

Fish Relationships with Large Wood in Small Streams

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Abstract.—Many ecological processes are associated with large wood in streams, such as forming habitat critical for fish and a host of other organisms. Wood loading in streams varies with age and species of riparian vegetation, stream size, time since last disturbance, and history of land use. Changes in the landscape resulting from homesteading, agriculture, and logging have altered forest environments, which, in turn, changed the physical and biological characteristics of many streams worldwide. Wood is also important in creating refugia for fish and other aquatic species. Removing wood from streams typically results in loss of pool habitat and overall complexity as well as fewer and smaller individuals of both coldwater and warmwater fish species. The life histories of more than 85 species of fish have some association with large wood for cover, spawning (egg attachment, nest materials), and feeding. Many other aquatic organisms, such as crayfish, certain species of freshwater muskels, and turtles, also depend on large wood during at least part of their life cycles.

Introduction

Large wood can profoundly influence the structure and function of aquatic habitats from headwaters to estuaries. In streams and rivers flowing through forests worldwide, large wood slows, stores, and redirects surface water and sediments and provides cover, substrate, and food used by fish and other vertebrates, aquatic invertebrates, and microbes (Table 1). We here review the role of large wood in small streams and highlight specific examples of how wood influences the distribution, abundance, and life history of various organisms. Our focus in this chapter will be on small streams, defined here as fourth-order or lower and having a bank-full width of 10 m or less.

Physical Effects in Stream Channels

Woody material of all sizes—from tiny fragments to intact trees—plays a role in stream systems.

Because decay rate and probability of displacement are a function of size, large pieces have a greater influence on habitat and physical processes than small pieces. In general, rootwads, branches, snags, detached boles, and other pieces 1.0–1.5 m long and wider than 10 cm in diameter are defined as large wood. Although somewhat arbitrary, this size approximates the wood that is entrained rather than simply passed through channels of small perennial streams. Smaller pieces and fragments, even those too small to count, also play a role in forming habitat (for example, as part of the matrix of material that forms debris dams; Bilby and Likens 1980; Dolloff and Webster 2000). Depending on the characteristics of the stream channel (for example, the presence of hydraulic controls, channel constrictions, channel roughness) and relative size and quality (for example, surface area and resistance to decay) of the wood, wood accumulations or dams of both large and small wood create habitat diversity and may persist for a few months to hundreds of years (Bilby and Likens 1980).

TABLE 1. The physical and biological roles of large wood in small streams.

Physical		Biological	
<u>Water</u> storage quality	<u>Substrate</u> storage routing	<u>Food</u> substrate abundance availability delivery substrate type	<u>Cover</u> protect from predators isolate competitors protect from displacement
<u>Channel shape</u> width, depth habitat type			

Nearly all wood that impinges on stream channels has the capacity to influence habitat and aquatic communities. Large wood oriented perpendicular to the thalweg is often associated directly with pool formation (Cherry and Beschta 1989; Richmond and Fausch 1995; Hauer et al. 1999). Even wood outside or above the wetted portion of the channel influences pool formation by directing patterns of scour at bank-full flows. Wood bridges eventually weaken with decay, break into two or more pieces, and exert entirely different influences on channel shape and habitat formation.

The amount of large wood in streams (wood loading) varies with age of the riparian forest, species of riparian vegetation, size of stream, time since disturbance, and land-use history. All of these factors interact with the frequency and magnitude of natural disturbances as well as human perturbations. Of these human alterations, history of land use, particularly urbanization, agriculture, and logging, has changed not only the physical and biological characteristics of streams but also our perception of what is natural. Natural disturbances like fire, wind, and floods do not typically affect all parts of a landscape equally. A flood-producing storm in one watershed may not similarly affect an adjacent watershed. Because of the dynamic spatial effects of natural disturbance regimes, large wood loading and hence stream habitat features across natural landscapes vary greatly. At any one time, some stream corridors may have large amounts of large wood configured into highly complex habitats, but others—perhaps even in the same watershed—may lack wood and have greatly simplified habitats (Sedell et al. 1990).

Today, the lack of large wood in streams near urban centers or in those draining agricultural regions is readily apparent, but even streams flowing through forested regions often lack significant amounts of wood (Maser and Sedell 1994). Nearly all of the riparian forests across the eastern United States have been harvested at least once, if not

multiple times, in the last 150 years. Most have not had time to produce the large trees that are not only the source of instream wood, but are also critical in forming complex, long-lasting habitat configurations (Dolloff and Webster 2000). The loss of old or late-successional riparian forests in the last century constitutes a new disturbance regime. The drastically reduced recruitment of large wood coupled with natural processes of decay and downstream transport have resulted in unnaturally low accumulations of large wood in streams across entire landscapes. Recovery of stream ecosystems through formation of wood dams may not occur for many decades (Golladay et al. 1989; Webster et al. 1990). The absence of large wood in riparian forests over much of North America has greatly reduced habitat complexity in streams and also reduced variability among streams draining a given ecoregion or geoclimatic setting. Without adequate large wood, these systems become more homogeneous with reduced habitat complexity, species diversity, and productivity.

Habitats in small streams are particularly sensitive to changes in large wood loading, and the full implications of reduced amounts of wood over large areas are unknown but potentially far-reaching for certain groups and life stages of organisms. Risk to the persistence, distribution, and abundance of pool-dependent species may be compounded after a natural disturbance, particularly if the abundance of suitable alternative habitats is already low or fragmented because of a previous disturbance.

Directly removing wood typically results in loss of pools and habitat complexity; in sand-bed streams, it may trigger or exacerbate destructive channel incision (Shields and Smith 1992). Removing wood from the channel or floodplain reduces numbers, average size, and biomass for both warmwater (Angermeier and Karr 1984; Shields et al. 1994) and coldwater (Elliott 1986; Dolloff 1986) fish species. Adding wood typically increases total pool area and depth, but simply add-

ing wood may not produce the same result in all streams. The quality of habitat produced by large wood is a function of geomorphic characteristics, such as channel size, channel form, gradient, and substrate size. For example, pool habitat more than doubled within 1 year of adding large wood to a small, low gradient (1.0% slope) Virginia stream (Hilderbrand et al. 1997). In contrast, pool area remained essentially unchanged after similar amounts of large wood were added to a moderate gradient (3–6%) stream where boulders were the dominant pool-forming element.

Wood is deposited and accumulates in small streams by a combination of chronic and episodic processes (Table 2). Inputs of the greatest amounts of large wood usually can be traced to specific, weather-related events; piles of logs deposited by floodwaters along stream sides are obvious indicators of the importance of episodic events. But for perspective, the annual input of organic material to small upland streams from seasonal litter fall (leaves, twigs, small branches) typically exceeds the input of large wood (Webster et al. 1990). In general, large wood input rates vary with tree species and age, slope and shape of surrounding land forms, health and history of surrounding forest (insects, disease, land use), and size of the watershed. Recruitment rates are generally lower in second-growth forests; in eastern North America, input rates tend to be very low because many riparian forests have been completely removed or have been harvested repeatedly (three or more timber rotations).

Hydraulic processes control the particular arrangement of large wood after it enters a stream channel, but the mechanism of entry can also be influential. Stream size, which incorporates differences in flow magnitudes, has a major influence on the fate and distribution of large wood (Bisson et al. 1987). In small streams (first- and second-order), the dominant spatial pattern appears random: dams may form at predictable intervals from leaves and litter; however, large pieces tend to stay where they fall because transport power is low. Accumulations of wood in in-

termediate-size streams (second to fourth-order) tend to be larger, more variable in size, and clumped at or near bends or changes in channel gradient. The mechanism of entry also influences the arrangement of large wood accumulations. In contrast to the relatively loose architecture of wood jams that form incrementally from the transport and entrainment of individual pieces in a stream, large wood pieces from landslides, debris flows, and snow avalanches tend to deposit in interlocking wood accumulation's (see Benda et al. 2003, this volume). Although formed by different processes, both types of accumulations make important contributions to habitat.

Some large wood accumulations in small streams last for hundreds of years. However, the total amount of large wood is dynamic, changing, sometimes dramatically, over the course of a year. As an illustration of this variability, the half-life of individual pieces of large wood ranges from 2.3 to 230 years (Harmon et al. 1986). The half-life of wood dams in very small streams tends to be less, about 6–24 months, depending on size and composition of the material in the dam and characteristics of flow. Whether limbs or whole trees, decay begins with death. The longevity of intact pieces of large wood is thus influenced by decay rates (resistance to abrasion, breakage, and rot) and transport processes. Softwoods generally decay faster than hardwoods, but certain softwood species, like hemlock, that contain high levels of decay-resistant tannins and other substances, last longer than many "soft" hardwoods, such as tulip poplar and aspen. Temperature of both the air and water, exposure to sunlight and humidity, and frequency and duration of flow all affect the rate of wood decay and its longevity at a particular site. Wood buried in the streambed or continually submerged resists decay better than wood that is only partly or periodically submerged, alternating between being wet and dry.

The loading of large wood in streams flowing through forests varies greatly, from 2.5 to 4,500 m³/ha (Harmon et al. 1986). In general, streams flowing through forests undisturbed by human

TABLE 2. Mechanisms of large wood input to small streams.

Chronic processes	Episodic processes
Litterfall, self-pruning from riparian areas	Tree fall from stream bank failures
Mortality of trees from insects and disease	Tree fall from windthrow
Tree fall from streambank undercutting	Snow and ice accumulation and melting
	Avalanches, debris flows

activities have the greatest volumes or density of large wood. High loads are well documented in the Pacific Northwest, but small streams flowing through forests in eastern North America also have substantial loads (Hedman et al. 1996). By inference, historical amounts of large wood in many small eastern streams probably were high. In the southern Appalachians, streams draining old-growth forests contained amounts of large wood comparable to those in northwestern old-growth forests and up to four times more large wood than in eastern wilderness streams draining forests cleared early in the century (Flebbe and Dolloff 1995). Likewise, small streams in unlogged watersheds of the Great Smoky Mountains National Park contained 4 times the volume of wood and 10 times the material in wood dams than streams logged early in the 20th century (Silsbee and Larson 1983; Table 6 in Harmon et al. 1986). In small streams of southern New Zealand, researchers determined that the amount of large wood in older forest streams was greater than in young forests, with overall amounts much smaller relative to those found in North American forested streams (Evans et al. 1993).

Habitat Relations

For many aquatic organisms, particularly fishes, large wood is most important in creating and maintaining deepwater or pool habitat. Pools and other habitats associated with large wood are attractive to fish for a variety of reasons. Conspicuous among them are the lower water velocities and greater depths associated with pools during low-flow periods. Salmonids and drift-feeding minnows inhabit areas with low velocity water and make forays into fast water to capture food items in the drift (Matthews 1998). Trout and minnows of eastern England were also found to be strongly associated with large wood (Punchard et al. 2000). Several American species also seek the lower velocities behind logs to avoid swift, cold winter flows. Refuges from high velocities, such as those found in the lee of logs, may significantly affect overwintering survival of the federally listed bayou darter *Etheostoma rubrum* (Ross et al. 1992) and many other small benthic fishes, particularly in sand-bottomed coastal plain streams. Still other fishes use the cover of logs in pools for nest sites and spawning (for example, centrarchids) or attach their eggs to logs (for example, shiners *Cyprinella* spp. and relict darter *Etheostoma chienense*). Pools typically harbor more

and larger fish than shallower areas because of the greater space (volume) of habitat available, particularly during times of exceptionally low flow, such as in late summer or winter. Streams with poorly developed, shallow pools have a low residual pool volume (Lisle and Hilton 1992) and consequently tend to support fewer species, have simple trophic structure, and show higher variability in fish abundance (Schlosser 1987).

Pools can form around any obstruction that creates friction and resists displacement by flowing water, and large wood is often the dominant pool-forming element. In small streams in forested areas, large wood can be responsible for 50–90% of all pools (Andrus et al. 1988; Hedman et al. 1996). The proportion of pools formed by large wood tends to be much lower (<10%) in streams flowing through second-growth and younger forests.

Large wood is an important habitat that is included in the definitions of many fluvial habitat types (Bisson et al. 1982; Hawkins et al. 1993; Armantrout 1998). Large wood can contribute to pool formation in a variety of ways depending on factors such as the size of the piece, the mechanism of entry into a stream channel, channel size and gradient, and streamflow. The most commonly envisioned orientation is channel spanning and perpendicular to the channel, which often results in forming plunge pools in the downstream and dam pools in the upstream direction. Perpendicularly oriented large wood that juts into but does not span a channel may create eddies and backwater pools. The deepest pools form behind pieces that span the entire width of the channel and are oriented perpendicular to flow. Large wood helps maintain the diversity of physical habitat by delimiting pool position and increasing depth variability.

Although the role of large wood in deep pool formation is important, its contribution as an element of channel roughness in shallow stream reaches should not be overlooked. In many coastal plain streams of the eastern United States, riffles and cobble substrate are absent and gravel is rare (Meffe and Sheldon 1988). Here, large wood is often the only element contributing to channel roughness and, hence, to the forming of complex, flowing habitats (Smock and Gilinsky 1992). The presence of wood accumulations, even relatively small-diameter pieces, in shallow, sandy, flowing areas creates a heterogeneous zone of variable velocities and depths. These wood-formed "riffles and runs" in turn support a significant proportion of the stream fish diversity in coastal plain

streams and likely are critical to the persistence of many darters (*Percina* spp. and *Etheostoma* spp.) and madtom catfishes *Noturus* spp. (Chan and Parsons 2000; Warren et al. 2002).

Large wood creates sediment storage sites (floodplains and terraces), the wetted portions of which contribute to producing food (algae and macroinvertebrate) and spawning habitat. Forming new sediment terraces is particularly important in drainages where natural floodplain deposits and terraces have been lost, such as in many small watersheds in the Cascade Range of Oregon and across much of eastern North America. Conversely, large wood also encourages scour and promotes transportation of fine sediments, thereby exposing gravel where fish spawn and benthic macroinvertebrates thrive. In general, streamflow determines the influence of large wood on routing and rates of sediment scour and fill. At low flow, pools formed by wood tend to fill and riffles tend to scour, but when flow is high, pools scour and riffles are depositional.

Although many researchers have focused on how large wood affects physical processes in streams, large wood also has a major impact on many, if not all, biological processes, such as substrate type, water depth, and velocity. These physical processes are influenced by large wood. Large wood also facilitates primary production by providing attachment sites for microbes and algae, sources of nutrients, and storage zones for organic matter. Biofilms, composed of microorganisms and the mucoidal matrix that surrounds them, develop readily on wood, a substrate that also provides a portion of the nutrients required to maintain them (Aumen et al. 1990; Golladay and Sinsabaugh 1991; Tank and Winterbourn 1995; Benke and Wallace 2003, this volume). Wood also creates conditions favorable to the entrainment and processing of terrestrially derived fine particulate organic material (FPOM) from riparian vegetation. Microbes and macroinvertebrates process this material more readily than wood. Large wood also traps and retains carcasses of spent fish in streams that are home to runs of anadromous fish (Cederholm and Peterson 1985). Nutrients, particularly nitrogen, from decomposing carcasses boost primary production by enhancing both algal and biofilm development (Richey et al. 1975; Wold and Hershey 1999).

Large wood enhances secondary production both directly, such as by increasing the surface area available to macroinvertebrate grazers and scrapers (Benke et al. 1985), and indirectly, by

physical habitat partitioning. Angermeier and Karr (1984) experimentally removed large wood from one side of a reach of a small Illinois stream and found that, in addition to more and larger fish, the side of the stream with wood had more litter and benthos. In coastal plain headwater streams of Virginia, invertebrate densities were 10 times and biomass 5 times higher in wood dams than on sandy substrates (Smock et al. 1989). In pumice-bed streams of New Zealand, summer densities of macroinvertebrates were higher in streams where wood was present, providing either increased habitat or greater food resources or a combination of both (Collier and Halliday 2000). Wood snags in southeastern Australian lowland streams serve as important habitat for macroinvertebrates, influencing not only the diversity of species, but also their abundance (O'Connor 1991). Invertebrates associated with wood substrates form essential elements of the diet of many fishes in these streams (Felley and Felley 1987).

Aside from its role in creating pools and velocity breaks, large wood can be an important source of cover and habitat complexity for aquatic species. Wood cover can be simply an overhanging log or intricate accumulation of wood and other material, often referred to a wood jam. In northern Japanese streams, masu salmon *Oncorhynchus masou* density was correlated with wood cover in both pool and nonpool habitats (Inoue and Nakano 1998). In general, streams with complex habitats tend to have more fish and fish species than streams lacking complexity. Complexity provides a measure of security from predators (Harvey and Stewart 1991), isolation from competitors, and points of refuge from severe environmental conditions, such as flood or drought. Wood provides shadow, which not only makes fish harder for predators to see, but also aids fish in seeing approaching predators (Helfman 1981). Large wood protects fishes from aquatic predators (Everett and Ruiz 1993), and complexity thwarts diving and wading predators (Power 1987; Harvey and Stewart 1991). Complexity is critical for many fishes, particularly aggressive species like salmonids, which do not tolerate conspecifics in close proximity. Submerged branches and other wood partition habitat and visually isolate individual fish, allowing more fish per unit of available space (Dolloff 1986). Field observation of this "condominium effect" provides part of the rationale for enhancing habitat by using discarded Christmas trees, brush bundles, and

tops from softwood trees (Boussu 1954; Reeves et al. 1991).

Complex cover and habitat, like that created by large wood, is especially important during times of stress, such as when streamflows are exceptionally low or high (Swales et al. 1986; Pearsons et al. 1992). In small, drought-prone streams, large wood and other channel obstructions may provide the only refuge during low flows. White pines planted near Benson's Run, Virginia toppled into the stream by the laterally migrating channel caused local scour and increased numbers and distribution of pools that are used as low-flow refugia by a host of fish species, including brook trout *Salvelinus fontinalis* (Figure 1). Species other than fish also frequent these pools; predators such as raccoons, herons, water snakes, and anglers are known to exploit the dense congregations of fish whose only escape lies in the tangled roots of the toppled trees. Adult cutthroat trout *O. clarki* in northern California small streams occupied habitat influenced by large wood during winter floods and showed a strong fidelity to wood-formed pools during normal fall and winter flows (Harvey et al. 1999).

In individual habitat units, fish tend to seg-

regate by species and size. Particularly among fish with aggressive natures, physical habitat partitioning is an important element of coexistence. Larger or more aggressive individuals tend to occupy the most efficient positions in small streams (Fausch and White 1981), which often are characterized by structure at the heads of pools, near but out of high-velocity currents. Juvenile salmonids of different species and sizes are known to segregate in small streams where large wood is the dominant pool-forming element. For example, Dolloff and Reeves (1990) observed that coho salmon *O. kisutch* and Dolly Varden *S. malma* occupied distinct regions in small (2–10-m²) pools in Alaska streams. One-year-old and older coho salmon typically occupied positions at the heads of pools near the water surface, but similar-sized Dolly Varden were associated more closely with the stream bottom and dense (frequently wood) cover. Young-of-the-year coho salmon and Dolly Varden occupied positions similar to the larger fish but farther down stream in the pools and associated less closely with cover.

Multivariate studies of warmwater, stream fish communities often demonstrate habitat partitioning based on factors involving amount of



FIGURE 1. Refuge habitat created by the rootwads of toppled streamside trees in Benson's Run, Virginia.

wood and cover after depth and velocity are taken into account (Baker and Ross 1981; Felley and Hill 1983; Felley and Felley 1987; Taylor et al. 1993; Warren et al. 2002). The actual association of species-rich, warmwater fish assemblages with wood and cover is often a complex mix of velocity preferences, behavioral responses (such as predator avoidance), or feeding responses, which can only be partially resolved in fish assemblage-habitat studies (Meffe and Sheldon 1988). In small northern Mississippi streams, many of which are affected by stream incision, the relative abundance of sunfishes was positively associated with wood in relatively deep habitats, a response attenuated by stream incision (Warren et al. 2002). In flowing habitats, large wood was associated positively with the relative abundance of darters (genera *Etheostoma* and *Percina*) and catfishes (mostly madtoms *Noturus* spp. and bullheads *Ameiurus* spp.; Warren et al. 2002). In Ozark streams, stream-dwelling rock bass and smallmouth bass showed high association with wood, but habitat use showed distinct differences in segregation by species, size, and relation to current velocities (Probst et al. 1984). Rock bass *Ambloplites rupestris* were more often associated with rootwads, regardless of size, but larger smallmouth bass *Micropterus dolomieu* (>350 mm) used log complexes in higher velocities than velocities associated with rock bass cover (Probst et al. 1984).

As fish mature, their use of large wood in streams can shift in relation to their size and food preferences. For example, in a prairie stream in Kansas, growth increments of some stream fishes were associated strongly with amounts of large wood (Quist and Guy 2001). Creek chubs *Semotilus atromaculatus* were strongly associated with amounts of large wood for only the first year of growth, but all growth stages of green sunfish *Lepomis cyanellus* were associated with wood (Quist and Guy 2001). The authors attributed the response of creek chubs to shifts from eating invertebrates while small to eating fish when they were larger. Green sunfish likely exploited invertebrates on wood at small sizes but, at large sizes, continued to use large wood as cover (Quist and Guy 2001).

Many other fish species are also associated with accumulations of large wood. In Kentucky's Beaver Creek, for example, divers found the highest concentrations of the federally threatened blackside dace *Phoxinus cumberlandensis* in pools with a complex mixture of large and small wood. Two nocturnally active fishes, the brown madtom *Noturus phaeus* and the pirate perch *Aphredoderus*

sayanus, are strongly associated with complex wood habitats in small coastal plain streams (Monzyk et al. 1997; Chan and Parsons 2000) of the southeastern United States. Large wood is a requisite feature of the diurnal cover of these species, but specific characteristics (for example, cavity space, entrained leaves, adjacent flow) also influence fish use (Monzyk et al. 1997). Brush bundles, leaf packs, and faux rootwads experimentally placed in northern Mississippi streams were used by 32 species of small-stream fishes. Strong position effects on fish numbers and identity reflected depth and velocity at individual samplers. Brush bundles and leafpacks held equal numbers of fish; smaller root samplers held fewer fish, but darters used them regularly. In January (water 2–5°C), up to 70 lethargic cyprinids occupied a single bundle, suggesting that such refuges are critical winter habitat (A. J. Sheldon, University of Montana, M. L. Warren, Jr. and W. R. Haag, USDA Forest Service, unpublished data). Even in the arid Southwest, large wood forms important habitat for native fishes. Presence of pools with root masses of standing or uprooted trees was the best predictor of the occurrence and abundance of the federally threatened Gila chub *Gila intermedia* (Probst and Stefferud 1994).

A cursory compilation of southeastern U.S. fishes that have some association with large wood is instructive (Table 3.). For many of these species, presence of large wood is facultative, particularly where rocky substrates or other elements can substitute for cover. For other species, large wood is the primary element of habitat complexity, especially in streams of predominantly fine substrates. Although not exhaustive, our compilation of fish associated with large wood habitat includes 12 families and more than 86 species of warmwater fishes. For these species, association with large wood includes diurnal cover, cover for adult or juvenile stages, food sources (such as algae or macroinvertebrates on wood), and reproductive uses (such as spawning and nesting cover, egg attachment). These species, and likely others that live in small streams, find protection from predators, as well as resting and foraging areas and spawning sites among the branches and pieces that comprise the matrix of wood jams.

Much information has accumulated showing the relation of large wood to fish populations, particularly of salmonids in western North America. Clear demonstration of similar relations in other regions and for other species, however, has often been problematic. For example, though Flebbe and

TABLE 3. Warmwater fish species associated with large wood in the southeastern United States

Species	Common name	Association with large wood	Reference
<i>Ichthyomyzon castaneus</i>	Chestnut lamprey	Spawning cover	Becker 1983
<i>Lampetra aepyptera</i>	Least brook lamprey	Cover for transforming larvae	Walsh and Burr 1981
<i>Amia calva</i>	Bowfin	Cover, nesting materials, nesting cover	Scott and Crossman 1973
<i>Esox niger</i>	Chain pickerel	Cover	Scott and Crossman 1973
<i>Cyprinella analostana</i>	Satinfin shiner	Egg attachment	Gale and Buynak 1978
<i>Campostoma</i> spp.	Stonerollers	Feeding on algae	Matthews 1998
<i>Cyprinella callitaenia</i>	Bluestripe shiner	Probable egg attachment	Wallace and Ramsey 1981
<i>Cyprinella galactura</i>	Whitetail shiner	Egg attachment	Pflieger 1997
<i>Cyprinella lutrensis</i>	Red shiner	Feeding, egg attachment	Quist and Guy 2001; Pflieger 1997
<i>Cyprinella spiloptera</i>	Spotfin shiner	Egg attachment	Pflieger 1965
<i>Cyprinella venusta</i>	Blacktail shiner	Egg attachment	Pflieger 1997
<i>Cyprinella whipplei</i>	Steelcolor shiner	Egg attachment	Pflieger 1965
<i>Exoglossum laurae</i>	Tonguetied minnow	Nesting cover	Trautman 1981; Jenkins and Burkhead 1994
<i>Exoglossum maxillingua</i>	Cutlips minnow	Nesting cover	Jenkins and Burkhead 1994
<i>Opsopoeodus emiliae</i>	Pugnose minnow	Probable egg attachment	Johnston and Page 1990
<i>Nocomis leptcephalus</i>	Bluehead chub	Nesting cover	Jenkins and Burkhead 1994
<i>Phoxinus cumberlandensis</i>	Blackside dace	Cover	Starnes and Starnes 1978
<i>Phoxinus tennesseensis</i>	Tennessee dace	Cover	Starnes and Jenkins 1988
<i>Pimephales notatus</i>	Bluntnose minnow	Nesting cover, egg attachment	Hubbs and Cooper 1936; Scott and Crossman 1973
<i>Pimephales promelas</i>	Fathead minnow	Nesting cover, egg attachment	Wynne-Edwards 1932; Scott and Crossman 1973
<i>Pimephales vigilax</i>	Bullhead minnow	Nesting cover, egg attachment	Parker 1964
<i>Pteronotropis euryzonus</i>	Broadstripe shiner	Cover	Mettee et al. 1996
<i>Semotilus atromaculatus</i>	Creek chub	Feeding (juvenile), diurnal cover	Pflieger 1997; Quist and Guy 2001
<i>Erimyzon oblongus</i>	Creek chubsucker	Cover	Mettee et al. 1996
<i>Erimyzon tenuis</i>	Sharpfin chubsucker	Cover	Mettee et al. 1996
<i>Ameiurus melas</i>	Black bullhead	Nesting cover	Breder and Rosen 1966
<i>Ameiurus natalis</i>	Yellow bullhead	Nesting cover	Carlander 1969
<i>Ameiurus nebulosus</i>	Brown bullhead	Nesting cover	Blumer 1985
<i>Ameiurus serracanthus</i>	Spotted bullhead	Cover	Mettee et al. 1996
<i>Noturus flavater</i>	Checkered madtom	Cover	Pflieger 1997
<i>Noturus flavipinnis</i>	Yellowfin madtom	Diurnal cover	Dinkins and Shute 1996
<i>Noturus funebris</i>	Black madtom	Cover	Mettee et al. 1996
<i>Noturus gyrinus</i>	Tadpole madtom	Cover, nesting cover	Burr and Warren 1986; Burr and Stoeckel 1999
<i>Noturus gilberti</i>	Orangefin madtom	Nesting cover	Burr and Stoeckel 1999
<i>Noturus hildebrandi</i>	Least madtom	Cover, nesting cover	Mayden and Walsh 1984; Etnier and Starnes 1993
<i>Noturus leptacanthus</i>	Speckled madtom	Cover, probably nesting cover	Mettee et al. 1996
<i>Noturus miurus</i>	Brindled madtom	Cover, nesting cover	Burr and Warren 1986; Mettee et al. 1996; Burr and Stoeckel 1999
<i>Noturus munitus</i>	Frecklebelly madtom	Cover	Etnier and Starnes 1993
<i>Noturus nocturnus</i>	Freckled madtom	Cover	Burr and Warren 1986; Mettee et al. 1996

TABLE 3. Continued.

Species	Common name	Association with large wood	Reference
<i>Noturus phaeus</i>	Brown madtom	Diurnal cover, probably nesting cover	Monzyk et al. 1997
<i>Noturus stigmosus</i>	Northern madtom	Cover	Etnier and Starnes 1993
<i>Pylodictis olivaris</i>	Flathead catfish	Cover, nesting cover	Jackson 1999
<i>Aphredoderus sayanus</i>	Pirate perch	Cover, feeding	Benke et al. 1985; Monzyk et al. 1997
<i>Fundulus olivaceus</i>	Blackspotted topminnow	Cover	Mettee et al. 1996
<i>Lucania goodei</i>	Bluefin killifish	Cover	Mettee et al. 1996
<i>Cottus bairdi</i>	Mottled sculpin	Nesting cover, egg attachment	Rohde and Arndt 1982
<i>Ambloplites ariommus</i>	Shadow bass	Cover	Mettee et al. 1996
<i>Ambloplites rupestris</i>	Rock bass	Cover	Probst et al. 1984; Matthews 1998
<i>Centrarchus macropterus</i>	Flier	Cover	Mettee et al. 1996
<i>Enneacanthus gloriosus</i>	Bluespotted sunfish	Cover	Mettee et al. 1996
<i>Lepomis spp.</i>		Cover (various life stages), feeding	Benke et al. 1985; Matthews 1998
<i>Micropterus dolomieu</i>	Smallmouth bass	Cover	Probst et al. 1984
<i>Etheostoma asprigene</i>	Mud darter	Cover, probable egg attachment	Page et al. 1982; Burr and Warren 1986; Pflieger 1997
<i>Etheostoma artesiae</i>	Redfin darter	Cover	Mettee et al. 1996
<i>Etheostoma boschungii</i>	Slackwater darter	Cover	Etnier and Starnes 1993
<i>Etheostoma chlorosomum</i>	Bluntnose darter	Cover, egg attachment	Page et al. 1982; Etnier and Starnes 1993
<i>Etheostoma chienense</i>	Relict darter	Cover, nesting cover, egg attachment	Piller and Burr 1999
<i>Etheostoma collis</i>	Carolina darter	Cover	Jenkins and Burkhead 1994
<i>Etheostoma colorosum</i>	Coastal darter	Cover	Mettee et al. 1996
<i>Etheostoma coosae</i>	Coosa darter	Egg attachment	Mettee et al. 1996
<i>Etheostoma corona</i>	Crown darter	Nesting cover, egg attachment	Mettee et al. 1996
<i>Etheostoma cragini</i>	Arkansas darter	Cover	Pflieger 1997
<i>Etheostoma davisoni</i>	Choctawhatchee darter	Cover	Mettee et al. 1996
<i>Etheostoma gracile</i>	Slough darter	Cover, egg attachment	Braasch and Smith 1967
<i>Etheostoma histrio</i>	Harlequin darter	Cover, juvenile cover	Warren 1982; Pflieger 1997
<i>Etheostoma lachneri</i>	Tombigbee darter	Cover	Mettee et al. 1996
<i>Etheostoma neopterum</i>	Lollipop darter	Cover, nesting cover, probable egg attachment	Etnier and Starnes 1993
<i>Etheostoma nigrum</i>	Johnny darter	Nesting cover, egg attachment	Jenkins and Burhead 1994
<i>Etheostoma olmstedi</i>	Tessellated darter	Cover, nesting cover, probable egg attachment	Jenkins and Burhead 1994
<i>Etheostoma oophylax</i>	Guardian darter	Cover, nesting cover, probable egg attachment	Etnier and Starnes 1993
<i>Etheostoma parvipinne</i>	Goldstripe darter	Cover, egg attachment	Robison 1977; Johnston 1994
<i>Etheostoma proeliare</i>	Cypress darter	Cover, egg attachment	Burr and Page 1978; Pflieger 1997
<i>Etheostoma punctulatum</i>	Stippled darter	Cover	Pflieger 1997
<i>Etheostoma pyrrhogaster</i>	Firebelly darter	Probable egg attachment	Carney and Burr 1989; Etnier and Starnes 1993

TABLE 3. Continued.

Species	Common name	Association with large wood	Reference
<i>Etheostoma ramseyi</i>	Alabama darter	Cover	Mettee et al. 1996
<i>Etheostoma swaini</i>	Gulf darter	Cover	Etnier and Starnes 1993
<i>Etheostoma tallapoosae</i>	Tallapoosa darter	Spawning cover, probable egg attachment	Mettee et al. 1996
<i>Etheostoma trisella</i>	Trispot darter	Cover	Etnier and Starnes 1993
<i>Etheostoma vitreum</i>	Glassy darter	Egg attachment	Winn and Picciolo 1960
<i>Etheostoma zonale</i>	Banded darter	Juvenile cover	Pflieger 1997
<i>Percina cymatotaenia</i>	Bluestripe darter	Cover	Pflieger 1997
<i>Percina macrocephala</i>	Longhead darter	Cover	Etnier and Starnes 1993
<i>Percina maculata</i>	Blackside darter	Cover, particularly for juveniles	Etnier and Starnes 1993; Pflieger 1997
<i>Percina nigrofasciata</i>	Blackbanded darter	Cover	Etnier and Starnes 1993
<i>Percina sciera</i>	Dusky darter	Cover	Page and Smith 1970; Etnier and Starnes 1993; Pflieger 1997
<i>Percina stictogaster</i>	Frecklebelly darter	Cover	Burr and Page 1993; Etnier and Starnes 1993

Dolloff (1995) demonstrated high use by trout of habitat created by large wood, they were unable to document a direct relation of trout density to the amount of wood in three streams draining wilderness areas in the eastern United States.

Unpublished information regarding the role of large wood as habitat for fishes of the Amazon Basin provides preliminary insights about the role of wood in tropical streams (P. Petry, Fish Division, Field Museum of Natural History, Chicago, personal communication). Many species of fishes are believed to use large wood as their habitat in the Amazon River and its tributaries. This includes several groups of catfishes (families Loricariidae, Pseudopimelodidae, Auchenipteridae, and Ageneosidae). Species of the family Auchenipteridae live among dead trees and branches; they are called driftwood catfishes because they are always found inside logs. Several species of electric knifefishes (Order Gymnotiformes) are also frequently found inside logs. In addition to those fish that actually live inside the logs, many species are associated with the log jams, including many cichlids and characins.

Large wood can be a vital resource for completing life history phases for a host of fish species. Almost half the species associations with large wood are related to reproduction or juvenile rearing (Table 3). Fishes living in streams of the coastal plain, where streambed materials tend to be fine-grained and highly mobile (Fellely 1992), often use large wood for attaching their eggs, spawning cover, or nest cover. For example, logs with intact, deeply ridged bark provide suitable

spawning habitat for minnows of the genus *Cyprinella* (Pflieger 1997), which deposit their eggs in crevices. The large range of the blacktail shiner *Cyprinella venusta* across southeastern U.S. coastal plain streams is thought to be at least partially attributable to its ability to use large wood for egg attachment. Madtom catfishes *Noturus* spp. provide extensive care to nests, eggs, and young and several species nest on the undersides of large wood (Burr and Stoeckel 1999). The federally endangered relict darter attaches its eggs to the underside of sticks or logs, and the male remains to guard the nest site; paucity of woody spawning substrates in its sandy coastal plain habitat is a primary factor limiting recruitment of the species (Piller and Burr 1999). A similar case can be made for other egg attaching darters inhabiting coastal plain and piedmont streams (Table 3).

Beyond Fish

Adding wood to Puerto Rican headwater streams for the purpose of increasing cover for freshwater shrimp did not appear to affect total numbers of shrimp per pool area (Pyron et al. 1999). However, large wood in streams around the world has been found to influence a broad array of aquatic and riparian dependent organisms in addition to fishes and insects. One of the most spectacular examples of dependence on large wood is the giant freshwater crayfish of Tasmania. These animals, known to live for 30 years and reach weights of 4 kg, depend on wood both for food (they peel

and eat layers of rotting eucalyptus logs) and for habitat (Hamr 1996). Instream habitat for the Tasmanian giant crayfish includes submerged logs, root masses, and wood accumulations, all of which are generally available and abundant in streams flowing through intact riparian areas. Another equally unique example is the interaction of large wood and the "fishing mussels" (*Lampsilis australis*, *L. perovalis*, and *L. subangulata*) of the southeastern United States (Haag et al. 1995). Females in this group release their larvae, which are obligate parasites on fishes, in two discrete masses that resemble a pair of small fishes in shape and color. After release, the lures are tethered to the female by a long, transparent mucous strand. As it undulates in the current, the tethered lure mimics movement of small fishes (Haag et al. 1995). After some time, the strand detaches from the female, drifts downstream, catches on wood, and continues "fishing" for the host fish (*Micropterus* spp.) (Haag et al. 1995; Haag and Warren 1999). Although the importance of this "snag and fish" strategy to recruitment has not been documented empirically, the strategy obviously extends temporal and spatial exposure of the lure (and, hence, the larvae) to the target host-fish species.

Perhaps less spectacular, but nevertheless important, is the association of aquatic turtles and wood. A frequently cited cause of decline of turtles in streams and rivers is the loss or deliberate removal of large wood from the channel (Felley 1992; Buhmann and Gibbons 1997). Although few studies have focused on the relationship of turtles to large wood, snags and logs provide them with basking sites (Conant and Collins 1998), particularly the map and false map turtles (genus *Graptemys*). Other turtle species seem to prefer habitats where wood is present. In Whiskey Chitto Creek, a tributary of the Calcasieu River, Louisiana, Shively and Jackson (1985) found that the Sabine map turtle was limited to stream reaches with high numbers of snags. The snags provided both basking areas and a substrate for algae used as food by the turtle (Shively and Jackson 1985; Felley 1992).

In the last 20 years, the list of species associated with, if not dependent on, large wood has grown dramatically. New relationships between wood in the water and many taxa of animals emerge regularly, and there clearly is much to be learned (see also Steel et al. 2003, this volume). Additional research is needed to provide managers with a more complete understanding of the

role of wood in streams including variables such as tree species, amounts, distribution, relations to biota (not only fishes but other vertebrates and invertebrates), and influence on habitat features in small streams. Knowledge gaps notwithstanding, our current knowledge provides a rigorous basis for resource managers to protect, maintain, and begin the complex task of restoring the functional character and features of small streams in forested regions.

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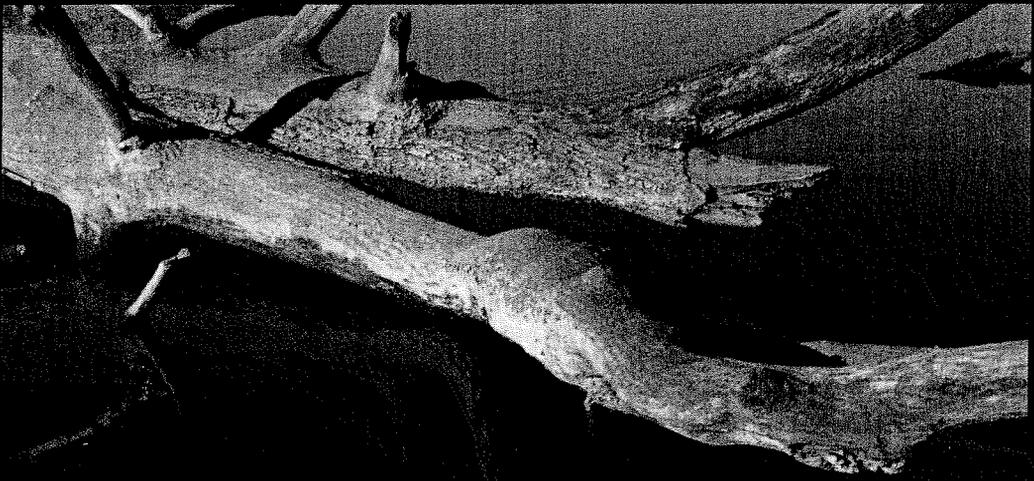
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The Ecology and Management of Wood in World Rivers

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American Fisheries Society Symposium 37

International Conference on Wood in World Rivers
held at Oregon State University, Corvallis, Oregon
23–27 October 2000

American Fisheries Society
Bethesda, Maryland
2003

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