs within the southeastern plains and coastal plain of Alabama, Georgia, and Northern Florida (Hobbs 1984). This species is confined to sandy streams of variable sizes containing coarse woody debris (CWD) and leaf litter, and occurs in areas with moderate to high flow (Hobbs 1981). Density of *P. versutus* varies greatly with habitat conditions, with the highest densities occurring with high CWD (R. Mitchell, unpublished data). In general, this crayfish is small compared to other species with a maximum size of ~39 mm CL (first-form male).

We quantified *Procambarus versutus* (hereafter crayfish) from 3 adjacent run and pool habitat units within each study reach. Crayfish were sampled at each habitat using a backpack electroshocker (Smith-Root LR-24[®]) and block seines, using the 2-pass removal-depletion method similar to fish sampling (Seber 1982). Crayfish were sampled at each habitat over 3 seasons, spring (March), summer (July), winter (December) 2003. In a study comparing different crayfish sampling methods, Rabeni et al. (1997) demonstrated electroshocking was the most effective for collecting crayfish from multiple habitats (i.e., in providing the highest abundance estimates). In our study, we counted all crayfish sampled, measured them for carapace length (CL, nearest 0.1 mm), and sexed them (for animals with CL >6 mm) before returning them to the collection point. CL was used to estimate biomass using a length-biomass regression equation for Cambaridae (Benke et al. 1999).

3.3.5 Statistical analysis

We used Pearson's correlation to assess relationships between landscape disturbance, catchment area and instream habitat variables. The purpose of this analysis was to determine the strength of the relationship among different scales, and to determine the potential mechanism through which landscape disturbance and catchment area indirectly influences crayfish populations through habitat influences. Next, we examined the multivariate relationships between instream habitat and crayfish population metrics using stepwise multiple regression to determine which instream habitat measures had the greatest potential influence on crayfish populations. We then tested for differences in crayfish population metrics between microhabitats (pools vs.

runs) using a nested ANOVA (pool/run within streams), for each season sampled. Coefficient of variation (CV, as %) was calculated for all run and pool instream habitat measures for comparison within and among streams. Additionally, CV was used to assess differences in habitat stability between pools and runs, with lower CV values indicating higher stability. Last, we examined relationships between crayfish population metrics and catchment disturbance using linear regression to assess if disturbance had an equal influence on both run and pools. Crayfish population measures were tested for normality and population variables that were not normal were log-transformed except for proportional data, which was transformed using arcsine-square-root transformation (Zar 1999). All statistical analysis was performed using SAS software (version 9.1, SAS Institute, Cary, North Carolina). α level was set at 0.05 for all analyses.

3.4 RESULTS

3.4.1 Instream habitat conditions

Instream habitat variables varied among streams and seasons (Table 3.2). Percent areal coverage of CWD ranged from 12.4 (LC) to a low of 3.3 (SB3) and %BPOM ranged from a high of 4.1 (LC) in summer, to a low of 0.06 (LPK) in winter. Mean current velocity varied among streams and seasons, whereas mean width and depth differed more by stream than among seasons, with KM1 and LPK (and BC2 for depth) showing the highest and lowest mean widths and depths, respectively. Mean stream area was roughly equivalent between runs (5.32 m²) and pools (5.05 m²). Discharge did not differ substantially among seasons; however, mean discharge

differences were substantial among some streams, with LC and BC2 showing the highest and lowest discharge (0.044 and 0.001 m³/s, respectively; Table 3.2).

3.4.2 Landscape-scale relationships with instream habitat

Stream habitat variables showed strongly contrasting associations with disturbance intensity at the catchment scale. There was a significant negative inverse relationship between annual (spring) CWD and disturbance intensity (Table 3.3). %BPOM also was negatively correlated with disturbance intensity during spring and summer, but not winter (Table 3.3). Depth was the only local-scale variable correlated (negatively) with disturbance intensity (Table 3.3), and only in summer and winter. Catchment area was unrelated to CWD or %BPOM; however, catchment area was correlated with mean width and discharge for all seasons, and with mean velocity and depth for spring and summer, respectively, as would be expected due to the relationship between catchment size and discharge (Table 3.3). Mean CV of stream depth was positively correlated with disturbance intensity across all seasons in runs (Fig. 3.1); however, for pools, mean CV of stream depth was correlated with disturbance intensity only in summer. No other mean CV of habitat measures were related to disturbance intensity and, subsequently, there were not significant differences between pool and run microhabitats.

3.4.3 Instream habitat relationships with crayfish measures

Stepwise multiple regression identified only models with only 1 or 2 significant habitat variables showing relationships with crayfish population variables. Overall,

CWD was the strongest correlate (positive) of mean crayfish density across seasons (Table 3.4). In addition, CWD was the strongest correlate (positive) of mean crayfish biomass in spring. In contrast, %BPOM and discharge were stronger correlates (again positive) of biomass in summer, whereas mean depth was the best correlate of biomass in winter (Table 3.4). Mean crayfish CL was unrelated to any instream habitat variable (Table 3.4).

Nested ANOVA revealed significant differences in crayfish density, biomass, and mean CL among streams for most seasons, but not sex ratio (Table 3.5). There were no significant difference in density or % females between runs and pools habitats for any season, but crayfish biomass was higher in pools than runs in spring and winter, and crayfish were larger in pools than runs in all seasons (Table 3.5, Fig. 3.2). Sex ratio differed among streams in summer only but did not differ between pools and runs (Table 3.5, Fig. 3.2). There was no significant interaction between stream and microhabitat for any crayfish variable, indicating that differences in crayfish measures between pools and runs were independent of differences among streams (Table 3.5).

Multiple regression of instream habitat variables revealed CWD to be the most important factor explaining crayfish variables in runs (Table 3.6), whereas crayfish variables in pools were explained by several microhabitat factors (CWD, %BPOM and discharge; Table 3.6). Crayfish density in runs was positively related to CWD in spring, and to CWD and % BPOM in summer, whereas biomass in runs was positively related to CWD in both spring and summer. Summer was the only season when CL was correlated with microhabitat variables (discharge in runs, depth in pools; Table 3.6). Crayfish biomass was positively related to CWD and %BPOM in spring and in summer.

Similar to runs, summer was the only season showing a significant relationship to mean CL, whereas discharge was positively related to mean CL.

3.4.4 Disturbance relationship with crayfish population measures

Analysis of the influence of catchment disturbance on crayfish measures showed that density in runs was significantly related to disturbance intensity across all seasons (Fig. 3.3a, b, c), whereas crayfish density in pools and combined pool and run density showed little or no relationship to disturbance intensity, except in winter where crayfish density in combined pool and run was significantly related to disturbance ($R^2 = 0.55$, $p = 0.035$). Similar to density, crayfish biomass was strongly related to disturbance intensity in runs (Fig. 3.4c), whereas pools and combined pool and run biomass showed no relationship to catchment disturbance, except spring where both pool and combined pool and run biomass were significantly related to catchment disturbance (Fig. 3.4a, b; $R^2 = 0.76$, $p = 0.042$, $R^2 = 0.53$, $p = 0.005$, respectively).

3.5 DISCUSSION

3.5.1 Influence of disturbance on instream habitat

Our results indicate that instream habitat, specifically CWD abundance, was negatively correlated with catchment disturbance as was % BPOM and stream depth. Catchment disturbance has been suggested by others in FBMI studies to affect instream habitat and, thus, communities (Houser et al. 2005, Maloney and Feminella 2006,). The primary source of stable habitat in FBMI streams is CWD, similar to other low-gradient sandy streams (Benke et al. 1984, Benke and Wallace 1990), and loss of

CWD from burial or scour in disturbed catchments may dramatically impact ecosystem function (Houser et al. 2005, Maloney and Feminella 2006). Beyond contemporary land use and its effects, historic land use, prior to military activities, also may exert a long-term influence on stream ecosystems (Maloney et al. 2008). In many lowland streams, sand intrusion into stream channels from upland disturbance can alter instream habitat for decades to centuries (Hyatt and Naiman 2001, Wallace et al. 2001, Downes et al. 2006).

% BPOM and depth were negatively correlated with disturbance intensity, but such relationships were not observed across all seasons. The absence of a relationship between % BPOM and disturbance during winter likely occurred because of a lush riparian zone in all study streams (> 90% cover, KOM, unpublished data) and correspondingly high allochthonous inputs of leaf litter during late fall-early winter that equaled or exceeded breakdown or export rates. Allochthonous inputs are the primary source of BPOM in most small temperate-deciduous streams (Mulholland 1997), and disturbed streams with low instream retention structures (e.g., CWD) likely will have low BPOM, a pattern that would be exacerbated in highly disturbed catchments because of high stream flashiness (Smock 1997, Maloney et al. 2005). Similarly, depth was correlated with disturbance intensity only in summer and winter. These depth relationships appear to be greatly influenced by habitat type. Within-habitat variation (as CV) for depth in run microhabitats increased with increasing disturbance intensity across all seasons, whereas for pools this relationship occurred only in summer. Others have suggested that sediment intrusion into channels from eroding uplands decreases streambed stability (Jain and Park 1989, Krone 1999, Maloney et al. 2005). In our

study, runs showed higher variability (i.e., less stable substrate) in depth than pools, which may indicate runs are more influenced by sediment movement through channels from upland/upstream sources than pools. Unfortunately, CWD was only measured at the reach (vs. microhabitat) scale, so we cannot assess if CWD abundance also varied more in runs than pools. Pools often form downstream of CWD (Wallace et al. 1995, Quinn et al. 1997) and these deposition zones often are more stable and contain higher BPOM than areas upstream of CWD (Smock et al. 1989). Thus, in our study, high % BPOM and lower variability of depth in pools compared to runs in highly disturbed catchments may be indicative of a more stable stream bed in pools than runs.

3.5.2 Influence of instream habitat on crayfish

Analysis of relationships between instream habitat and crayfish population metrics suggests that crayfish are strongly influenced by abundance of CWD. Crayfish density for both pools and runs combined was positively related to increasing CWD across all seasons. Spring crayfish biomass also appeared to be strongly influenced by CWD, whereas summer biomass appeared more related to % BPOM. Habitat variables that influenced crayfish biomass were different than those that correlated with density, and the strong inverse correlation of % BPOM with disturbance intensity suggests that upland disturbance indirectly influenced biomass through different habitat measures than those influencing density. Our findings are similar to others reporting land use impacts on instream habitat and biota (Roy et al. 2003, Parkyn and Collier 2004, Maloney and Feminella 2006). Upland disturbance can be considered an indirect

influence on stream biota by directly influencing instream habitat. For example, in streams from New Zealand, Parkyn and Collier (2004) demonstrated that land use changes can reduce habitat quality and quantity for crayfish, thus reducing density and potential for population recovery from flood disturbance. In addition, the presence of wood as tree roots and CWD, as well as instream cover such as leaf litter, was shown to be positively related to crayfish abundance in streams in Britain (Smith et al. 1996) and New Zealand (Naura and Robinson 1998). Streams depth also may decrease with increasing catchment disturbance because of reduced CWD, the latter of which may be important in pool formation (Parkyn and Collier 2004); others have shown that crayfish populations are positively associated with water depth because deeper pools typically have slower velocity and act as sinks for BPOM, thus increasing food availability in pools compared to higher velocity microhabitats (Usio and Townsend 2000).

Crayfish typically showed higher population biomass and larger individual size in pools than runs, but not higher density. Results of other studies also showing differential crayfish size structure or microhabitat use, but the factors affecting such patterns varied. Flinders and Magoulick (2007) found that small crayfish used shallow habitats whereas large crayfish used shallow and deep habitats equally, suggesting increased predation risk of smaller crayfish from fish in deep habitats and higher quality food resources in shallow habitats. Others have suggested that larger crayfish find refuge from terrestrial predators, and thus larger crayfish will more likely be found in deeper water (Englund and Krupa 2000). Additionally, Lodge and Hill (1994) suggested that juvenile crayfish are more susceptible to cannibalism than adults, which would explain why smaller crayfish are less common in deeper water where larger crayfish

occur. This latter point may explain the observation in our study with a higher mean size of crayfish in pools than runs. Further, fish predation risk is not likely a major factor in our study. Maloney et al. (2006) reported low presence and relative abundance of predacious fish in these same streams, sampled during the sample time period. Finally, this pattern appears to be independent of sex ratio, with the ratios being equal between run and pool habitats. Habitat quality and the influence of disturbance of the microhabitats is a more likely reason for the decreasing density and biomass with increasing disturbance observed in the current study.

Our findings suggest that instream habitat, specifically CWD abundance, is an important variable for crayfish populations in runs but less so in pools. Other research has shown a positive relationship between CWD and crayfish density. In addition, the presence of riparian tree roots in the stream has been shown to influence crayfish density, possibly providing a refuge for crayfish in disturbed catchments (Parkyn and Collier 2004). Whereas crayfish density and biomass showed a positive relationship with CWD, no relationship was found with crayfish size. Our findings suggest that CWD acts as a refuge for crayfish, but it appears that increased CWD does translate to increased food quality for *P. versutus* in the study streams.

3.5.3 Relationship between catchment disturbance and crayfish

One mechanism with which catchment disturbance influences streams is through transport of sediment from upland areas of the catchment into streams via ephemeral streams (Howarth et al. 1991, Quist et al. 2003). Most studies of catchment disturbance have emphasized assemblage or community measures, rather than focus on single

populations. Many aquatic taxa are currently under pressure of species loss, and nowhere are aquatic taxa more vulnerable than in southeastern US, particularly crayfish (Master et al. 2000, Strayer 2006, Taylor et al. 2007). Changes to instream habitat have caused significant impacts to stream biota, but it can be difficult to determine which instream habitat component has the greatest direct influence. A measure of catchment-level disturbance that can predict instream biological conditions may be useful to managers and conservation biologists for monitoring imperiled stream biota.

That CWD and %BPOM were highly correlated with catchment disturbance intensity suggests that disturbance acts indirectly on crayfish populations through the CWD abundance and %BPOM in the stream channel. Our findings suggested that catchment disturbance intensity was a good predictor of crayfish density and biomass, with its greatest influence in runs. This result suggests that pools may act as a refuge for crayfish under increased disturbance pressure, but perhaps only in streams where aquatic crayfish predator presence and cannibalistic behavior is low. Others have found that catchment disturbance can have a disproportionate impact on instream habitat availability for benthic macroinvertebrate communities. Findings by Roy et al. (2003) suggest that riffle habitats are more influenced by catchment disturbance than pools or bank habitats. Additional results from Quinn et al. (1997) suggest that pool formation is highly related to the presence of CWD. In our study, similar observations were made where pools were typically associated with CWD in the form of debris dams or tree roots (personal observations). This relationship would suggest that pools are a more stable habitat than runs and that as the amount of the reach scale CWD decreases there should be a disproportionately negative effect on habitat stability in runs.

In summary, *P. versutus* appears to be influenced by upland disturbance similar to other aquatic macroinvertebrates through the degradation of habitat availability. However, because of its use of both run and pool habitats it appears that this species can occupy the more stable pool habitats as a refuge from increasing upland disturbance. Such microhabitat flexibility may allow this species to avoid extirpation under all but the most extreme cases of upland disturbance. Additionally, our research suggests a strong land-cover cascade relationship between land-use and crayfish (sensu Burcher et al. 2007), mediated through the direct linkage of land-use and habitat availability (i.e. CWD). The likely association between CWD and pool habitats suggests that these areas of the stream are more stable than run microhabitats, thus providing more optimal conditions for survival of this crayfish.

3.6 LITERATURE CITED

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Table 3.1. Study stream locations, with catchment and disturbance characteristics.

UTM = Universal Transverse Mercator, %BGRD = percentage of catchment as bare ground on slopes > 5% and % of unpaved roads in catchment. Catchments were ordered in terms of increasing landscape disturbance.

Stream	Stream code	UTM	Military land use	Stream order	Catchment area (km ²)	Disturbance intensity (% BGRD)
Bonham Tributary	BC2	0710627N, 3588976E	Infantry/ Ranger	2	0.75	3.15
Lois Creek	LC	0715377N 3597908E	Infantry/ Ranger	2	3.32	3.67
Kings Mill Creek	KM1	0720701N, 3600036E	Infantry/ Ranger	2	3.69	4.63
Hollis Branch	HB	0717848N 3583123E	Infantry/ Ranger	2	2.15	6.62
Sally Branch Tributary	SB2	0716808N 3584787E	Heavy Machinery	2	1.23	8.12
Sally Branch Tributary	SB3	0716673N 3584684E	Infantry/ Ranger	1	0.72	10.49
Little Pine Knot Tributary	LPK	0719223N 3585421E	Heavy Machinery	2	0.33	11.26
Sally Branch Tributary	SB4	0716005N, 3584889E	Heavy Machinery	1	1.00	13.65

Table 3.2. Mean (+1SE) instream habitat-scale variables. CWD = coarse woody debris relative abundance. %BPOM = benthic particulate organic matter. Catchments were ordered in terms of increasing landscape disturbance (see Table 3.1).

Stream	Stream code	CWD (% areal coverage)	Season	%BPOM	Velocity (m/s)	Depth (m)	Wetted stream width (m)	Run area (m ²)	Pool area (m ²)	Discharge (m ³ /s)
Bonham Creek Tributary	BC2	10.1	Spring	2.20 (0.29)	0.05 (0.03)	0.09 (0.02)	1.2 (0.14)	2.72 (0.14)	3.96 (0.31)	0.004
			Summer	1.85 (0.46)	0.03 (0.03)	0.24 (0.02)	1.1 (0.04)	5.43 (2.09)	3.47 (0.18)	0.001
			Winter	0.83 (0.46)	0.06 (0.01)	0.19 (0.03)	1.0 (0.02)	4.05 (0.93)	3.46 (0.10)	0.005
Lois Creek	LC	12.4	Spring	3.33 (0.61)	0.17 (0.02)	0.14 (0.02)	2.0 (0.11)	10.81 (2.68)	8.90 (2.32)	0.044
			Summer	4.10 (0.37)	0.11 (0.04)	0.12 (0.02)	2.0 (0.11)	6.97 (2.27)	7.56 (2.27)	0.013
			Winter	1.90 (0.87)	0.07 (0.02)	0.14 (0.02)	1.9 (0.06)	9.77 (0.43)	6.86 (0.57)	0.022
Kings Mill Creek	KM1	7.5	Spring	1.06 (0.52)	0.13 (0.02)	0.21 (0.02)	2.1 (0.13)	9.51 (2.44)	6.28 (1.51)	0.037
			Summer	1.85 (0.25)	0.13 (0.02)	0.22 (0.02)	1.9 (0.23)	7.85 (0.89)	8.96 (2.68)	0.020
			Winter	1.13 (0.80)	0.09 (0.004)	0.21 (0.01)	1.8 (0.09)	5.00 (1.02)	8.39 (1.37)	0.029
Hollis Branch	HC	6.5	Spring	2.30 (0.81)	0.08 (0.04)	0.17 (0.01)	2.0 (0.12)	5.71 (0.58)	8.47 (1.69)	0.018
			Summer	0.79 (0.06)	0.08 (0.02)	0.13 (0.02)	1.8 (0.14)	5.89 (0.42)	6.99 (1.29)	0.013
			Winter	2.45 (0.50)	0.07 (0.01)	0.17 (0.02)	1.9 (0.18)	8.60 (0.52)	10.80 (4.10)	0.018
Sally Branch Tributary	SB2	8.7	Spring	0.95 (0.35)	0.15 (0.02)	0.12 (0.01)	1.4 (0.14)	3.27 (1.26)	4.24 (0.90)	0.027
			Summer	1.64 (0.16)	0.13 (0.02)	0.11 (0.01)	1.4 (0.09)	5.89 (1.47)	4.05 (0.60)	0.009
			Winter	1.02 (0.04)	0.12 (0.01)	0.12 (0.01)	1.5 (0.11)	3.35 (0.52)	5.84 (2.67)	0.016
Sally Branch Tributary	SB3	3.3	Spring	1.14 (0.21)	0.09 (0.01)	0.10 (0.01)	1.3 (0.09)	2.21 (0.39)	2.52 (0.35)	0.007
			Summer	1.37 (0.45)	0.08 (0.01)	0.07 (0.01)	1.3 (0.08)	3.78 (1.27)	2.39 (0.11)	0.004
			Winter	1.39 (0.21)	0.08 (0.01)	0.09 (0.02)	1.3 (0.07)	4.76 (0.68)	2.79 (0.30)	0.008
Little Pine Knot Tributary	LPK	3.98	Spring	1.15 (0.28)	0.06 (0.01)	0.19 (0.01)	1.9 (0.05)	3.61 (0.88)	1.85 (0.61)	0.003
			Summer	1.13 (0.45)	0.12 (0.02)	0.06 (0.01)	1.0 (0.13)	1.83 (0.18)	1.49 (0.18)	0.002
			Winter	0.06 (0.23)	0.06 (0.004)	0.08 (0.03)	1.0 (0.12)	3.51 (0.87)	1.94 (0.58)	0.003
Sally Branch Tributary	SB4	3.6	Spring	0.57 (0.03)	0.11 (0.02)	0.11 (0.01)	1.5 (0.13)	4.31 (0.59)	3.43 (0.84)	0.012
			Summer	0.56 (0.07)	0.01(0.02)	0.07 (0.01)	1.4 (0.08)	4.66 (0.64)	4.32 (0.61)	0.006
			Winter	0.53 (0.10)	0.08 (0.02)	0.11 (0.02)	1.5 (0.15)	4.30 (0.80)	2.40 (0.51)	0.009

Table 3.3. Pearson's correlation coefficients summarizing relationships between landscape variables with instream habitat variables, by season. Bold correlation coefficients were significant at $\alpha=0.05$. Disturbance intensity = %BGRD (percent of bare ground on slopes >5% and unpaved roads within catchment). ND= no data (CWD was measured in spring only).

Variable	CWD	%BPOM	Velocity	Depth	Width	Discharge
Spring						
Disturbance intensity	-0.92	-0.74	-0.13	-0.09	0.39	-0.52
Catchment area	0.59	0.36	0.72	0.20	0.72	0.91
Summer						
Disturbance intensity	ND	-0.67	0.28	-0.78	-0.51	-0.41
Catchment area	ND	0.52	0.49	0.90	0.96	0.95
Winter						
Disturbance intensity	ND	-0.45	0.17	-0.74	-0.36	-0.52
Catchment area	ND	0.54	0.30	0.90	0.91	0.96

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CWD = coarse woody debris relative abundance. %BPOM = benthic particulate organic matter.

Table 3.4. Stepwise multiple regression results for crayfish population variables across instream habitat variables. CWD = coarse woody debris relative abundance. Size = carapace length (CL). %BPOM = benthic particulate organic matter.

Population variables	Season	Range	Model variables	R^2	β coefficient	F	p
	Spring						
Density		0.2-1.1	CWD, % BPOM	86.1	1.45, -0.97	25.23	0.003
Biomass		35.4-273.1	CWD	71.5	0.85	15.06	0.008
Size		11.6-16.1	—	—	—	—	NS
	Summer						
Density		0.2-0.7	CWD	71.4	0.85	14.97	0.008
Biomass		48.7-426.1	% BPOM, Discharge	87.7	0.71, 0.43	17.71	0.005
Size		13.0-20.0	—	—	—	—	NS
	Winter						
Density		0.2-1.0	CWD	51.2	0.72	6.29	0.046
Biomass		0.0-263.7	Depth	47.46	0.69	5.42	0.057
Size		12.3-19.7	—	—	—	—	NS

Table 3.5. ANOVA summary showing differences for crayfish population variables among streams and between microhabitats. Habitat represents pools vs. runs. Mean size = mean crayfish size (as carapace length). DF = degrees of freedom. Values are *F*-statistics (*p*-value).

Effect	Season	DF	Density	Biomass	Mean Size	Sex Ratio
	Spring					
Stream		8	8.84 (<0.0001)	6.12 (0.0002)	2.71 (0.024)	0.14 (0.996)
Habitat		1	1.64 (0.209)	11.41 (0.006)	11.47 (0.002)	0.79 (0.381)
Stream*Habitat		7	0.45 (0.883)	0.56 (0.799)	1.31 (0.282)	0.65 (0.709)
	Summer					
Stream		8	11.09 (<0.0001)	3.57 (0.004)	0.86 (0.362)	2.85 (0.026)
Habitat		1	0.06 (0.804)	3.44 (0.071)	5.48 (0.024)	0.27 (0.606)
Stream*Habitat		7	2.01 (0.073)	1.29 (0.219)	0.32 (0.856)	1.13 (0.377)
	Winter					
Stream		8	3.06 (0.010)	0.89 (0.537)	3.07 (0.015)	1.51 (0.212)
Habitat		1	0.03 (0.857)	4.75 (0.036)	7.91 (0.009)	0.02 (0.899)
Stream*Habitat		7	0.31 (0.958)	0.54 (0.815)	0.83 (0.575)	1.12 (0.385)

Table 3.6. Stepwise multiple regression results for run and pool crayfish samples. Size = carapace length (CL). CWD = coarse woody debris abundance. %BPOM = benthic particulate organic matter.

Crayfish variables	Season	Range	Model variables	Adj. R^2	β coefficient	F	P
Runs							
	Spring						
Density		0.0-1.1	CWD	64.3	0.80	10.79	0.017
Biomass		0.0-300.6	CWD	59.4	0.77	8.77	0.025
Size		8.3-19.1	—	—	—	—	NS
	Summer						
Density		0.0-1.0	CWD, % BPOM	95.8	0.42, 0.63	81.10	<0.001
Biomass		0.0-235.9	CWD	84.0	0.91	31.53	0.001
Size		7.0-18.6	Depth	59.8	0.77	8.91	0.024
	Winter						
Density		0.0-1.3	—	—	—	—	NS
Biomass		0.0-137.9	—	—	—	—	NS
Size		10.1-17.9	—	—	—	—	NS
Pools							
	Spring						
Density		0.4-1.4	—	—	—	—	NS
Biomass		44.07-392.0	CWD, % BPOM	81.68	1.36, -0.74	16.61	0.006
Size		14.7-19.9	—	—	—	—	NS
	Summer						
Density		0.3-1.1	—	—	—	—	NS
Biomass		66.5-616.4	% BPOM	53.31	0.73	6.85	0.040
Size		13.0-21.8	Discharge	52.8	0.72	6.71	0.041
	Winter						
Density		0.0-0.9	CWD	53.04	0.73	6.78	0.040
Biomass		0.0-392.5	—	—	—	—	NS
Size		13.7-16.7	—	—	—	—	NS

Figure 3.1. The amount of streambed variability expressed as coefficient of variation (%CV) of depth in runs and pools plotted against the catchment disturbance intensity for the 8 study streams across 3 seasons (top panel = spring, middle panel = summer, bottom panel = winter).

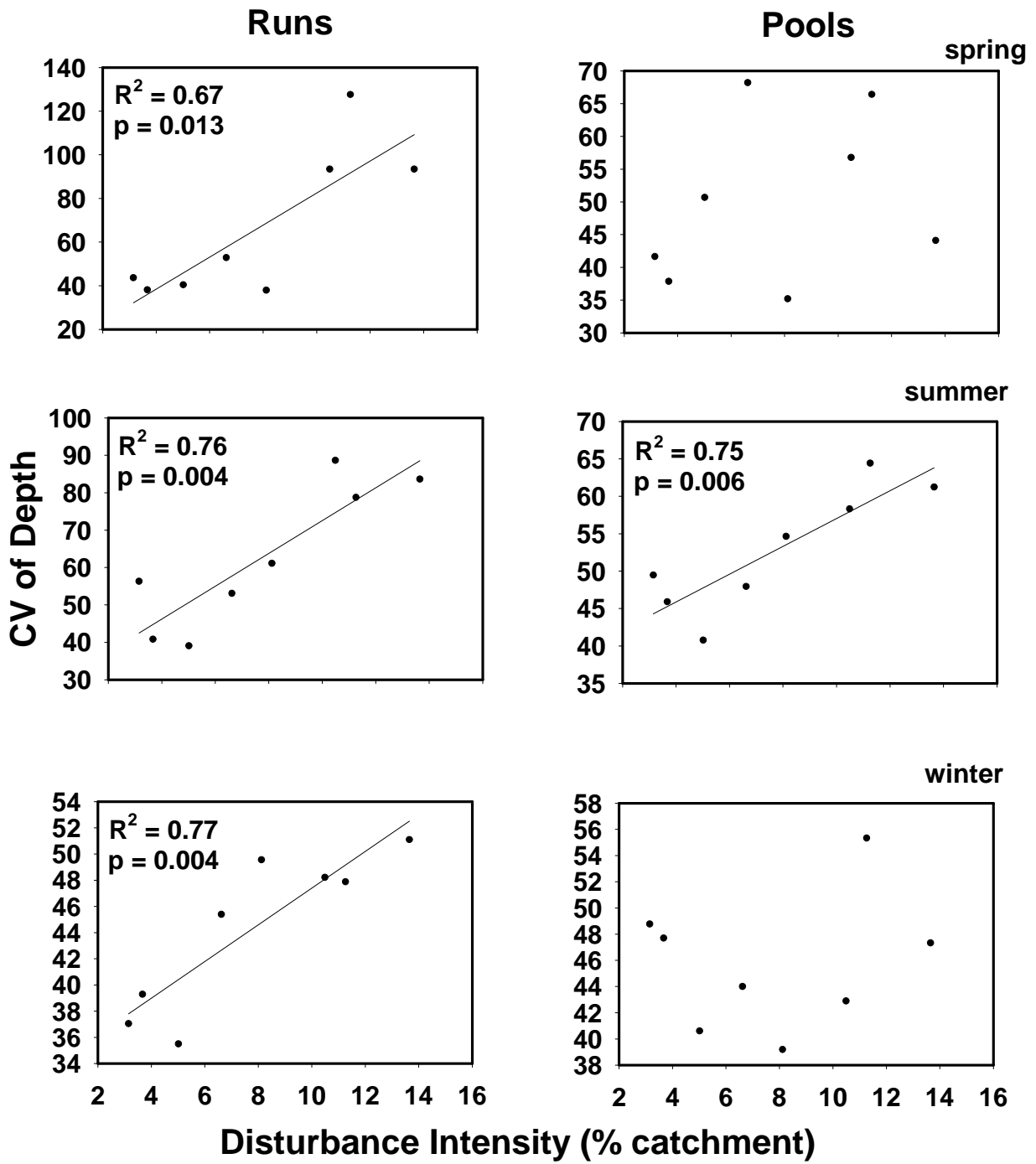


Figure 3.2. Comparison of mean (+1SE) crayfish density, biomass, carapace length (CL) and % of the population as females (% female) between run and pool microhabitats across 3 seasons (spring, summer, winter). * $p < 0.05$.

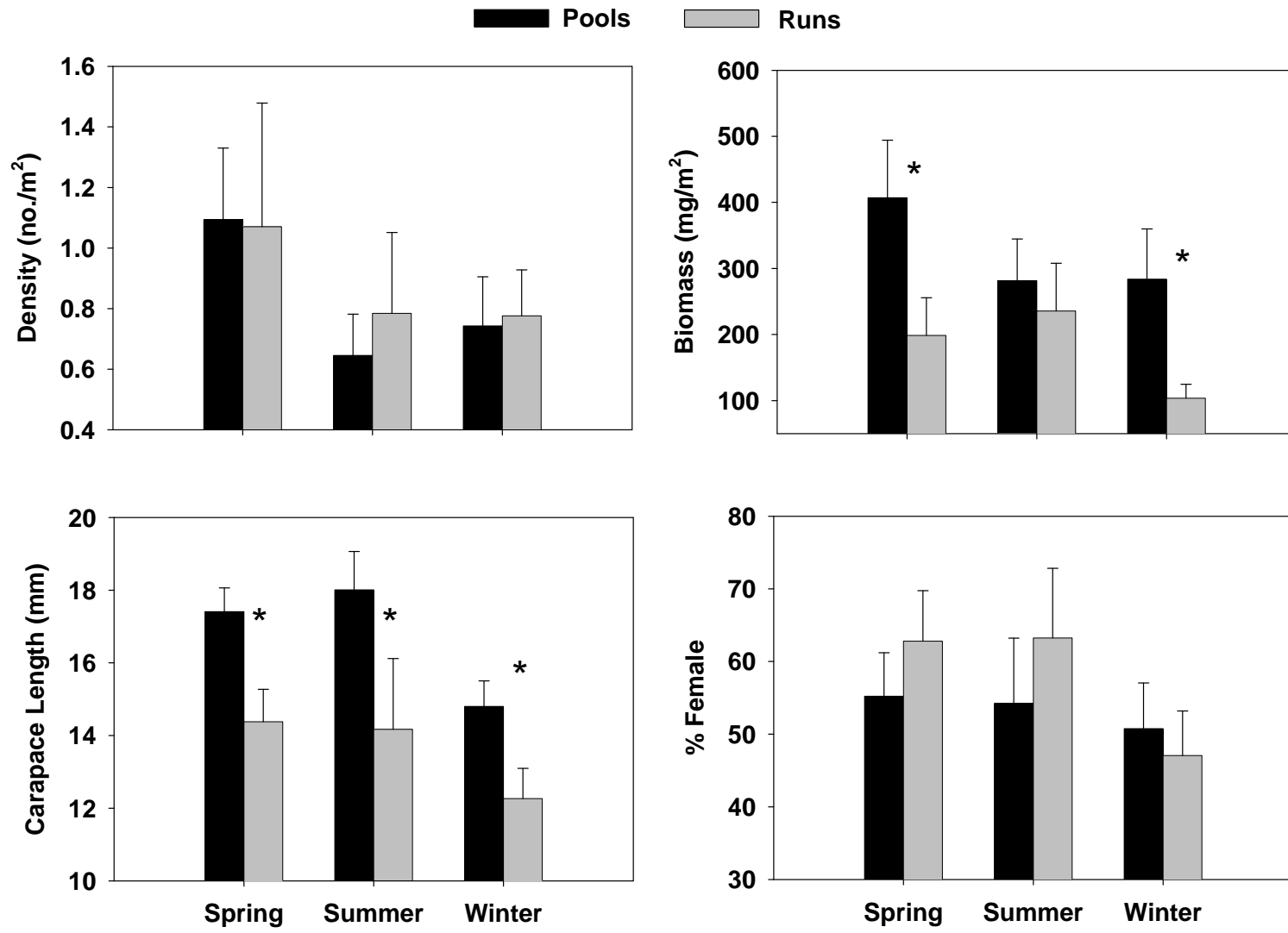


Figure 3.3. Mean density of crayfish (number per m²) in runs plotted against catchment disturbance intensity for the 8 study streams for spring (A), summer (B), and winter (C).

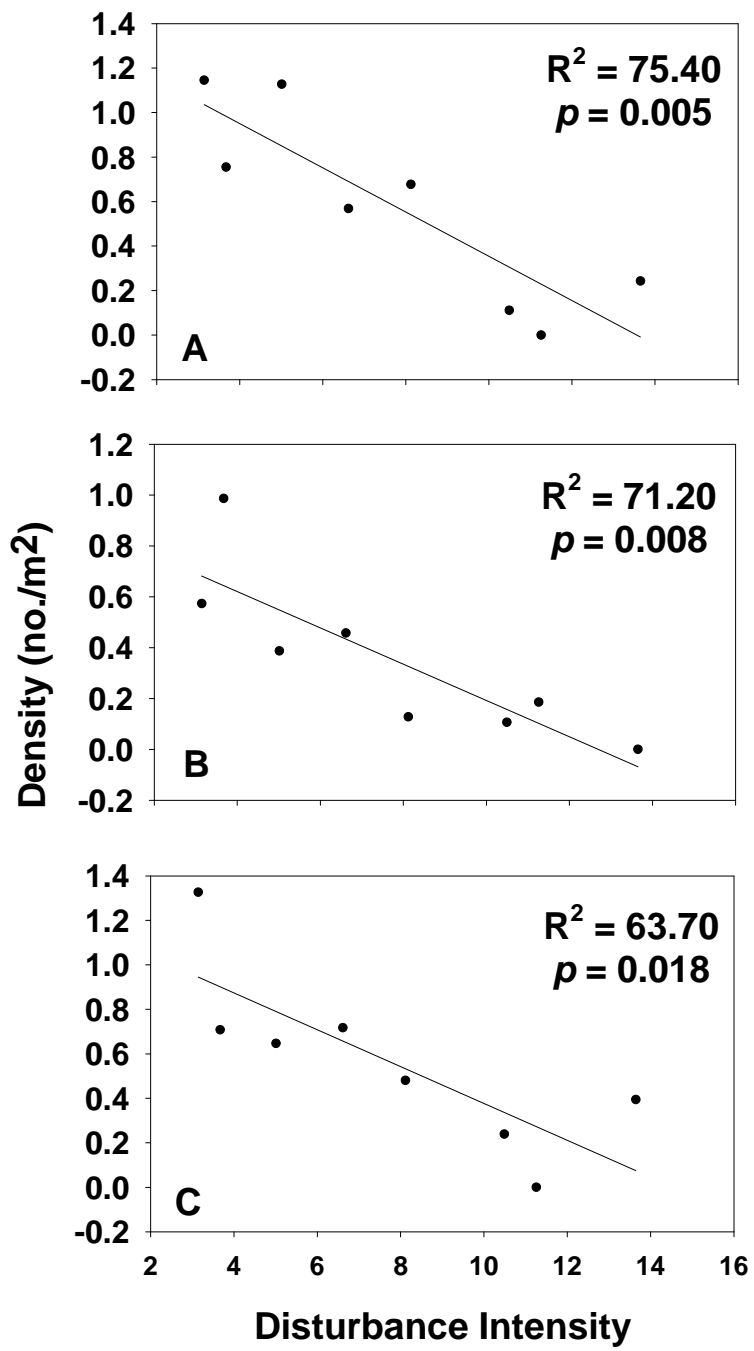
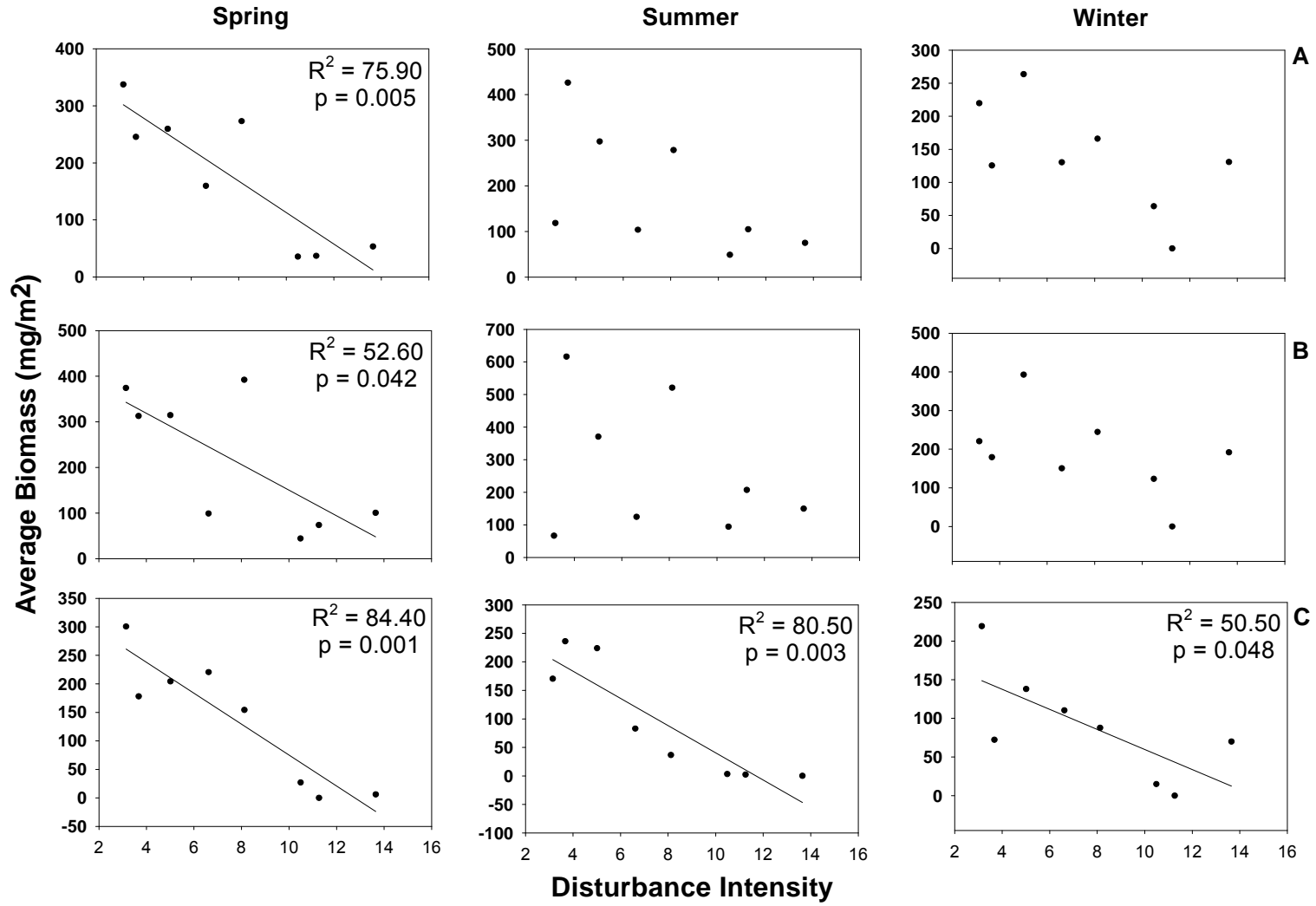


Figure 3.4. Mean biomass of crayfish per m² plotted against catchment disturbance intensity for the 8 study streams across season. A = pools and runs, B = pools, and C = runs.



4. INFLUENCE OF THE CRAYFISH *PROCAMBARUS VERSUTUS* ON LEAF BREAKDOWN AND BENTHIC MACROINVERTEBRATES IN A SANDY STREAM

4.1 SUMMARY

Crayfish have been shown to have strong effects on both basal resources (e.g. algae, leaf litter) and benthic macroinvertebrate assemblages in high-gradient upland streams; however, the trophic crayfish role within structurally simpler lowland, sandy streams where leaf detritus is the primary basal resource is unknown. We conducted a 6-wk enclosure-exclosure experiment in a sandy stream in eastern Alabama, USA, to assess effects of the crayfish *Procambarus versutus* on leaf litter breakdown and macroinvertebrate assemblage structure. We used hardware cloth cages as experimental units, and 3 crayfish density treatments (0, 4, 12/m²), 1 cage control treatment, and a no cage treatment containing artificial leaf packs of *Fagus grandifolia* (American Beech), and quantified breakdown and macroinvertebrate assemblages. Litter breakdown was unaffected by crayfish density, but macroinvertebrate density, biomass, and richness all were significantly lower in the high- crayfish density (vs. exclusion) treatment. *Procambarus versutus* appears to be an important determinant of macroinvertebrate assemblage structure, but unlike other species of crayfish, has a limited effect on leaf litter processing. Results from stable isotope analysis of *P.*

versutus muscle suggested this crayfish functioned more as a predator than a detritivore, which confirms the results of the field experiment.

4.2 INTRODUCTION

Crayfish constitute the bulk of benthic macroinvertebrate biomass in many freshwater systems (Mason 1974, Momot and Gowing 1977, Momot et al. 1978, Momot 1995, Rabeni et al. 1995), but a debate remains over their exact trophic role. Most researchers have considered crayfish to be primarily omnivores (Webster and Patten 1979, Huryn and Wallace 1987, Hart 1992, Creed 1994), whereas others have argued that because crayfish diets must contain enough high-protein from animal material to maintain their biomass and growth, crayfish function more as carnivores (Momot et al. 1978, Momot 1995). Irrespective of their trophic position, crayfish have the potential to exert a substantial effect on benthic macroinvertebrates in many freshwater systems because of their high biomass, polyphagous feeding, and large size relative to other benthic macroinvertebrates (Lodge et al. 1994, Usio and Townsend 2004, Usio et al. 2009).

Crayfish can influence macroinvertebrate assemblages and basal resources (e.g. leaf litter, algae; Creed 1994, Parkyn et al. 1997), sometimes through ecosystem engineering (Creed and Reed 2004), which involves creating or modifying habitats and influencing resource availability for other species (Jones et al. 1994, 1997, Usio and Townsend 2004, Helms and Creed 2005). Modifications of substrate conditions by crayfish can either increase or decrease distributions of other benthic organisms, depending on species or the nature of the change (Parkyn et al. 1997).

Researchers have suggested that the reason crayfish act as ecosystem engineers is because of their omnivorous feeding and relatively large size compared to other macroinvertebrates (Huryn and Wallace 1987, Parkyn et al. 1997, Usio and Townsend 2000). Unlike keystone predators (sensu Paine 1966) whose direct effects on secondary consumers cascade through food webs and indirectly affect basal resources (Carpenter et al. 1985, Menge and Sutherland 1987, Power 1990), omnivorous crayfish exert effects directly on multiple trophic levels. In this context, crayfish often show strong direct trophic influences, thus offsetting or ameliorating cascading effects developed from a top consumer (Diehl 1995).

Omnivore size may influence the likelihood and magnitude of effects on intermediate consumers (animal prey) and basal resources, with influence increasing with the size differential between omnivores and intermediate consumers (Diehl 1993, 1995). Experimental studies indicate that when top omnivores are disproportionately larger than intermediate consumers, strong direct trophic effects of omnivores on intermediate consumers and basal resources occur, often negating indirect effects and trophic cascades (Polis and Holt 1992, Diehl 1993, Creed 1994, Pringle and Hamazaki 1998).

Previous experiments involving crayfish trophic position have focused on large, long-lived species (Huryn and Wallace 1987, Lodge et al. 1994, Parkyn et al. 1997, Usio 2000, Helms and Creed 2005). For example, Huryn and Wallace (1987) studied the effects of a long-lived (up to 13 y), slow maturing (~5 y) crayfish (*Cambarus bartonii*) on leaf litter breakdown, and reported that litter breakdown and crayfish size were correlated. Additionally, Creed and Reed (2004) reported this same species (~20 mm

carapace length) increased litter breakdown but also reduced abundance of large chironomid larvae. In general, large long-lived crayfish have a significant impact on both basal resources and macroinvertebrates, where impacts on benthic macroinvertebrates can be both direct and indirect, mediated through alteration of basal resources or habitat (Lodge et al. 1994).

Few studies have assessed trophic influences of crayfish from warm, low-latitude streams. Momot (1984) hypothesized that such species are short lived (2 y or less) and require high amounts of animal protein to meet their metabolic demands. Species of *Procambarus* primarily inhabit warm environments or the southeastern United States where temperatures rarely go below freezing (Hobbs 1984), and have been shown to grow and mature more rapidly than species from other crayfish genera (Pratten 1980, Momot 1984, Huryn and Wallace 1987). Maintaining a high growth rate is likely to require a greater need for a high protein diet, which, in streams, requires a high reliance on animal material (Momot 1984, Whitley and Rabeni 1997). In cases where crayfish species rely on animal prey, they are more likely to influence benthic macroinvertebrate assemblages and food web structure, relative to other predacious benthic macroinvertebrates (Nystrom et al. 1996).

We present results from a field experiment designed to assess the influence of a small, short-lived crayfish species on both a basal resource (leaf detritus) and benthic macroinvertebrates colonizing leaf litter. In addition, we described crayfish trophic position to assess its potential influence on the benthic food web.

4.3 Methods

4.3.1 Study area

The experiment was conducted in a forested section of Choctafaula Creek (32° 29' N, 85° 36' W), Macon County, Alabama, within the Tuskegee National Forest. Choctafaula Creek is a 3rd-order stream that flows through the Piedmont and Southeastern Plains ecoregions (Omernik 1987). Soils in the catchment range from Cretaceous-age loamy to sandy sediments (USDA 1981). The dominant forest type in the catchment is oak-hickory-pine, with riparian areas being dominated by hardwoods. The study reach was approximately 150 m, composed mainly of pools and runs, with few riffles and substrate reach was mostly sand with some gravel and coarse woody debris in the active channel.

4.3.2 Study species

The study animal, *Procambarus versutus* (Hagen, subgenus *Pennides*) occurs within the southeastern plains and coastal plain of Alabama, Georgia, and Northern Florida (Hobbs 1984). This species is confined to sandy streams of variable sizes containing coarse woody debris (CWD) and leaf litter, and occurs in areas with moderate to high flow (Hobbs 1981). Density of *P. versutus* varies greatly with habitat conditions, with the highest densities occurring with high CWD (R. Mitchell, unpublished data). In general, this crayfish is small compared to other species with a maximum size of ~39 mm carapace length (CL; first-form males).

4.3.3 Experimental design

We conducted an in-situ enclosure-exclosure experiment from October to November 2005 (6-wk) to assess the effect of *P. versutus* (hereafter crayfish) density on leaf pack and benthic macroinvertebrate assemblages within leaf packs. Cages (50 cm L x 50 cm W x 35 cm H) were used either to enclose or exclude crayfish. Cages were constructed of 3-mm-mesh hardware cloth, and positioned with one corner pointing upstream to reduce accumulation of extraneous material by the current. We used a randomized block design with 5 blocks with 5 treatments per block: 1) high density (enclosure with 12 crayfish/m²), 2) low density (enclosure with 4 crayfish/m²), 3) no crayfish (exclosure), 4) a cage control (downstream portion of cage open), and 5) an uncaged control (base of cage only). Treatment densities bracketed those observed within the study site (2–7/m²). All crayfish used in the experiment were collected from runs within the study stream. Only male crayfish with a CL of 17 mm to 20 mm were used. Males were used to standardize the influence of sex and size on the experiment. Cage control and uncaged treatments were accessible to all benthic organisms, whereas coarse mesh in enclosures and exclosures effectively excluded both large and small crayfish but not smaller macroinvertebrates. We placed cages in 5 rows (blocks), with each row placed in a separate run with approximately equal depth (~0.25m) and velocity (~0.39m/s).

We used abscised American beech (*Fagus grandifolia*) leaves, from the riparian area of the study reach, for construction of artificial leaf packs placed in each cage (1 pack/cage), and secured packs with cable ties at the upstream-end of the cage. Leaf packs were chosen for the experimental substrate because of its importance as both

food and habitat for many benthic macroinvertebrates, and was common throughout the study reach. Packs weighed ~10 g (9.8–10.3 g dry mass), and were held with metal binder clips at the leaf petiole. Beech was chosen because of its high abundance within the riparian zone of the study reach. Cages were checked and cleaned daily by gently scrubbing the hardware cloth to ensure adequate flow into cages, and water temperature (recorded every 15 min with a HOBO temp logger) ranged from 7 to 22° C over the experiment.

After the experiment we retrieved leaf packs from the cages by gently removing them with a 250 µm-mesh net. Leaf packs and associated macroinvertebrates were placed on ice and transported to the laboratory and kept frozen until processed. In the laboratory, leaves were thawed and individually rinsed over a 250-µm sieve to separate macroinvertebrates and whole leaves/leaf fragments. Macroinvertebrates were identified to the lowest possible taxonomic level (usually genus) using keys in Merritt and Cummins (1996), except for larval Chironomidae, which were grouped into Tanypodine and non-Tanypodine larvae. Macroinvertebrate biomass was estimated by measuring length of animals (nearest mm) and converted length into ash-free dry mass (AFDM) using length-mass equations in Benke et al. (1999).

4.3.4 Crayfish trophic position and foodweb analysis

Crayfish, conditioned detrital litter collected from the stream, and selected primary and secondary consumers (below), were quantified for analysis of stable isotopes at the end of the experiment (November 2005). We collected Macroinvertebrates (10-20 individuals per sample) and a mixture of leaf litter from pools

and runs in the study reach to account for spatial variation in the isotope compositions of foodweb components. Litter and macroinvertebrate samples were transported on ice to the laboratory and then frozen (-10°C) until processed. Frozen samples were thawed, then were dried at 50°C for 24 to 48 h, and then homogenized into a fine powder with a mortar and pestle. Three to 5 samples were analyzed for isotope analysis for each taxonomic group, except crayfish where $n = 30$. A higher number of crayfish were collected, compared to other macroinvertebrates, to encompass a wide range of crayfish sizes (5 to 34mm). Here, we chose to include a range of crayfish sizes to incorporate ontogenetic changes in feeding, if they occurred. Isotopic analysis was done at Colorado Plateau Stable Isotope Laboratory, Flagstaff, AZ, using a Thermo Electron gas isotope-ratio mass spectrometer. Isotope ratios are reported in standard delta (δ) notation defined as the parts per thousand deviation from the standard reference materials (air for N, Vienna Pee Dee belemnite carbonate for C), as:

$$\delta^{13}\text{C} \text{ or } \delta^{15}\text{N}_{\text{sample}} = [(R_{\text{sample}} - R_{\text{standard}}) / R_{\text{standard}}] \times 1000$$

where R is $\text{C}^{13}/\text{C}^{12}$ or $\text{N}^{14}/\text{N}^{15}$ (Peterson and Fry 1987, Hershey et al. 2007).

Organisms generally were identified to genus or species, except for Chironomidae, which was grouped by subfamily. Leaf litter was readily available for sampling, whereas because of interference with other biofilm components instream primary producers (algae) were more difficult to sample; therefore, we used 2 primary consumers to determine the isotopic baseline of the food web for both algae and leaf litter sources (see Post 2002). *Stenonema* sp., a grazing mayfly, was used to represent the algal source and *Tipula* sp., a shredding crane fly, was used to represent the leaf litter source (Merritt and Cummins 1996). Absolute trophic position (TP), defined as an

organisms position relative to a basal resource (i.e. algae and detrital leaf litter), was estimated for each taxon sampled. A 2-source (i.e., detritus leaf litter and algae) mixing model was used to evaluate the relative contribution of each food source to a consumer's diet and TP (Post et al. 2000, Klinge et al. 1990). estimated as:

$$TP = \lambda + (\delta^{15}N_{sc} - [\delta^{15}N_{Tipula} \times \alpha + \delta^{15}N_{Stenonema} \times (1 - \alpha)]) / \Delta_n$$

where λ is the trophic position of the organism used to estimate $\delta^{15}N_{base\ of\ food\ web}$ (i.e., $\lambda = 2$ for primary consumers), α is the proportion of N in the consumer ultimately derived from litter and $(1 - \alpha)$ is the proportion of N contributed by algae, $\delta^{15}N_{sc}$ is the N isotope value for any given secondary consumer, and Δ_n is the fractionation or enrichment in N that occurs between trophic levels ($\Delta_n = 3.4$). The proportion of the dietary C derived from litter (used in the previous equation) was estimated from the following equation (Post et al. 2000):

$$\alpha = (\delta^{13}C_{sc} - \delta^{13}C_{Stenonema}) / (\delta^{13}C_{Tipula} - \delta^{13}C_{Stenonema})$$

4.3.5 Predictions and Analysis

We predicted that crayfish would have limited effects on basal resources because of their relatively small size compared to other species of crayfish and, thus, would have a low effect on altering available benthic habitat. In turn, because of their relatively rapid growth rate and high protein requirements, compared to other larger species of crayfish, we predicted *P. versutus* to have a strong direct effect on benthic macroinvertebrates within litter, an effect that should vary depending on density of *P. versutus*. Additionally, we predicted that *P. versutus* TP would be similar to other benthic food web predators.

All data were analyzed for normality using a Kolmogorov-Smirnov test for normality and homogeneity of variance using Levene's test for equal variance (Zar 1999). Any response variables determined to be nonnormal or heteroscedastic were \log_{10} -transformed, which then satisfied parametric assumptions. We used multivariate analysis of variance (MANOVA) to test for overall effect of treatments and blocks on leaf pack loss and macroinvertebrate response variables. We used ANOVA to test for effects of treatments on specific response variables. For response variables showing a significant difference we used Tukey's pairwise comparison tests to determine where differences among specific treatments resided.

4.4 RESULTS

4.4.1 Field experiment

Effects of crayfish on leaf breakdown.—Litter breakdown for individual treatment units ranged from 31.1 to 88.4% loss, with the lowest individual loss occurring in the open cage treatment and the highest loss in the moderate crayfish density treatment. However, there was high variability across all blocks and treatments, with no significant block effect ($F_{4,16} = 0.80$, $p = 0.545$) and no significant treatment effect ($F_{4,16} = 0.17$, $p = 0.953$) for % leaf pack loss (Fig. 4.1). High among-treatment block variability may have been because of differences in water velocity at each experimental unit (mean %CV within block = 29.72 and treatment = 34.76). Velocity ranged from 0.25 m/sec to 0.69 m/sec. There was no treatment effect on velocity ($F_{4,16} = 0.86$, $p = 0.511$); however, there was a marginally significant block effect ($F_{4,16} = 2.96$, $p = 0.052$), suggesting that

velocity, through mechanical breakage, explained the high variability in leaf pack loss during the experiment.

Effects of crayfish on macroinvertebrates.—The degree to which crayfish influenced macroinvertebrate assemblages within leaf packs varied with treatment and the macroinvertebrate measure. MANOVA showed an overall treatment effect for all macroinvertebrate variables analyzed (Wilk's λ , $F_{24,39} = 2.74$, $p = 0.002$), but no block effect (Wilk's λ , $F_{24,39} = 0.605$, $p = 0.914$). Most macroinvertebrate response variables showed a significant difference in relation to the crayfish exclusion-enclosure treatments. Overall, total macroinvertebrate density differed among treatments (ANOVA, $F_{4,16} = 5.02$, $p = 0.008$), being highest in the crayfish exclusion and lowest in high-crayfish density and cage control treatments (Fig. 4.2A); a similar pattern occurred for total biomass ($F_{4,16} = 3.94$, $p = 0.021$, Fig. 4.2B), although the no-cage treatment did not differ from the crayfish exclusion. Mean density of the mayfly *Stenonema* sp. also differed among treatments ($F_{4,16} = 5.42$, $p = 0.004$), being highest in crayfish exclusion, low-density, and cage controls treatments, and lowest in the no-cage and high-density treatments (Fig. 4.2C). Density of predacious Plecoptera followed a similar pattern ($F_{4,16} = 4.26$, $p = 0.015$), except means were highest in exclusion and low-density treatments and cage controls and lowest in the no cage and high-density treatments (Fig. 4.2D). Mean *Cheumatopsyche* sp. density was highest in exclusions, intermediate in cage control, and lowest in all other treatments ($F_{4,16} = 5.00$, $p = 0.008$; Fig. 4.2E). Similar patterns occurred for non-tanypodine Chironomidae ($F_{4,16} = 5.22$, $p = 0.005$) and mean *Tipula* sp. density ($F_{4,16} = 4.54$, $p = 0.012$), except that the low-density crayfish

treatment was intermediate between the exclusion and the other treatments (Fig. 4.2F,G). Tanypodine chironomids showed no significant difference among blocks or treatments.

In addition to an effect on *Tipula* sp. density, mean larval size of *Tipula* sp. also strongly differed among treatments ($F_{4,16} = 9.88, p < 0.0001$). Pairwise comparisons showed that larval size in the crayfish exclusion was significantly higher than all other treatments (Fig. 4.3) with larvae being almost twice as large in the crayfish exclusion than in other treatments.

4.4.2 Foodweb analysis

The wide separation in C^{13} and N^{15} between 2 focal primary consumers (the grazer *Stenonema* sp. consuming algae and the shredder *Tipula* sp. consuming detritus, Fig. 4.4) suggested the presence of 2 distinct basal resources, algae and leaf detritus. Crayfish position in the foodweb biplot indicated reliance on other macroinvertebrates that obtained most of their energy from detritus ($\alpha = -0.28$, Fig. 4.4). In contrast, collector-filterer taxa (as *Cheumatopsyche* sp. and *Chimarra* sp.) received C from a mixture of algae and detritus ($\alpha = 0.48$). Unlike crayfish, other predacious macroinvertebrates (as *Perlesta* sp. and *Progomphus* sp.) appeared to obtain most C from grazers ($\alpha = 0.67, \alpha = 0.70$), whereas other Odonata taxa ($\alpha = -0.26$) and *Hexatoma* sp. ($\alpha = 0.04$) were more similar to crayfish in relying mostly on detritus as a basal resource (Fig. 4.4). Last, benthic fishes in the food web appeared to receive C from a combination of algae and detritus (Fig. 4.4).

The highest TP within the benthic food web was held by the blackbanded darter (*Percina nigrofasciata*), with an absolute value of ~4. Crayfish held a TP (3.05) was similar to predacious odonates (i.e., 3.24, 3.23, and 2.29, for Coenagrionidae, *Cordulegaster* sp. (Odonata in Fig. 4), and *Progomphus* sp., respectively). TPs of collector-filterers (caddisflies *Cheumatopsyche* sp. and *Chimarra* sp.) also were similar to crayfish with absolute values of 2.97 and 2.87, respectively. Last, TPs of collector-gatherer taxa (as non-tanypodine chironomids and Baetidae) were lower than crayfish, with values of 2.56 and 2.12, respectively.

4.5 DISCUSSION

4.5.1 Influence on leaf litter breakdown

Our findings suggest that *P. versutus* may be similar other benthic macroinvertebrate shredders in its inability to process leaf litter; however, it appears to play a less important role in litter breakdown compared with other crayfish species (Huryn and Wallace 1987, Parkyn et al. 1997, Usio 2000, Creed and Reed 2004). For example, Huryn and Wallace (1987) found that leaf litter processing by the large long-lived (~13 y) crayfish *Cambarus bartonii* was positively related to individual size. They reported a litter consumption rate for this species to be 36 g dry mass m⁻² y⁻¹, with its greatest impact in late spring and summer when other shedder taxa were less abundant or absent. In contrast, Usio and Townsend (2004) demonstrated that smaller-bodied *Paranephrops zealandicus* crayfish (<23 mm orbital carapace length) had minimal or no effect on litter breakdown. In our study, we observed *P. versutus* actively on leaf packs; however, it is likely this species had little influence on overall leaf litter loss. One reason

why smaller-sized species such as *P. versutus* have limited impact on breakdown may relate to latitudinal influences on growth and final size. In a study of crayfish across a wide latitudinal gradient Momot (1984) suggested that individuals grow and mature more slowly in cooler regions than in warmer regions, such that individuals in streams from warmer regions may not reach sizes of species from streams in cooler regions. This environmental influence on crayfish growth may have a substantial effect on a crayfishes ability function like an omnivore, thus causing it to act more as a predator in warmwater streams of the southeastern United States, and potentially in other similar latitudes.

Researchers have speculated the primary reason why litter breakdown rates and crayfish body size are related is because of ontogenetic differences in crayfish growth rate, with older individuals growing more slowly and requiring less animal material to maintain this lower growth rate than more rapidly growing younger crayfish. For example, growth rate of *Orconectes punctimanus* from Missouri streams between 0- to 0.5-y was twice that of the 1.5- to 2.0-y old individuals (4.79 vs. 0.28 mg/mg AFDM/y, Rabeni et al. 1995). It has been hypothesized that relative to older individuals younger crayfish require a higher amount of animal protein to maintain their high growth rate, but once they reach maturity this need is reduced, with a litter-based diet sustaining metabolic demand (Lorman and Magnuson 1978, Momot 1995). In addition to crayfish size, sex also can have a strong impact on litter breakdown, as males showing a disproportionably higher effect on breakdown than females (Usio and Townsend 2002, see also Chambers 1990). In our study, despite using only male crayfish no differences

in breakdown among treatments were observed; this result further supports the idea that *P. versutus* has an extremely limited influence on leaf litter processing in streams.

4.5.2 Crayfish influence on macroinvertebrate assemblages

Unlike that for litter breakdown, results of our experiment suggest that *P. versutus* has a significant effect on benthic macroinvertebrate assemblages within leaf packs. Contrasting crayfish densities, particularly presence (vs. absence of *P. versutus*), had a substantial influence on both benthic macroinvertebrate density and biomass. However, *P. versutus* appears unlikely to act as an ecosystem engineer because of its limited ability to affect litter breakdown; rather, biotic effects appear to be from direct consumption of macroinvertebrates rather than indirect effects on benthos through alteration of the leafpack habitat. Similar to our findings, one study within macrophyte habitats of ponds reported that high crayfish density decreased macroinvertebrate biomass and richness (Nystrom et al. 1996). However, other studies have found that crayfish influence only certain macroinvertebrate taxa within the benthic assemblage (Usio and Townsend 2002, 2004). Our findings suggest that *P. versutus* has a greater influence on some macroinvertebrates compared to others.

Crayfish can be selective predators on benthic macroinvertebrates, altering prey density and/or size structure (Crowl and Covich 1990, Weber and Lodge 1990, Lodge et al. 1994). A primary reason for selective predation is that crayfish feed more on sedentary (vs. mobile) taxa, which are less able to escape consumption (Nystrom et al. 1996, Usio and Townsend 2004); sedentary chironomid larvae often are a common prey item (Whitledge and Rabeni 1997, Nystrom et al. 1996). In our study, a wide range of

taxa were affected by crayfish presence, even at low crayfish density; however, the degree of vulnerability of individual taxa may be related to their mobility. Density of both highly mobile *Stenonema* sp. and predacious Plecoptera nymphs (*Acroneuria* sp., *Neoperla* sp., *Paragnetina* sp.) were negatively affected by crayfish, but only at high crayfish density. Crayfish effects on these 2 groups likely occurred through indirect emigration rather than from direct consumption. These more mobile taxa were less prevalent in *P. versutus* guts (<10% of gut content for both groups, R. Mitchell, unpublished data), suggesting that while they are prey items for *P. versutus*, they compose a small portion of the overall diet.

Relative to mobile taxa, sedentary taxa (i.e., Chironominae and *Cheumatopsyche* sp.) appeared more vulnerable to crayfish presence, occurring at low densities even when crayfish density was low. Others have found chironomids to be vulnerable to crayfish predation, although effects appear to be size class-specific. Usio and Townsend (2004) found that medium- and large-sized tanypodine chironomid density varied with crayfish density, with medium-size larvae being reduced in high-density treatments and large larvae reduced in both high- and low-density treatments. However, tanypods are more mobile than other chironomid taxa, whereas non-tanypods (Chironominae) are relatively sessile and, thus, more vulnerable, usually remaining in their tubes (Hershey 1986). Our study showed that non-tanypodine density was substantially lower in all treatments except crayfish exclusion treatments. Additionally, we found that tanypodine density did not differ between treatments, suggesting they were less affected by crayfish than non-tanypod chironomids. This pattern also may explain why sedentary net-spinning caddisflies (*Cheumatopsyche* sp.) were affected by

a range of crayfish densities in our study. Together, these findings suggest that *P. versutus* greatly influences sedentary taxa, compared with more mobile taxa.

Density of *Tipula* sp., an abundant shredder in Choctafaula Creek, was reduced in only the high-density crayfish treatment; larvae in the low-density treatment showed an intermediate response compared with exclusion and high crayfish treatments. However, mean size of *Tipula* sp. was strongly reduced in all treatments except those where crayfish were absent. These data strongly suggest that *P. versutus* selectively feeds on larger larvae and has a stronger effect on *Tipula* size structure than density. Gut analysis of *P. versutus* verified *Tipula* sp. was consumed by crayfish, composing up to 80% of *P. versutus* gut content (R. Mitchell, unpublished data), and this estimate is likely to be conservative because of the digestive soft-body of *Tipula* sp. larvae. Others also have reported higher effects of crayfish on prey size structure than density (Nystrom et al. 1996, Usio and Townsend 2002, 2004), whereas others hypothesized that crayfish indirectly influence prey by altering habitat conditions by bioturbation of sediments (Creed and Reed 2004, Helms and Creed 2005). That leaf litter breakdown did not differ among treatments suggests that *P. versutus* compensated for shredder taxa (i.e., *Tipula* sp.) loss in the crayfish enclosure treatments. The relatively high density and large size of some taxa in the exclusion treatment suggests that crayfish probably had a more direct predatory influence on *Tipula*, which may apply to other sedentary prey with wide size spectra (Usio and Townsend 2002).

4.5.3 Crayfish trophic relationships in leaf litter food webs

Stable isotope analyses of the leaf litter food web also indicated that *P. versutus* is an important benthic predator. Other research has indicated that stable isotope analysis is a good means of quantifying crayfish energy sources and thus indicating its trophic position (Whitledge and Rabeni 1997, Nystrom 2005). Indeed, others using stable isotope and gut content analyses have concluded crayfish are important predators that consume as much animal material as all other benthic predators combined (Rabeni et al. 1994). In our study, it appears *P. versutus* relies on taxa that consume a greater amount of leaf litter than autotrophic matter; as a result, their absolute trophic position is similar to other important benthic macroinvertebrate predators, such as Odonata, but higher than predacious Plecoptera. Our results also showed that taxa supported either completely or partially by primary production (i.e., algae) were enriched in N¹⁵ compared to taxa supported by detritus. This pattern may explain why some taxa, such as *Cheumatopsyche* sp. and *Chimarra* sp., were determined to be at a higher trophic level than would have been expected if the entire food web was supported on detritus alone. Others have shown that many predaceous stoneflies exhibit ontogenetic shifts from a herbivore-detritivore to a carnivorous diet, which suggests that a predator's trophic position will be reduced relative to predators with a less variable diet over the course of its life history (Fuller and Stewart 1979, Feminella and Stewart 1986). If *P. versutus* is predacious through most of its life, then this may explain why this species has a higher trophic position than other benthic invertebrate predators with more variable diet. Our results also suggest that *P. versutus* influence on *Stenonema* sp. and predacious Plecoptera is indirect because, unlike

these taxa, most of its C appears to come from leaf litter rather than autotrophic sources.

Our results and those from other studies (Huryn and Wallace 1987, Usio 2000, Helms and Creed 2005) suggest that crayfish can have a substantial influence on macroinvertebrate assemblages in streams. However, unlike other studies that have focused on large long lived species, our findings suggests small short-lived crayfish may have a different influence on stream ecosystems than larger species, acting less as an omnivore or ecosystem engineer, and more like a predator. These findings further help our understanding of the role crayfish play in heterotrophic ecosystems. Even though this crayfish appears to play less of a role on basal resource processing such as leaf litter breakdown, it still appears to have a substantial influence on the benthic macroinvertebrate assemblages.

Our findings extend an understanding of the influence of crayfish from lower temperate latitudes on stream ecosystem food webs; however, more experimental evidence documenting the impact of small crayfish species from warmer latitudes and from more sandy streams is needed, and further comparison to previous studies of crayfish needed to fully assess the difference that crayfish may play in warmer sandy coastal plain stream systems.

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Figure 4.1. Mean (± 1 SE) % remaining of American beech leaf litter within contrasting crayfish density treatments. Differences among treatments are designated by different letters using Tukey's pair-wise comparisons and treatments with the same letter were not significantly different. Treatments were crayfish exclusion (E), 1 crayfish enclosure (1C), 3 crayfish enclosure (3C), open cage (CC), and no cage (NC).

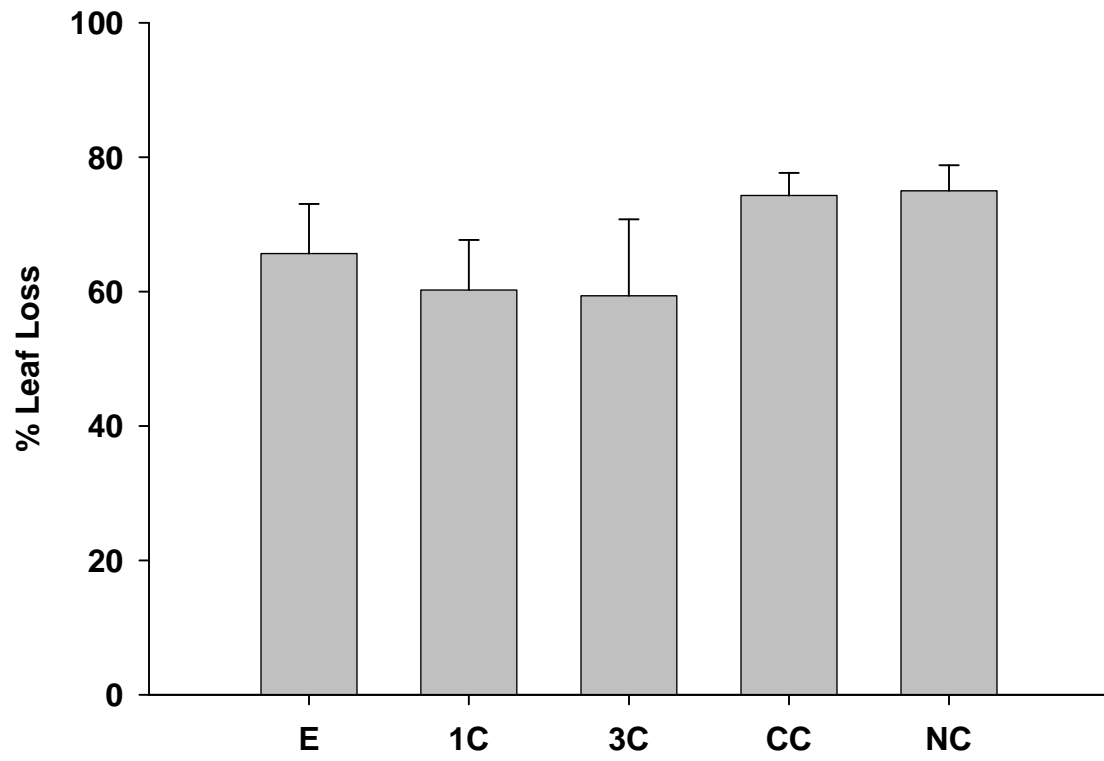


Figure 4.2. Mean (± 1 SE) abundance of focal macroinvertebrate taxa in contrasting crayfish density treatments. A.—macroinvertebrate density, B.—macroinvertebrate biomass, C.—log₁₀-transformed *Stenonema sp.* density, D.—log₁₀-transformed predacious Plecoptera density, E.—*Cheumatopsyche sp.* density, F.—non-Tanypodine Chironomidae density, G.—*Tipula sp.* density. Differences among treatments are shown by different letters using Tukey's pair-wise comparisons and treatments with the same letter were not significantly different. Treatments were crayfish exclusion (E), 1 crayfish per enclosure (1C), 3 crayfish per enclosure (3C), open cage (CC), and no cage (NC).

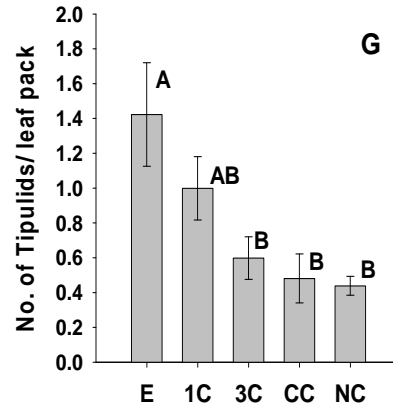
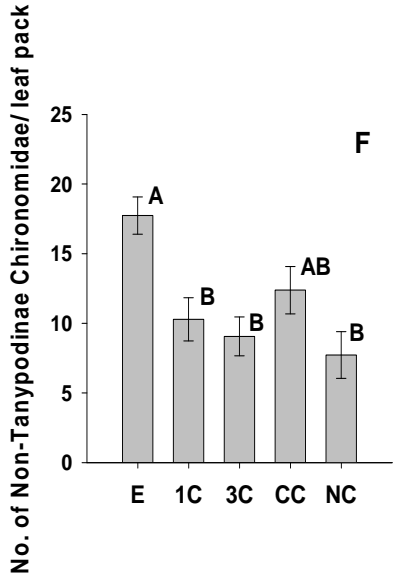
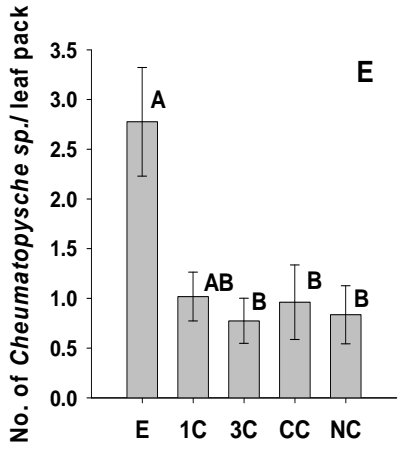
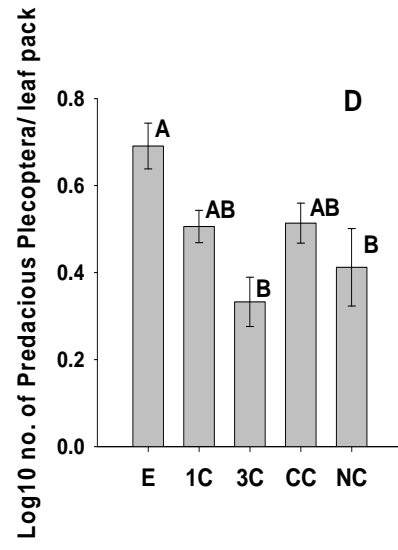
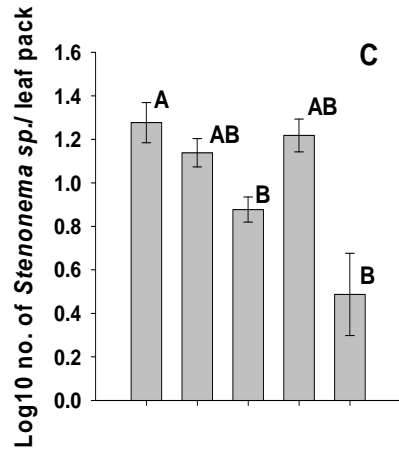
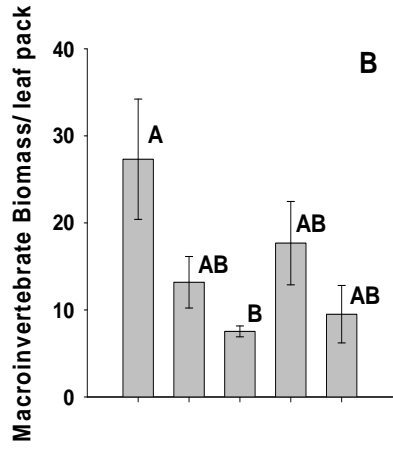
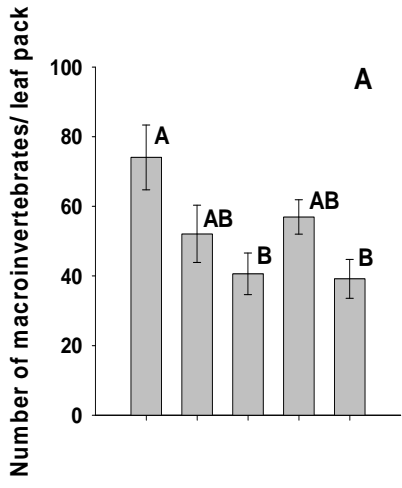


Figure 4.3 Mean (± 1 SE) length of *Tipula* sp. larvae in contrasting crayfish density treatments. Differences among treatments are designated by different letters using Tukey's pair-wise comparisons such that treatments with the same letter were not significantly different. Treatments were crayfish exclusion (E), 1 crayfish per enclosure (1C), 3 crayfish per enclosure (3C), open cage (CC), and no cage (NC).

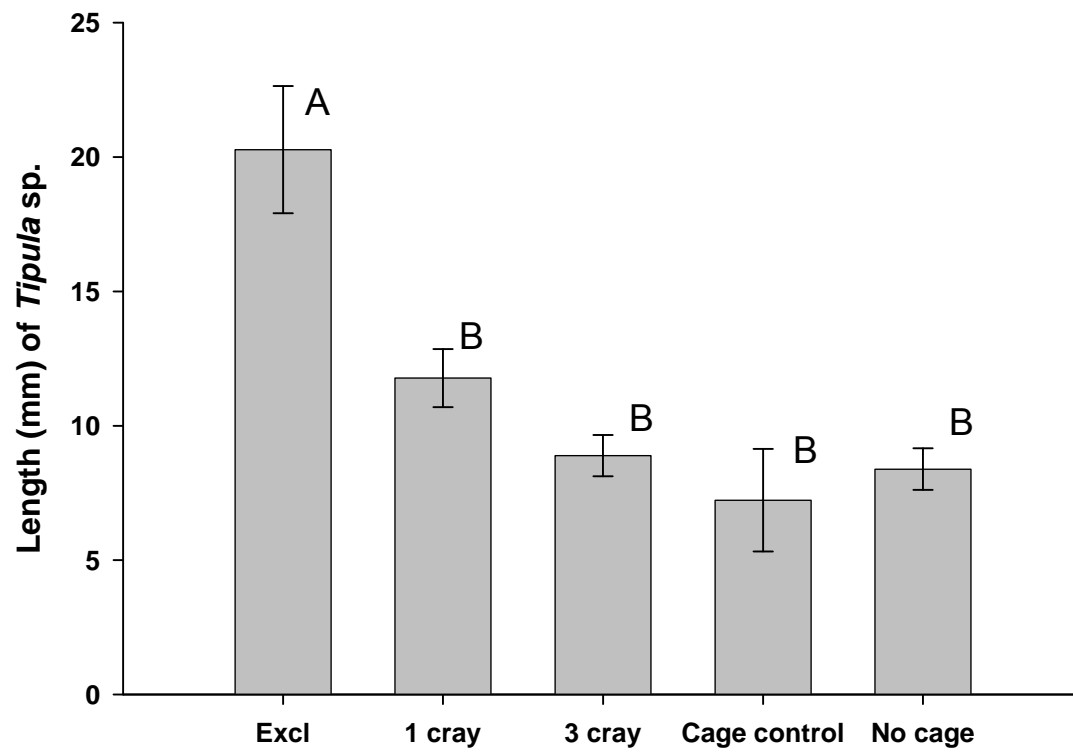
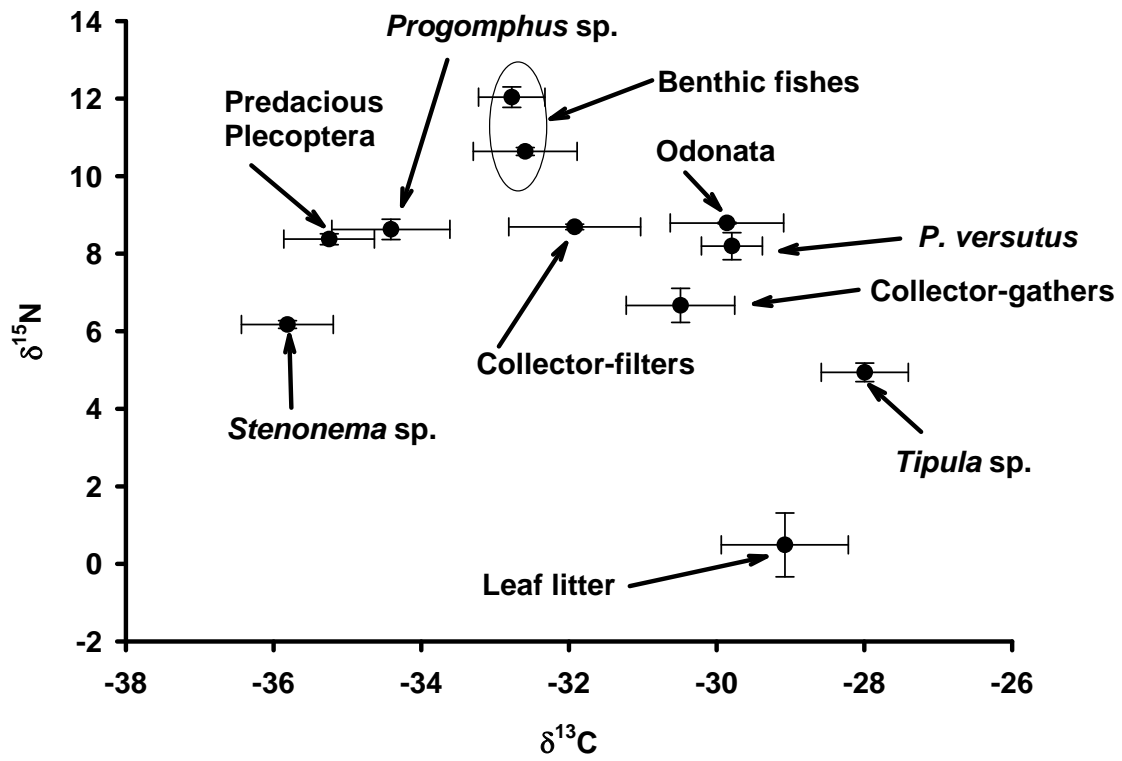


Figure 4.4. Stable isotope cross-plots of the Choctafaula Creek benthic food web. All $\delta^{15}\text{N}$ and $\delta^{13}\text{C}$ values are mean values (± 1 SE) from 3 to 5 samples per taxon, except *P. versutus*, which was composed of 30 individuals.



**5. CONTRASTING DIET AND PRODUCTION OF THE CRAYFISH
PROCAMBARUS VERSUTUS FROM 3 COASTAL PLAINS STREAMS
IN WESTERN GEORGIA, USA**

5.1 SUMMARY

We quantified diet, density, growth, and secondary production of populations of the crayfish *Procambarus versutus* (Cambaridae) in 3 small coastal plain streams at Fort Benning, Georgia, USA. Study streams had strongly contrasting levels of coarse woody debris (CWD, 3–13% of streambed surface) and benthic particulate organic matter (BPOM, particles ≤ 2 cm diameter; 1–5% of bed substrate). We explored to degree to which habitat and basal resource availability influenced crayfish production and trophic position in benthic food webs. Instream habitat (as CWD) was assessed annually and BPOM was assessed seasonally over the study. Crayfish were sampled monthly for 1y, to estimate population density, individual size, and secondary production. In addition, we sampled crayfish during spring and fall to assess trophic position. Mean annual crayfish density and biomass was lowest in the stream with the lowest CWD and BPOM, whereas density was highest in the high-CWD/BPOM stream, but not biomass. Mean size of crayfish was highest in the intermediate-CWD stream. Annual crayfish production tracked instream CWD, being highest in the high-CWD stream, intermediate in the intermediate-CWD stream, and lowest in the low-CWD stream. Diet and stable isotope analysis showed that annual production was derived primarily from consumption

of animal matter and secondarily from plant detritus. Variation in crayfish density, biomass, size, and production may be explained by among-stream differences in food quality and associated feeding behavior.

5.2 INTRODUCTON

Crayfish play an important role in many freshwater ecosystems, functioning as processors of detritus, predators of other macroinvertebrates, and as important food resources for fishes and terrestrial vertebrates (Taylor et al. 2007). Crayfish also compose a significant portion of the benthic macroinvertebrate biomass in many freshwater ecosystems (often >50% of total biomass; Huryn and Wallace 1987, Momot 1995), so changes in abundance of crayfish populations resulting from human perturbations (e.g., habitat loss, chemical pollution, nonnative species invasions, see Allan and Flecker 1993, Richter et al. 1997) could alter ecosystem function (Taylor et al. 2007).

Crayfish use a wide range of biotic and abiotic benthic habitats (e.g., gravel, cobbles, submersed vegetation, wood, etc.) as refuge from predation by fishes and terrestrial vertebrates (Stein 1977). Research has shown the importance of habitat availability in reducing the impact of predation on crayfish populations; however, surprisingly few studies have assessed the role of habitat conditions on intrinsic factors regulating crayfish population dynamics such as growth and production (Stein 1977, Mitchell and Smock 1991, Contreras-Balderas and Lozano-Vilano 1996). In addition, most crayfish research has been done in upland streams containing primarily gravel and/or cobble substrate (Momot 1995, Whitledge and Rabeni 1997, Evans-White et al.

2003), with virtually similar studies conducted in low-gradient sandy streams. High-gradient streams often show a diverse mix of abiotic (gravel, cobble, boulder), and biotic (CWD, macrophytes) substrates and, thus, high structural heterogeneity. In contrast, in low-gradient sandy streams CWD is the main structural feature (Benke et al. 1984, Roeding and Smock 1989, Rinella and Feminella 2005); hence, abundance of CWD can be the primary determinant of benthic habitat in lowland streams (Huryn and Wallace 1987, Mitchell and Smock 1991).

Few studies have investigated the importance of available CWD habitat on crayfish and macroinvertebrate populations in lowland streams. In addition to providing primary habitats, CWD also retains benthic particle organic matter (Smock et al. 1989, Maloney and Feminella 2006), which can increase energy flow from primary to secondary consumers in benthic food webs (Wallace et al. 1997). For example, Hall et al. (2000) found that reduction of leaf litter caused energy flow to become more even across taxa and increased the number of predator pathways, which resulted from increases in both prey abundance and diversity. The polyphagous behavior of crayfish, however, may reduce their dependency on any single food resource, although crayfish populations may still depend on CWD as a refuge from predators (interspecific and intraspecific) (Huryn and Wallace 1987).

The purpose of our study was to quantify the influence of contrasting abundance of instream CWD on crayfish population dynamics in sandy streams where CWD is the primary benthic habitat. Specifically, we explored if crayfish density, biomass, diet, and production would track variation in streams showing contrasting CWD abundance. We predicted that high instream CWD would be associated with high crayfish density,

biomass, and secondary production because of high survival of individual crayfish over time. We also assessed diet composition and trophic position of crayfish among streams with contrasting CWD. Here, we predicted that high CWD would be associated with high benthic particulate organic matter retention and macroinvertebrate density, which, in turn, would increase 1) the amount of detrital matter in crayfish diets, and 2) crayfish trophic position through high availability of prey resource abundance.

5.3 METHODS

5.3.1 Study streams

The study was done in small catchments at the Fort Benning Military Installation (FBMI) in west-central Georgia (Fig. 5.1). FBMI is in the Southeastern Plains Level-3 ecoregion (Omernik 1987) encompassing an area of 735 km², with a humid and mild climate and year-round precipitation (mean = 105 cm/y). The predominant land use is military training and includes dismounted infantry, tracked-vehicle maneuvers (i.e., tanks), heavy weapons usage, and airborne training drop zones. Upland vegetation in study catchments consisted of longleaf pine (*Pinus palustris*) and loblolly pine (*P. taeda*), with some hickories (*Carya* spp.), dogwood (*Cornus florida*), and oaks (*Quercus* spp.). Riparian vegetation is largely intact (canopy coverage often >90%, Maloney et al. 2005), and was dominated by mesic hardwoods including sweetbay magnolia (*Magnolia virginiana*), water oak (*Q. nigra*), yellow poplar (*Liriodendron tulipifera*), red maple (*Acer rubrum*), black gum (*Nyssa sylvatica*) and sweet gum (*Liquidambar styraciflua*). Land management at FBMI includes extensive restoration long-leaf pine forests by use of

selective harvesting and control burning to reduce density of nonnative trees (USAIC 2001, Dale et al. 2002).

Three low-order streams (1 per catchment) with bed substrate primarily of sand and clay were selected for study. Study streams showed generally similar physicochemical conditions, although catchment size differed somewhat and affected parameters such as stream depth and discharge (Table 5.1). Dissolved O₂ (DO) also varied among streams, with SBT having the highest DO, and KMC and SBT having similar DO (Table 5.1). Conductivity was uniformly low among study streams, ranging from $14.3 \pm 0.63 \mu\text{S/cm}$ (mean $\pm 1\text{SE}$) in BCT to 22.6 ± 3.2 in SBT (Houser et al. 2006).

5.3.2 Study animal

We studied the crayfish *Procambarus versutus* (subgenus *Pennnides*), which was common in the study streams, FBMI in general, and throughout the Southeastern Plains of Alabama, Georgia, and Northern Florida (Hobbs 1984). This species is confined to lotic systems and occurs across a wide size range of sandy streams containing variable amounts of coarse woody debris and leaf litter; it also been associated with beds of *Orontium aquaticum* L. (Hobbs 1981). *Procambarus versutus* is a tertiary burrower, showing little or no burrowing behavior (Hobbs 1981), and is small compared to other species in the genus with a maximum size of ~39 mm carapace length (CL, first-form male). Little is known about the biology of this species other than its general habitat and life cycle. Hobbs (1981) reported that first-form males occur year-round and females in berry (reproductive state) occur in April. In our study, we also found first-form males year-round, although females in berry were found in late

April and July in SBC (personal observations). No previous studies have examined the feeding habitats of this species, and ours also is the first study investigating production and trophic position of this species.

5.3.3 Coarse woody debris and benthic particulate organic matter sampling

To assess among-stream differences in habitat availability for *P. versutus*, we used a modified transect method to quantify the relative abundance of instream CWD associated (Wallace and Benke 1984). CWD surveys were conducted annually in spring 2002 and 2003 by measuring all live, dead-submerged, and dead-buried wood pieces >2.5 cm in diameter in 15 cross-stream transects per stream. Area sampled for CWD included a 0.5 m upstream and downstream (1-m swath) along the center of the cross-stream transects. CWD data were converted to planar area (m^2 of CWD per m^2 of stream bed) by multiplying the CWD diameter by length and then dividing by the area sampled within each transect. We then expressed CWD abundance as an areal percentage of the streambed area. Live wood was combined with dead wood in our surveys because some sites had prominent exposed roots in the stream bed, which can provided function similarly to dead wood as benthic habitat and/or a source of organic matter retention.

We quantified abundance of benthic particulate organic matter (BPOM) using sediment cores (PVC pipe, area = 2.01 cm^2) taken from the upper 10 cm of the stream bed ($n = 24/\text{stream}/\text{date}$) seasonally (spring, summer, winter), with 12 cores collected randomly from both the thalweg (mid-channel) and the outer-third of the wetted channel. In the laboratory, BPOM samples were oven-dried at 80°C for 24-48 h, desiccated and

weighed to determine total dry mass, and then ashed in a muffle furnace at 550°C for 3 h, desiccated, and reweighed. %BPOM was determined as the difference between the dry and ashed masses divided by the total dry mass (Minshall 1996).

5.3.4 Crayfish sampling

We sampled *P. versutus* (hereafter “crayfish”) monthly from each stream to estimate population density, biomass, mean size, and production. Crayfish were sampled from November 2002 to November 2003 using kick seines downstream of a quadrat (area = 1 m²; mesh size = 0.32 mm; 5 samples/stream). Sampling usually was done between 0900 and 1300 standard time, but 2 additional nighttime samplings were done (April and September 2003) to ensure that capture rates did not vary over the 24-h day-night cycle. Because of this species non-borrowing behavior (Hobbs 1981), the non-significant difference between the daytime and nighttime sample suggests that the daytime sampling adequately represented the crayfish population of each stream. Five samples were collected randomly over a 100-m reach in each stream per date. All crayfish collected were sexed and measured for carapace length (CL, nearest 0.1 mm) in the field, and then returned to the collection point.

5.3.5 Crayfish density, biomass, and production

Crayfish density was estimated from captured individuals (from 1-m² quadrats, see above), and enumerated in the field, whereas crayfish biomass was estimated from CL using the Cambaridae length-biomass regression equation from Benke et al. (1999). Biomass estimates was then converted to stream-specific monthly ash free dry mass

(AFDM)/m². Monthly size class distribution was based on separating individuals into 5-mm intervals (i.e. size class 1 = 0-5 mm; size class 2 = 6-10 mm; etc).

Crayfish production (P) was estimated using the size-frequency method (Hynes and Coleman 1968, Hamilton 1969, Benke 1984). This method estimates a mean cohort from samples taken throughout the year, and is the appropriate method in cases when an actual cohort cannot be followed over time (Benke 2007). The mean cohort is determined from the size-specific density (annual weighted means), and is assumed to approximate the survivorship from one size class to the next. The size-frequency method first determines production lost between adjacent size classes, by multiplying mortality between adjacent size classes (ΔN : see table 5.2) by the mean biomass of adjacent classes (\bar{W} : see table 5.2) and then by the number of size classes (6 size classes). Total production is then calculated by summing each individual size-specific production loss. The size-frequency method assumes a development time of 1 y; however, previous research has suggested that *P. versutus* has a lifespan of at least 2 y. For this reason, the production must be corrected by multiplying by 12/cohort production interval (CPI), which we assumed was 24 mo, the interval defining the lifespan of an individual of this species. Annual production/biomass ratios ($P:\bar{B}$) were calculated for each stream from the mean annual biomass and annual production data to estimate crayfish turnover rate (Benke 1984, 1993, 2007).

5.3.6 Crayfish diet and trophic position

We used stable N and C isotope ratios ($\delta^{15}\text{N}$ and $\delta^{13}\text{C}$, respectively) to generate simplified food webs and determine crayfish trophic position. Additionally, crayfish diet

data were used to estimate the amount of each food resource that contributed to annual crayfish production. Crayfish were collected in April 2006 (n = 175) and October 2006 (n = 189) for diet analysis (~60 per stream). Thirty-three and 50 crayfish were collected in October 2005 and October 2006, respectively, for stable isotope analysis. Crayfish collected for stable isotope and diet were transported on ice to the laboratory and then frozen (-10°C) until processed. Only crayfish tail muscle was used for the stable isotope analysis. Crayfish used for diet analysis had their stomachs removed and flushed into a gridded Petri dish, distributed evenly, and examined at 40x under a dissecting microscope. Gut contents were sorted into 4 categories: sediment, detritus, animal, or diatom/algae, and the relative composition of each category was estimated as an areal percentage of the total gut composition (Helms and Creed 2005). We further separated animal material into finer taxonomic categories, when possible. In addition, we determined organic matter content of crayfish diets by flushing the gut contents into pre-weighed aluminum dishes, drying samples at 60°C for 48h, desiccating and weighing them, ashing them at 550°C for 3 h, and then re-desiccating and weighing them to determine % AFDM (Minshall 1996). Proportional diet and AFDM content data were analyzed for normality and, if non-normal, were arcsine-transformed (Zar 1999) before comparing them among streams using one-way ANOVA.

We estimated material flow between basal resources and crayfish (as mg AFDM $\text{m}^{-2} \text{y}^{-1}$) for each stream, using the trophic basis of production method (Benke and Wallace 1980, Benke et al. 2001). Briefly, we calculated total ingestion by individual crayfish from annual crayfish production estimates divided by gross production efficiency (GPE), which is equal to assimilation efficiency ($\text{AE} = \text{assimilation}/\text{ingestion}$)

multiplied by net production efficiency (NPE = production/assimilation). Crayfish AE varies greatly with their diet, so we used AE values of 90% for animal matter, 40% for algae, and 14% for leaf detritus based on data from Whittledge and Rabeni (1997). We used an NPE value of 50% based on data from large predacious and omnivorous stream macroinvertebrates (Benke and Wallace 1980, Smock and Roeding 1986, Smith and Smock 1992, Benke et al. 2001). Finally, mean trophic position (TP) based on gut content for crayfish was calculated as 1 plus the sum of the TP of the food item multiplied by its fraction consumed by crayfish. For this calculation, detritus and algae/diatoms would be considered at a TP = 1; an organism feeding only on detritus (e.g. *Tipula* sp.) would be considered at TP = 2; and we assumed that animals feeding on other animals (e.g. predacious Plecoptera) would be considered at TP = 3. We only did analyzed gut content analysis of crayfish, so the above TPs were assumed for each of the food items consumed by crayfish.

We used stable N isotope ratios ($\delta^{15}\text{N}$) to assess the stream-specific level of ^{15}N -enrichment and TP of crayfish sampled in autumn for 2 consecutive years (2005 and 2006, $n = 35$ and 49 , respectively). We also quantified basal resources (as submerged leaf litter) during both years ($n = 4$ per stream). Because of high variability in estimating basal $\delta^{15}\text{N}$ among streams, we standardized $\delta^{15}\text{N}$ samples for each stream by setting the mean basal resource (i.e. leaf litter) TP = 1. Next, we subtracted the difference between the mean basal resource from mean crayfish $\delta^{15}\text{N}$ value for that stream (Cabana and Rasmussen 1996, Vander Zanden et al. 1997). Once we adjusted mean crayfish $\delta^{15}\text{N}$, TP was determined as:

$$\text{TP} = \lambda + (\delta^{15}\text{N}_{\text{crayfish}} - \delta^{15}\text{N}_{\text{base}}) / \Delta\text{N}$$

where λ is the TP of leaf litter (i.e. 1) used to estimate $\delta^{15}\text{N}_{\text{base}}$, $\delta^{15}\text{N}_{\text{crayfish}}$ is the isotope signature of an individual crayfish, $\delta^{15}\text{N}_{\text{base}}$ is the mean isotope signature of the basal resource (litter), and Δ_{N} is the trophic fractionation of N, reported as 3.4 ‰ per trophic level (Hershey et al. 2007). We used one-way ANOVA to test for differences in crayfish levels of ^{15}N enrichment and TP among streams.

5.4 RESULTS

5.4.1 CWD and BPOM

CWD relative abundance (as % of the stream bed surface as CWD) significantly varied among streams from a low of 3.26% in SBT to a high of 15.13% in BCT ($F = 13.39$, $p < 0.0001$). % CWD values in BCT and KMC were significantly higher than SBT, whereas the difference in % CWD between BCT and KMC was nonsignificant (Fig. 5.2). The ratio of mean CWD to mean wetted stream width was highest in BCT (12.61), lowest in SBT (2.50), and intermediate in KMC (4.30).

% BPOM values from mid-channel and near-bank were similar, so these data were combined for each stream. Among-season variation in % BPOM was low in KMC and SBT ($< 2 \text{ mg AFDM/m}^2$), and somewhat more variable in BCT ($\sim 4\text{-}6 \text{ mg AFDM/m}^2$, depending on season; Fig. 5.3). Among-stream patterns in % BPOM overall were similar, being highest in BCT and lowest in KMC and SBT (Fig. 5.3). % BPOM in BCT was higher than KMC and SBT in each season (spring: $F = 19.54$, $p < 0.0001$, summer: $F = 17.25$, $p < 0.0001$, $F = 7.61$, $p = 0.002$; Fig. 5.3).

5.4.2 Crayfish density, biomass, size, and production

Daytime and nighttime sampling showed similar numbers of crayfish collected during spring 2003 ($F = 0.92$, $p < 0.36$) and summer 2003 ($F = 0.87$, $p < 0.28$), so we assumed that daytime sampling adequately reflected true abundance. Monthly crayfish density varied seasonally, with highest densities in early spring and fall (Fig. 5.4A). Among streams, BCT showed the highest density and SBT showed the lowest, whereas KMC had intermediate densities. Biomass was lowest in winter and highest throughout summer and early fall, especially in BCT (Fig. 5.4B). Mean crayfish size (as CL) followed the same seasonal pattern as biomass although, unlike density and biomass, monthly CL was highest in SBT especially in June and October (Fig. 5.4C). Examination of crayfish size-frequency distributions did not easily suggest a 2-y lifespan, hence the reason for using the size-frequency method to estimate production for the 3 populations (Fig. 5.5).

Annual mean density ranged from 1.09 individuals/m² in SBT to 5.06 individuals/m² in BCT, Fig. 5.6). Annual density was significantly different among streams ($F = 33.89$, $p < 0.0001$; Fig. 5.4A), with densities in BCT being higher than KMC and SBT, and higher in KMC than SBT. Mean annual biomass ranged from 211.8 to 587.0 mg AFDM/m² (Fig. 5.4B, Fig. 5.6), which also differed among streams ($F = 3.91$, $p = 0.029$), being highest in BCT and lowest in SBT; biomass in KMC did not differ from BCT or SBT. Mean annual CL also differed among streams ($F = 5.13$, $p = 0.007$) and ranged from 11.6 mm in BCT to 13.4 mm in KMC (Fig. 5.4C). Tukey's pairwise comparisons showed that CL in KMC was higher than BCT, but because of high among-date variation CL in SBT did not differ from KMC or BCT (Fig. 5.4C).

Annual crayfish production ranged from a low of 566.80 mg AFDM/m²/y in SBT (Table 5.2) to a high of 1870.83 mg AFDM/m²/y in BCT (Table 5.4). Annual P:̄B was highest in BCT (3.29, Table 5.4), lowest in KMC (2.50, Table 5.3), and intermediate in SBT (2.57, Table 5.2).

5.4.3 Crayfish diet and trophic position

Amorphous detritus was the predominant food type in crayfish diets from all 3 streams, composing >50% of the total diet (Fig. 5.7). Animal matter was the 2nd-most abundant food type (15–20%), with diatoms composing a comparatively smaller proportion of the diet (0.16 to 2.8%). Detritus was the predominant food type in all crayfish diets, but its relative amount differed among streams (spring 2006, $F = 7.15$, $p = 0.001$; fall 2006, $F = 5.87$, $p = 0.004$). Pairwise comparisons revealed that BCT and KMC were similar to each other, which were both higher than SBT (Fig. 5.7). The % of animal matter in the diet did not differ among streams in spring 2006 but differ in fall 2006 ($F = 7.15$, $p = 0.001$), with BCT and KMC both showing higher % animal matter in the diet than SBT (Fig. 5.7). The % diatom category strongly differed among streams in both seasons (spring 2006, $F = 6.02$, $p = 0.003$; fall 2006, $F = 15.00$, $p < 0.0001$), with KMC showing higher % diatoms than both BCT and SBT (Fig. 5.7). In addition to among-stream variation in food items, the proportion of the total diet as organic matter also varied (Fig. 5.8). % organic matter was lower in SBT than BCT and KMC in both seasons ($F = 14.20$, $p < 0.0001$, $F = 4.41$, $p = 0.018$), whereas BCT and KMC did not differ (Fig. 5.8).

Animal matter contributed most to annual crayfish production, followed by detritus and diatoms, in all 3 streams (Tables 5.5, 5.6, 5.7), accounting for 66.89% of production in BCT, 62.44% in KMC, and 63.57% in SBT. In contrast, detritus accounted for only 31.15% of production in SBT, 36.19% in BCT, and 34.47% in KMC. Diatoms accounted for a substantially lower amount of crayfish annual production than animal matter or detritus (i.e., 3.09% in KMC, 1.24% in SBT, and 0.24% in BCT). Crayfish TP calculated from gut content analysis showed little variation among streams, with SBT having the highest TP (2.23), whereas KMC and BCT were almost identical with TP values of 2.19 and 2.18, respectively.

Use of stable isotopes to estimate crayfish TP showed significant differences among streams. In 2005, crayfish from SBT were less enriched in ^{15}N than KMC and BCT ($F= 12.21$, $p < 0.0001$, Fig. 5.9), whereas in 2006 crayfish in SBT were less ^{15}N -enriched than KMC, but not different from BCT ($F= 8.42$, $p = 0.001$, Fig. 5.9). Mean TP of crayfish also differed among streams, with crayfish from SBT being lower than crayfish from KMC and BCT in 2005 ($F= 12.09$, $p < 0.0001$, Fig. 5.9); however, in fall 2006 only crayfish from SBT and KMC differed from each other; crayfish from BCT showed an intermediate TP between KMC and SBT ($F= 8.45$, $p < 0.001$, Fig. 5.9). TP estimates from the stable isotope analysis were higher in both 2005 and 2006, compared to the TP estimates from the gut content analysis.

5.5 DISCUSSION

5.5.1 Importance of CWD and its influence on basal resources

Instream habitat availability has been shown to influence both structure and function of benthic macroinvertebrate assemblages, with decreases in both habitat quality and quantity having negative effects on assemblages (Wallace and Benke 1984, Bilby and Likens 1984, Benke and Wallace 1990, Maloney and Feminella 2006). Our results also suggest that abundance of instream CWD has a substantial influence on population density, production, diet, and trophic position of the crayfish *Procambarus versutus*. However, our study included unreplicated streams of contrasting CWD, so these results are only suggestive of the importance of CWD habitat on crayfish populations. Few studies have investigated the influence of instream habitat availability on crayfish populations across streams with varying habitat availability. Our research thus adds to a general understanding of how CWD availability may influence benthic macroinvertebrate assemblages in headwater systems of the southeastern US.

CWD is a key factor in retaining BPOM in a wide array of high- to low-gradient streams (Bilby and Likens 1980, Bilby 1981, Smock et al. 1989, Wallace et al. 1995) and, in many sandy low-gradient streams, instream CWD and roots from riparian vegetation are the primary structures facilitating BPOM retention (Angermeier and Karr 1984, Smock et al. 1989). In our study, %BPOM was substantially higher in the stream containing the highest CWD (BCT); however, and somewhat surprisingly, the intermediate-CWD stream (KMC) did not display an intermediate %BPOM relative to the low-CWD stream (SBT). One explanation for this disparity could be that our BPOM sampling effort was inadequate to discriminate low levels of %BPOM in KMC and SBT.

Additionally, because of its smaller size relative to KMC, debris dams in BCT typically crossed the entire channel, and accounted for a higher ratio of mean CWD to stream width in BCT compared to KMC; in contrast, debris dams and logs in KMC rarely crossed the entire channel and stream flow moved more easily around individual debris dams or logs (R. M. Mitchell, *personal observations*). Smock et al. (1989) also found that debris dams structure within the channel substantially influenced benthic organic matter, with a stream with <50% perched logs (i.e. logs lying above stream channel or only partially in stream channel) and only 21% of logs parallel to flow having ~9x as much non-woody organic matter as the stream with >70% perched logs and ~50% of the logs parallel to the flow.

Others have reported seasonal variation in organic matter storage in the stream bed, with higher organic matter storage during and just after leaf fall, which decreases with decomposition through spring and summer (Smock et al. 1989, Wallace et al. 1995). However, in our study there was no difference in % BPOM among seasons; rather, %BPOM was highest in summer, at a time when other studies report lowest BPOM storage (Smock et al. 1989). There are 2 possible explanations for this pattern. First, several of the riparian tree and shrub species at FBMI show relatively slow breakdown rates, including *M. virginiana*, *N. sylvatica*, rhododendron (*Rhododendron* sp.), and American holly (*Ilex opaca*), and these litter inputs may persist longer in the channel (Allan 1995), and drop their leaves later or continually throughout the year. Second, high %BPOM in summer could have been resulted from drought conditions over the study (R. M. Mitchell, *personal observations*), which could have decreased processing rates. Others have equated the rapid decline of BPOM in late winter with

the increase in the number of high-energy flow events, and related increased downstream transport of organic matter (Roeding and Smock 1989, Smock et al. 1989). Additionally, drought conditions may cause trees to drop their leaves during summer and thus increase the amount of BPOM during the summer, compared to winter BPOM levels.

5.5.2 Crayfish density, biomass, and production

Crayfish often display habitat preferences and are thus influenced by habitat quality (Huryn and Wallace 1987, Quinn and Janssen 1989, Mitchell and Smock 1991, Jones and Bergey 2007). This prior research has focused on understanding crayfish habitat use based on direct observation of habitat preference. However, unlike these earlier studies we instead focused on understanding how instream habitat, in the form of CWD, influenced *P. versutus* populations by quantifying CWD habitat at the reach scale and relating it to population measures.

Direct complementarity between reach-scale crayfish density and CWD abundance is consistent with observations by others. In a New Zealand stream, densities of *Paranephrops planifrons* decreased with decreasing CWD as a function of increasing catchment disturbance (Parkyn and Collier 2004). Unlike the latter study, *P. versutus* density, biomass, and individual size did not show a similar pattern in our study. The high and intermediate-CWD streams had similar crayfish biomass, both being higher than the low-CWD stream, and mean size was highest in the high- and intermediate-CWD and lowest in the low-CWD stream. It is possible that the similar biomass observed in the high and intermediate-CWD streams was caused by higher

mean individual size in the intermediate-CWD stream and higher density in the high-CWD stream, patterns that would suggest stream-specific variation in competition and predation and their effects on crayfish biomass. Others have suggested that these processes limit crayfish populations in combination with habitat availability (Stein 1977, Mitchell and Smock 1991). In our study, high instream cover (as CWD) in the high-CWD stream could have reduced intraspecific competition for available habitat, as well as reducing predation because of high refuge, the combination of which would increase survivorship. Alternatively, lower habitat availability in the intermediate-CWD stream may have increased competition and individual mortality, resulting in increased individual size by reducing the abundance of smaller individuals in the population. Such competition would be expected to occur in systems with minimal predator control of crayfish by size-selective aquatic vertebrate predators (Stein and Magnuson 1976). Such predation is unlikely in small streams at FBMI, as vertebrate predator abundance is low (Maloney et al. 2006); however, the degree of crayfish consumption by terrestrial predators, which can affect crayfish survivorship (Stein and Magnuson 1976), is unknown. Others have reported that juvenile crayfish show high survival and growth under high habitat complexity, especially when adult crayfish are present (Olsson and Nystrom 2009). In our study, there was no evidence that adult crayfish directly affected juveniles, although others have reported juveniles are less active during day and night under low habitat complexity and when adults are present, which may reduce feeding and decrease juvenile growth and survival (Olsson and Nystrom 2009).

Crayfish annual production in lotic ecosystems is highly variable, ranging from 200 to 8800 mg AFDM m⁻² y⁻¹ (Momot and Gowing 1977, Momot 1984, Huryn and

Wallace 1987, Mitchell and Smock 1991, Whitemore and Huryn 1999, Evan-White et al. 2003), which likely is caused by several environmental factors. Annual production of crayfish from our study (530.15 – 1779.17 mg AFDM m⁻² y⁻¹) was within the low to middle range of measured production for any stream. Others have observed that low habitat availability strongly influences crayfish production, and have suggested that low productivity suboptimal conditions for growth (Mitchell and Smock 1989). However, unlike annual production, annual $P:\bar{B}$ was in the upper end of ratios from other systems (e.g., 0.5 – 2.4; Momot and Gowing 1977, Momot 1984, Evan-White et al. 2003), suggesting that turnover of *P. versutus* populations may be less influenced by habitat availability than population production. One possible reason for the low production of crayfish populations relates to low overall productivity of these systems. Houser et al. (2005) reported low gross primary productivity and high ecosystem respiration from these and other streams at FBMI, suggesting that these systems are highly heterotrophic. However, heterotrophy does not necessarily imply a system is unproductive; but low basal resources in the form of allochthonous BPOM inputs in the study streams may severely limit their productivity (Pimm 1984).

5.5.3 Crayfish diet and trophic position

The predominance of plant detritus in the diet of *P. versutus*, along with the secondary importance of animal matter and diatoms, is consistent with other studies of stream crayfish (Evan-White et al. 2003, Whitley and Rabeni 1997, Momot et al. 1978). However, whereas plant detritus was the dominant component in the diets of all 3 crayfish populations studied, there was a difference in the amount of BPOM (primarily

allochthonous plant detritus) among streams, during both spring and fall. Crayfish from both the high- and intermediate-CWD streams had significantly more plant detritus in their diet compared to the low-CWD stream. This pattern may reflect differential BPOM availability in the study streams and, thus, a potentially strong influence of BPOM on crayfish diet. Individual *P. versutus* from SBT tended to show a higher amount of inorganic material in their gut compared to the other 2 streams, suggesting a reduced food base in this stream. Catchment disturbance is likely to cause a decrease in BPOM and previous research in FBMI streams found that %BPOM decreased with increasing watershed disturbance (Maloney et al. 2005). Additionally, previous work at FBMI has shown a direct link between several benthic macroinvertebrate parameters and instream CWD (i.e. habitat) abundance, which, in turn, are both linked to catchment disturbance (Maloney and Feminella 2006).

A somewhat surprising result was the high amount of inorganic material in crayfish diets from the low-CWD stream (SBT) relative to BCT and KMC showing higher CWD. Some studies have reported sediment constituting a large portion of crayfish diets (Capelli 1980, Whiteledge and Rabeni 1997, Evans-White et al. 2003). However, Helms and Creed (2005) reported that gut contents of *Orconectes cristavarius* were 50 to 100% sediment, suggesting this species actively consumes large amounts of inorganic sediment, ostensibly to collect BPOM. In our study, *P. versutus* may show similar sediment-based feeding in streams or conditions where plant detritus and animal matter are low. In such streams particularly where sediment-laden BPOM is low, food quality may significantly affect individual crayfish growth and survivorship.

After correcting the diet data for different AEs of the different diet components, our estimates were similar to other studies (Whitledge and Rabeni 1997, Evans-White et al. 2003). Animal matter contributed most to production, approximately twice as much as plant detritus and considerably more than diatoms. We did not account for the energetic influence of sediment to crayfish considerable production; however, others have suggested crayfish may obtain energy from consumed sediment (Helms and Creed 2005), largely from bacterial cells and exudates (Allan 1995, Hall and Meyer 1998). Future studies addressing the importance in conditioned sediments to crayfish production may be needed to understand the energy sources available to crayfish more fully.

Crayfish from the low-CWD stream (SBT) had the lowest ^{15}N enrichment for both years of our study; relative to the high- and intermediate-CWD streams where enrichment was less. This result suggests overall food quality is lower in the low-CWD stream (SBT), as observed in the reduced detrital and animal matter in crayfish diets, which, in turn, indicates that these crayfish are less likely to obtain adequate energy for production. In addition, the trophic position of crayfish in SBT was lower than either of the other study streams, suggesting that crayfish were feeding at a lower trophic level and on lower-quality food than the other 2 streams. Others have shown that changes to low habitat quality and food resources had bottom-up effects on crayfish populations, specifically yielding smaller crayfish when food was limited by habitat conditions (Nystrom et al. 2006). Others also have suggested that food resource alteration from watershed disturbance may influence TP of predatory organisms (Parker and Huryn 2006), and result from higher TP and omnivores feeding behavior of crayfish,

disturbance is likely to impact crayfish similar to other benthic macroinvertebrates. We did not sample the entire benthic macroinvertebrate assemblage; however, previous research at FBMI indicated that increased disturbance and decreased CWD abundance had negative effects on benthic macroinvertebrate assemblages in general (Maloney and Feminella 2006). This result may suggest that benthic macroinvertebrate prey for crayfish are reduced in SBT compared with KMC and BCT, which could explain both the lower ^{15}N and TP in this stream.

In summary, our findings suggest that *P. versutus* may be influenced by instream habitat conditions, which, in turn, have been shown to be influenced by catchment disturbance (Maloney et al. 2005). Multiple factors are attributable to the decline of many crayfish species, including chemical pollution, introduction of nonnative species, overexploitation, and habitat alteration linked to catchment land use (Richter et al. 1997, Wilcove et al. 2000). Despite the importance of crayfish in many aquatic ecosystems, >50% of all crayfish populations from North America are at risk of extinction; yet, there remains only scant information on the life history and habitat requirements for most species (Taylor et al. 2007). Understanding the influence of instream habitat conditions on crayfish populations in general will aid in conservation efforts of this imperiled group.

Our study demonstrates that *P. versutus* populations exhibit considerable variation in population and dietary measures, which appeared to track variation in instream CWD abundance. *Procambarus versutus* populations appear denser under conditions of high-CWD, however it also appears that mean size is highest under intermediate-CWD populations. Under low-CWD conditions, *P. versutus* populations appear to be highly impaired from both reduced habitat cover and food resource quality.

Even though *P. versutus* is a relatively widespread species, these results could be useful in understanding how habitat degradation may influence crayfish populations, and help further efforts to conserve more imperiled species of crayfish.

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Table 5.1. Watershed and physicochemical characteristics for streams where *Procambarus versutus* were collected.

Average stream slope (%) is from a 100 m stream reach where crayfish were collected. **Mean temperature** (°C) is the mean annual temperature of each stream during the period crayfish were collected (Mean ±1SE). **DO** (dissolved oxygen, mg/L), **pH**, and **Ca⁺** (mg/L) were taken from the downstream most point of study sites. **Velocity** (m/s), **Depth** (m), and **Wetted stream width** (m) are reach averages from collection sites (Mean ±1SE). **Discharge** (m³/s) was taken from the downstream most point of study sites.

Stream	Stream code	Drainage area (km ²)	Mean temperature (°C)	Season	DO (mg/L)	pH	Ca ⁺ (mg/L)	Velocity (m/s)	Depth (m)	Wetted stream width (m)	Discharge (m ³ /s)
Bonham Creek Tributary	BCT	0.75	16.78 (5.07)	Spring	6.6	4.87	0.25	0.05 (0.03)	0.09 (0.02)	1.2 (0.14)	0.004
				Summer	7.46	5.27	--	0.03 (0.03)	0.24 (0.02)	1.1 (0.04)	0.001
				Winter	8.36	6.42	0.28	0.06 (0.01)	0.19 (0.03)	1.0 (0.02)	0.005
Kings Mill Creek	KMC	3.69	16.98 (4.73)	Spring	7.08	5.08	--	0.13 (0.02)	0.21 (0.02)	2.1 (0.13)	0.037
				Summer	7.88	5.54	--	0.13 (0.02)	0.22 (0.02)	1.9 (0.23)	0.020
				Winter	7.23	7.50	0.26	0.09 (0.004)	0.21 (0.01)	1.8 (0.09)	0.029
Sally Branch Tributary	SBT	1.95	17.25 (5.16)	Spring	10.08	4.85	0.84	0.09 (0.01)	0.10 (0.01)	1.3 (0.09)	0.045
				Summer	10.81	6.95	--	0.08 (0.01)	0.07 (0.01)	1.3 (0.08)	0.007
				Winter	11.36	6.50	1.44	0.08 (0.01)	0.09 (0.02)	1.3 (0.07)	0.025

Table 5.2. Calculation of *P. versutus* production by the size-frequency method, from Sally branch tributary (SBT), Fort Benning Military Reservation, Georgia.

Size Group Length (mm)	Density (No./m ²) <i>N</i>	Ind. Mass (mg) <i>W</i>	No. Lost (No./m ²) ΔN	Biomass (mg/m ²) $B = N \times W$	Weight at Loss $\bar{W} = (W_1 + W_2)/2$	Weight Loss $\bar{W} \Delta N$	$\times 6$ (mg/m ²)
1 to 5	0.06	2.95		0.18			
			-0.43		10.66	-4.59	-27.56
6 to 10	0.50	18.37		9.05			
			0.20		38.49	7.70	46.19
11 to 15	0.29	58.61		17.13			
			0.06		153.00	9.41	56.49
16 to 20	0.23	247.39		57.09			
			0.06		446.13	28.60	171.59
21 to 25	0.17	644.88		107.48			
			0.15		816.17	123.47	740.83
26 to 30	0.02	987.45		19.75			
			0.02		987.45	19.75	118.49
				Biomass = 210.68	Production (uncorrected) = 1133.59		
					Annual Production (corrected) = 566.80		
					Cohort P/B = 5.38		
					Annual P/B = 2.69		

Table 5.3. Calculation of *P. versutus* production by the size-frequency method, from Kings Mill creek (KMC), Fort Benning Military Reservation, Georgia.

Size Group Length (mm)	Density (No./m ²) <i>N</i>	Ind. Mass (mg) <i>W</i>	No. Lost (No./m ²) ΔN	Biomass (mg/m ²) $B = N \times W$	Weight at Loss $\bar{W} = (W_1 + W_2)/2$	Weight Loss $\bar{W} \Delta N$	$\times 6$ (mg/m ²)
1 to 5	0.23	2.92		0.67			
			-0.86		11.30	-9.73	-58.39
6 to 10	1.09	19.67		21.49			
			0.03		39.25	1.21	7.25
11 to 15	1.06	58.83		62.45			
			0.34		155.21	52.53	315.19
16 to 20	0.72	251.59		181.92			
			0.44		382.16	168.05	1008.30
21 to 25	0.28	512.72		145.27			
			0.21		699.42	144.37	866.20
26 to 30	0.08	886.11	0.08	70.89	886.11	70.90	425.33
				Biomass = 482.69	Production (uncorrected) = 2622.27		
					Annual Production (corrected) = 1311.14		
					Cohort P/B = 5.43		
					Annual P/B = 2.72		

Table 5.4. Calculation of *P. versutus* production by the size-frequency method, from Bonham creek tributary (BCT), Fort Benning Military Reservation, Georgia.

Size Group Length (mm)	Density (No./m ²) <i>N</i>	Ind. Mass (mg) <i>W</i>	No. Lost (No./m ²) ΔN	Biomass (mg/m ²) $B = N \times W$	Weight at Loss $\bar{W} = (W_1 + W_2)/2$	Weight Loss $\bar{W} \Delta N$	$\times 6$ (mg/m ²)
1 to 5	0.52	2.84		1.49			
			-2.85		14.02	-39.92	-239.49
6 to 10	3.37	25.21		84.93			
			1.65		43.68	71.90	431.39
11 to 15	1.72	62.15		107.08			
			0.92		137.20	126.65	759.89
16 to 20	0.80	212.26		169.81			
			0.57		374.06	211.96	1271.79
21 to 25	0.23	535.85		125.03			
			0.19		835.33	156.36	938.14
26 to 30	0.05	1134.80		56.74			
			0.05		1134.80	56.74	340.44
				Biomass = 545.08	Production (uncorrected) = 3741.65		
					Annual Production (corrected) = 1870.83		
					Cohort P/B = 6.86		
					Annual P/B = 3.43		

Table 5.5. Calculation of production attributed to each food type and amount consumed by *P. versutus*, from Sally branch tributary (SBT), Fort Benning Military Reservation, Georgia (annual production = 566.80 mg/m²/yr).

	Food type in foregut (%)	Assimilation efficiency* (AE)	Net production efficiency* (NPE)	Relative amount to production	Production attributed to food type (%)	Production attributed to food type (mg/m ² /yr)	Gross production efficiency* (AE x NPE)	Amount food type consumed (mg/m ² /yr)
Detritus	74.18	x 0.14	x 0.5	= 5.19	31.15	176.56	÷ 0.07 =	2522
Algae/Diatoms	1.65	x 0.39	x 0.5	= 0.32	1.95	11.05	÷ 0.20 =	55
Animals	24.17	x 0.92	x 0.5	= 11.12	66.89	379.13	÷ 0.46 =	824
Chironomidae	20.22	x 0.92	x 0.5	= 9.30	55.94	317.07	÷ 0.46 =	689
Tipulidae	1.48	x 0.92	x 0.5	= 0.68	4.07	23.07	÷ 0.46 =	50
Ephemeroptera	0.00	x 0.92	x 0.5	= 0.00	0.00	0.00	÷ 0.46 =	0
Trichoptera	1.36	x 0.92	x 0.5	= 0.62	3.74	21.20	÷ 0.46 =	46
Predacious Plecoptera	0.24	x 0.92	x 0.5	= 0.11	0.68	3.85	÷ 0.46 =	8
Non-predacious Plecoptera	0.88	x 0.92	x 0.5	= 0.40	2.46	13.94	÷ 0.46 =	30

Table 5.6. Calculation of production attributed to each food type and amount consumed by *P. versutus*, from King's Mill creek (KMC), Fort Benning Military Reservation, Georgia (annual production = 1311.14 mg/m²/yr).

	Food type in foregut (%)	Assimilation efficiency* (AE)	Net production efficiency* (NPE)	Relative amount to production	Production attributed to food type (%)	Production attributed to food type (mg/m ² /yr)	Gross production efficiency* (AE x NPE)	Amount food type consumed (mg/m ² /yr)
Detritus	63.72	x 0.14	x 0.5	= 5.27	34.47	457.94	÷ 0.07 =	6542
Algae/Diatoms	2.04	x 0.39	x 0.5	= 0.47	3.09	40.51	÷ 0.20 =	203
Animals	18.80	x 0.92	x 0.5	= 10.45	62.44	818.68	÷ 0.46 =	1779
Chironomidae	12.06	x 0.92	x 0.5	= 6.70	42.89	562.34	÷ 0.46 =	1222
Tipulidae	2.66	x 0.92	x 0.5	= 1.48	9.43	123.64	÷ 0.46 =	269
Ephemeroptera	1.20	x 0.92	x 0.5	= 0.67	4.25	55.72	÷ 0.46 =	121
Trichoptera	1.26	x 0.92	x 0.5	= 0.70	4.48	58.74	÷ 0.46 =	128
Predacious Plecoptera	0.14	x 0.92	x 0.5	= 0.08	0.46	6.03	÷ 0.46 =	13
Non-predacious Plecoptera	1.44	x 0.92	x 0.5	= 1.70	5.10	66.87	÷ 0.46 =	145

Table 5.7. Calculation of production attributed to each food type and amount consumed by *P. versutus*, from Bonham creek tributary (BCT), Fort Benning Military Reservation, Georgia (annual production = 1870.83 mg/m²/yr).

	Food type in foregut (%)	Assimilation efficiency* (AE)	Net production efficiency* (NPE)	Relative amount to production	Production attributed to food type (%)	Production attributed to food type (mg/m ² /yr)	Gross production efficiency* (AE x NPE)	Amount food type consumed (mg/m ² /yr)
Detritus	65.60	x 0.14	x 0.5	= 5.43	36.19	677.05	÷ 0.07 =	9672
Algae/Diatoms	0.16	x 0.39	x 0.5	= 0.04	0.24	4.49	÷ 0.20 =	22
Animals	17.56	x 0.92	x 0.5	= 9.76	63.57	1189.29	÷ 0.46 =	2585
Chironomidae	10.32	x 0.92	x 0.5	= 5.74	37.39	699.50	÷ 0.46 =	1521
Tipulidae	2.98	x 0.92	x 0.5	= 1.66	10.78	201.68	÷ 0.46 =	438
Ephemeroptera	0.03	x 0.92	x 0.5	= 0.01	0.08	1.50	÷ 0.46 =	3
Trichoptera	3.10	x 0.92	x 0.5	= 1.72	11.25	210.47	÷ 0.46 =	458
Predacious Plecoptera	0.17	x 0.92	x 0.5	= 0.09	0.63	11.79	÷ 0.46 =	26
Non-predacious Plecoptera	0.96	x 0.92	x 0.5	= 0.53	3.46	64.73	÷ 0.46 =	141

Figure 5.1. Locations of study catchments within Fort Benning Military Reservation, GA. The dotted line within the western portion of the military reservation designates the Chattahoochee River. BCT (Bonham Creek Tributary) is the high-CWD stream, KMC (King's Mill Creek) is the intermediate-CWD stream, and SBT (Sally Branch Tributary) is the low-CWD stream.

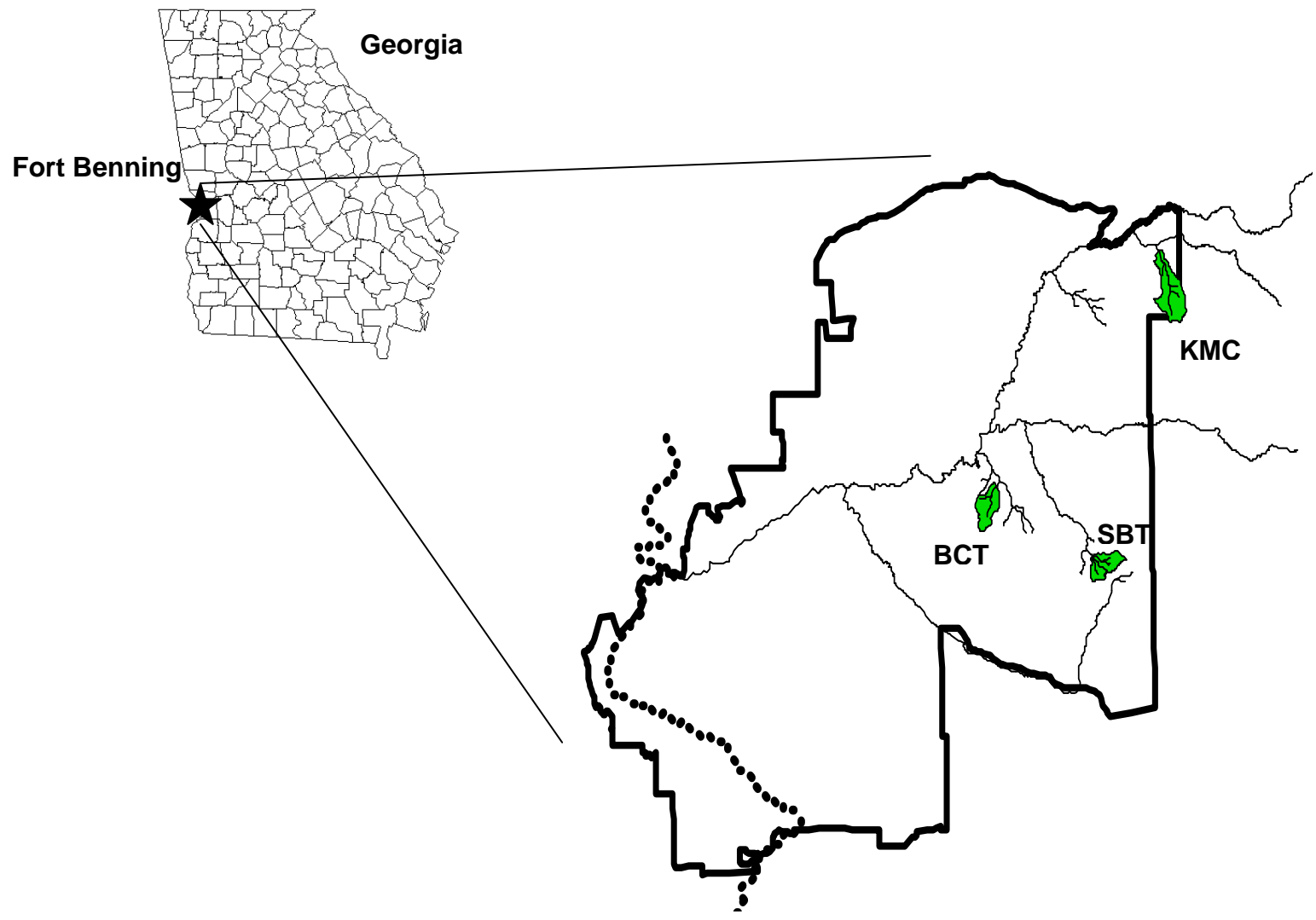


Figure 5.2. Mean (± 1 SE) percentage of stream bottom covered by coarse woody debris (CWD) for each of the 3 study streams. Differences among streams are shown by letters above bars such that streams with the same letter are not significantly different (Tukey's pairwise test).

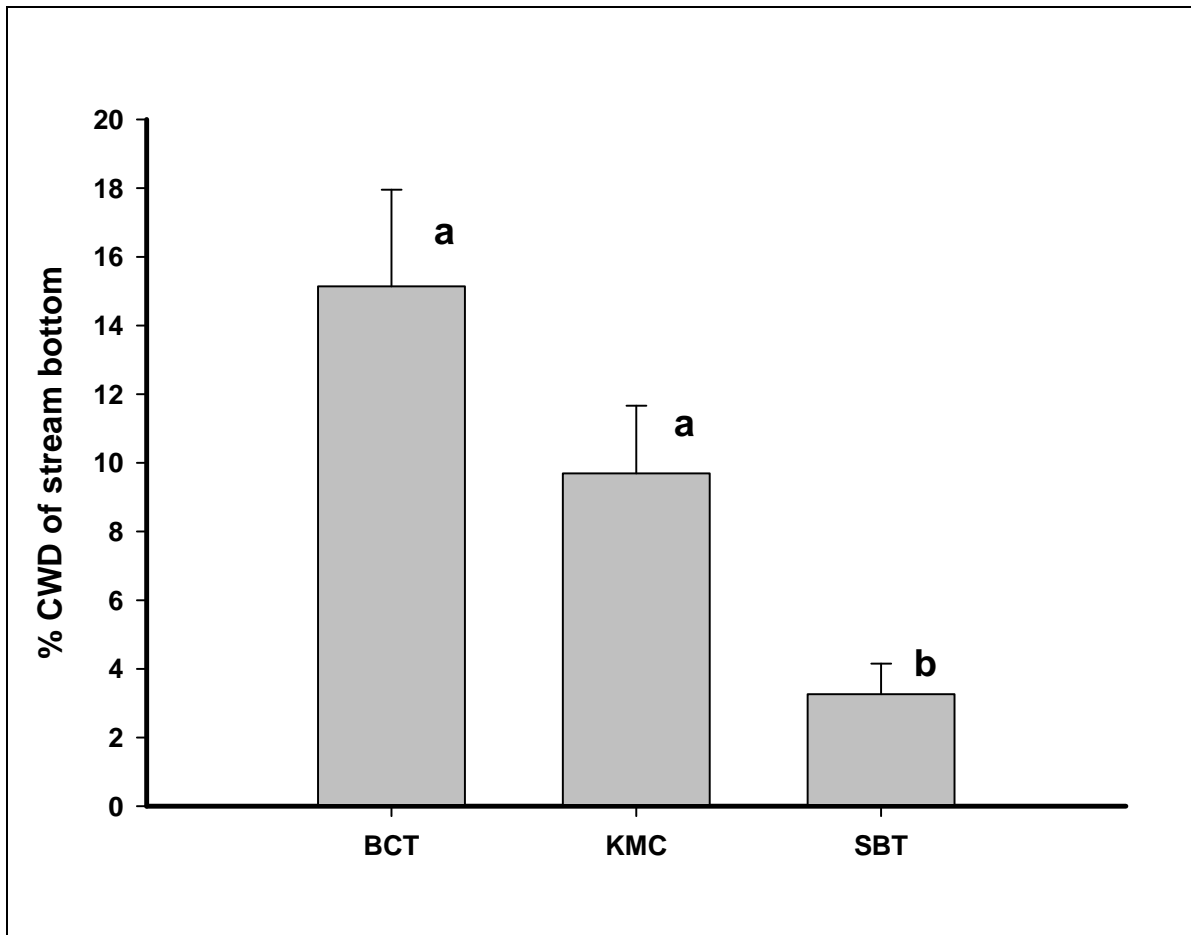


Figure 5.3. Mean (± 1 SE) percentage of benthic particulate organic matter from sediment core samples. Differences among streams are shown by letters above bars such that streams with the same letter are not significantly different (Tukey's pairwise test). A= spring, B= summer, and C= winter.

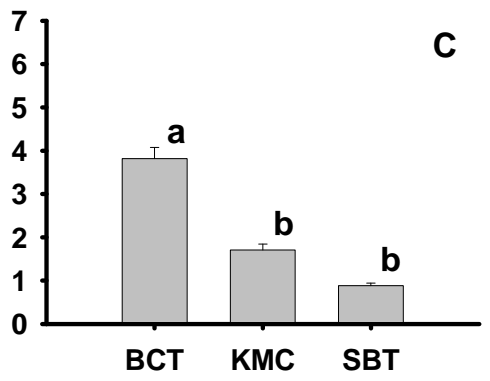
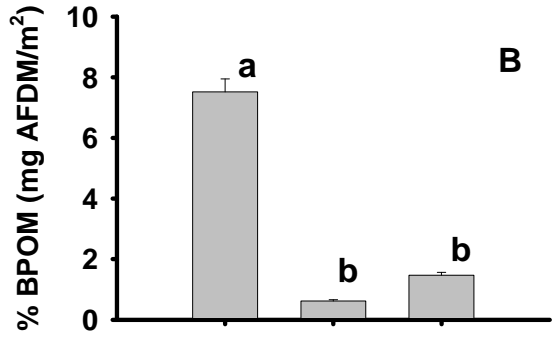
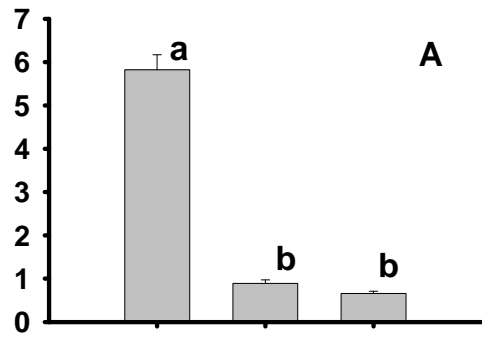


Figure 5.4. Mean (\pm 1SE) monthly density (A), biomass (B), and individual size as carapace length (C) of the crayfish *Procambarus versutus* within the 3 study streams.

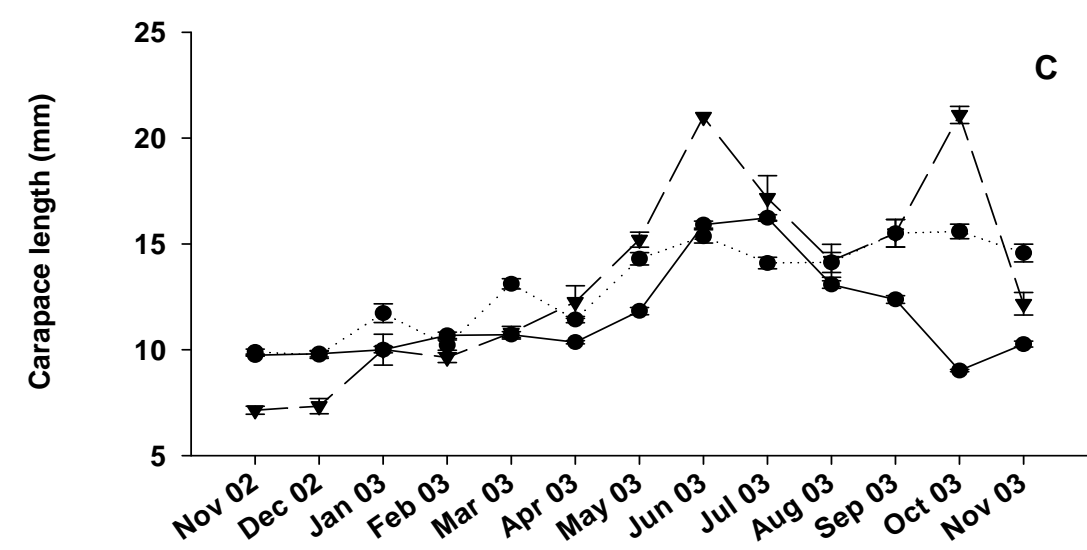
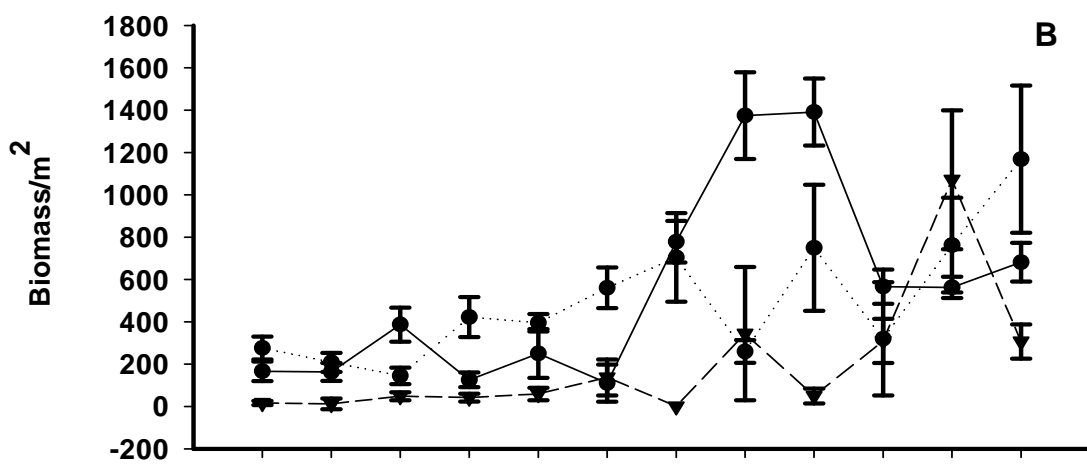
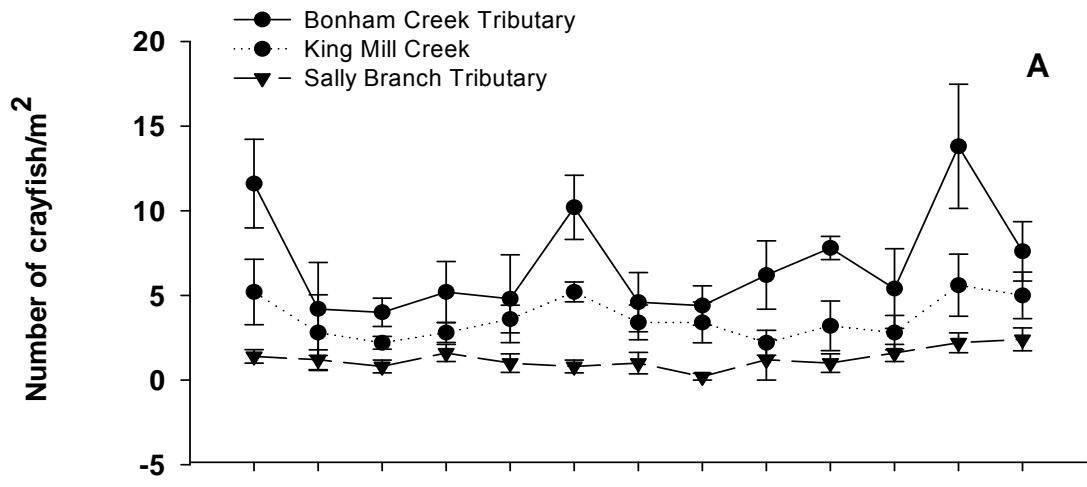


Figure 5.5. Monthly size frequency distribution of the crayfish *Procambarus versutus* within the 3 study streams. Width of each bar represents the percentage of total individuals within each size class.

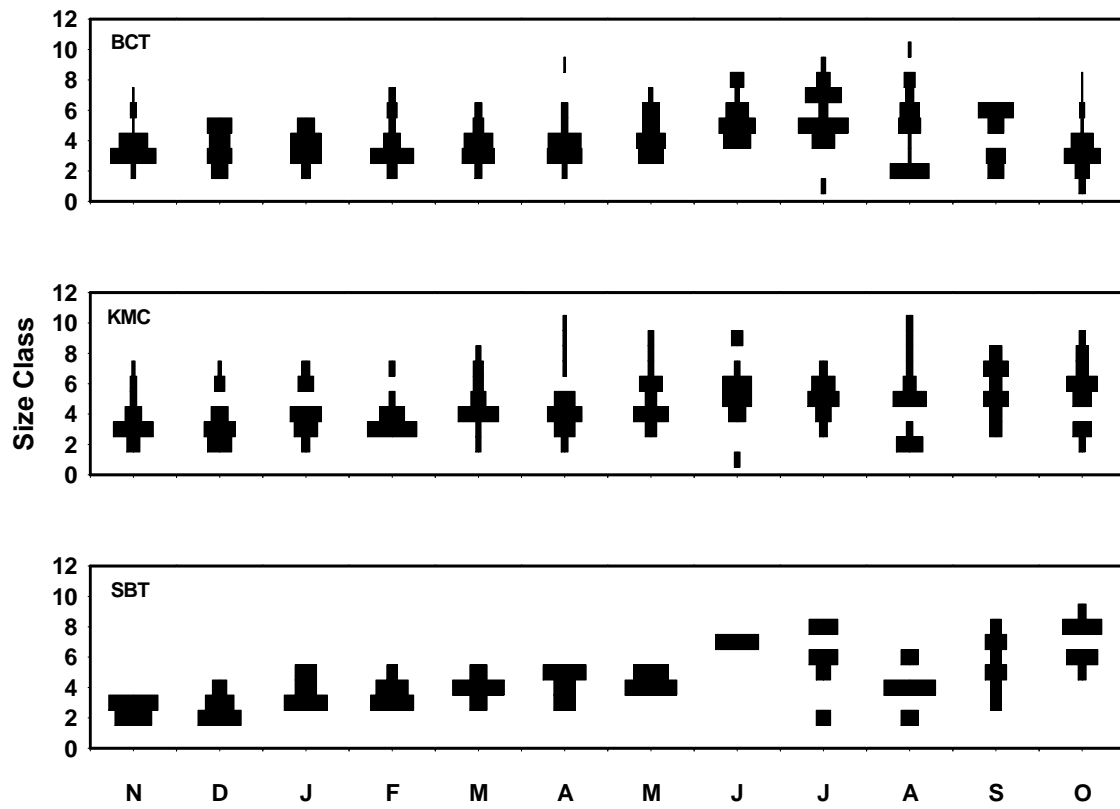


Figure 5.6. Mean (\pm 1SE) annual density and biomass of the crayfish *Procambarus versutus* within the 3 study streams. Differences among streams for annual density and biomass are shown by different letters, such that streams with the same letter are not significantly different (Tukey's pairwise test).

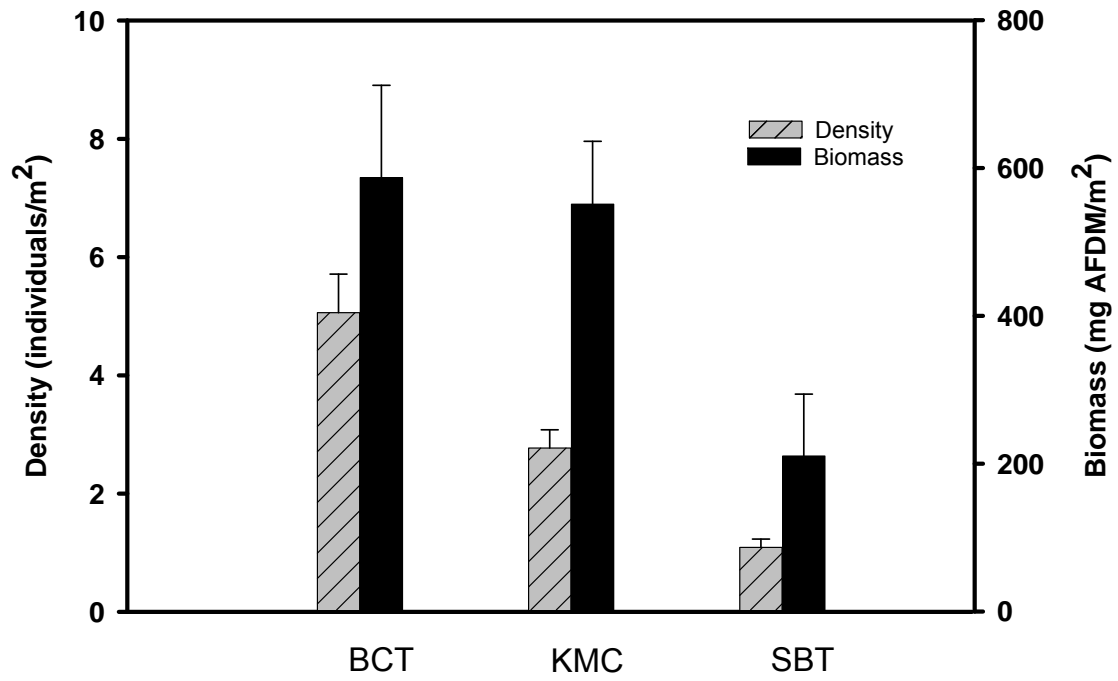


Figure 5.7. Mean (\pm 1SE) diet of the crayfish *Procambarus versutus* within the 3 study streams as % gut-content for 4 gut-content categories. A = BCT (Bonham Creek Tributary), B = KMC (King's Mill Creek), and C = SBT (Sally Branch Tributary).

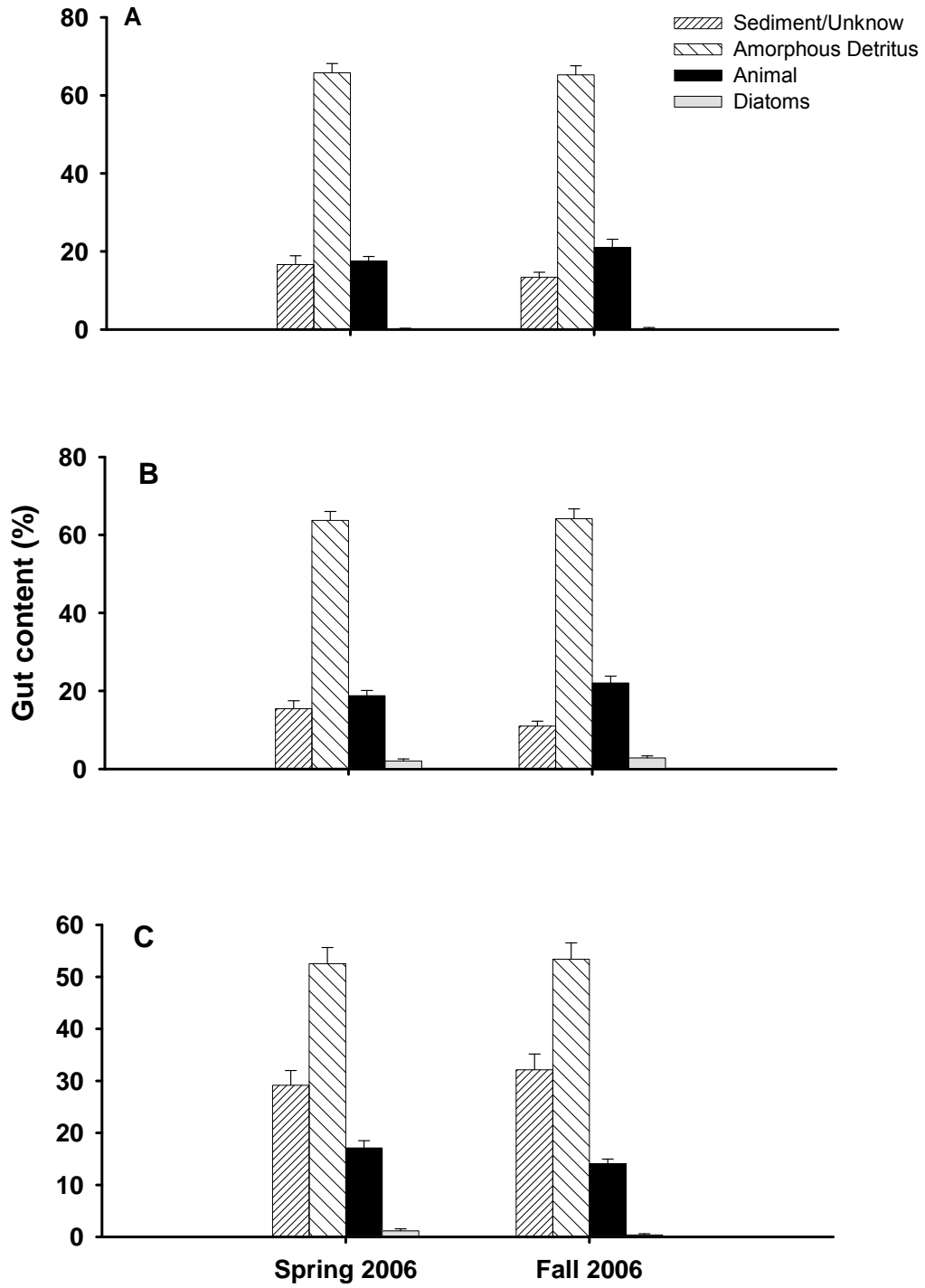


Figure 5.8. Mean transformed % organic content of the diet of the crayfish *Procambarus versutus* within the 3 study streams. Differences between study streams are designated by different letters using Tukey's pair-wise comparisons and treatments with the same letter were not significantly different. A= spring 2006, B = fall 2006.

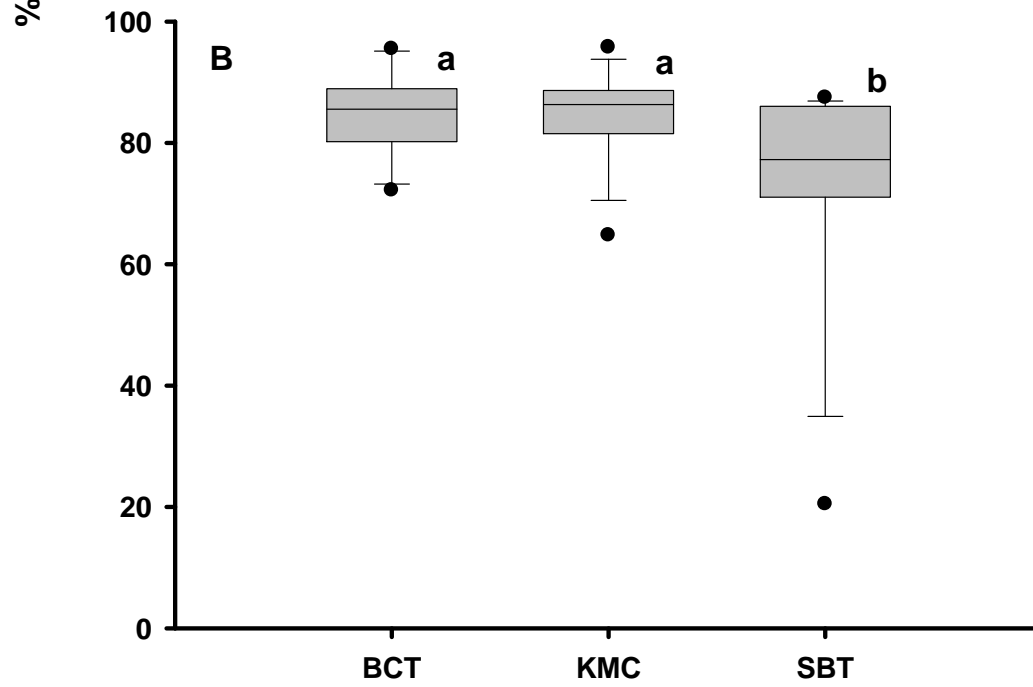
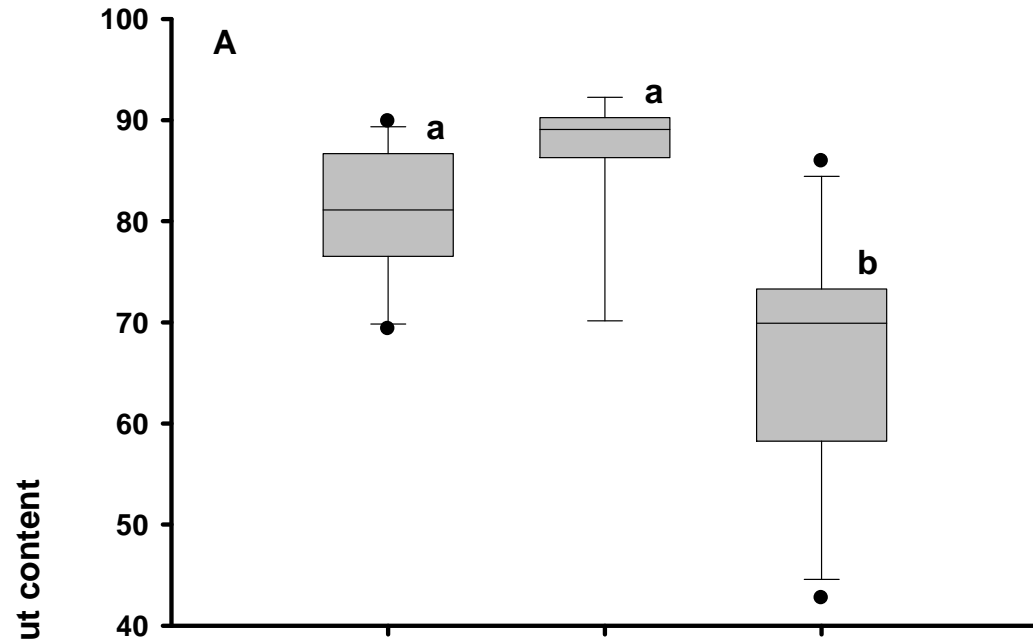


Figure 5.9. Mean (± 1 SE) ^{15}N values for the crayfish *Procambarus versutus* (A) and mean (± 1 SE) crayfish trophic position (B) for fall 2005 and 2006. Within-year differences among study streams are designated by letters above bars such that streams with the same letter within a given year are not significantly different (Tukey's pair-wise test).

