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Autumn use of woody snags by fishes in backwater and channel border habitats of a large river

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Synopsis

Snags are important to fish communities in small rivers and streams, but their importance to fishes in large rivers has not been investigated. This study examined snag use by fishes during autumn in backwater and channel border habitats in the upper Mississippi River, and compared these to fish communities in reference sites without snags. Species assemblages differed significantly between backwater and channel border habitats, and between snag and reference sites within the channel border, likely responding to differences in substrate, depth, and current velocity. In both habitats, average fish biomass and abundance were higher (2 to 50 ×) at snag sites than at reference sites, but these differences were significant only for channel border biomass. Fish taxa richness differed between backwater and channel border habitats, but not between snag and reference sites. Most large piscivorous fishes (e.g., *Micropterus* spp., *Stizostedion* spp.), several insectivorous fishes (*Lepomis macrochirus, Ambloplites rupestris, Minytrema melanops*), and a few prey fishes (*L. macrochirus, Notropis atherinoides*) were significantly more abundant at snag sites than at reference sites, suggesting active selection of snags for foraging or protection. Snag quality, as assessed by a snag rating index, had a direct effect on attracting fish communities with greater biomass, especially within the channel border habitat. These results indicate that snags are important habitat for fish communities in both backwaters and channel border habitats of the upper Mississippi River.

Introduction

Submerged fallen trees, or snags, and other forms of woody debris have a strong influence on the quality of food and habitat resources available to fish in a variety of aquatic systems (Angermeier & Karr 1984, Johnson et al. 1988, Van Den Avyle & Petering 1988, Reeves et al. 1993). Fish may use snags as foraging sites (Wallace & Benke 1984, Benke et al. 1985, Van Den Avyle & Petering 1988), as spawning substrates (Van Den Avyle & Petering 1988), as protection from current (Todd & Rabeni 1989), or as camouflage from predators or prey (Angermeier & Karr 1984, Johnson et al. 1988). Woody debris is important to fish in many different systems, including lakes and ponds (Johnson & Stein 1979, Johnson et al. 1988), reservoirs (Van Den Avyle & Petering 1988; but see Moring et al. 1986), and coldwater (Hunt[1, 2], Thorn[3, 4], Reeves et al. 1993) and warmwater (Angermeier & Karr 1984, Todd & Rabeni 1989, Lobb & Orth 1991) streams.

In lotic systems, the significance of snags to fish communities most often has been examined in small and medium-sized streams (Angermeier & Karr 1984, Benke et al. 1985, Todd & Rabeni 1991, Reeves et al. 1993). In streams of this size, snags interact with stream hydraulic processes to influence water depth, current velocity, and substrate composition, thereby enhancing overall habitat diversity (Angermeier & Karr 1984, Bilby & Ward 1991, Reeves et al. 1993). As a result of these important interactions, snags have been found to have a strong influence on fish communities in streams within this size range (Angermeier & Karr 1984, Benke et al. 1985, Todd & Rabeni 1989). However, the impact of snags on the fish communities in larger rivers has been largely ignored (Lobb & Orth 1991, Shields & Smith 1992). Snag removal was a common activity on large, navigable rivers in North America during the 1800s and early 1900s (e.g., Wallace & Benke 1984, Fremling et al. 1989). Although this practice has largely been discontinued, it still is used on smaller waterways to clear snags that either block a portion of the shipping channel or accelerate bank erosion by redirecting current (D. Krumholz, U.S. Army Corps of Engineers, Fountain City personal communication). At the present time, our understanding of large river ecosystems is expanding rapidly (Johnson et al. 1995), and attempts are being made to rehabilitate or restore selected river reaches to some predetermined structure and function (Gore & Shields 1995). The U.S. Army Corps of Engineers currently is incorporating snags into some of its shoreline stabilization and habitat improvement projects within the upper Mississippi River (D. Krumholz personal communication), even though data on snag use by fish in large rivers is lacking. More information on the effects of various types of instream cover on fishes in large rivers is needed so that these restoration projects will produce the proper physical habitat diversity necessary to attract and hold fish communities with good diversity and density (Gore & Shields 1995).

This study was undertaken to evaluate snag habitats and the composition and abundance of the fish communities associated with them in a large river. Snags in backwaters and main channel border habitats in Pool 6 of the upper Mississippi River were examined to accomplish two basic objectives: (1) to examine possible differences in fish community structure, biomass, and abundance among snag and non-snag habitats in backwater and main channel border areas, and (2) to assess what physical variables may be important in predicting the use of snag habitat by fish. This paper will demonstrate that snags provide important fish habitat in both backwater and main channel border areas, and that snag quality is an important factor affecting fish standing stock.

Study area

Pool 6 (44°02′ N, 91°34′ W) of the upper Mississippi River is one of 26 regions delineated by a series of locks and low-head dams constructed to support passage of commercial barge traffic. The pool extends 22.9 km upstream from Lock and Dam 6 (River km 1150.0 upstream from Cairo, Illinois) at Trempealeau, Wisconsin, to Lock and Dam 5A (River km 1172.9) at Winona, Minnesota, U.S.A. Pool elevation is maintained at 196.8 m above sea level. The Mississippi River at Winona has an

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[1] Hunt, R.L. 1988. A compendium of 45 trout stream habitat development evaluations in Wisconsin during 1953–85. Wisconsin Department of Natural Resources Technical Bulletin Number 162. 80 pp.

[2] Hunt, R.L. 1992. Evaluation of trout habitat improvement structures in three high-gradient streams in Wisconsin. Wisconsin Department of Natural Resources Technical Bulletin Number 179. 40 pp.

[3] Thorn, W.C. 1988. Brown trout habitat use in southeastern Minnesota and its relationship to habitat improvement. Minnesota Department of Natural Resources, Fisheries Investigational Report 395. 28 pp.

[4] Thorn, W.C. 1993. Summer habitat requirements of large brown trout in southeastern Minnesota streams. Minnesota Department of Natural Resources, Fisheries Investigational Report 428. 15 pp.

average discharge of 703 m^3 sec^{-1} (range = 71 to 7 595 m^3 sec^{-1}) and drains an area of approximately 153 500 km^2 (Fremling et al.[5]). The upper pool, where this study was conducted, is characterized by braided channels (main channel maintained for barge traffic), forested islands, and a variety of backwater lakes and sloughs, some connected to and others separated from the main channel during base flows. The backwater sites used in this study were located in an area connected to a river side channel by a single, narrow (10 m) low-water passage at the downstream end. The lower pool is primarily lacustrine.

Channel and backwater riparian zones are primarily forested. Eastern cottonwood *Populus deltoides* Marsh, silver maple *Acer saccharinum* L., river birch *Betula nigra* L., willow *Salix* spp., and swamp white oak *Quercus bicolor* Willd. are common shoreline trees that often drop into the river during storm and flood events and become snag habitats. Some riparian zones bordering the main channel have been armored with large rock riprap to protect banks from erosion, whereas others have received deposits of sand dredged from the shipping channel.

Eighty-four species of fish have been collected in Pool 6 (Van Vooren[6]): six species are considered abundant, 30 are common, 22 are collected occasionally, and 26 appear infrequently in collections. Fish standing stock within Pool 6 has been estimated to be between 335 and 900 kg ha^{-1} (Fremling et al.[5]). These fish stocks support both commercial and recreational fishing activities.

Methods

Fish community assessment

Fish sampling was performed during October 1994. Twenty-five sites were sampled in the backwaters and main channel border of Pool 6. All sites were located between River km 1162 and 1170. Twelve snag sites (six backwater, six channel border) and 13 reference sites (six backwater, seven channel border) were sampled. Snag sites consisted of individual snags of varying size (see below), whereas reference sites consisted of similar-sized areas lacking obvious structural elements. All snags sampled remained attached to the shoreline by rootwads. Sites were chosen only in natural shoreline areas, avoiding habitats in proximity to riprap, wing dams, closing dams, and dredge spoil deposits.

Fish collecting was performed exclusively by electrofishing during daylight hours with a Coffelt CPS boomshocker (pulsed DC current, 20 amps at peak output) mounted on a 5.5 m flat-bottom boat. Electrofishing was accomplished by approaching each site perpendicular to the shoreline and maneuvering in and around snags, fishing each site until no more fish appeared. A similar procedure, with a sample area of similar size, was used at reference sites. Ideally we would have liked to isolate each

Table 1. Variables and criteria for quantification of snags. For each variable, ratings ranged from 0 to 4. Total snag score range was 0 (minimum) to 12 (maximum).

Rating value	Variable		
	Number of major branches	Trunk circumference	Roughness
0	0–2	0–40 cm	smooth, no bark
1	3–6	40–80 cm	some bark
2	7–10	80–120 cm	most bark, shallow ridges
3	11–14	120–160 cm	most/all bark, medium ridges
4	15 +	> 160 cm	most/all bark, deep ridges

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[5] Fremling, C.R., D.V. Gray & D.N. Nielsen. 1973. Phase III report: environmental impact study of Pool 6 of the northern section of the upper Mississippi River valley. Winona State College, Winona. 304 pp.

[6] Van Vooren, A. 1983. Distribution and relative abundance of upper Mississippi River fishes. Upper Mississippi River Conservation Committee. 19 pp.

Table 2. Physical characteristics (mean ± SE) of backwater and channel border reference and snag sites in Pool 6 of the upper Mississippi River, October 1994.

Variable	Backwater		Channel border	
	Reference	Snags	Reference	Snags
Depth (m)	0.48 (0.02)	0.78 (0.09)	0.64 (0.03)	1.58 (0.38)
Current velocity (m s^{-1})	0.00 (0.00)	0.00 (0.00)	0.05 (0.02)	0.11 (0.07)
Substrate	silt, detritus	silt, detritus	sand	sand
Water temperature (° C)	all sites combined		14.4 (1.1)	
Flow (m^3 sec^{-1})	–	–	1193 (16)	

area with block nets before sampling, but river currents, irregular bottom contours, and underwater obstacles made this impractical. Our data, therefore, are conservative estimates of the fish actually occupying the habitats sampled. Fish captured by electrofishing were measured to the nearest mm (total length), weighed to the nearest gram (wet weight), identified to species, and released. Questionable specimens were preserved and returned to the laboratory for identification. Electrofishing time (sec) was recorded for each site for use in catch-per-effort (CPE) estimates.

We determined total fish abundance and biomass, CPE (both numbers and biomass), and species richness at each individual site. Bray-Curtis community similarity tests were used to examine the relative similarities of fish communities in the various habitats.

Habitat assessment

A snag rating index was devised to quantify snags according to their potential attractiveness (i.e., quality) as fish habitat. Snag quality was determined by assigning each of three snag characteristics (number of major branches, trunk circumference within 2 m of rootwad, bark presence/roughness) a numerical score ranging from 0 to 4 (Table 1), and totaling the scores. Larger snags with more branches and intact,

Table 3. Snag characteristics and snag rating index scoring (in parentheses) of backwater and channel border snags in Pool 6 of the upper Mississippi River, October 1994.

Habitat	Variable			Total snag score
	Number of major branches	Trunk circumference (cm)	Roughness	
Channel border				
Snag 1	9 (2)	60 (1)	medium, all bark (3)	6
Snag 2	8 (2)	96 (2)	medium, most bark (3)	7
Snag 3	17 (4)	123 (3)	deep, all bark (4)	11
Snag 4	5 (1)	168 (4)	deep, most bark (4)	9
Snag 5	10 (2)	145 (3)	medium/deep, all bark (4)	9
Snag 6	15 (4)	175 (4)	deep, most bark (4)	12
Backwater				
Snag 1	2 (0)	57 (1)	shallow, some bark (1)	2
Snag 2	16 (4)	151 (3)	medium, most bark (3)	10
Snag 3	10 (2)	79 (1)	shallow, all bark (2)	5
Snag 4	20 (4)	177 (4)	deep, some bark (3)	11
Snag 5	21 (4)	224 (4)	deep, some bark (3)	11
Snag 6	11 (3)	86 (2)	shallow, some bark (1)	6

deeply grooved bark were assumed to provide fish with the best habitat because of their potential for modifying currents, providing shade and protection, and presenting a greater surface area for invertebrate colonization. Hence, this type of snag received a higher score than did a smaller snag with fewer branches and less or smoother bark. Possible snag score ranged from a minimum of 0 (low-quality snag) to a maximum of 12 (high-quality snag). Linear regression analyses were performed on snag rating score versus total fish abundance and total fish biomass to determine whether snag rating score was a significant factor in predicting fish numbers and biomass associated with snags.

Additional physical data also were collected at each site. These included substrate type, water temperature (° C), current velocity (m sec^{-1}), and depth (m). All physical variables were measured approximately 2–3 m from shore at each site. Substrate types were classified in the field on the basis of tactile and visual inspection. Temperature was measured with a TRW digital thermometer, and current velocity was measured at 0.6 depth with a Gurley pygmy current velocity meter to yield an average value for the entire water column.

Table 4. Common and scientific names of fish collected in Pool 6 of the upper Mississippi River, October 1994.

Family/ common name	Scientific name
Petromyzontidae	
silver lamprey	*Ichthyomyzon unicuspis* Hubbs & Trautman
Clupeidae	
gizzard shad	*Dorosoma cepedianum* (Lesueur)
Esocidae	
northern pike	*Esox lucius* Linnaeus
Cyprinidae	
common carp	*Cyprinus carpio* Linnaeus
emerald shiner	*Notropis atherinoides* Rafinesque
Catostomidae	
shorthead redhorse	*Moxostoma macrolepidotum* (Lesueur)
smallmouth buffalo	*Ictiobus bubalus* (Rafinesque)
bigmouth buffalo	*Ictiobus cyprinellus* (Valenciennes)
quillback	*Carpiodes cyprinus* (Lesueur)
spotted sucker	*Minytrema melanops* (Rafinesque)
Moronidae	
white bass	*Morone chrysops* (Rafinesque)
Centrarchidae	
rock bass	*Ambloplites rupestris* (Rafinesque)
bluegill	*Lepomis macrochirus* Rafinesque
green sunfish	*Lepomis cyanellus* Rafinesque
pumpkinseed	*Lepomis gibbosus* (Linnaeus)
largemouth bass	*Micropterus salmoides* (Lacepède)
smallmouth bass	*Micropterus dolomieu* Lacepède
black crappie	*Pomoxis nigromaculatus* (Lesueur)
Percidae	
yellow perch	*Perca flavescens* (Mitchill)
walleye	*Stizostedion vitreum* (Mitchill)
sauger	*Stizostedion canadense* (Smith)
logperch	*Percina caprodes* (Rafinesque)
mud darter	*Etheostoma asprigene* (Forbes)
Sciaenidae	
freshwater drum	*Aplodinotus grunniens* Rafinesque

Statistical analyses

Various statistical analyses were used to compare physical and fish community variables between backwater and channel border habitats, and between snag and reference sites. When data sets met normality and variance homogeneity assumptions, analysis of variance (ANOVA) and t-tests were used to test for possible differences among habitats and sites. When data were not normally distributed or did not exhibit variance homogeneity, nonparametric tests (Kruskal-Wallis test, Wilcoxon two-sample rank sum test) were used. Chi-square tests were used to assess individual fish species distribution patterns (numbers of individuals) among snag and reference habitats. Simple linear regression was used to examine relationships between snag rating index scores and corresponding fish biomass and abundance measures.

Results

Physical variables

Current velocities were significantly different among the backwater and main channel habitats ($p = 0.001$, Kruskal-Wallis test). No current was detected at any of the backwater sites, whereas velocities at channel border sites averaged slightly less than 0.1 m sec^{-1} (Table 2). Velocities did not differ between channel border snag and reference sites

($p > 0.10$, Wilcoxon two-sample rank sum test). Depths also differed significantly among habitats ($p < 0.001$, Kruskal-Wallis test), with the areas associated with snags being deeper than reference areas ($p < 0.01$ and $p < 0.05$ [Wilcoxon two-sample rank sum test] for channel border and backwater sites, respectively). Temperature and river discharge were relatively constant throughout the study period. Substrates at all backwater sites were comprised of mixtures of silt and detritus, whereas channel border sites were comprised largely of sand, with only sporadic occurrences of cobble, silt, and detritus.

Snags sampled in channel border habitats were identified as fallen cottonwood and willow. Backwater snags consisted of silver maple, swamp white oak, and river birch. Channel border snags generally were oriented pointing diagonally away from shore and downstream, whereas backwater snags exhibited no common orientation. The snag rating index produced snag scores ranging from 2 to 12 (Table 3). Average snag score was 9.0 in the channel border and 7.5 in the backwaters, but this difference was not significant ($p = 0.42$, t-test).

Fish communities

Altogether, 455 fishes were collected by electrofish-

Table 5. Numbers of fish collected at reference and snag sites in Pool 6 of the upper Mississippi River, October 1994. Species are grouped according to backwater versus channel border distribution patterns.

Species	Backwater		Channel border		Total
	Reference	Snags	Reference	Snag	
Backwater sites only					
northern pike	2	–	–	–	2
spotted sucker	–	6	–	–	6
bluegill	18	64	–	–	82
green sunfish	–	1	–	–	1
pumpkinseed	1	2	–	–	3
largemouth bass	19	19	–	–	38
black crappie	1	3	–	–	4
yellow perch	13	22	–	–	35
walleye	–	3	–	–	3
Channel border sites only					
silver lamprey	–	–	–	1	1
shorthead redhorse	–	–	1	1	2
smallmouth buffalo	–	–	–	3	3
bigmouth buffalo	–	–	–	6	6
quillback	–	–	7	1	8
white bass	–	–	6	3	9
smallmouth bass	–	–	1	2	3
logperch	–	–	1	–	1
mud darter	–	–	1	–	1
freshwater drum	–	–	6	–	6
Backwater and channel border sites					
gizzard shad	62	56	13	–	131
common sharp	–	1	–	18	19
emerald shiner	1	18	13	41	73
rock bass	–	2	–	8	10
sauger	1	2	1	2	6
Total individuals	118	199	50	86	455
Total species	9	13	10	11	24

ing at the 25 sites. Twenty-four species were identified (Table 4), with nine restricted to backwater sites, 10 restricted to channel border sites, and five collected in both major habitat types (Table 5). Of the total number of fishes caught, over 70% were collected in the backwaters.

Gizzard shad was the most abundant species captured, comprising 28.8% of the total catch (Table 5). Four additional species (bluegill, emerald shiner, largemouth bass, and yellow perch) each also comprised > 5% of the total catch. Together these five species accounted for nearly 80% of the fishes collected during the study. Interestingly, bluegill, largemouth bass, and yellow perch were captured only in the backwaters.

Many of the fish species collected exhibited distinct preferences for either snag or reference habitat (Table 6). Most insectivorous fishes, piscivores (five species combined because of small sample sizes), small prey species, and common carp were significantly more common in snag habitats than in reference habitats. However, several relatively common species (e.g., yellow perch, small largemouth bass, and gizzard shad) displayed no significant habitat preference.

The average number of fish captured per site ranged from a low of seven for channel border reference sites to a high of 34 for backwater snag sites. Although differences among sites were not significant ($p = 0.11$, Kruskal-Wallis test), backwater sites generally contained more fish on average than channel border locations, and many snag sites had twice as many fish as reference sites within the same habitat (Figure 1a). When expressed on a CPE (fish min^{-1}) basis, no significant differences were detected among habitat types ($p = 0.25$, Kruskal-Wallis test), although the trend for more fish at backwater locations was still evident (Figure 1b). The longer electrofishing times needed to adequately sample snag habitats reduced CPEs for snags, eliminating any possible differences between snag and reference habitats.

Average total biomass of fish collected per site displayed a significant difference among habitat types ($p = 0.008$, Kruskal-Wallis test; Figure 2a). Significantly greater fish biomass was associated

Table 6. Proportional distribution of fish among snag and reference sites in Pool 6 of the upper Mississippi River and results of Chi-square distribution tests.

Species	Proportion collected in each habitat		Chi-square tests	
	Snags	Reference	p-value	Preferred habitat
Insectivores				
bluegill	0.78	0.22	< 0.001	snags
rock bass	1.00	0.00	< 0.005	snags
yellow perch	0.63	0.37	> 0.10	none
spotted sucker	1.00	0.00	< 0.025	snags
smallmouth buffalo	1.00	0.00	< 0.10	none/snags
bigmouth buffalo	1.00	0.00	< 0.025	snags
Piscivores				
combined*	0.77	0.23	< 0.005	snags
largemouth bass < 15 cm TL	0.44	0.56	> 0.10	none
Prey species				
emerald shiner	0.81	0.19	< 0.001	snags
bluegill	0.78	0.22	< 0.001	snags
gizzard shad	0.43	0.57	> 0.10	none
Other species				
quillback	0.13	0.87	< 0.10	none/reference
freshwater drum	0.00	1.00	< 0.025	reference
common carp	1.00	0.00	< 0.001	snags

* Includes largemouth bass > 15 cm TL, smallmouth bass, black crappie, walleye, and sauger.

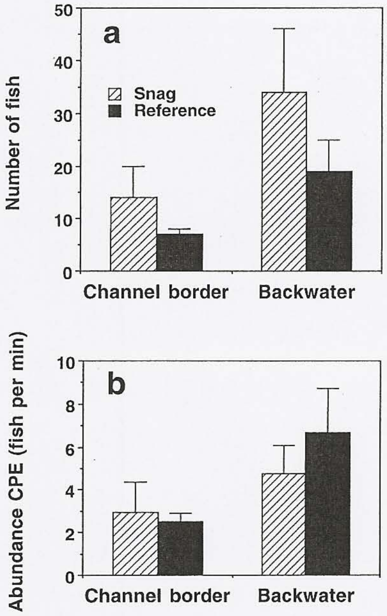

Figure 1. Mean (± SE) fish abundance at snag and reference sites in channel border and backwater habitats in Pool 6, upper Mississippi River in October 1994: a – Total number of fish collected per snag and reference site. b – Catch-per-effort (fish min^{-1}) for snag and reference sites.

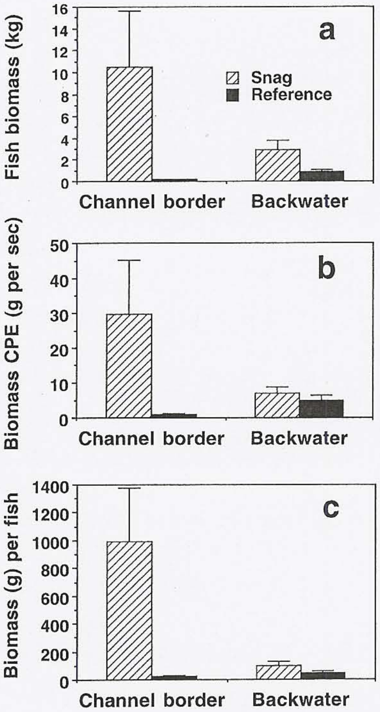

Figure 2. Mean (± SE) fish biomass at Mississippi River (Pool 6) snag and reference sites in channel border and backwater habitats, October 1994: a – Total fish biomass per site. b – Biomass catch-per-effort (g sec^{-1}) for snag and reference sites. c – Biomass per fish at channel border and backwater sites.

with snags than with reference sites within the channel border habitat ($p < 0.05$, Wilcoxon two-sample rank sum test), where fish biomass averaged > 50 × greater at snag sites than at reference sites. Although backwater snag sites averaged 3 × greater fish biomass than that of the reference sites, this difference was not significant ($p = 0.10$, Wilcoxon two-sample rank sum test). These same general trends were still evident even when biomass was expressed on a CPE (g sec^{-1}) basis (Figure 2b). These differences among habitat types primarily were the result of differences in average fish size among the sites. Fishes collected at snag sites were much larger than those at reference sites ($p = 0.007$, Kruskal-Wallis test; Figure 2c), especially in channel border areas.

In addition to differences in fish biomass among habitats sampled, the number of different species

Table 7. Fish taxa richness (mean ± SE) and Bray-Curtis community similarity comparisons of backwater and channel border reference and snag sites in Pool 6 of the upper Mississippi River, October 1994. Brackets around Bray-Curtis values indicate habitat pairs being compared.

<table>
<tr><th rowspan="2">Variable</th><th colspan="2">Backwater</th><th colspan="2">Channel border</th></tr>
<tr><th>Reference</th><th>Snags</th><th>Reference</th><th>Snags</th></tr>
<tr><td>Number of taxa</td><td>3.7
(0.5)</td><td>5.8
(1.1)</td><td>3.3
(0.4)</td><td>2.5
(0.8)</td></tr>
<tr><td>Bray-Curtis, community similarity</td><td colspan="2">|- - - - - - - 0.690 - - - - - - -|</td><td colspan="2">|- - - - - - - 0.302 - - - - - - -|</td></tr>
<tr><td></td><td colspan="3">|- - - - - - - - - - - - - - - - - 0.179 - - - - - - - - - - - - - - - -|</td><td></td></tr>
<tr><td></td><td></td><td colspan="3">|- - - - - - - - - - - - - - - - - 0.178 - - - - - - - - - - - - - - - -|</td></tr>
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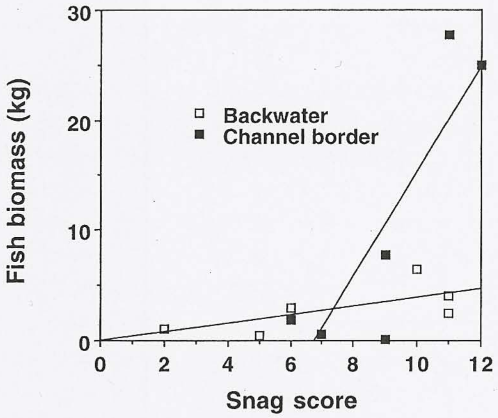

Figure 3. Total fish biomass at backwater and channel border snag sites with varying snag scores, as determined by the snag rating index. Relationship for backwater snags: $Y = -0.0028 + 0.3889 \times$, $r^2 = 0.462$, $p = 0.135$. Relationship for channel border snags: $Y = -32.2972 + 4.7537 \times$, $r^2 = 0.739$, $p = 0.028$.

collected per site also differed between backwater and channel border sites ($p = 0.022$, two-factor ANOVA). Backwater sites averaged approximately four to six species per site, whereas channel border sites averaged approximately three species each (Table 7). However, there were no differences in taxa richness between snags and reference sites ($p = 0.343$, two-factor ANOVA).

Bray-Curtis community similarity tests indicated differing levels of similarity between fish communities in various paired habitats (Table 7). Fish communities in the two backwater habitats were highly similar to one another, but communities occupying the two channel border habitats were different from one other and from communities in backwater habitats.

Snag scores from both channel border and backwater sites were compared to both fish abundance and fish biomass. Although there was no significant relationship between snag score and fish abundance ($p = 0.174$, $r^2 = 0.149$), a significant positive correlation was detected between snag score and total fish biomass ($p = 0.048$, $r^2 = 0.337$). When this analysis was subdivided into channel border and backwater habitats, this correlation increased, although only the relationship between channel border snag score and fish biomass was significant (Figure 3). Larger snags, therefore, had greater fish biomass associated with them than did smaller snags. Also, the slope of the channel border regression line was significantly steeper ($p < 0.05$, ANCOVA) than the backwater regression line, indicating that snags in the channel border produced a larger biomass response than those in the backwater areas. Finally, the regression lines suggest that channel border snags may be unattractive to fish unless they are of a certain quality (i.e., they have a certain minimum snag score).

Discussion

Snags in the upper Mississippi River appear to have some of the same effects on channel morphology as they do in smaller lotic systems. Snags can reduce average current velocities and promote accumulation of detritus in low-velocity areas (Malmquist et al. 1978, Angermeier & Karr 1984), but they also can restrict the channel in small rivers and streams, increasing a stream's erosion potential and enhancing pool formation and maintenance in low-gradient, fine-substrate streams (Angermeier & Karr 1984, Reeves et al. 1993). Snags in the Mississippi River occurred in areas deeper than associated reference sites, suggesting that snags in larger rivers also redirect current and cause scouring (only during high spring flows in backwaters). Since the Mississippi River is so large and the deepening effects of snags appear to be highly localized, it is likely that snags have little effect on overall channel morphology. However, their presence increases the heterogeneity of both backwater and channel border habitats, potentially influencing fish communities in these habitats.

Several studies in river and stream ecosystems (e.g., Angermeier & Karr 1984, Benke et al. 1985, Todd & Rabeni 1989, Lobb & Orth 1991, Reeves et al. 1993) have demonstrated the close association between fish and areas with woody debris. Snags provide suitable and often preferred substrate for invertebrate colonization (e.g., Angermeier & Karr 1984, Wallace & Benke 1984, Benke et al. 1985), and many species of fish feed heavily on invertebrates produced on snags (Benke et al. 1985). Snags in the upper Mississippi River are colonized by large numbers (up to 16 000 organisms m^{-2} of snag surface area) of invertebrates (K. Marley & M. Delong unpublished data), providing prime foraging areas for many insectivorous fishes such as bluegill, spotted sucker, and small rock bass which were significantly more common at snag sites than at reference sites (Table 6). Common carp and buffalo, predominantly bottom feeders, may have been attracted to snags because of the enhanced ability of these structures to accumulate detritus and, along with this material, a certain type of invertebrate community (Malmquist et al. 1978).

Snags also may allow fish to save energy and enhance growth rate by providing pockets of reduced current velocity (e.g., Tarzwell 1938, Bachman 1984, McClendon & Rabeni 1987, Todd & Rabeni 1989, Putman et al. 1995). Fish can hover or feed in these lower-velocity areas (Todd & Rabeni 1989), while still remaining near faster currents for other activities. Ninety percent of smallmouth bass and rock bass collected in channel border habitats during the present study were associated with snags.

Fish may use snags or areas near them as protection from a wide variety of potential predators. Cover provided by snags may reduce predation risk from other fish, birds, or mammals (Angermeier & Karr 1984, Johnson et al. 1988), while deep water (often associated with snags) may be just as effective as the physical structure in reducing attacks from birds and mammals (Power 1984, Matthews et al. 1986). In the upper Mississippi River, piscine predators are abundant, and fish-eating birds and mammals are very abundant (Fremling et al.[5]). Snags may protect Mississippi River fishes such as emerald shiners and bluegill, which demonstrated particularly strong preferences for snag habitats, from this plethora of predators. Bluegill are known to seek out dense habitat structure when potential predators are present (e.g., Savino & Stein 1982, Johnson et al. 1988), and emerald shiners, which likely do not feed on snag-dwelling invertebrates (Benke et al.[7]), were probably using snag sites in both channel border and backwater habitats (presence and absence of current) primarily as protection from predators.

Snags also may be important foraging sites for piscivorous fishes, using the shade produced by snags as camouflage while waiting for prey to pass nearby (Helfman 1981, Angermeier & Karr 1984). In the present study, most piscivores (100% of walleye, 83% of largemouth bass > 15 cm TL, 75% of black crappie, 67% of sauger and smallmouth bass) were collected at snag sites. These findings are similar to those of several other investigators (e.g., Angermeier & Karr 1984, Todd & Rabeni 1989, Lobb & Orth 1991) who observed that several species of piscivores preferentially utilized snag habitats in rivers and streams.

Our findings indicate that, in both backwater and channel border habitats, snag quality (as measured by snag score) explained a large portion (74% in channel borders, 46% in backwaters) of the variability in fish biomass among individual snags. However, snag quality accounted for less (18% in channel borders, 37% in backwaters) of the variability in fish numbers. In contrast, Sowa & Rabeni (1995) reported no significant relationship between bass density or biomass and total snag and rootwad area within a stream reach, whereas Todd & Rabeni (1989) observed that better-quality boulders provided shelter for greater numbers of smallmouth bass. Why better-quality snags in the Mississippi River should support greater fish biomass but not greater numbers of fishes is not clear. While it is possible that the snag characteristics we chose to assess simply were more important estimators of fish biomass rather than fish number, it is more likely that the differences in average fish size observed between snag and reference sites interfered with the suspected snag score-fish abundance relationship. In backwaters where average fish size did not differ significantly between snag and reference sites, snag scores accounted for fairly similar amounts of variability in fish numbers (37%) and biomass (46%) among individual sites. However, in channel borders where average fish size differed 40-fold between habitat types, snag scores explained vastly disimilar proportions of fish numbers (18%) and biomass (74%) variability. Perhaps the presence of

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[7] Benke, A.C., D.M. Gillespie, F.K. Parrish, T.C. Van Arsdell, Jr., R.J. Hunter & R.L. Henry, III. 1979. Biological basis for assessing impacts of channel modification: invertebrate production, drift, and fish feeding in a southeastern blackwater river. Environmental Resources Center Publication No. ERC 06–79, Georgia Institute of Technology, Atlanta. 187 pp.

very large fish, whether conspecifics or potential predators, at most of the channel border snags resulted in the displacement of smaller, more numerous fishes to other habitats. Other investigators (e.g., Fraser & Mottolese 1984, Power et al. 1985, Harvey et al. 1988, Johnson et al. 1988) have shown that smaller fishes often abandon or avoid preferred underwater habitats when a larger fish is present.

Contrary to expectations, fish community taxa richness was not significantly different between snag and reference areas. Since habitat complexity is a primary factor influencing the diversity of fish communities (Gorman & Karr 1978, Angermeier & Karr 1984, Reeves et al. 1993) and snags represent a heterogeneous, complex type of habitat, these areas might be expected to exhibit greater fish taxa richness than areas without snags. Why fish taxa richness was not higher in snag habitats is unknown, since more species preferred snags than reference areas (Table 3). As suggested above, one or a few large fish within a snag habitat may have prevented other, smaller fish from occupying the same area, thereby having a negative effect on fish taxa richness within the snag.

The fish communities that occupied snags in backwater and channel border habitats of the Mississippi River were largely disimilar. Of the 20 species total captured at snags, only four were collected at both backwater and channel border snags, and the Bray-Curtis community similarity index score was low (< 0.2). Reference sites displayed a similar pattern (16 species total, three in common; similarity index score < 0.2). This was not unexpected, since these two habitats generally support different overall fish communities (Fremling et al. 1989). However, backwater snag and reference sites supported similar fish communities (similarity index score > 0.6), whereas channel border snag and reference site communities exhibited much lower similarity (similarity index score = 0.3). These comparisons suggest that even though snags are important to fish communities in both backwater and channel border habitats, they may play a much more important role in channel border habitats since they support a much different fish community than is found at reference sites. In addition, the snag score-total fish biomass relationships indicate that channel border snag fish communities respond more dramatically than backwater snag communities to changes in snag quality. These differences probably exist in response to such physical factors as current velocity and substrate type, and also may be influenced by various life history characteristics of the fish species present. The relative value of snags to these different fish communities warrants further examination.

Since our study only examined fish use of snag habitats during autumn, it is likely that investigations during other seasons may produce slightly different results. Preferences of some species of fish for woody debris are known to change with the seasons (Moring et al.[8], Todd & Rabeni 1989), and changing interactions among some species may allow different fish communities to develop in different seasons in certain habitats (Harvey et al. 1988). Some species also may seek out woody debris for use as spawning substrate (Miller 1960, Lambou 1965), or woody debris may serve as nursery habitat for fish larvae and juveniles (Van Den Avyle & Petering 1988). Consequently, the types of fish associated with snag and non-snag habitats in the upper Mississippi River may change seasonally. However, given the many similarities between the present study and previous investigations of fish use of snags in smaller rivers and streams during various seasons, we suspect that the same general patterns observed in autumn would persist during other seasons.

The abundance of snags in backwater and channel border habitats of the upper Mississippi River varies greatly, most likely the direct result of differences in flow between these two habitats. Although snags numbers per shoreline length were not directly quantified, general observations indicate that snag abundance appeared to be < 10 snags km^{-1} of main channel border shoreline and > 30 snags km^{-1} of backwater shoreline. How this abundance of

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[8] Moring, J.R., K.E. Gibbs, P.D. Eiler, M.T. Negus, T.E. Robertson & R.D. McCullough. 1981. The ecological effects of log driving in relation to navigable rivers. University of Maine at Orono, Report to U.S. Fish and Wildlife Service, Washington, D.C.

snags compares to natural abundances prior to river development of the past two centuries is unknown. Snag removal was common along the main shipping channel prior to 1930 (Fremling et al. 1989), but it has virtually ceased since construction of the lock and dam system in the 1930s (D. Krumholz personal communication). Accelerated shoreline erosion induced by increased boat traffic today may be increasing the rate of snag development in both channel border and backwater habitats (C. Fremling personal communication). Consequently, snag abundance in the upper Mississippi River today may be similar to, or possibly even greater than, pre-development levels. In smaller rivers and streams, snag abundance may exceed several hundred km^{-1} (Wallace & Benke 1984, Reeves et al. 1993, Gore & Shields 1995), since these systems may have insufficient power to move large woody debris (Wallace & Benke 1984). Although snags in the upper Mississippi River may not be as abundant or have as great an influence on channel structure as snags in smaller systems, the results of the present study indicate that snags provide important habitat for many species of fish in both backwater and channel border habitats.

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