Woody Debris as a Resource for Aquatic Macroinvertebrates in Stream and River Habitats of the Southeastern United States: A Review

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Introduction

Woody debris is a valuable resource to most stream and river ecosystems, especially for the resident aquatic macroinvertebrate fauna (see review by Wallace et al. 1996). In terms of food, macroinvertebrates can directly consume wood (xylophagy; Anderson et al. 1978, Hoffman and Hering 2000) or feed on the biofilms (bacteria, fungi, algae) that develop on wood surfaces (Hax and Golladay 1993, Drury and Kelso 2000, Johnson et al. 2003, Spanoff et al. 2006, Eggert and Wallace 2007). Macroinvertebrates also use wood as habitat, finding refuge inside the wood itself, under residual bark, or in crevasses on the surface (O'Connor 1991). For those taxa that require hard substrates for attachment (e.g., black fly larvae), wood is often used as substrate (Cudney and Wallace 1980, Minore and Weatherly 1994), especially in the absence of stable rocky material. Some insects use wood that extends above the water surface as sites to emerge into adults, and adult females may use that same wood as locations to deposit new eggs into the habitat (Wallace et al. 1993). Large pieces of wood can also affect flow dynamics and retention of organic matter (leaf litter, other wood) in streams (Benke and Wallace 1990). These functions in total would suggest that the presence or absence of woody debris, or variation in wood volume, should have a profound impact on macroinvertebrate diversity, abundance, biomass, and production among streams and rivers of the Southeastern United States. In this review, we assess the literature on woody debris-aquatic macroinvertebrate interactions, specifically in Southeastern U.S. habitats, and focus on variation among three different ecoregions: Coastal Plain, Appalachian Mountains, and Piedmont; updating a similar effort by Wallace et al. (1996).

Coastal Plain Ecoregion

The Southeastern Coastal Plain (Atlantic and Gulf Coast) is a broad area of minimal topographic relief from Maryland south to Florida and west to Louisiana. The area is characterized by very low gradient streams and rivers. Because the Coastal Plain was relatively recently covered by ocean (in terms of geology), streams and rivers have sandy or muddy substrates with minimal bedrock outcrop or cobble/gravel substrate. A "blackwater" stream or river refers to a Coastal Plain habitat where the headwaters originate on the plain itself, and do not flow down from the Piedmont or Appalachians.

Benke et al. (1984) assessed the distribution of macroinvertebrate diversity, abundance, biomass, and secondary production (biomass production over time) of macroinvertebrates at two locations along the Satilla River, a blackwater river in southeast Georgia. When macroinvertebrate taxa of submerged wood (snags) were compared to sandy and muddy benthic substrates, they found that diversity was higher in snag habitat (40 genera from 7 orders) than either sand (20 genera from 4 orders) or mud (17 genera from 4 orders). Ephemeroptera (mayflies) and Plecoptera (stoneflies) were only collected from woody snags. Caddisflies (Hydropsychidae) and blackflies (Simuliidae) numerically dominated snags while non-snag habitat (sand and mud) was dominated by non-biting midges (Chironomidae) and oligochaete worms. While snags accounted for only ~6% of habitat, the habitat contributed half of the biomass and 15-16% of total macroinvertebrate production. In terms of functional feeding groups, collector-filterers dominated on snags and collector-gatherers dominated on sand and mud.

In a sepearate paper, Benke et al. (1985) further assessed macroinvertebrate production in the Satilla River between snags and benthic habitats and related the impact of invertebrate distribution to predatory fish. Standing stock biomass and secondary production was greater on snags (5.8 g/m^2, 57.4 g/m^2/yr) than mud (0.094 g/m^2, 13.9 g/m^2/yr) or sand (0.59 g/m^2, 13.7 g/m^2/yr). The stomach contents of eight fish species were analyzed and invertebrates were identified to genus. The diets of three of the four *Lepomis spp.* as well as pirate perch (*Aphredoderus sayanus*) consisted of at least 60% snag taxa. The spotted sucker (*Minytrema melanops*) was the only fish to feed more from benthic habitats than snags. All eight fish species assessed had consumed some snag-associated invertebrates.

Wallace and Benke (1984) assessed wood habitat in the Ogeechee River (6^{th} order) of eastern Georgia, and Black Creek (4^{th} order), a tributary of the Ogeechee. Adapting line-intersect methods from upland forestry (Warren and Olsen 1964), they calculated wood volume, mass, and surface area in each habitat. They then sampled macroinvertebrates from representative samples of wood, and numbers and biomass or organism was converted to values per unit of wood surface. Back converting to actual wood availability, Wallace and Benke (1984) found that invertebrate biomass on wood in these habitats was at least 1.88 g/m^2 of channel bottom. In an artificial stream-side channel study, Benke et al. (1992) found that the mayflies that commonly occur on snag habitat in the Ogeechee River had rapid growth rates, and diets were primarily based on the bacterial seston and organic matter that flocculates on the wood surface rather than algae.

Smock et al. (1985) studied stream macroinvertebrate production at three sites in a small (2nd order) blackwater stream in South Carolina. When production was compared among five habitat types (wood snags, stream channel sediments, muddy banks, leaf packs, and emergent plants), production on snags was the highest (9.33, 5.77, and 6.99 $g/m^2/yr$ at each site), comprising 28–32% of total production. Biomass exhibited similar trends to production. Filter-feeders and collector-gatherers dominated snags, while only collector-gatherers dominated other habitats. The importance of snag habitat as substrate for filter-feeding insects was also emphasized by Cudney and Wallace (1980) for net-spinning caddisflies in the Savannah River. They suggest that competition for space on snags might be a significant issue structuring populations.

Smock et al. (1989) found that dead wood in two small south Virginia blackwater creeks accumulated into debris dams. These structures altered flow dynamics and they found that organic matter of all types (coarse and fine particles) tended to accumulate around the wood. Further, macroinvertebrate density and biomass was also greatest around the debris dams, probably because the organisms were tracking the levels of organic matter.

In a sandy coastal plain stream (3rd order) in Alabama, Rinella and Feminella (2005) compared macroinvertebrate assemblages between coarse woody debris (CWD) and sandy substrates. Overall biomass was almost 10 times higher in sand than on wood. But diversity (Shannon's index) was lower in sand because the habitat was strongly dominated by chironomid midge larvae. Unlike Benke et al. (1984), they found that percent EPT taxa (Ephemeroptera, Plecoptera, Trichoptera) was not significantly different between CWD and sand. However, 11 taxa collected from woody debris were not collected from sand, including three Megaloptera genera. Rinella and Feminella (2005) also tested whether samples from an artificial substrate sampler (Hester-Dendy) reflected macroinvertebrate compositions on either natural substrate, and concluded that they did not, with results differing significantly from both wood and sand.

In two low-gradient coastal streams of Louisiana, Six Mile and Mill Creeks, Kaller and Kelso (2006, 2007) used experimental approaches to assess the impact of variable CWD surface area on stream macroinvertebrates. In one study (Kaller and Kelso 2006), they collected recently fallen woody debris (with leafs and green bark) and returned it to the laboratory where they aged it for 0, 2, or 6 weeks, which resulted in three different decay classes (II, 0 weeks; III, 2 weeks; and IV, 6 weeks) based on criteria in Robison and Beschta (1990). They then returned the wood to the source habitats to permit macroinvertebrate communities to develop for 5 weeks. However, they did not find a significant relationship between wood decay state, and the density, diversity, evenness, or richness of stream macroinvertebrates. In their second study (Kaller and Kelso 2007), CWD was collected from debris piles on the floodplain; the material was sterilized with an autoclave and then divided into two groups: large (> 10 mm diameter) and small (1–5 mm diameter). This wood was then placed into the streams in pairs, one large with one small, and placement was stratified to include areas with high, medium, and low dissolved oxygen (DO) levels. DO levels were higher in Six Mile Creek (3.4–7.3 mg l^{-1}) than Mill Creek (2.7–3.1 mg l^{-1}). After 5 weeks, they assessed the macroinvertebrates that colonized the wood. Organisms on ambient wood were sampled as a control. Total abundance of macroinvertebrates was higher on the larger pieces of wood, but patterns were driven by only two Diptera genera (*Atherix* and *Corynoneura*). Unexpectedly, total abundance, generic richness, and Shannon's diversity index were all highest in the low DO treatment. Patterns in ambient wood largely mimicked those on the manipulated pieces of wood. Many taxa were generalists, and did not respond to either wood size or DO level.

Everett and Ruiz (1992) demonstrated that the importance of CWD to macroinvertebrates can extend out into tidally influenced channels of a river estuary of Maryland. Using manipulative wood additions and laboratory experiments, they found that grass shrimp (*Palaemonetes pugio*) used CWD more frequently when predatory fish were present, and the presence of CWD increased survivorship of this ecologically important macroinvertebrate.

Braccia and Batzer (2001, 2008) demonstrated that the importance of CWD can also extend out into the lateral floodplains of the 4^{th} order, blackwater Coosawhatchie River in coastal South Carolina. In a descriptive study of floodplain wood (Braccia and Batzer 2001), they found that wood in the wetlands supported greater macroinvertebrate abundance and biomass during winter flooded periods than the dry summer period. However, perhaps unexpectedly, most of the macroinvertebrates on wood during winter floods were non-aquatic, rather than aquatic, and many were probably using the wood as refugia from high water. In an experimental study, Braccia and Batzer (2008) tethered dead sweet gum logs in the Coosawhatchie river channel, the seasonally flooded floodplain, and the adjacent uplands, and then monitored macroinvertebrates on and in the wood over a three year period. Wood in the river was colonized mostly by chironomid midges and wood in the uplands was colonized by an assortment of terrestrial arthropods (elaterid click beetles, termites). Macroinvertebrate assemblages colonizing wood in the floodplain included both aquatic and terrestrial species, but overall shared more similarities with upland wood than river wood.

Appalachian Ecoregion

The Appalachian ecoregion extends from northern Alabama and Georgia through the borders of Tennessee, South Carolina, North Carolina, Kentucky, Virginia, through all of West Virginia, and into Pennsylvania. Stream and rivers tend to be high gradient, with extensive bedrock outcrops, and abundant cobble, gravel, and sand. Small headwater streams dominate this landscape. In terms of macroinvertebrate ecology, Appalachian streams are among the most extensively studied in the world. Remarkably, studies directly assessing the interaction between woody debris and stream macroinvertebrates in the Appalachians are quite limited, being produced largely by a single laboratory group and at a single site.

Wallace et al. (1995) experimentally assessed the impact on the macroinvertebrate community of additions of large woody debris (LWD) to a high-gradient headwater stream in the Coweeta Hydrologic Laboratory of the southern Appalachian Mountains in North Carolina. Large tulip poplar logs (20–30 cm diameter) were placed perpendicular to flow across the entire channel (bank-to-bank) and anchored to create debris dams. Macroinvertebrates were monitored for 4 years in the benthic substrates in stream reaches with and without anchored logs. Log additions reduced scraper and filterer abundance, biomass, and secondary production, and increased collector and predator abundance, biomass, and production. Overall shedder biomass did not change, but trichopteran and dipteran shredder biomass increased, while plecopteran shredder biomass decreased.

Like Wallace et al. (1995), Lemley and Hilderbrand (2000) also assessed the impacts of adding LWD on macroinvertebrates. Their stream, North Fork Stony Creek, Virginia, was somewhat larger (3^{rd} order) and lower gradient. Trees adjacent to the stream were felled, and cut into 4-m length and ~25 cm diameter sections. Fifty logs of seven species were placed systematically in a 250 m section of the stream, while another 250 m upstream section served as a control. Macroinvertebrates were collected from both sections in May just prior to additions, and again one year later; sampling was stratified to cover 5 riffles and 3 pools per reach. In paired riffle and pool treatments, macroinvertebrate assemblages were similar with or without

LWD additions. However, assemblages in pools differed from those in riffles, and LWD additions increased the amount of pool habitat available. Hence, assemblages over the entire reach probably shifted towards a pool macroinvertebrate assemblage of collector gatherers and away from a riffle assemblage of shredders and scrapers.

In a second headwater stream in North Carolina, rather than an addition experiment, Wallace et al. (1999, 2001) conducted a removal experiment to assess the relationship between wood and leaf litter and the aquatic macroinvertebrate fauna. After excluding terrestrial leaf litter inputs for 3 years, all small woody debris (< 10 cm diameter) was removed from the treatment stream (Wallace et al. 1999, 2001); two years later all large woody debris (> 10 cm) was removed (Wallace et al. 2001). After the initial leaf litter exclusion, macroinvertebrate numbers, biomass, and production plummeted (Wallace et al. 1999) and remaining macroinvertebrates focused their consumption on wood (Hall et al. 2000). After 1 year of small wood removal, macroinvertebrate abundance, biomass, and secondary production decreased an additional 47–50% in the exclusion stream over the previous litter-only exclusion levels (Wallace et al 1999). Papers assessing the longer term impacts of small wood removal, and impacts of large wood removal are being prepared.

Eggert and Wallace (2007) used laboratory experiments to assess the relative values of leaf litter, wood itself, and wood biofilms to three macroinvertebrate detritivore species (plecopteran, dipteran, trichopteran) common in southern Appalachian headwater streams. Abilities of detritivores to assimilate wood bioflims and leaves were determined by calculating assimilation efficiencies and ingestion rates. They found that assimilation efficiencies of the three species were greater on wood biofilms (26–36%) than leaves (9–17%), but ingestion rates were higher for leaves (0.09–0.47 g/day) than wood (0.04–0.07 g/day). Coupling these two measures, Eggert and Wallace (2007) determined that the plecopteran (*Tallaperla*) and dipteran (*Tipula*) species were better able to use wood bioflims, but the trichopteran (*Pycnopsyche*) species functioned better on leaf litter. This suggests that wood biofilms might be a more important food resource than previously recognized.

Piedmont Ecoregion

The Piedmont, extending from Pennsylvania to Alabama, is sandwiched between the Coastal Plain and the Appalachians. As such, streams and rivers there tend to be geomorphologically intermediate to the other ecoregions, with intermediate gradients with some rock outcrop but also stream bottoms with extensive shifting sands. Probably because streams in the Piedmont are more impacted by human activities than streams in the Coastal Plain or Appalachians, research on the interaction between woody debris and aquatic macroinvertebrates from the Piedmont is very limited (see also Wallace et al. 1996). In fact, for this review, we only located two studies potentially relevant to our topic, both from the northern extreme of the Piedmont, and even these deal with woody debris and macroinvertebrates in a cursory manner.

Sweeny (1993), in a study of White Creek, Pennsylvania, mostly focused on the impacts of streamside vegetation, but noted that woody debris provided valuable substrate for macroinvertebrates, added heterogeneity to stream habitats, and helped retain organic matter in the channel. He observed that non-forested reaches of stream had minimal woody debris, with stocks decreasing by 15 g/m^2, and speculated that this factor contributes to habitat degradation for macroinvertebrates.

Snyder et al. (2002), in a study on the Pennsylvania/New Jersey border, compared habitat condition and macroinvertebrate community structure between streams with riparian forest dominated by hemlock forest versus those with mixed hardwood forest. Streams with hemlock inputs supported more macroinvertebrate taxa, and 11 taxa strongly favored the hemlock-dominated area (17 weakly favored hemlock, while 5 weakly favored hardwood). Species distribution was more even in hemlock streams. However, overall macroinvertebrate densities were higher in streams with a mixed hardwood riparian zone. The authors speculated that the quality of hemlock woody debris as substrate for macroinvertebrates may play a role in community differences, and further speculated that hemlock decline from a severe insect infestation may have consequences to streams.

Synthesis

Studies from all ecoregions of the Southeastern U.S. suggest that woody debris can be important to macroinvertebrates in streams and rivers. However, as previously maintained by Wallace et al. (1996), the impact of wood on macroinvertebrates appears to differ somewhat between the Coastal Plain and the Appalachians. In the Coastal Plain, the mineral substrate is composed largely of sifting sand and mud, and wood comprises much of the stable substrate in the streams and river. With low gradients, large woody debris may rarely move. While some taxa such as midges and oligochaete worms find sand and mud desirable habitat, the majority of macroinvertebrate taxa focus on the wood as habitat (Benke et al. 1984). Wood condition seems to have minimal influence on its use by macroinvertebrates (Kaller and Kelso 2006), and most organisms associated with wood consume the organic matter that accumulates on or around the wood rather than feeding on the wood itself (Benke et al. 1992), thus it appears that the major value of wood to macroinvertebrates is provided by the physical structure of the material.

In rocky Appalachian streams, macroinvertebrates have ample physical structure to colonize, and that role of wood may be less important. However, much of the importance of wood in the headwater Appalachian streams may still be structural. The presence of large wood in small Appalachian streams appears to alter flow dynamics and organic matter accumulations, and thus results in compositional shifts in macroinvertebrate communities (Wallace et al. 1995, Lemly and Hilderbrand 2000). Wallace et al. (1999) and Hall et al. (2000) indicate that wood could be an important food resource to macroinvertebrates, but their exclusion studies were complicated by the fact that they had already eliminated leaf litter as food, and thus the residual organisms were forced to focus on wood as food. Under more natural conditions, the reliance on wood might be less pronounced. However, Eggert and Wallace (2007) clearly demonstrate that wood can provide macroinvertebrates with highly nutritious food.

Due to a lack of information, we cannot draw conclusions about the importance of wood to aquatic macroinvertebrates in the Piedmont. However, because stream and river substrates have extensive shifting sands (like the Coastal Plains), further exacerbated by high sedimentation rates from human activity, the relatively stable habitat provided by wood is likely quite important.

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