Hydrobiologia (2008) 610:235–244
DOI 10.1007/s10750-008-9438-5

PRIMARY RESEARCH PAPER

Structural complexity of woody debris patches influences fish and macroinvertebrate species richness in a temperate floodplain-river system

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Received: 27 November 2007 / Revised: 2 May 2008 / Accepted: 21 May 2008 / Published online: 10 June 2008

Abstract A field experiment was conducted to examine the influence of variable density (complexity) of small patches of woody debris on the abundance and taxonomic richness of macroinvertebrates and fishes in the Brazos River, a meandering lowland river in east-central Texas. Woody debris patches contained bundles of either 8 or 16 sticks of two sizes, and reference plots contained no woody debris. The experiment was conducted in the littoral zone in the river channel and a nearby oxbow lake. Organisms were collected from each patch after 14 days. Abundance and taxonomic assemblage structure of macroinvertebrates in both the river channel and oxbow were significantly and positively influenced by complexity of woody debris. For fish in the oxbow, abundance and species richness were greater in woody debris than sites lacking structure, but the opposite trend was observed for fish in the river channel. This difference could be associated with isolation from source habitats and low colonization of the constructed woody debris patches in the river by fishes with affinities for complex habitats. Small lotic-adapted minnows were captured from reference habitats in the channel, but these species were rare in woody debris patches. This was in contrast to aquatic insects in the river channel, such as caddisfly and midge larvae, that efficiently colonized the small isolated patches of woody debris. In a lotic environment, woody debris provides vertical surfaces that intercept drifting insect larvae and provides protection from the water current. We speculate that greater abundance of macroinvertebrates in woody debris patches in both habitats results from the combined influence of high food resource availability and refuge from predation provided by structurally complex habitats.

Keywords Benthic · Flow · Habitat heterogeneity · Lentic · Lotic · Oxbow lake · Species assemblage

Handling editor: R. Bailey

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Introduction

The structural complexity of habitats is hypothesized to increase the diversity of local species assemblages according to several potential mechanisms. Greater levels of physical complexity in habitats create barriers to movement and lines of sight as well as refuges among interstitial spaces that can reduce animal encounter rates and the intensity of interference competition (Petren & Case, 1995; Sundland & Näslund, 1998) and predator–prey interactions (Beukers & Jones, 1997; Hixon & Beets, 1993; Huffaker, 1958; Janssen et al., 2007; Persson & Eklov, 1995). Greater physical complexity provides more diverse substrates, resource states, and foraging opportunities (MacArthur, 1970; Petren & Case, 1995; Sarty et al., 2006). Greater three-dimensional complexity also can mediate extreme levels of certain abiotic factors, such as wind or water velocity (Boström & Bonsdorff, 2000; Wallace et al., 1995). Several empirical studies have demonstrated greater levels of species density (number of species per unit area) or richness (number of species per sampling unit) in habitats with higher structural complexity in marine (e.g., Lingo & Szedlmayer, 2006) and freshwater (e.g., Wright & Flecker, 2004) systems.

The richness and structure of fish and macroinvertebrate assemblages in streams and rivers are strongly associated with local habitat characteristics, with spatial heterogeneity and structural complexity among the most prominent aspects (Angermeier & Karr, 1984; Brown & Warburton, 1997; Brooks et al., 2004; Scott & Angermeier, 1998; Shields et al., 2006; Willis et al., 2005). In aquatic ecosystems, woody debris enhances habitat structural complexity and is used as cover by macroinvertebrates and fishes (Arrington et al., 2005; Hrodey & Sutton, 2008; O'Connor, 1991). Woody debris also provides important hard substrate for colonization by algae, microorganisms, and invertebrates that are food resources for macroinvertebrates and fishes (Angermeier & Karr, 1984; Benke et al., 1985; Crook & Robertson, 1999; Smock et al., 1989). Studies revealing positive associations between species richness and the density or complexity of woody debris in fluvial systems usually have investigated intermediate or large spatial scales (Angermeier & Winston, 1998; Evans & Norris, 1997; Gerhard & Reich, 2000; Inoue & Nakano, 1998; Palmer et al., 1996; Wright & Flecker, 2004). In a study examining fish–habitat relationships at the patch scale, Willis et al. (2005) showed that species density and morphological diversity in littoral habitats of a tropical floodplain river were positively correlated with habitat complexity and negatively correlated with flow velocity.

In the present study, we manipulated patches of woody debris in the littoral zone of a temperate floodplain river and associated oxbow lake to examine responses of biota to variation in structural complexity at a small spatial scale. We examined responses by both fishes and macroinvertebrates and compared patterns in lotic (river channel) and lentic (oxbow) habitats of a lowland river ecosystem. We hypothesized that the abundance and richness of both fishes and macroinvertebrates would be positively associated with structural complexity in both habitats.

Methods

Study site

We sampled fishes and macroinvertebrates within a 200-m section of the lower Brazos River (30°37′42″ N; 96°32′49″ W) and in Moehlman's Slough oxbow (30°36′53″ N; 96°31′36″ W) near the Brazos–Burleson County line in southeastern Texas. The Brazos River arises in northeastern New Mexico and flows across Texas in a southeasterly direction before entering the Gulf of Mexico 2 km south of the city of Freeport. The catchment area of the Brazos River is approximately 120,000 km^2. The period of highest average monthly discharge is late fall through spring, but high flow pulses can occur during any time of the year (Winemiller, 1996). Moehlman's Slough contains high fish biomass and is recorded to have high richness and diversity of fish species compared to other oxbows along the middle and lower reaches of the Brazos River where the gradient is low and the channel meanders strongly (for detailed descriptions of these habitats and biological communities, see Winemiller et al., 2000 and Zeug et al., 2005). Seine samples from littoral habitats of river channel reveal a fish fauna strongly dominated by minnows (Cyprinidae), with catfishes (Ictaluridae), gars (Lepisosteidae), sunfishes (Centrarchidae), and darters (Percidae) also common (Winemiller et al., 2000; Zeug et al., 2005). The fish fauna of Moehlman's Slough is dominated by sunfishes, shad (Clupeidae), mosquitofish (Poeciliidae), minnows, silversides (Atherinidae), suckers (Catostomidae), and catfishes. The overall density of fishes in the oxbow lake is much higher than that in littoral habitats of the river channel (Winemiller et al., 2000).

The aquatic macroinvertebrate fauna of the Brazos River channel is dominated by mussels (Corbiculidae), mayflies (Baetidae, Caenidae, Heptageniidae), dragonflies (Gomphidae, Aeshnidae, Macromiidae), water boatmen (Corixidae), caddisflies (Hydropsychidae), and midges (Chironomidae) (Lanza, 2003). The aquatic macroinvertebrate fauna of Moehlman's Slough is dominated by snails (Physidae), amphipods (Hyalellidae), mayflies (Caenidae), dragonflies (Gomphidae, Libellulidae), damselflies (Coenagrionidae), waterboatmen (Corixidae), water treaders (Mesoveliidae), beetles (Haliplidae, Hydrophilidae), and midges (Chironomidae) (Lanza, 2003). In Lanza's (2003) survey, Shannon's species diversity values for aquatic macroinvertebrates were similar for the Brazos River channel and Moehlman's Slough (3.8 and 3.7, respectively) despite that fact that species composition was different, with some shared taxa and others unique to either the lotic or lentic habitat.

Experimental procedures

We collected woody debris (sticks) submerged in Moehlman's Slough oxbow and used this material to construct 40 small woody debris patches with a low or high level of complexity. Sticks were first sorted into two groups based on diameters (1–1.5 and 3–4 cm), and then all were cut to a uniform length of 40 cm (Fig. 1). Sticks with intact bark were stored underwater near the shoreline of a local pond to maintain their condition as submerged woody debris. On November 17, 2005, we created 20 woody debris patches (10 low-density + 10 high-density) that were spaced 4 m apart in both the Brazos River and Moehlman's Slough (40 total patches). Sites for placement of bundles within the river and oxbow were selected based on accessibility and appropriate water depth within the littoral zone along the western river bank and lake shoreline (Fig. 1). Woody debris patches were constructed by driving unwashed, conditioned sticks into the substrate to a depth of approximately 5 cm and positioning them into bundles shaped like an inverted funnel ("teepee"). The oxbow substrate was dominated by clay with overlying silt, and the substrate at the river channel site was sand with overlying silt. Each bundle was secured near the top with a thin metal wire. Low-density (low complexity) patches had 8 sticks (4 small diameter [1–1.5 cm] + 4 large diameter [3–4 cm]), and high density (high complexity) patches contained 16 sticks (8 small diameter + 8 large diameter). To facilitate detection, each bundle was marked with a surveyor's flag attached to a stiff wire that was anchored in the sediment (Fig. 1). All bundles had gaps between the sticks that ranged up to 15 cm, which allowed fishes to enter inside. Within each habitat, the low-density and high-density patches were alternated in a linear array that followed the 40–50 cm depth contour parallel to the west

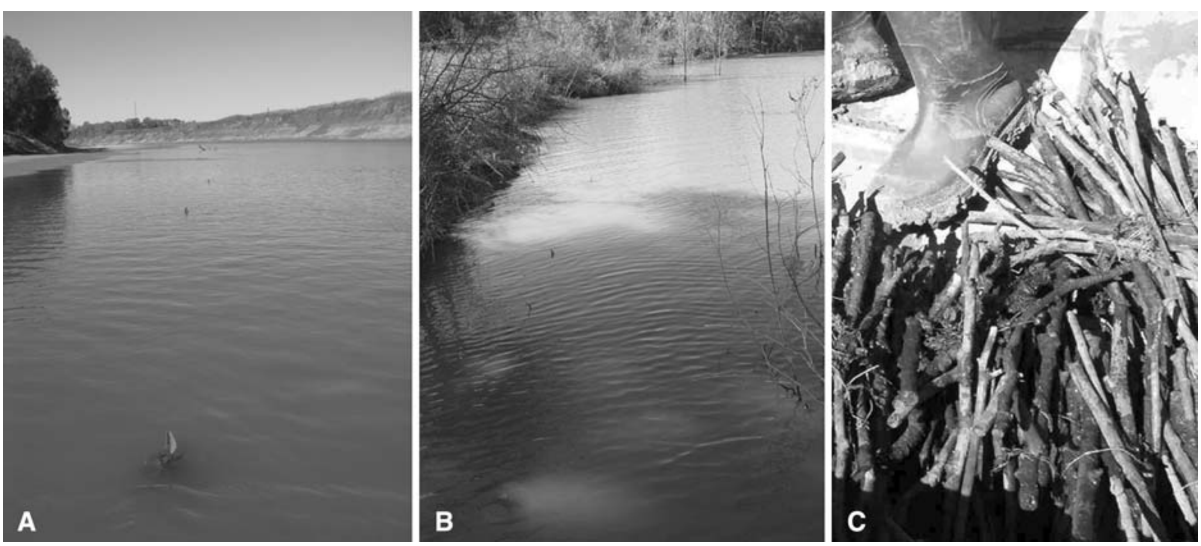

Fig. 1 Photographs of the habitats in which woody debris patches were placed in arrays within the littoral zone: (**A**) main channel of the Brazos River; (**B**) Moehlman's Slough (oxbow); (**C**) conditioned sticks prior to placement into bundles arrayed along the bank of the Brazos River

shoreline. Reference sites were plots of unmanipulated substrate located halfway between adjacent low- and high-density bundles in each of the two arrays. There was no aquatic vegetation in the river channel, but a few emergent willows (*Salix nigra*) were near the area where the bundles were placed in the oxbow (Fig. 1). The slope of the channel was nearly horizontal in the littoral habitats where the arrays were positioned; thus, there was no abrupt transition to deep-water habitats. There was no flow in the oxbow habitat, but flow in the Brazos River channel was 0.26 m/s in the littoral zone where experimental patches were located.

All woody patches and reference sites were surveyed 14 days later. Discharge in the Brazos River at the site was 21.9 m^3 s^{-1} at the start of the experiment and 16.85 m^3 s^{-1} at the end. Discharge ranged from 14.6 to 23.9 m^3 s^{-1} during the 14-day interval. The peak discharge occurred on day 12 of the experiment, and on day 14 woody debris patches in the river channel were at depths of 52–72 cm. Water level in the oxbow lake was unchanged, and no over-bank flooding occurred during the experiment.

Patches and reference sites were sampled by slowly approaching on foot and then quickly sealing off the area by dropping a 189-l plastic barrel with both ends open. This manual drop sampler technique is highly effective for collecting relatively sedentary aquatic macroinvertebrates and fishes that have affinity for cover, such as sunfishes, catfishes, and darters. Fast swimming fishes, such as minnows and suckers, were probably sampled less effectively; however, it may be assumed that whenever these large fishes flee into cover, they are vulnerable to the drop sampler as well. After the area was sealed by the barrel, sticks were removed and examined for macroinvertebrates while held over a large dipnet (mesh 3 mm). Invertebrates were placed into labeled plastic bags containing 10% formalin with rose-bengal solution. Once all sticks had been removed and examined, the water within the barrel was swept with dipnets of two different mesh sizes (1 and 3 mm), and fishes and macroinvertebrates were removed and placed in labeled plastic bags. Dipnet sweeps were continued for several minutes until three consecutive sweeps yielded no specimens. Temperature, conductivity, and dissolved oxygen (DO) were measured with a YSI 85 multiparameter meter, and flow was measured in the river channel with a Marsh-McBirney digital flowmeter. Temperature was 16.7°C in the oxbow and 17.9°C in the river; conductivity was 420 μS in the oxbow and 1,800 μS in the river, and both sites had saturated DO (>8 mg/l).

In the laboratory, fishes and macroinvertebrates from each experimental and reference plot were sorted, identified, and counted. Invertebrates were identified to family using characters described in Pennack (1978) and Peckarsky et al. (1990), and fishes were identified to species using keys and illustrations in Page and Burr (1991).

Data analysis

We used a 3 × 2 ANOVA to examine the main effects of patch complexity (reference [0 sticks], low-density [8 sticks], high-density [16 sticks]), habitat (river channel, oxbow), and the interaction between these two independent variables on dependent variables. Four dependent variables were examined: number of fish species, abundance of fish, number of macroinvertebrate families, and abundance of macroinvertebrates. Normal Q–Q plots of standardized residuals indicated that distributions of raw data for the dependent variables were significantly different ($P < 0.05$) from a normal distribution. Hence, dependent variables were logarithmically transformed to reduce skew in the distributions. Post hoc, pairwise comparisons of mean values for treatments were conducted using Tukey's test. Correlation between macroinvertebrate abundance and fish abundance in woody debris patches was evaluated with Pearson's product–moment correlation. Statistical tests were performed using SPSS (2004).

Results

Fish and invertebrate abundance and taxonomic richness were significantly associated with the complexity of patches (0, 8, or 16 sticks) in both lotic and lentic habitats (Fig. 2, Table 1). There was a significant interaction ($P < 0.05$) between the two independent variables (complexity of woody debris and habitat type) for both fish abundance and taxonomic richness data. There was no significant interaction for macroinvertebrate abundance and taxonomic richness data (Table 1).

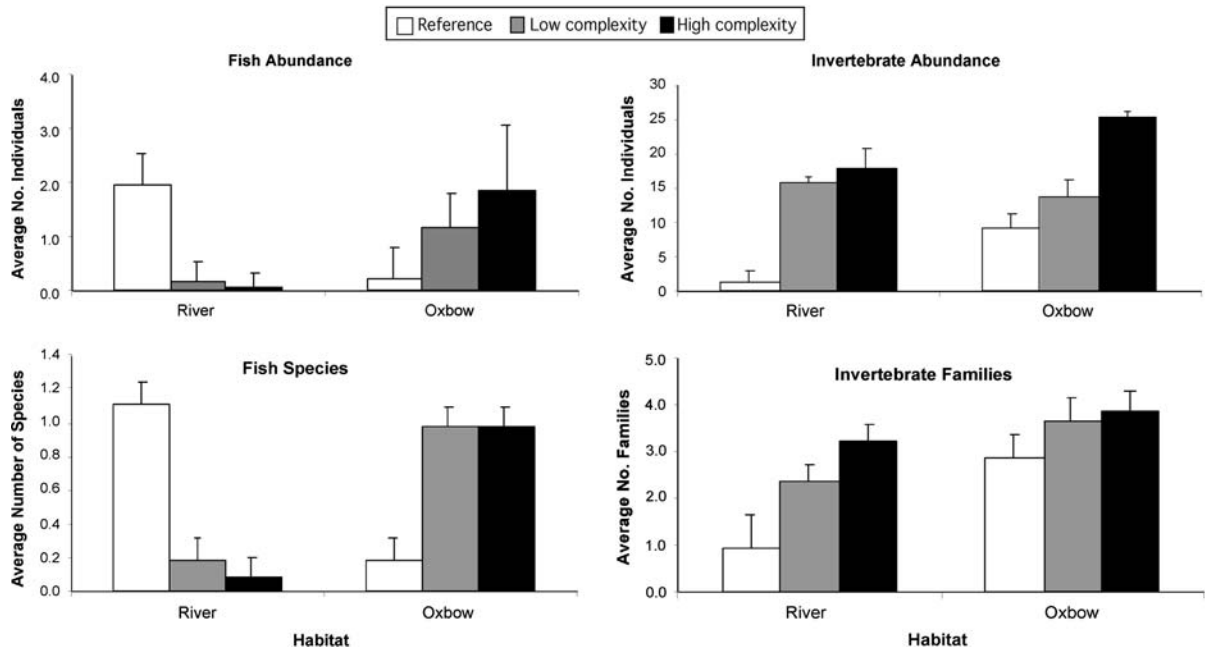

Fig. 2 Mean numerical abundances and species richness of fishes and family richness of macroinvertebrates (error bars = 1 SD) in relation to three levels of structural complexity of woody debris patches (open bar = no sticks added; gray bar = 8 sticks; black bar = 16 sticks) in two habitat types (river channel versus oxbow lake) of the middle Brazos River

Table 1 ANOVA results for effects of habitat and level of complexity of woody debris patches on fish and macroinvertebrate abundance and taxonomic richness

Dependent variable	Independent variable	*F*	df	*P*
Fish abundance	Habitat type	3.022	1	0.089
	Complexity level	0.527	2	0.594
	Interaction	16.053	2	<0.0001
Macroinvertebrate abundance	Habitat type	3.908	1	0.054
	Complexity level	10.315	2	<0.0001
	Interaction	2.817	2	0.070
Fish species richness	Habitat type	3.293	1	0.076
	Complexity level	0.239	2	0.789
	Interaction	14.141	2	<0.0001
Macroinvertebrate family richness	Habitat type	13.279	1	0.001
	Complexity level	7.606	2	0.001
	Interaction	2.370	2	0.105

Abundance

Overall, fish numerical abundance was not significantly different in the two habitat types. Fish abundance was greater with higher levels of habitat complexity in the oxbow habitat, but the reverse pattern was observed in the river channel (Fig. 2). When analyzed separately according to habitat, these fish abundance–habitat complexity patterns were statistically significant ($P < 0.05$). In the river channel, the average abundance of fish captured from reference plots lacking structure (approximately 2 individuals/patch) was significantly greater than the average abundance from patches with woody debris at either high or low levels of habitat complexity (much less than 1 individual/patch in each case). The oxbow revealed greater fish abundance in patches with greater habitat complexity, with an average of just over 1 individual/patch for low complexity and an average of nearly 2 individuals/patch for high complexity.

Macroinvertebrate numerical abundance was not significantly different in the two habitats overall and was significantly affected by the amount of woody debris in local patches within both habitats (Table 1). Mean invertebrate abundance was greater in patches with greater structural complexity within both habitats (Fig. 2). In the river, the difference between average macroinvertebrate abundance in complex patches versus reference patches was nearly 10-fold. In the oxbow, the high complexity patches had an average macroinvertebrate abundance that was twice that of the reference patches.

Taxonomic richness

Fish species richness in habitat patches was not significantly different between the two habitat types (Table 1), but there were differences in species composition. The oxbow samples were strongly dominated by *Lepomis* species, especially *L. macrochirus* and *L. megalotis* (these two species comprised 84% of 45 fish specimens captured from the oxbow), and the river channel samples were dominated by minnows (*Cyprinella lutrensis* [16 specimens], *Pimephales vigilax* [3], and *Macrhybopsis hyastoma* [1]). A single specimen of the ghost shiner, *Notropis buchanani*, was captured from the oxbow, and a single specimen of the dusky darter, *Percina sciera*, was captured from the river channel. The significant interaction effect between habitat type and complexity level resulted from opposite patterns of fish species richness in relation to habitat complexity within the two habitats. Species richness data showed the same pattern that was observed for fish abundance data: a positive association with complexity in the oxbow and the reverse pattern in the river channel (Fig. 2). When analyzed separately according to habitat, these differences were statistically significant ($P < 0.05$). In the river channel, the average species richness of fishes captured from reference plots lacking structure was more than fivefold greater than the average number captured from patches with woody debris at either high or low levels of complexity (Tukey's post hoc test, $P < 0.05$). The reverse pattern was observed in the oxbow where average species richness of fishes was five times greater in complex patches relative to the reference patches, with no difference in the mean species richness of fishes in the low versus high complexity patches.

Overall, macroinvertebrate family richness in habitat patches tended to be greater in the oxbow than the river channel, and richness tended to be greater within more complex habitat patches in both habitat types (Table 1, Fig. 2). The dominant taxon in the oxbow was the grass shrimp, *Palaemonetes kadiakensis* (Palaemonidae), followed by mayflies (Caenidae), midges (Chironomidae), dragonflies (Aeshnidae, Gomphidae, Libellulidae, Macromiidae), damselflies (Coenagrionidae), waterboatmen (Corixidae), and beetles (Halipidae). In the river channel, the dominant taxa were midges (264 specimens) and caddisflies (Hydropsychidae, 210 specimens), almost all of which were taken from the woody debris patches. In the river, there was significantly greater family richness in patches with greater structural complexity (reference < low complexity < high complexity; Tukey's test; $P < 0.05$). In the oxbow, invertebrate family richness was lower in the reference plots than the patches with woody debris, but family richness in the low versus high complexity patches was not significantly different.

Correlation between macroinvertebrate and fish abundance

In the oxbow, the correlation between fish total abundance and macroinvertebrate total abundance in woody debris patches (including both low and high density samples) was 0.16 (Pearson's correlation, $df = 19$, $P < 0.01$). Too few fishes were captured from woody debris patches in the river to permit examination of correlation between their abundance and that of macroinvertebrates.

Discussion

Small patches of woody debris were associated with greater abundance and diversity of macroinvertebrates in shallow habitats within both the Brazos

River channel and an associated oxbow, and with greater abundance and diversity of fishes in the oxbow habitat but not in the river channel. For many species of fishes and invertebrates, woody debris provides important microhabitats where they encounter food resources and refuge from predators or swift water currents (Angermeier & Karr, 1984; Braccia & Batzer, 2001; Crook & Robertson, 1999; Flebbe & Dolloff, 1995; Inoue & Nakano, 1998). Woody debris has been shown to enhance accumulation of organic sediment (Bilby & Likens, 1980; Drury & Kelso, 2000; O'Connor, 1991) and detritus that are food resources for certain aquatic macroinvertebrates (Egglishaw, 1969; González & Graça, 2005). The high densities of aquatic macroinvertebrates in woody debris patches, in turn, provide foraging opportunities for invertivorous fishes. Lehtinen et al. (1997) showed that insectivorous and piscivorous fishes were more abundant in snags than open water reference sites in channel and backwater habitats of the upper Mississippi River. They inferred that these fishes were attracted to woody debris due to higher prey availability compared to surrounding habitats. In their study, the densities of detritivorous and omnivorous fishes were not significantly greater in woody debris habitats.

In Moehlman's Slough, all except one of the fishes taken from woody debris patches were sunfishes (*Lepomis cyanellus, L. gulosus, L. macrochirus,* and *L. megalotis*), and most of these were juvenile size classes that are strongly invertivorous. The three species taken from woody debris patches in the Brazos River channel were invertivores (dusky darter, *Percina sciera*) and omnivores (red shiner, *Cyprinella lutrensis*, and bullhead minnow, *Pimephales vigilax*). Dusky darters tend to be associated with cover, whereas the latter two species are common in open habitats and were more abundant in the reference patches than wood bundles placed within the river channel. Sunfishes are common in the Brazos River channel, but not in open stretches lacking woody debris like the reach where our experiment was conducted.

In addition to providing more foraging opportunities, woody debris also provides prey species with cover from predators. Many sight-oriented predators experience decreased hunting success in structurally complex habitats (Beukers & Jones, 1997; Gotceitas, 1990; Savino & Stein, 1982), and prey may adjust their habitat use according to perceived predation risk (Brown & Warburton, 1997; Everett & Ruiz, 1993; Vince et al., 1976). Woody debris may act as a refuge from predators by reducing visual contact between individuals (Everett & Ruiz, 1993; Minello & Zimmerman, 1983) and by providing shelter from predators too large to enter small interstitial spaces (Brown & Warburton, 1997; Crook & Robertson, 1999; Johnson et al., 1988). In addition to reducing predation, physical habitat complexity could moderate the intensity of competitive interactions and allow more individuals to occupy an area. In a tropical floodplain river, ecomorphological diversity of fishes was greater in local assemblages occupying littoral zone habitats with higher levels of structural complexity (Willis et al., 2005). This pattern was inferred to be a response to interspecific competition and predation.

Substrate characteristics and water velocity affect the distribution and abundance of fishes and invertebrates in fluvial ecosystems (Poff et al., 1997; Shields et al., 2006; Thorp et al., 2006). In rivers and streams, woody debris provides solid vertical substrates that intercept drifting macroinvertebrates and onto which they can colonize (Johnson et al., 2003). This colonization aspect probably accounted for the higher abundance of aquatic insects, particularly net-spinning caddisfly larvae (Hydropsychidae), on woody debris patches in the Brazos River. More than 90% of all macroinvertebrates on woody debris patches in the channel were net-spinning caddisflies and chironomid larvae, groups that can move large distances by drifting. In contrast, most of the macroinvertebrates on woody debris patches in the oxbow were Odonota nymphs that colonized by crawling. Only two net-spinning caddisflies were captured from the oxbow lake, and their low abundance was likely due to the lack of water current for foraging and dispersal. Woody debris in rivers and streams also creates microhabitats that are sheltered from strong current (Drury & Kelso, 2000; McMahon & Hartman, 1989; Scott & Angermeier, 1998) and may enable fishes and macroinvertebrates to reduce energetic costs (Crook & Robertson, 1999).

Within the channel of the Brazos River, fish abundance and diversity were higher in unstructured reference patches than patches containing woody debris over sandy-bottom habitats—a pattern that was opposite to that observed in the lentic oxbow. The fish species captured in the river channel were small, lotic-adapted cyprinids. The red shiner and bullhead minnow are the two most abundant (in terms of numbers of individuals) fish species in the Brazos River channel (Winemiller et al., 2000; Zeug et al., 2005). These fishes are most abundant in open shallow habitats with slow to moderate current velocities and thus were captured in low abundance in our reference survey plots that lacked woody debris patches. These species may have avoided isolated patches of woody debris (one individual of each species captured). Again, the only other fish species captured from the woody debris patches in the river channel was the dusky darter.

The composition and structure of fish species assemblages in woody debris in streams and rivers have been observed to vary in association with flow and proximity to source habitats (Angermeier & Karr, 1984; Arrington et al., 2005). Sunfishes, darters, juvenile catfishes, and other fish taxa often associated with woody debris were not captured in our channel patch samples, and this could have been due to the isolation of the constructed patches relative to large natural woody debris patches in the river. There were very few natural snags in the channel within the reach where the experimental plots were located. We speculate that more sunfishes and perhaps other species with affinities for structurally complex habitats would colonize woody debris patches placed in closer proximity to large natural snags in the river. Moreover, the moderate current velocity in our experimental channel reach probably negatively affected colonization by sunfishes and other lentic-adapted fishes.

In summary, our field experiment demonstrated that abundance and taxonomic richness of macroinvertebrates in both the river channel and oxbow were significantly and positively influenced by the complexity (density) of woody debris patches. This response likely reflects enhanced food resources and refuge from predation provided by structurally complex habitat. Moreover, the vertical structure of the woody debris probably enhanced colonization by insect larvae that drift with the current and also could have created microhabitats with lower water currents. Caddisfly and midge larvae efficiently colonized the small isolated patches of woody debris via passive drifting within the current. Odonata, which dominated the taxonomic diversity of macroinvertebrates on woody debris patches in the oxbow, was uncommon on woody debris patches in the river channel, possibly due to low rates of active movement from natural snags in the river. Fish response to the complexity of woody debris patches was strongly dependent on habitat type. In the oxbow, fish abundance and species richness were greater in woody debris than sites lacking structure, but the opposite trend was observed in the river channel. This difference might be explained by the isolation of the constructed woody debris patches relative to natural snags in the river. Small lotic-adapted minnows were captured from unstructured reference patches in the channel, but these species may have avoided woody debris patches.

Conclusions

Our experimental manipulation of small patches of woody debris in lotic and off-channel lentic habitats in the Brazos River revealed habitat-specific patterns for fishes but not macroinvertebrates. The taxonomic richness and abundance of macroinvertebrates always were greater in woody debris than reference sites. Results suggest that fishes do not rapidly colonize small, isolated patches of wood in shallow, flowing stretches of large floodplain rivers. In fact, channel areas with wood patches had fewer fish than reference sites lacking vertical structures. This contrasts with results from the oxbow lake in this study and with other research conducted in pool habitats of streams where fishes were strongly associated with woody debris (e.g., Angermeier & Karr, 1984; Flebbe & Dolloff, 1995; Sundland & Näslund, 1998). We speculate that placement of small woody patches into lentic marginal habitats (backwaters) of the river channel, or near large natural snags in areas with flow, would yield higher fish colonization rates.

Acknowledgments We thank Clint Robertson, Allison Pease, Bibiana Correa, and Jenny Cochran for assistance with fieldwork. We also thank Ellen Toby for assistance with statistical analyses. The research was supported by NSF grant DEB-0089834.

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