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Influence of Wood on Invertebrate Communities in Streams and Rivers

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Abstract.—Wood plays a major role in creating multiple invertebrate habitats in small streams and large rivers. In small streams, wood debris dams are instrumental in creating a step and pool profile of habitats, enhancing habitat heterogeneity, retaining organic matter, and changing current velocity. Beavers can convert sections of free-flowing streams into ponds and wetlands by killing trees and building dams. In low-gradient rivers, undercut trees that fall into the main channel (snags) are often the only stable habitat for invertebrates and provide a refuge and food resource for fishes as well. Invertebrates may use or require wood as food, but many species simply occupy wood as habitat. Although some species adapt to the woody environment by gouging and tunneling into the wood surface, others obtain their food from allochthonous and autochthonous resources that accumulate on the wood surfaces or are directly filtered from the water column. In streams of all sizes, accumulations of wood are often the hot spots of invertebrate diversity, and snags in Coastal Plain rivers of the southeastern United States support invertebrate production that is among the highest in lotic systems. The distribution of biomass and production among functional groups on wood varies greatly depending on the type of system. Loose streambed wood is colonized especially by shredders (gougers), and stable snags in larger streams and rivers are dominated by filterers and gatherers. High diversity of snag predators can result in complex food-web pathways, and snag taxa can be the major components of invertebrate drift in low-gradient rivers. Snag sampling is becoming a standard part of bioassessment, particularly in low-gradient systems, because snags are recognized as a major site of invertebrate diversity and production. Re-introduction of wood in streams and rivers is becoming an important aspect of restoration and management strategies around the world, as attempts are made to increase biodiversity and refuges both for fishes and their invertebrate prey.

Introduction

> It is interesting to contemplate an entangled bank ... with various insects flitting about, and worms crawling through damp earth ... the production of higher animals, directly follows. [Darwin 1859.]

Charles Darwin chose an entangled bank to illustrate the complexity of life in the final paragraph of his landmark book. What he may not have realized was that this entangled habitat probably continued beneath the surface of the stream or pond in the form of tree roots and dead wood. Associated with this submerged entanglement would have been an entirely different community of aquatic insects and other invertebrates. And similarly, the production of higher life forms (crayfishes, fishes, and so on) would directly follow in the aquatic as well as the terrestrial realm. The value of submerged wood as an important habitat for aquatic invertebrates, particularly in streams and rivers, has been known for at least 50 years (see early references in Hynes 1970), but it has received increased attention in the past 25 years. Although

recognition has been slow, that wood can influence invertebrate communities in many ways is now apparent: creating habitats such as pools, providing substrate on which invertebrates can live, and serving as food. Consequently, wood and its associated invertebrates can be important in the functioning of aquatic systems.

The general study of invertebrates on wood in streams and rivers has coincided with an abundance of related work on the importance of wood to stream structure and function and as fish refuge and food source (for example, Harmon et al. 1986; Dolloff and Warren 2003; Wondzell and Bisson 2003; both this volume).

Much of the work on wood-dwelling invertebrates has been concentrated at specific sites in the United States: Midwestern U.S. rivers (Berner 1951; Morris et al. 1968; Modde and Schmulbach 1973; Nilsen and Larimore 1973; Nord and Schmulbach 1973), Oregon's Coast and Cascade range streams (Anderson et al. 1978, 1984; Dudley and Anderson 1982), southeastern U.S. Coastal Plain rivers (Benke et al. 1979, 1984, 1985, 2001; Cudney and Wallace 1980; Wallace et al. 1987; Benke and Wallace 1997), southeastern U.S. Coastal Plain streams (Smock et al. 1985, 1989, 1992; Thorp et al. 1985), southeastern U.S. Appalachian Mountain streams (Golladay and Webster 1988; Wallace et al. 1995, 1996, 1999), and south-central U.S. streams (Golladay and Hax 1995; Hax and Golladay 1998; Phillips 1997a, 1997b). Several relatively recent studies have been conducted in streams and rivers in Australia (O'Connor 1991, 1992; Humphries et al. 1996, 1998; McKie and Cranston 1998; Sheldon and Walker 1998; Growns et al. 1999), New Zealand (Tank and Winterbourn 1995, 1996; Quinn et al. 1997; Collier et al. 1998; Collier and Halliday 2000), and central Europe (Weigelhofer and Waringer 1999; Hoffmann and Hering 2000; Warmke and Hering 2000).

Some of the earliest hints of the importance of wood-dwelling invertebrates were related to their being a source of fish food (Berner 1951; Morris et al. 1968). Subsequent studies, however, have focused on a wide variety of questions: the role of wood-eating (xylophagous) taxa in processing wood, using wood as invertebrate habitat and food by nonxylophages, wood food webs, invertebrate production on wood, the role of debris dams in creating other habitats and affecting resource availability, effects of flow disturbance on wood invertebrates, and using wood-dwelling species in bioassessment.

Previous reviews of invertebrates on wood have focused on identifying species associated with wood (Dudley and Anderson 1982), how invertebrates use wood for habitat and food (Hoffmann and Hering 2000), and how wood contributes to invertebrate biodiversity in the southeastern United States (Wallace et al. 1996). We attempt to review and synthesize a wide variety of approaches that suggest wood is important for invertebrates in habitats ranging from small streams to large rivers. Unfortunately, wood has been removed from lotic systems of all sizes, often being associated with channelization and navigation in medium-to-large rivers. Consequently, much of the invertebrate diversity and production supported by woody habitats have disappeared, and their ecological functions can be studied and appreciated only in relatively undisturbed systems.

Wood-Created Habitat

The physical presence of wood creates invertebrate habitats in any freshwater ecosystem because it provides a solid substrate that decays slowly when submerged, and large wood lasts from decades to centuries (Harmon et al. 1986; Wallace et al. 1996, 2001a; Hyatt and Naiman 2001; Bilby 2003, this volume). Wood habitat often is found along the shoreline of natural lakes, where it blows in from surrounding forest, or in newly created reservoirs, where entire trees may be submerged (McLachlan 1970; Boon 1984; Bowen et al. 1998). More commonly, however, wood is a major natural feature of streams and rivers, where it accumulates from mortality of riparian trees or branches (Anderson and Sedell 1979; Triska and Cromack 1980; Wallace and Benke 1984). The major types of wood-created habitats in lotic systems are loose stream wood, represented by individual branches that lay on the stream bottom; wood dams, formed when trees fall across small-to-medium streams or when smaller branches fall and accumulate at specific stream sites; beaver ponds and wetlands, formed behind dams built by beavers (*Castor canadensis* in North America) on small-to-medium streams; and snags (fallen trees and branches), accumulating and often anchored along the banks of medium-to-large rivers (Figure 1).

Wood accumulations

Wood accumulations dramatically alter a stream's longitudinal profile by disrupting the flow of wa-

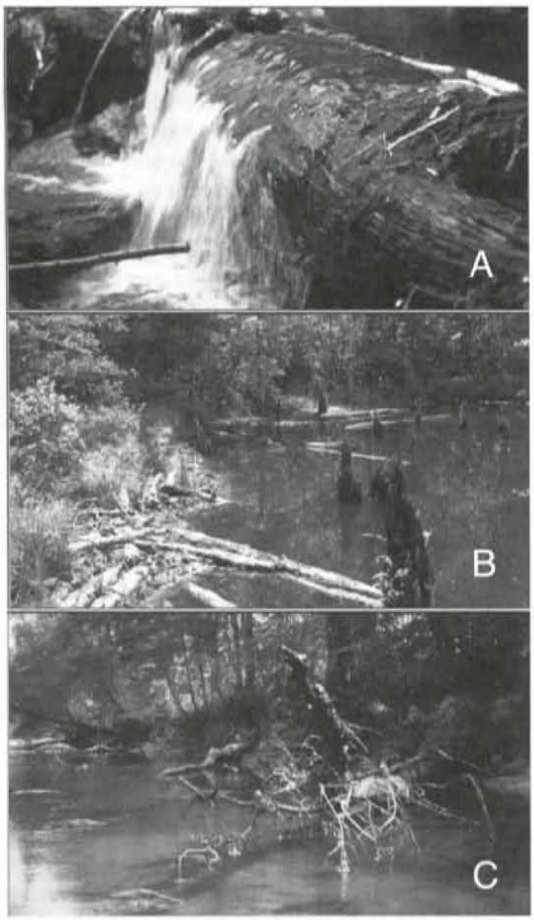

FIGURE 1. Wood-created habitats in lotic systems: (A) wood dam created by a log in a small stream in the southern Appalachian Mountains (note the plunge pool to the left and sediment accumulation to the right); (B) beaver dam built on a small stream in the southeastern U.S. Coastal Plain (note dam to the left consisting of logs and mud, and wetland with stumps of killed trees to the right); (C) snags along bank of a medium-sized river in the southeastern U.S. Coastal Plain at a very low river stage (note, all wood in the photograph will be submerged and colonized by aquatic invertebrates when the river rises.

ter and influencing an array of habitat features that affect the invertebrate assemblages and their role in the structure and function of stream communities (Swanson and Lienkaemper 1978; Harmon et al. 1986; Huryn and Wallace 1987; Trotter 1990; Gregory 1992; Wallace et al. 1995, 1999). In small, high-gradient streams, such obstructions create a stair-step profile that dramatically alters the streams' physical nature (Bilby and Likens 1980). Upstream of the dam, streams are deeper, current velocities lower, retention of particulate inorganic and organic matter higher, and substrate particles smaller. This depositional zone creates an invertebrate habitat different from that provided by erosional zones (such as riffles), with higher current velocities, larger substrate, and so on. A turbulent plunge pool may develop downstream of the dam, followed by riffle areas. All of these factors influence the composition of invertebrate assemblages, such as the distribution among functional feeding groups, and the role that they play in trophic and nutrient dynamics of stream ecosystems (Bilby 1981; Molles 1982; Newbold et al. 1982; Melillo et al. 1983; Smock et al. 1989).

Wood accumulations also are important features in low-gradient streams. Although the stair-step profile is far less pronounced, these obstructions still create depositional areas upstream that retain organic matter and represent a more pool-like environment (Smock et al. 1989). Alternatively, wood accumulations can develop along the margins of larger low-gradient streams and increase the diversity of benthic habitat patches (Palmer et al. 1996). The wood-formed dams of low-gradient streams, however, appear to be more of a hot spot for invertebrate diversity, abundance, biomass, and secondary production than those of high-gradient systems, given the unstable nature of sediments both upstream and downstream of the dam (Roeding and Smock 1989; Smock et al. 1989, 1992; Weigelhofer and Waringer 1999).

Beaver dams

In addition to debris dams formed by tree and limb fall and physical processes, dam-building by beavers can be a major force in creating ponds and wetlands, typically on first- to fourth-order streams (McDowell and Naiman 1986; Naiman et al. 1988; Clifford et al. 1993; Gurnell 1997; Pollock et al. 2003, this volume). These ecosystem engineers (Jones et al. 1994) topple trees, cut wood, and build and repair their dams. In doing so, they create pond and wetland habitats, many of which last for decades. Rather than simply creating a pool and riffle sequence like those with most dams formed by fluvial accumulations of wood, multiple beaver dams along a stream can create a major shift in the balance between lotic and lentic habitats for invertebrates (Naiman et al. 1988). Such lentic environments are colonized by an entirely different invertebrate assemblage than

found in lotic habitats (McDowell and Naiman 1986; Benke et al. 1999; Wissinger and Gallagher 1999; Rolauffs et al. 2001). Beaver dams create pond-like environments in regions of relatively high gradient or shallow wetland environments in areas of low gradient. The beaver dam itself represents a habitat that can be colonized by invertebrates (Clifford et al. 1993; Rolauffs et al. 2001). Like most dams, beaver dams tend to modulate discharge regimes and alter stream chemistry downstream, which strongly affect invertebrate diversity and abundance (Smith et al. 1991).

River snags

In addition to the profound effect of wood in forming impoundments on first- to fourth-order streams, stabilized wood can itself be a major habitat, especially in medium-to-large rivers and particularly in Coastal Plain regions where the gradient is low (Wallace and Benke 1984; Maser and Sedell 1994). Riparian trees are undercut and fall along the bank of the channel, creating snag habitats that can remain from decades to centuries because the rate of decomposition of inundated wood is so slow. Historical records show that wood was abundant in many rivers of the United States (Sedell and Luchessa 1982; Sedell et al. 1982, 1990; Sedell and Froggatt 1984; Wallace and Benke 1984). During much of the 19th century and early 20th century, however, extensive snag removal eliminated most wood from all large rivers in the United States, including the Mississippi, and we can only speculate about the importance of this wood to these historical aquatic habitats and to the invertebrate species that must have colonized them. Today, wood is still seen in considerable abundance in some of the medium-sized low-gradient rivers of the U.S. Coastal Plain (Wallace and Benke 1984; Benke and Wallace 1990), and its important role for invertebrate communities has become apparent (Benke et al. 1979, 1984; Cudney and Wallace 1980).

In some large rivers, the accumulation of wood in the channel rivaled the influence of wood dams and beaver dams in altering the character of small streams. A well-documented example was the formation of the "Great Raft" on the Red River in northwestern Louisiana, USA (Triska 1984; McCall 1988). Over a period from the late 1400s to the mid-1800s, wood from riparian trees formed enormous debris dams that blocked the channel for more than 400 km and formed a series of large lakes along the Red River (Triska 1984). About 70 years (1833–1904) of wood dam and snag removal, levee projects, and dredging ultimately resulted in a cleared, wide meandering channel (Triska 1984). We do not know how many lowland rivers had wood similar to the Great Raft (Triska 1984). The Great Raft and studies of wood in smaller rivers only provide a clue to what ecological conditions and invertebrate assemblages of larger rivers must have been. Even in desert rivers, where snags are uncommon, driftwood can provide an important substrate that expands the diversity of niches available to invertebrates, as has been shown by recent work in the Colorado River (Haden et al. 1999).

In summary, wood plays a major role in creating habitats in streams and rivers of many sizes and in many geographic areas, and this role is often in forming dams that create lentic depositional environments along the river's course. In spite of this very important habitat-creating role of wood, much of the remainder of our review will primarily address the invertebrates that actually colonize wood surfaces and use it for habitat and food.

Wood as Habitat and a Potential Food Source

That invertebrates colonize any solid substrate in flowing water is widely known (Berner 1951; Fremling 1960). For example, artificial substrate samplers made of mineral (such as a rock basket) or organic (such as a Hester-Dendy multiplate sampler) materials have been used for many years to assess water quality. Similarly, that invertebrates readily colonize the branches of inundated trees in both lotic (Berner 1951; Nilsen and Larimore 1973; Benke et al. 1979, 1984; Cudney and Wallace 1980) and lentic systems (McLachlan, 1970; Boon 1984) has been known for decades. Invertebrates are also known to colonize leaves and small branches deposited on stream bottoms (Anderson et al. 1978; Anderson and Sedell 1979). Although mineral substrates have received much more attention, wood sometimes can provide a superior invertebrate habitat. Like mineral substrates, wood can be relatively stable if anchored in the stream, can provide good sites for invertebrate attachment, and can allow colonization of biofilms and plants that provide additional habitat and food. Unlike mineral substrates, however, wood can be eaten by some species, is soft enough to be gouged to create refuges, and is particularly effective in trapping other organic matter with its

branching structure. Thus, wood can provide access to a wider variety of food than is available on mineral substrates. This same complexity also creates habitats and provides refuges for motile animals that do not necessarily colonize the wood itself, a well known phenomenon for fishes (Fausch and Northcote 1992; Lehtinen et al. 1997; Monzyk et al. 1997; Quist and Guy 2001; Dolloff and Warren 2003; Zalewski et al. 2003, this volume) but a less well-established one for large invertebrates such as shrimp (Everett and Ruiz 1993; Pyron et al. 1999).

Invertebrates use wood in many ways during all stages of their life cycle, regardless of their food source (Table 1). Adults use wood for resting and reproductive activities, and they deposit eggs on wood both above and below the water line. Many invertebrates, particularly insect larvae, use wood as a refuge by hiding under loose bark, by tunneling, and by occupying crevices or creating them by gouging (such as the filtering caddisfly *Macrostemum*). Some insect larvae use small pieces of bark and twigs to build mobile cases, such as the caddisflies *Heteroplectron* and *Pycnopsyche*. Perhaps the major reason for invertebrates being found on submerged wood is that they can exploit numerous food resources by using a wide variety of feeding strategies. Finally, many insects enter the pupal stage firmly attached to the wood surface or in the wood or use partially submerged wood to climb out of the water for emergence.

Dudley and Anderson (1982) were among the first to draw attention to the potential for wood as an invertebrate food source by surveying various wood-associated invertebrates in North America. More recently, Hoffmann and Hering (2000) classified the fauna associated with wood into three categories based on the relative degree of wood-feeding (xylophagy) exhibited by various species of macroinvertebrates. Some species are found *only* on wood and restricted to feeding on it (obligate xylophages). Others feed on wood to some degree (facultative xylophages) but also eat leaf litter. And some species have an affinity for wood substrates, but little of their diet is contributed by wood itself (nonxylophage). A more traditional classification would place xylophages into the shredder functional feeding group (Cummins and Merritt 1996; Wallace and Webster 1996). Nonxylophagous species would fall into any of the other functional groups (scrapers, gatherers, filterers, and predators).

Obligate xylophagous macroinvertebrates are dominated by miners, gougers, and tunnelers (Hoffmann and Hering 2000). These authors recognized some caddisflies (Trichoptera), beetles (Coleoptera), and true flies (Diptera) as obligate xylophages in central Europe (their Table 3), but many examples come from other parts of the world. Examples common to Europe and North America include caddisflies such as several *Heteroplectron* spp., elmid beetles, chironomids such as *Stenochironomus* spp., and tipulids such as *Lipsothrix* spp. Many species of chironomids can be especially common as wood miners and tunnelers (Cranston and Oliver 1988; Borkent 1984; Kaufman and King 1987; Anderson 1989; Cranston and Hardwick 1996). The chironomid *Xylopus par* tunneled into soft (decayed) wood to depths of 2 cm, and attained densities of 7,600/m^2 on natural wood and more than 20,000/m^2 on wood baits (Kaufman and King 1987). *Lipsothrix* spp. are associated with wood in advanced stages of decomposition, but the elmid *Lara avara* and the caddisfly *H. californicum* are gougers of firm waterlogged wood (Anderson et al. 1978; Anderson 1989). Presumably, the wood gouged and consumed by *L. avara* is very low in food quality because the beetle's larvae have the slowest growth rates and the longest life cycles (5–6 years) published for a stream insect (Steedman and Anderson 1985). On the other hand, many species of chironomids, such as *X. par*, can complete development in a year or less (Kaufman and King 1987). Collier and Halliday (2000) used gut and stable isotope analyses to demonstrate that 66% of the body carbon of *Pycnocentria funera* was derived from wood, with lesser amounts coming from wood for other coexisting species, in several New Zealand streams.

Facultative xylophagous macroinvertebrates are common in small streams where wood forms dams or lies on the streambed, rather than as a fixed element in the current. Dudley and Anderson (1982) identified several invertebrates that were associated with wood in North America, but the degree of xylophagy was not specified. In a companion paper, however, Pereira et al. (1982) examined gut contents of 108 taxa of lotic insects and found that 45 of them contained a large amount of wood; some of the insects probably required wood as food and others did not. Other early studies suggested that xylophagy was relatively common in streams in New Zealand (Anderson 1982) and Australia (Chessman 1986). Hoffmann and Hering (2000) recognized several species of facultative xylophages in Europe (their Table 2), but many additional taxa were suspected

TABLE 1. Potential uses of wood by stream invertebrates (modified from Wallace et al. 1996).[a]

Invertebrate use of wood	Comments	References
Adult activities	Resting sites; copulation; emergence	Dudley and Anderson 1982 Steedman and Anderson 1985 Dudley and Anderson 1987
Oviposition site	Eggs deposited above or below waterline	Dudley and Anderson 1982 Hoffman 2000
Direct food source		
Xylophagy (obligate or facultative)	Feeding directly on wood and epixylic biofilm coating it	Pereira et al. 1982 Anderson et al. 1984 Anderson et al. 1978 Hoffmann 2000 Steedman and Anderson 1985 Chergui and Pattee 1991 Roeding and Smock 1989 Collier and Halliday 2000
Predators of primary consumers	Invertebrate predators feeding on other snag invertebrates	Wallace et al. 1987 Benke et al. 2001 Smith and Smock 1992
Habitat and indirect food source		
Retention of coarse particulate organic matter as food	Litter trapped by wood and consumed by shredders	Wallace et al. 1987 Bilby and Likens 1980 Wallace et al. 1995 Smock et al. 1989 Roeding and Smock 1989 Díez et al. 2000
Retention of fine particulate organic matter as food	Seston (microbially enriched) trapped by wood and consumed by gatherers	Wallace et al. 1987 Edwards and Meyer 1990 Benke et al. 1992 Bilby and Likens 1980 Wallace et al. 1995 Díez et al. 2000
Biofilm on wood as food	Biofilm growth on snags consumed by grazers or gatherers	Wallace et al. 1987 Couch and Meyer 1992 Wallace et al. 1996 Tank and Winterbourn 1995, 1996 Golladay and Sinsabaugh 1991 Tank and Webster 1998 Tank et al. 1998
Filter-feeding of seston	Insect attachment to snags (such as black flies) or net building (hydropsychid caddisflies) for filtering	Wallace et al. 1987 Benke and Wallace 1997 Edwards and Meyer 1987 Edwards 1987 Wallace et al. 1977
Refuge from predators		
Woody material for cases	Caddisfly cases	Anderson et al. 1978 Wiggins 1998
Retreat construction	Gouging to build retreats (hydropsychid caddisflies)	Wallace and Sherberger 1974 Wallace et al. 1977
Hiding places	Crevices, loose bark	Anderson et al. 1978
Pupation site	Stable substratum or refuge under loose bark	Dudley and Anderson 1982 Hoffman 2000

[a] See also Hoffman and Hering (2000).

of requiring wood (their Table 4). One interesting example of a facultative xylophagous insect is the lepidostomatid caddisfly *Lasiocephala basalis* (Kol.), described from a third-order German stream by Hoffmann (2000). This "shredding" caddisfly's gut contents varied according to the substrate with which larvae were associated, consisting largely of wood fragments when the insect was found on wood or alder roots, leaf material and amorphous detritus when it was found in leaf litter, and amorphous detritus when it was collected from stone substrates. Similarly, Hall et al. (2000) showed that when litter was experimentally excluded from a southern Appalachian stream, *Tipula* spp. shifted from a diet of predominantly leaf litter to one of mostly wood.

Among the nonxylophagous invertebrates are scrapers and gatherers that feed on epixylic biofilms that often coat submersed wood. These biofilms consist of algae, fungi, bacteria, protists, amorphous detritus, and extracellular polysaccharides, which can develop from in situ production or from the deposition or flocculation of seston from the water column (Couch and Meyer 1992; Tank and Webster 1998). Virtually all components of epixylic biofilms are consumed by scrapers and gatherers; when gut contents are examined, what is found is distinguished only as amorphous detritus (Wallace et al. 1987). In some systems, fungi may develop more extensively on woody substrates than on leaf detritus (Golladay and Sinsabaugh 1991), and in New Zealand streams, ^{14}C-glucose incorporated into fungi and bacteria was at least partially assimilated by grazing amphipods (Tank and Winterbourn 1995). In U.S. Coastal Plain rivers, radio-labeled bacteria, deposited on snags from the seston, were shown to be readily assimilated by gathering mayflies (Edwards and Meyer 1990). Epixylic biofilms in Coastal Plain rivers may be enhanced by flocculated dissolved organic carbon and fine seston particles from the water column that provides the bulk of food for highly productive gathering invertebrates (Wallace et al. 1987; Benke et al. 1992; Couch and Meyer 1992; Benke and Jacobi 1994). Biofilms are known to develop within two weeks after exposure of wood to river water (Couch and Meyer 1992), which corresponds well with rapid invertebrate colonization on introduced woody substrates (Van Arsdall 1977; Thorp et al. 1985). Macroinvertebrate colonization and species richness has been positively correlated with development of biofilm on organic substrates (Hax and Golladay 1993).

Filterers also can be an important component of nonxylophagous invertebrates on wood, particularly on snags in Coastal Plain rivers where the benthic habitats are dominated by shifting sand and stable substrate is limited (Cudney and Wallace 1980; Benke et al. 1984; Smock et al. 1985; Benke and Wallace 1997). Filterers do not necessarily depend on biofilms because their food (drifting organic particles and drifting animals) is produced elsewhere in the system and delivered by the current. Gut analyses of snag-dwelling filterers from the Ogeechee River showed that they consumed large quantities of amorphous detritus from the seston (Wallace et al. 1987). Analyses of seston and feeding studies using labeled foods supplied to filtering black flies suggest that bacteria, bacterial extracellular polysaccharide, and protists may all be important components in the diet of filterers in the Ogeechee River (Edwards 1987; Edwards and Meyer 1987; Carlough and Meyer 1989, 1991; Carlough 1994; Couch et al. 1996). Other dominant filtering groups, such as chironomid midges and caddisflies (Wallace et al. 1987), are also likely to depend heavily on these microbial components.

Predators are a nonxylophagous group inhibiting wood substrates that have received relatively little attention. Most studies of wood-dwelling predators have been conducted in the southeastern United States; they suggest that predaceous species (dragonflies, damselflies, perlid stoneflies, megalopterans, ceratopogonids, and tanypodine chironomids) could be found on any solid substrate (Benke et al. 1984, 2001; Smock et al. 1985; Smith and Smock 1992). Nonetheless, the flattened bodies of several perlid stoneflies and the hellgrammite *Corydalus cornutus* are well adapted to hiding under loose bark of well-conditioned wood. Not surprisingly, these wood-dwelling predators consume coexisting primary consumers, but detailed analyses suggest that predators of differing sizes and species have specific preferences for prey (Smith and Smock 1992; Benke et al. 2001). In addition to insects generally considered to be predators, hydropsychid caddisflies from Ogeechee River snags are omnivores that consume substantial numbers of chironomids and mayflies (Benke and Wallace 1997; Benke et al. 2001).

Invertebrate Assemblages on Wood

Quantitative studies are often necessary for understanding the structural and functional characteristics of invertebrate assemblages found on wood. Such studies require both sampling inver-

tebrates and quantifying the wood itself. Invertebrate assemblages have been assessed in various ways: by determining invertebrate life history, density, biomass, population dynamics, functional groups, secondary production, and food webs; and by contributions to drift, fish prey, and stream biodiversity.

Quantifying invertebrate assemblages on wood

Sampling wood-dwelling invertebrates in lotic systems can be difficult, particularly in large rivers. Access to wood in large rivers is virtually impossible from depths greater than 1 m, especially with swift currents and high turbidity. Scuba diving or snorkeling in swift currents near submerged trees can be dangerous. Therefore, unless waters are shallow (<1 m), wood samples have usually been collected from a boat where portions of the wood are just below the surface or partially sticking out of the water. Large wood is especially difficult to sample because it cannot be lifted from the water by hand. Sampling wood in small streams can be somewhat easier, but it is fraught with problems—such as whether the wood is normally submerged or inaccessible to aquatic fauna because it is buried in sediments or out of the water, or obtaining a "representative" sample from a wood-formed dam.

To assess the importance of invertebrates on wood, not only must wood samples be retrieved, but their contributions must be compared to those found in traditional habitats on the streambed (that is, sand, mud, gravel, cobble, and bedrock). Such a comparison may include at least two major steps: developing a quantitative sampling approach in which population variables (density, biomass, production) can be calculated per unit area of habitat surface and quantifying the wood habitat itself to convert habitat-specific values to streambed values.

The general sampling approach is to remove the wood from the stream in a way that minimizes loss of invertebrates. Once the wood is removed from the stream, invertebrates are typically brushed, picked, and washed from the wood surface. Then, the wood surface area is calculated so that density, biomass, or production can be presented per square meter of wood surface. In the case of wood-mining chironomids, however, a combination of multiple washings and emergence over several months has been necessary to estimate density (Anderson 1989).

Removing wood from streams and rivers can be as simple as carefully lifting the wood from the water and cutting it into transportable pieces (Nilsen and Larimore 1973; Cudney and Wallace 1980; Golladay and Hax 1995; Phillips 1997b; Hax and Golladay 1998; Spänhoff et al. 2000). Alternatively, some investigators have surrounded the snag with a collecting device so that organisms are not lost during retrieval. Smock et al. (1985) sampled snags in small streams by placing a bucket around the wood before cutting it. Others have collected snags by placing a mesh net around the snag before cutting off a section with a saw (O'Connor 1992; Phillips and Kilambi 1994a, 1994b).

Some investigators have built devices specifically for snag sampling. Benke et al. (1984) used a 45-cm longitudinal sieve with handles and a notch at each end (Figure 2). It was placed under an intact snag (submerged tree branch) and then lifted out of the water so that the wood at each end could be cut off with clippers or a saw. Delong et al. (1993) designed a more elaborate sampler consisting of plastic tubing and Nitex mesh that could be closed around the snag before it is cut. Unlike previously described samplers, the one designed by Growns et al. (1999; snag bag) could be used for large wood (>10-cm diameter) impossible to retrieve from lowland Australian rivers. Their mesh bag was wrapped around the snag and held in place with Velcro strips as invertebrates were brushed from the snag into the net.

Once invertebrates are removed from individual snags, the surface area sampled must be

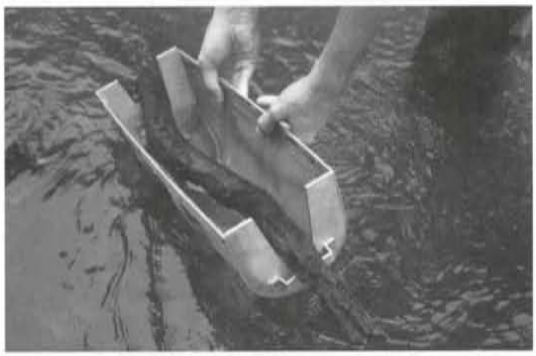

FIGURE 2. Longitudinal sieve sampler (45 cm long) for retrieving snags up to 8 cm in diameter. The sampler is placed under snag before it is pulled out of the water. Excess wood is clipped or sawed off each end, and the remaining piece is placed in a plastic bag, along with any invertebrates that dropped into the sieve.

measured if numbers are to be converted to square meter of snag surface. Most investigators measure the length and diameter of wood in the laboratory after the invertebrates have been removed (Cudney and Wallace 1980; Benke et al. 1984), but Growns et al. (1999) measured wood in place after they brushed invertebrates into their snag bag. Spänhoff et al. (2000) estimated wood surface area in the laboratory by covering the wood with aluminum foil after invertebrates were removed, then weighing it and determining an area-to-weight relation.

Sampling wood from accumulations can be more difficult than sampling individual branches because wood pieces are jammed together tightly and attempts to dislodge single pieces would likely lose many of the invertebrate colonists. Smock and others (Roeding and Smock 1989; Smock et al. 1989, 1992) sampled entire wood dams by placing a 5-mm seine downstream of each dam to collect large invertebrates swept away as the dam was disassembled. Numbers were converted to square meter of streambed, based on the surface areas covered by the dam. Weigelhofer and Waringer (1999) sampled the vertical distribution in invertebrates in wood dams by driving a 10-cm-diameter plastic tube (with a 100-mm mesh net at the bottom end) horizontally into the dam in an upstream direction. Protruding twigs were cut from the anterior opening with clippers as the tube was withdrawn from the dam. Their volumetric estimates of wood could also be converted to numbers per square meter of streambed. Quantitative sampling of invertebrates from beaver dams has proved extremely difficult because they are typically too large to be sampled as a unit as Smock et al. (1989) did with small wood accumulations. Clifford et al. (1993) collected qualitative samples by disturbing and disassembling small sections of dam so that invertebrates were swept into a net. Rolauffs et al. (2001) obtained indirect estimates of invertebrate abundance and production in stream, beaver dam, and beaver pond through the use of emergence traps.

Because natural snags are often difficult to retrieve from rivers, several investigators have used artificial snags in attempts to characterize and quantify the wood assemblages (Nilsen and Larimore 1973; Thorp et al. 1985; Anderson 1989; O'Connor 1991; Hax and Golladay 1993; Tank and Winterbourn 1995, 1996; Magoulick 1998; McKie and Cranston 1998; Spänhoff et al. 2000). Humphries et al. (1998) compared various methods for sampling invertebrates in large rivers and found that artificial snags were superior to onion bag baskets, airlift sampling of sediments, and sweep-net sampling of edges for both diversity and quantitative analyses. For some xylophagous taxa, however, it may be necessary to condition wood in the stream for several years before it becomes a suitable habitat (Anderson 1989). Although artificial snags can be useful for various purposes (such as estimating colonization fluxes), assessing how representative they might be is impossible without quantitative sampling of natural snags.

If numbers of invertebrates per snag surface area are to be converted to a common unit for an entire lotic system, the amount of wood in the stream or river must be quantified. Wallace and Benke (1984) modified a line-intersect technique used by foresters so that surface area of wood could be calculated per square meter of riverbed as a function of river height in the Ogeechee River, a Coastal Plain river in the southeastern United States. Then, the number of invertebrates per square meter of snag surface could be converted to number per square meter of riverbed (Benke and Parsons 1990). O'Connor (1992) and Humphries et al. (1996) used the same method to estimate invertebrate densities on wood in lowland Australian streams and rivers. In contrast, Smock et al. (1985) estimated the surface area of all inundated pieces of wood (a census) along a 50-m reach of a second-order Coastal Plain stream in South Carolina. Gippel et al. (1996) compared the line-intersect method with census estimates and aerial photography in a lowland Australian river and concluded that the line-intersect method overestimated wood abundance, and offered suggestions about how overestimation could be reduced. Similarly, when Wallace et al. (2001a) compared the line-intersect method with direct wood removal in a mountain stream, they also found the method produced overestimates for large wood. In contrast, small wood was slightly underestimated by the line-intersect method compared to actual wood removal (Wallace et al. 2001b). Because the line-intersect method is the only alternative means of quantifying wood, aside from a complete wood census or aerial photography, investigators should take steps to assess its accuracy in their specific situation.

Abundance, biomass, production, and biodiversity

Invertebrates on wood have been quantified in studies from around the world, but the variation

TABLE 2. Quantitative studies of invertebrates on wood in streams and rivers; studies are grouped by location (state or country).[a]

Stream and rivers (no. streams or sites)	Location (state or country)	Stream order	Discharge (m^3/s)	Taxa included	Type of analysis	Reference
Coast Range (3)	Oregon	1, 3, 6	0.3, 0.8, 38	All	B	Anderson et al. 1978 Anderson et al. 1984
Cascade Range (4)	Oregon	1, 3, 5, 7	0.15, 2.2, 20, 200	All	B	Anderson et al. 1978
Cascade and Coast ranges (13)	Oregon			Tipulidae	N	Dudley and Anderson 1987
Berry Creek	Oregon	2	<0.015	All	N	Anderson 1989
San Joaquin River (25)	California			All	N, R	Brown and May 2000
Satilla River (2)	Georgia	6	28-62	All	N, B, P, R	Benke et al. 1979, 1984
Ogeechee River	Georgia	6	67	Simuliidae	N, B, P, R	Benke and Parsons 1990
Ogeechee River	Georgia	6	67	Ephemeroptera	N, B, P, R	Jacobi and Benke 1991 Benke and Jacobi 1994
Ogeechee River	Georgia	6	67	Trichoptera	N, B, P, R	Benke and Wallace 1997
Ogeechee River	Georgia	6	67	Chironomidae	N, B, P, R	Benke 1998
Ogeechee River	Georgia	6	67	Coleoptera	N, B, P, R	Benke 2002
Ogeechee River	Georgia	6	67	Predators	N, B, P, R	Benke et al. 2001
Savannah River	Georgia			Trichoptera	N, B, P, R	Cudney and Wallace 1980
Cedar Creek	South Carolina	2	1.2	All	N, B, P, R	Smock et al. 1985
Steel Creek	South Carolina		1.3	All	N, R	Thorp et al. 1985
Little Tennessee River	North Carolina	6		All	B	Wallace et al. 1996
Buzzard's Branch and Colliers Creek	Virginia	1	<0.1	All	N, B, P, R	Smock et al. 1989, 1992

TABLE 2. Continued.

Stream and rivers (no. streams or sites)	Location (state or country)	Stream order	Discharge (m^3/s)	Taxa included	Type of analysis	Reference
Buzzards' Branch	Virginia	1	<0.1	predators	N, B, P, R	Smith and Smock 1992
Fleming Creek	Michigan	3		All	N, R	Magoulick 1998
Chippewa River	Michigan	4		Chironomidae	N, B	Kaufman and King 1987
St. Regis River	New York	4		All	N, R	Hax and Golladay 1993
3 streams	Arkansas	1, 2, 3, 4		Trichoptera	N, R	Phillips 1994
3 streams	Arkansas	1, 2, 3, 4		Coleoptera	N, R	Phillips 1995
3 streams	Arkansas	1, 2, 3, 4		Plecoptera	N, R	Phillips and Kilambi 1994a
3 streams	Arkansas	1, 2, 3, 4		Ephemeroptera	N, R	Phillips and Kilambi 1994b
3 streams	Arkansas	1, 2, 3, 4		Diptera	N, R	Phillips and Kilambi 1994c
3 streams	Arkansas and Texas	2, 3, 4		Coleoptera	N, B, P	Phillips 1997a
3 streams	Arkansas and Texas	2, 3, 4		Coleoptera	N, B, P	Phillips 1997b
Sister Grove Creek	Texas	Intermittent		All (macro)	N, R	Hax and Golladay 1998
Sister Grove Creek	Texas	Intermittent		Meiofauna	N	Golladay and Hax 1995
Elm Fork	Texas			Trichoptera	N, B, P	Johnson et al. 1998
Marmaton River	Missouri	7	8.8	All	N, B	Rabeni and Hoel 2000
Marais des Cygnes River	Missouri	7	61	All	N, B	Rabeni and Hoel 2000
Pranjip-Creightons Creek	Australia		2	15 most common	N, B	O'Connor 1992
Ladberger Mühlenback and Ibbenbürener Aa	Germany	2, 3		All	N, R	Spänhoff et al. 2000
Weidlingbach (Danube)	Austria	3	0.045	All	N	Weigelhofer and Waringer 1999

[a]N = density, B = biomass, P = production, R = taxonomic richness.

in approaches and lack of consistent units of measure make comparisons and generalities difficult (Table 2). Sampling has sometimes been done with natural snags and wood accumulations, and at other times, colonization of introduced woody substrates has been measured. Invertebrates on wood have been quantified by using density, biomass, or production, sometimes apportioning one of more of these measures into functional feeding groups (Cummins and Merritt 1996; Wallace and Webster 1996). Sometimes, entire invertebrate assemblages have been analyzed, but other studies have focused on single species, small species groups, or orders (Table 2).

Density (number per square meter of snag surface area) for entire invertebrate assemblages has been estimated in several studies and varies greatly (Table 3). Invertebrate density estimates on snags from Germany, Australia, Texas, and Missouri were relatively low (<5,000/m^2), but most other estimates approached or exceeded 10,000/m^2. In an early study on the small (about 1 m^3/s) Kaskaskia River, Illinois, densities averaged more than 22,000/m^2 on three natural logs but reached 96,000/m^2 on introduced wood substrates heavily colonized by oligochaetes (Nilsen and Larimore 1973). Average density on snags collected monthly from two sites on the Satilla River, a medium-sized Coastal Plain river in Georgia, exceeded 26,000/m^2 (Benke et al. 1984). Average density from the Ogeechee River, also in the Georgia Coastal Plain, was greater than 97,000/m^2, about 70% of which were chironomids (see Benke 1998 and other references for Ogeechee River in Table 2). Average density from Cedar Creek, a second-order Coastal Plain stream in South Carolina was somewhat lower (14,900/m^2) than that found in larger rivers (Smock et al. 1985). Mean density for wood accumulations in Buzzard's Branch, a small Coastal Plain stream in Virginia, was greater than 22,000/m^2, but this estimate was per square meter of streambed directly under the dam, not surface area of wood (Smock et al. 1989). High density also has been found in studies that addressed only a single group (for example, Cudney and Wallace (1980) found mean

TABLE 3. Density, biomass, and production for entire invertebrate assemblages on wood surfaces from streams and rivers throughout the world from sampling natural snags, wood dams, or from colonization studies; values from colonization studies are shown in parentheses. In some cases, mean values were calculated where there was more than one site, stream year, or sampling approach. For river size and literature sources, see Table 2.

Stream and location	Density (No./m^2)	Biomass (g dry mass/m^2)	Production (g dry mass/m^2/year)
Upper Satilla River, Georgia	33,315	3.4	72.2
Lower Satilla River, Georgia	26,207	5.8	57.4
Ogeechee River, Georgia	97,704	6.4	147.6
Collier Creek, Virginia	8,915	0.4	2.8
Buzzards Branch, Virginia (DD)[a]	22,302	5.2	27.4
Cedar Creek, South Carolina	14,900	1.1	7.4
Steel Creek, South Carolina	(6,777)		
Little Tennessee River, North Carolina		2.7	
Marmaton River, Missouri	977	0.5	
Marais des Cygnes River, Missouri	471	0.3	
Coastal Mountains streams, Oregon		1.0	
Cascade Mountains streams, Oregon		0.7	
Berry Creek, Oregon	2,475		
San Joaquin River, California	4,700		
Kaskaskia River, Illinois	22,110	0.7	
	(96,060)	(0.3)	
Sister Grove Creek, Texas	2,780		
Fleming Creek, Michigan	(14,000)		
Pranjip-Creightons Creek, Australia	3,086	1.6	
Ladberger Mühlenback and	1,464		
Ibbenbürener Aa, Germany	(3,382)		

[a] Wood dam

density for net-spinning caddisflies varied from almost 6,000/m² to more than 22,000/m² in the Savannah River, Georgia, depending on current velocity). Low density can sometimes be explained, particularly by sampling procedures. For example, the low density of macroinvertebrates (mean <2,800/m²) sampled in a Texas stream surely resulted from using a coarse mesh (500-µm) sieve (Hax and Golladay 1998). The same authors estimated meiofauna density of 22,000–224,000/m² using a fine mesh (45-µm) sieve (Golladay and Hax 1995). In German streams (Spänhoff et al. 2000), low invertebrate density were found on wood pieces lifted from the stream bottom where they were sometimes partially buried in sand. They probably did not experience the same type of environment as in those studies with extremely high density (such as in the Ogeechee and Satilla rivers). In summary, invertebrate density was usually very high on wood substrates, particularly those that were anchored and exposed to the current, suggesting that wood is a highly attractive habitat site for invertebrates in many lotic systems. If wood simply lies on the streambed where it may become partially buried, it will be attractive to shredders, but it is unlikely to be as attractive to filterers and gatherers that might otherwise reach high density.

Biomass (grams of dry mass per square meter of snag surface) for entire invertebrate assemblages also has been estimated in several studies but not necessarily for the same streams as for density (Table 3). Biomass estimates also varied greatly, possibly for some of the same reasons as suggested for density. In general, invertebrate biomass was relatively high, usually approaching or exceeding 1 g/m². The highest values were found on snags in the two Coastal Plain rivers in Georgia (Ogeechee and Satilla rivers) and for the wood accumulations in Buzzards Branch, Virginia. Invertebrate biomass on wood lying on the bottom of Oregon streams was generally lower than found on stabilized snags of the southeastern U.S. Coastal Plain.

Annual production (grams dry mass per square meter each year) studies for entire invertebrate assemblages have been done only in southeastern U.S. Coastal Plain streams and rivers (Table 3). Studies on the Satilla River were the first to establish that production on snags is often higher than in benthic habitats (Benke et al. 1979, 1984). Cudney and Wallace (1980) showed that production of net-spinning caddisflies on snag was similarly high in the Savannah River. The highest invertebrate production on snags was found in the Ogeechee River, a large fraction of which was from chironomids (Benke 1998; see other sources in Table 2), which function as the base of a complex invertebrate food web. Production on snags in the much smaller Cedar Creek (Smock et al. 1985) was substantially lower than on snags in the Satilla and Ogeechee rivers. Subsequent studies by Smock et al. (1989, 1992) showed that debris dams were a site of relatively high production in some (Buzzards Branch), but not all (Colliers Creek), Coastal Plain streams.

High invertebrate production on snags in southeastern Coastal Plain rivers results from both high biomass and high biomass turnover rate. In the Ogeechee River, growth rates were particularly high for chironomids (up to 90% per day; Stites and Benke 1989; Hauer and Benke 1991), black flies (up to 43% per day; Hauer and Benke 1987), and mayflies (up to 35% per day; Benke and Jacobi 1986; Benke et al. 1992), in part because of relatively high temperatures (>20°C) most of the year. High biomass and high growth rates are possible for invertebrates that colonize stable snags because they are able to exploit materials produced in other habitats and carried to them by the current (Cudney and Wallace 1980). Furthermore, the amorphous detritus carried to these insects by the current is microbially enriched and thus high in food value (Edwards 1987; Edwards and Meyer 1987, 1990; Carlough and Meyer 1989; Benke et al. 1992; Carlough 1994; Couch et al. 1996).

Several studies have shown that when invertebrate production is considered by specific habitat, snags can be a production "hot spot" compared to other habitats in some streams (Wallace et al. 1996). This phenomenon was particularly true for rivers in the southeastern U.S. Coastal Plain (Satilla and Ogeechee), where production on snags was much higher than was found in the shifting sand of the riverbed (Figure 3). It was also true of Cedar Creek, although total channel production was lower than in the larger rivers. Similarly, production in the wood dams of Buzzards Branch was higher than in sediments, but the reverse was true of Colliers Creek because of the relatively stable organic matter in the sediments. Some additional exceptions to the pattern in Figure 3 are notable. In the Ogeechee River, production was much higher on snags than in sediments, but biomass in sediments was almost as high on snags because of the nonnative mollusk *Corbicula fluminea* in sediments. In the Little Tennessee River, biomass was lower on snags than on macrophyte-covered cobbles that provide a stable three-dimensional habitat in the streambed.

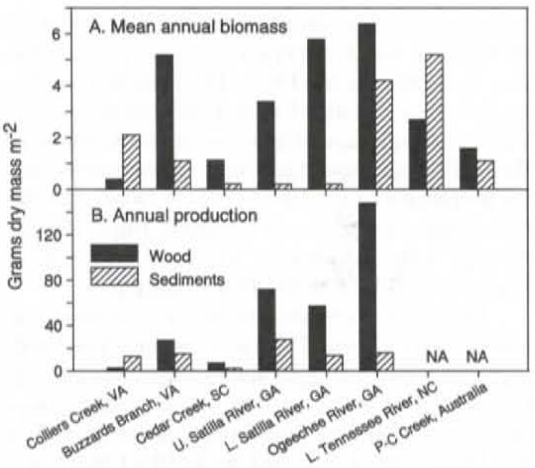

FIGURE 3. Mean annual biomass and production of invertebrates on wood surfaces compared to sediments for several streams. All units are per square meter of habitat surface area. Most wood surfaces are of snags, but Colliers Creek and Buzzards Branch are per square meter of streambed under wood dams. Sources: Colliers Creek and Buzzards Branch, Virginia (Smock et al. 1992); Cedar Creek, South Carolina (Smock et al. 1985); upper and lower Satilla River, Georgia (Benke et al. 1984); Ogeechee River, Georgia (from several papers in Table 2); Little Tennessee River, North Carolina (Wallace et al. 1996); and Pranjip-Creightons Creek, Australia (O'Connor 1992).

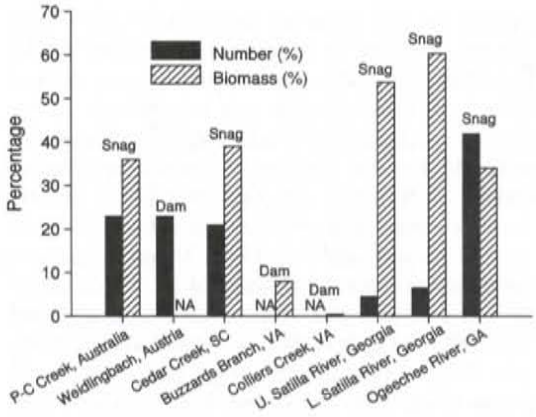

FIGURE 4. Percentage of snag invertebrates that contribute to total numbers and biomass in several streams. Some contributions are from invertebrates found in wood dams (Austria, Virginia) rather than snags. Sources: Pranjip-Creightons Creek, Australia (O'Connor 1992); Weidlingbach, Austria (Wiegelhofer and Waringer 1999); Cedar Creek, South Carolina (Smock et al. 1985); Buzzards Branch and Colliers Creek, Virginia (Smock et al. 1989, 1992); upper and lower Satilla River, Georgia (Benke et al. 1984); Ogeechee River, Georgia (Benke 2001). NA means values were not available.

Clearly, when wood is the only stable substrate in lotic systems, it will be a center of invertebrate biomass and production. When other stable substrates are abundant, however, wood may only be a hot spot for xylophagous species or shredders commonly associated with detritus (also see Humphries et al. 1996).

Although wood can be a site of intense invertebrate activity (Table 3; Figure 3), wood does not necessarily contribute significant invertebrate numbers, biomass, or production for the stream as whole. In studies that included attempts to quantify wood habitat, however, the numbers per habitat surface area can be converted to numbers per unit area of streambed and thus make direct comparisons among habitats possible (Wallace and Benke 1984; Smock et al. 1992; Benke 2001). Percentages of abundance and biomass on snag habitats compared to other habitats are shown for selected streams in Figure 4. Clearly, snags often contain more than 20% of total invertebrate numbers and more than 30% of invertebrate biomass when values are converted to area of streambed. The most extreme case was for the Satilla River, where biomass of snag-dwelling invertebrates was more than half of the total invertebrate biomass (Benke et al. 1984). Thus, snag invertebrates can comprise not only a habitat-specific concentration of invertebrates in streams and rivers (Figure 3), but also can make important contributions to the entire riverine ecosystem (Figure 4). On the other hand, if snags are only a tiny fraction of benthic habitats, perhaps because of wood removal at some time in the past, the contribution of invertebrates from snags may be minor (Rabeni and Hoel 2000).

In addition to being a site of high invertebrate biomass and production, wood can also be a "hot spot" of biodiversity. Wallace et al. (1996) compared invertebrate richness among habitats from six streams in the southeastern United States and found that half of the streams had more species associated with wood than with streambed habitats. Invertebrate richness on wood is particularly pronounced in Coastal Plain systems where few other stable habitats exist. For example, Benke et al. (1984) found 63 species inhabiting snags, but only 31 in sandy habitats and 41 in muddy backwaters in the Satilla River. A more intensive study on the Ogeechee River has found more than 108 invertebrate species on snags (Benke, author's unpublished data) and 70

in the sandy sediments (Stites 1986). The snags included 52 species of Ephemeroptera, Plecoptera, and Trichoptera, however, and the sediments had none from these orders. Collier and Halliday (2000) reported that species richness was greater on wood than on inorganic substrates in 11 of 12 pumice-bed streams in New Zealand, with a total of 81 species on wood and 64 on mineral substrates for all streams. Similarly, twice as many taxa were collected from wood (23) as from shifting sand and pumice (11) during the recovery of Clearwater Creek from the eruption of Mt. St. Helens (Dudley and Anderson 1982; Anderson 1992). Somewhat similar results have been found in other streams (Smock et al. 1985, 1992; O'Connor 1991; Hax and Golladay 1998). Wallace et al. (1996) noted that in lotic systems where snags are not prominent and extensive mineral substrates exist (such as cobble or cobble covered with macrophytes), biodiversity on snags may be less than on mineral substrates.

Wood colonization and drift

The availability of wood habitat to aquatic invertebrates is generally more variable than mineral substrates located on the riverbed. Unlike mineral substrates, wood is continuously supplied and lost to streams and rivers, even though it may be stabilized for decades. The greatest instability associated with wood is when it has a vertical orientation and is subjected to variable degrees of inundation (Figure 1C). Depending on where wood is positioned in the stream, it may be inundated for only a single day or for an entire year. Variable degrees of wetting and drying suggest the importance of two interrelated phenomena for invertebrates: colonization and drift. Colonization determines how quickly snags become populated as water rises to inundate previously dry habitat. Drift is probably a major source of this colonization (in addition to reproduction) because snag invertebrates cannot crawl easily across unstable habitats. Furthermore, if invertebrates found on snags are distinctly different from those in other habitats, quantification of drift can provide insight to both colonization and the origin of the drift assemblage.

Several studies have shown that invertebrate colonization of wood begins quickly, as does biofilm development, but it can take anywhere from one to several weeks to achieve maximum biomass and diversity. Nilsen and Larimore (1973) found that at least four weeks were required before maximum density (of mostly oligochaetes and chironomids) was reached on small logs in a slow-flowing section of the small Kaskaskia River, Illinois. In fast-flowing riffles, the assemblage shifted to caddisflies and black flies, although densities were not so high. Nord and Schmulbach (1973) used multiplate (masonite) samplers as surrogates for snags in an unchannelized section of the Missouri River; they found a diverse assemblage dominated by filter-feeding caddisflies in fast-flowing water after 32 d. Van Arsdall (1977), focusing only on caddisflies in the Satilla River, found substantial colonization in less than 10 d, with similar density near the water surface and at 2-m depth. Fremling (1960) had noticed earlier that hydropsychid caddisflies colonizing buoy chains (a snag surrogate) in the upper Mississippi River had similar abundance at the water surface and at 8 m deep. O'Connor (1991) found that 2 weeks was sufficient for natural colonization density in an Australian lowland stream, and Drury and Kelso (2000) found that abundance peaked on tree branches in Coastal Plain streams in Louisiana after two to three weeks. Thorp et al. (1985) examined the patterns of colonization over eight weeks at three sites in a low-gradient stream-swamp system in South Carolina. They found highest density with the fastest current; snags were well-colonized within a week but shifted from a predominance of filterers to gatherers in that period. Similarly, Hax and Golladay (1993) found more rapid colonization in higher velocity. Although colonization studies can be extremely useful in understanding population dynamics and succession on snags, caution should be exercised in interpreting patterns over various periods. The invertebrate assemblage found on an artificial snag at any given time is not only due to its length of submergence, but also to the stream's biological and environmental history (for example, species-specific life history patterns can cause a shift in assemblage structure from one week to the next, regardless of the colonization period).

Wood conditioning, surface texture, and gouging by invertebrates has been suggested to influence colonization. For example, O'Connor (1991) found that grooved woody substrates were colonized by more invertebrate species than was smooth wood. McKie and Cranston (1998) have even gone so far as to suggest that certain elmid beetles (particularly *Notriolus* spp.) function as "keystone" species because their gouging of *Eucalyptus* spp. wood facilitates colonization by other invertebrates and microbes. In a Michigan stream, however, Magoulick (1998) found no difference in colo-

nization of smooth and rough wood, although species richness was greater on conditioned (previously submerged) wood than on unconditioned wood. Furthermore, invertebrate colonization was greater on smooth wood than on smooth Plexiglas, indicating that natural organic substrates are more suitable than artificial substrates (Magoulick 1998). Spänhoff et al. (2000) found much higher invertebrate density on conditioned than on fresh wood in German lowland streams, but not on different wood species over 8-weeks exposure.

Stream drift is a well-known phenomenon that has been better studied in small streams than large rivers (Waters 1972; Benke et al. 1986). If wood-dwelling invertebrates in lotic systems are sufficiently distinct from those in other habitats, such as sandy or muddy riverbeds, then examining drift can be used to measure snag importance. Early studies in the Missouri River suggested that most of the drifting insects originated from brush piles (snags) rather than benthic habitats (Morris et al. 1968; Modde and Schmulbach 1973). Similarly, Kovalak (1978) found more drift leaving than entering a pool area of a small stream in Michigan and suggested that the pool was a drift source because of the logs and twigs along the pool margin. Benke et al. (1986) compared drift density with habitat density in the Satilla River, Georgia, and showed that snags contributed 72–81% of the numbers and 78–82% of the biomass to drift. A subsequent study in the Ogeechee River demonstrated similar contributions from snags (Benke et al. 1991), but snag abundance—and thus drift density—were substantially higher (>20 individuals/m^3 and >2.4 mg dry mass/m^3) than in the Satilla. Although invertebrates can drift from different habitats at different rates, these findings provide an independent demonstration of the importance of snag habitats in low-gradient rivers and a potentially important source of food for filtering invertebrates and drift-feeding fishes.

Although snags can be the major source of drifting invertebrates in natural streams, they also represent a stable refuge, particularly in low-gradient streams during periods of high discharge. For example, Borchardt (1993) showed that accumulated wood substantially reduced drift losses under experimentally induced hydraulic stress. Palmer et al. (1996) also conducted experiments suggesting that wood dams conferred increased resistance of chironomids and copepods to floods in certain habitats. Invertebrates are known to drift from snags to escape desiccation as water levels fall, and drift is important in the recolonization of newly inundated snags, but the understanding of the relation between drift density, hydrologic regime, and colonization of snags remains weak.

Functional feeding groups on wood

The number of wood-eating species appears to decrease from western to eastern North America (Dudley and Anderson 1982), suggesting that degree of xylophagy may differ among geographic regions. Determining the importance of xylophagy (or any other feeding mode) for entire invertebrate assemblages from different geographic regions, however, requires not only determination of invertebrates' trophic status (Dudley and Anderson 1982; Hoffmann and Hering 2000), but also a quantitative approach. Although quantitative data are limited, we have used published analyses from streams in Oregon, Virginia, South Carolina, and Georgia to summarize the distribution of either biomass or production among functional feeding groups (Figures 5 and 6). Although wood gougers are considered part of the shredder feeding group (Cummins and Merritt 1996; Wallace and Webster 1996), we have separated gougers from shredders (when possible) for our analysis of wood-associated invertebrates.

The distribution of biomass among functional groups clearly distinguishes two patterns (Figure 5). Those studies that identified wood as "snags" (Figure 5C through 5D) contained invertebrates that primarily fell into gatherer, filterer, and predator functional groups, with few contributions from gougers or shredders. All of these studies were from eastern U.S. Coastal Plain streams or rivers. In contrast, the Oregon streams were heavily weighted toward the gougers and shredders, consistent with the higher diversity of obligate xylophages, with no filterers or predators. Scrapers did not comprise a significant proportion of invertebrate biomass on wood from eastern streams, but they were important in some Oregon streams (Anderson et al. 1978, 1984).

The distribution of production among functional groups was limited to only the eastern U.S. Coastal Plain streams and rivers and included the two Virginia streams in which wood dams were sampled instead of snags (Figure 6). Production on snags from the South Carolina stream and the Georgia rivers were similar to their biomass distributions (Figure 5), except that the rela-

tive proportions shifted in the gatherer, filterer, and predator groups as a function of their turnover rates. The wood dams from Virginia streams, however, contained invertebrates that were primarily shredders and predators with low fractions of gatherers and filterers, suggesting a significantly different microhabitat than for snags.

Based on the distributions of biomass and production among functional feeding groups in this limited number of streams (Figures 5 and 6), we suggest that these differences are caused largely by the habitat in which the wood was sampled and the manner in which the wood was collected. Snags from Coastal Plain systems in South Carolina and Georgia typically were branches of fallen trees well anchored in the current above the sediments. In contrast, wood accumulations from the Oregon streams were typically loose or tethered sticks lying on the stream bottom. Wood accumulations in Virginia streams, on the other hand, were packed tightly, trapped other detrital material, and thus attracted a high fraction of shredders. Other studies using abundance of functional groups are reasonably consistent with the biomass and production data. Colonization of fixed snags in another South Carolina Coastal Plain stream again demonstrated high gatherer and filterer density, but also included scrapers (Thorp et al. 1985). Snags from an Australian stream consisted primarily of gatherers (O'Connor 1992). On the other hand, stick packs placed on the bottom of small Appalachian streams in North Carolina attracted only 11% shredders; most of the rest were collectors and scrapers (Golladay and Webster 1988). Similarly, stick packs placed on the bottom of streams in New York were composed of only 6% shredders and piercers with the majority gatherers and filterers (Hax and Golladay 1993). In contrast to the wood dam results from Virginia (Smock et al.

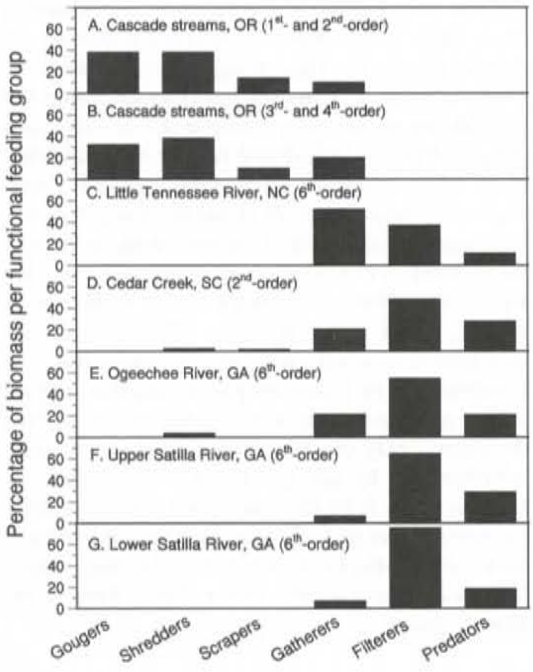

FIGURE 5. Distribution of invertebrate biomass percentages in functional feeding groups for streams and rivers. Sources: Cascade streams (first- and second-order and third- and fourth-order from Anderson and Sedell 1979); Little Tennessee River, North Carolina (Wallace et al. 1996); Cedar Creek, South Carolina (Smock et al. 1985); Ogeechee River, Georgia (see sources in Table 2), Satilla River, Georgia (upper and lower sites, Benke et al. 1984). Note: for the Cascade streams, we have arbitrarily placed those organisms identified as "other" into the gatherer functional group.

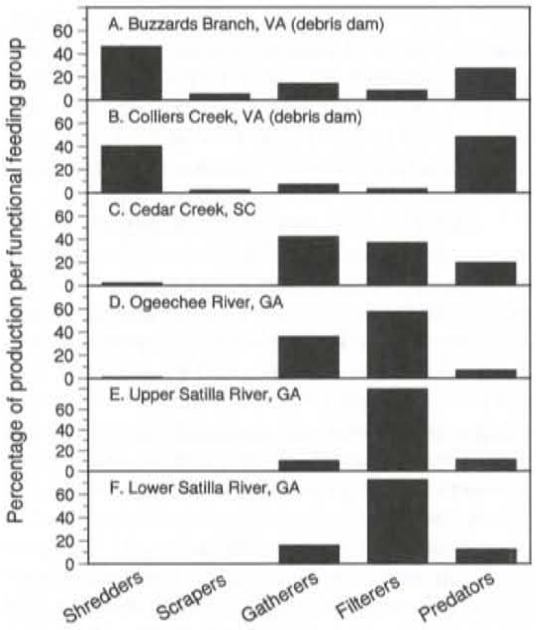

FIGURE 6. Distribution of invertebrate production percentages in functional feeding groups for streams and rivers. Sources: Virginia streams (Smock et al. 1989, 1992); Cedar Creek, South Carolina (Smock et al. 1985); Ogeechee River, Georgia (Benke et al. 2001, see other references in Table 2); Satilla River sites, Georgia (Benke et al. 1984).

1989), invertebrates from a beaver dam in Alberta, Canada consisted primarily of filtering black flies and more closely resembled the fauna of a lake outlet (Clifford et al. 1993). In summary, quantitative studies suggest that nonxylophagous taxa (particularly filterers and gatherers) can dominate wood habitat in a wide variety of conditions.

Although the geographical distribution of obligate xylophages across North America may play a role in affecting differences in functional feeding groups that colonize snags (Dudley and Anderson 1982), we believe that the limited quantitative data (relative density, biomass, and production) presented here support the view that habitat and sampling approaches are of overriding importance in determining assemblage composition. Xylophages (gougers and other shredders) and gatherers appear to be important on wood that has settled in depositional habitats, but filterers and gatherers dominate on snags anchored in erosive environments. Filterers and gatherers have their highest production as stream size and water velocity increases, and more enriched fine particulate organic matter is transported.

Food webs on wood: beyond functional groups

Identification of invertebrate food habits and classification into functional feeding groups can provide considerable insight into the role of wood-dwelling invertebrates in streams. Such analysis, however, is only a crude characterization of wood food webs, particularly beyond the primary consumers. Detailed analyses for the Ogeechee River snag assemblage (Wallace et al. 1987; Benke and Wallace 1997; Benke et al. 2001) demonstrated trophic pathways between individual groups and species that have been realized in few other stream habitats (Smock and Roeding 1986; Smith and Smock 1992). Most of the primary consumers on Ogeechee snags are filterers and gatherers (chironomids and mayflies) that depend on microbially enriched amorphous detritus collected from the seston (Figure 7). In spite of a complex feeding hierarchy, most of the chironomids and mayflies are consumed by omnivorous net-spinning caddisflies, possibly after they enter the current, and are later recaptured from the drift by caddisflies on another snag. The predatory portion of the food chain also includes larger, strictly predaceous insects such as perlid stoneflies, dragonflies, and the hellgrammite *Corydalus cornutus* as the top invertebrate predator (Benke et al. 2001). Production of these larger predators totaled 7.1 g dry mass/m^2 (wood surface)/year, which required a high consumption of about 52% of total prey production. Smith and Smock (1992) also estimated production of the predator component on the wood dam of Buzzards Branch (8.4 g dry mass · m^{-2} · year) and found that predators consumed about 94% of invertebrate prey production for the stream as a whole. Food webs on wood from other lotic systems (such as high-gradient streams) have yet to be described, but they would probably be more difficult to separate from coexisting food webs on mineral habitats.

In addition to the complexity of feeding levels in the invertebrate assemblage on the snag habitat in Coastal Plain rivers, invertebrates provide the foundation for higher trophic levels. In the Satilla River, snag invertebrates are a major source of food for insectivorous fishes; up to 60% of the diet of several fish species originated from snags (Benke et al. 1979, 1985). The insectivorous fishes are, in turn, consumed by fish-eating species (Benke et al. 1985). In spite of many studies demonstrating the importance of wood in creating habitat and as a refuge for fishes (Dolloff and Warren 2003; Zalewski et al. 2003), relatively little other research documents the importance of wood-dwelling invertebrates as a food source to fishes (Angermeier and Karr 1984; Lehtinen et al. 1997; Crook and Robertson 1999). Although direct evidence is sparse, Crook and Robertson (1999) provide an excellent review on the potential use of snags as foraging sites by fishes; they conclude that, at least in low-gradient rivers throughout the world, fish do indeed rely on snag-dwelling invertebrates, whether they forage directly or whether they obtain their prey from the drift. Quist and Guy (2001) have found that growth rates of some prairie stream fishes are related to the amount of instream wood, presumably because it is the source of their invertebrate prey.

Influence of invertebrates on wood: structure and process

Given that many xylophagous invertebrates are found on stream wood, whether they play a major role in wood decomposition is of paramount importance. In terrestrial environments, wood decomposition is relatively rapid, enhanced by invertebrates that create deep galleries into the interior of the wood, promoting fragmentation

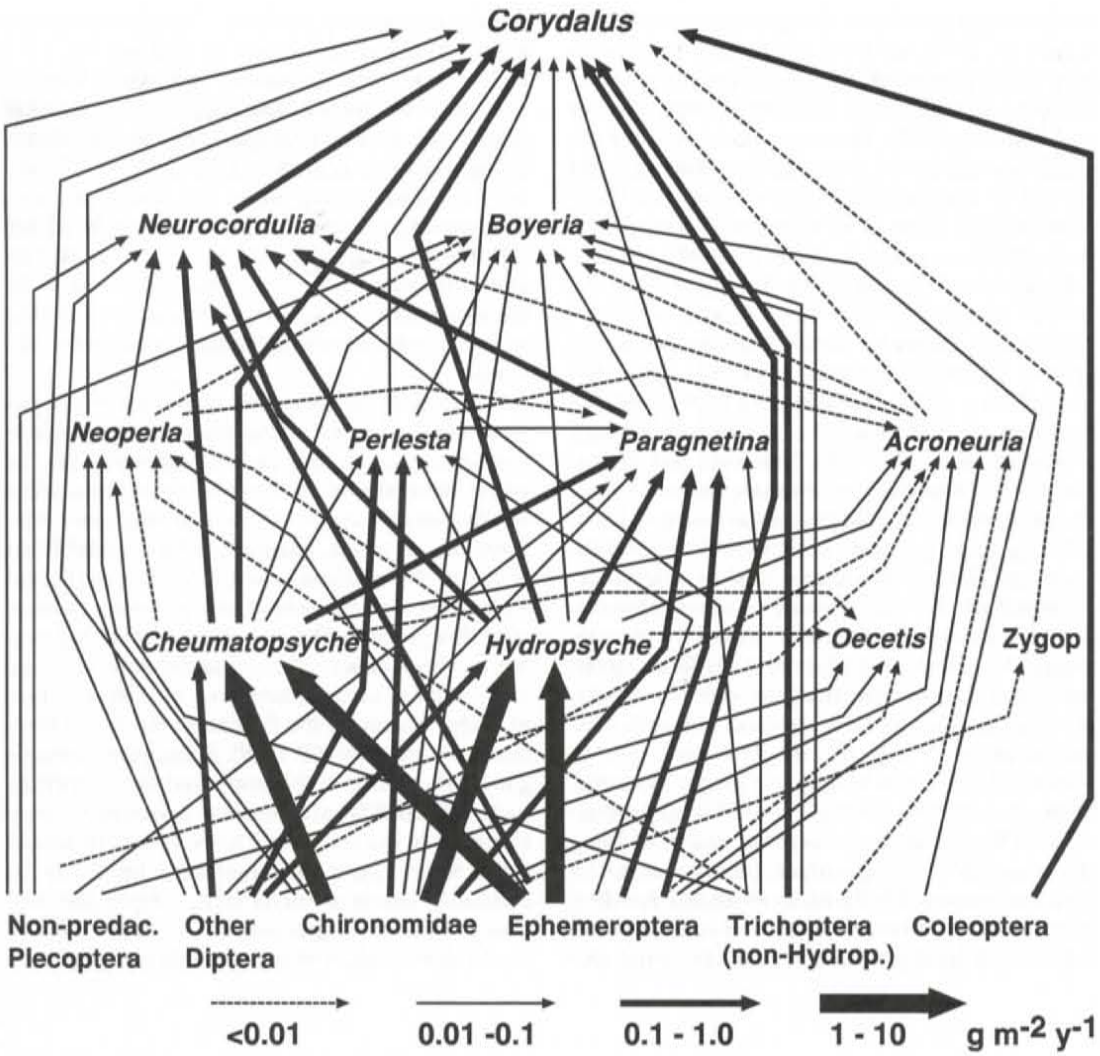

FIGURE 7. Quantitative food web on the snag habitat in the Ogeechee River, emphasizing the predator component (from Benke et al. 2001). Line thickness indicates the ingestion flux. See original paper for actual values. Note that *Cheumatopsyche* spp. and *Hydropsyche* spp. are omnivores, and their ingestion of basal food resources is not shown (see Figure 3 in Benke and Wallace 1997). Abbreviations: Zygop = Zygoptera, Non-predac. = non-predaceous, non-Hydrop. = non-Hydropsychidae. (reproduced with permission from *Freshwater Biology*).

and increased surface area for microbial decomposition (Harmon et al. 1986). In contrast, wood decomposition is much slower in freshwater environments, probably because oxygen concentrations in the interior of wetted wood are very low, serving as a barrier to bacteria, fungi, and invertebrates. Hence, wood decomposition in lotic systems is primarily a surface phenomenon, but the possibility still exists that invertebrates play an important role in this slow decomposition.

Although most invertebrates are limited to the wood surface, some evidence shows that they promote decomposition by scraping, gouging, and tunneling wood colonized by bacteria and fungi: these activities expose additional wood to further microbial decomposition (Anderson et al. 1984; Dudley and Anderson 1982). Unfortunately, relatively few quantitative studies exist, making comparative analysis difficult. Some species are incredibly effective in consuming wood; for example, the tipulid *Lipsothrix* spp. can produce feces from wood at a rate of 88% to 223% of its

body weight per day in Oregon streams (Anderson et al. 1984), and the caddisfly *Pycrocentria funerea* can produce feces 22% to 168% of its body weight per day in New Zealand streams (Collier and Halliday 2000). Because wood has a low assimilation efficiency, these fecal production rates should be comparable to (but slightly less than) consumption rates. Determination of the invertebrate effects on wood requires not only consumption rates per individual, but also quantitative estimates of consumer biomass or production. Fecal production fluxes by three major xylophagous species in Oregon streams have been estimated to be 17.5 g of feces per kilogram of wood per year or more than 20 g/m^2 of streambed per year. (Anderson et al. 1978, 1984; Steedman and Anderson 1985). These authors estimate that such fecal production rates would process as much as 2% of existing wood per year, which would be significant considering the otherwise slow rate of decomposition. We are unaware of other estimates of wood disappearance rates caused by invertebrates. Nonetheless, Collier and Halliday (2000) estimated that *Pycnocentria*, the dominant xylophagous species in New Zealand streams, consumed about 29 mg · m^{-2} · d^{-1} (11 g · m^{-2} · year^{-1}), comparable to that found in Oregon streams. Hoffmann (2000) estimated annual fecal production for the caddisfly *Lasiocephala basalis* of 100 g dry mass/m^2 of wood surface, but this cannot be directly compared to the other estimates. Roeding and Smock (1989) estimated wood consumption, rather than fecal production rates, by using secondary production analysis. Their consumption values of 12.6 g · m^{-2} · year^{-1} (or 34.5 mg · m^{-2} · d^{-1}) for the dominant shredders in Virginia Coastal Plain streams were surprisingly similar to fecal production fluxes in Oregon and New Zealand. Using a similar approach, Hall et al. (2000) estimated wood consumption for shredders in a southern Appalachian stream of 6 mg to 23 mg ash free dry mass · m^{-2} · d^{-1} in a reference stream and a higher wood consumption of 34 mg to 48 mg ash free dry mass · m^{-2} · d^{-1} in a litter-excluded stream, again reasonably similar to previous estimates.

Nonxylophagous species also have the potential to gouge and stimulate wood decomposition, even though they do not necessarily eat the wood. Several species of net-spinning caddisflies (Hydropsychidae) are known to gouge oval depressions in snags, particularly in Coastal Plain rivers of the southeastern United States (Figure 8), but we are unaware of any attempts to measure this process. The significance of such gouging has been observed from underwater damage to wooden structures, however. In 1988, a section of bridge spanning the Pocomoke River in Maryland collapsed (NTSB 1989). Subsequent investigation showed that the untreated timber pilings had a 53% to 58% reduction in cross-sectional area, resulting in the collapse. The National Transportation Safety Board attributed the reduction to the combined effects of microbial decomposition and many decades of gouging by larvae of *Hydropsyche incommoda*, which had colonized the pilings

FIGURE 8. Submerged log from the Sipsey River, Alabama. The deep gouges were apparently made by hydropsychid caddisflies, particularly *Macrostemum carolina*, which is abundant on snags in this river. Diameter of log is about 10 cm.

(NTSB 1989; Flint 1996). In conclusion, both xylophagous invertebrates and nonxylophagous gougers probably play a major role in wood decomposition in lotic ecosystems, although further research in this area is clearly needed.

Wood Invertebrates in Bioassessment

The importance of wood as invertebrate habitat in streams and rivers has not escaped the attention of investigators developing protocols for bioassessment. Lenat (1988) described wood sampling as one of the standardized qualitative collection techniques used for water quality assessment in North Carolina. Cuffney et al. (1993) summarized methods for collecting macroinvertebrates in the U.S. Geological Survey's National Water-Quality Assessment Program and described woody snags as an important habitat to be sampled. Similarly, the rapid bioassessment protocol developed for the U.S. Environmental Protection Agency for macroinvertebrates has recently recognized snags as one of the five basic habitat types that should be sampled in streams of any type (Barbour et al. 1999). The USEPA (1997) and Maxted et al. (2000) developed field and laboratory methods specifically for macroinvertebrate and habitat assessment in low gradient, nontidal streams in the eastern U.S. Coastal Plain. Because the mineral substrate of such streams is often sand or silt, which typically have few species that are pollution-sensitive, they recognized that snag sampling should be essential to their protocol.

Various investigators have now conducted field studies in which they have sampled snags as part of water quality studies. Rabeni (2000) sampled six common habitat types, including snags, from 45 streams in three ecoregions in Missouri and calculated a variety of metrics for assessing water quality. He found distinctive assemblages associated with each habitat type and concluded that bioassessments need to use habitat-specific sampling, including snags, if they are a common feature of streams. Brown and May (2000) effectively assessed the relation between wood-dwelling macroinvertebrates (by family) and environmental variables in the lower Sacramento and San Joaquin River basins, California, as part of the National Water Quality Assessment Program. In New Zealand, Collier et al. (1998) sampled mineral substrates, macrophytes, and wood in 18 lowland streams, and they applied various biotic indices to each habitat. They found that wood was relatively common in most streams and an important habitat to sample in bioassessments. Quinn et al. (1997) measured wood accumulation in 11 hill-country streams in New Zealand and collected invertebrates with a Surber sampler. They found that potential differences in invertebrate communities based on differences in pollution were ameliorated by the presence of wood habitat in all the streams. In short, now that wood substrates are well recognized as invertebrate habitat through basic research, stream biologists have incorporated this important finding into bioassessment protocols.

Managing and Restoring Streams

Given that wood plays an important role in the ecological characteristics of streams and rivers and given that invertebrate colonists are an essential functional component, such considerations should obviously be an integral part of managing streams and planning to restore them. We have known for many years that protecting riparian zones is essential for natural functioning of lotic systems, particularly as a source of allochthonous inputs for aquatic consumers and in maintaining healthy river-floodplain interactions (Gregory 1992; Sweeney 1993; Benke 2001). Increased knowledge of the importance of wood to streams and river channels reinforces this understanding, particularly from the viewpoint of wood as essential habitat for both invertebrate and vertebrate animals. Not only is protecting riparian zones important, but also, the destructive practices of channelization and "snagging" should be eliminated or reduced in many systems, now that their harm to natural wood habitats is appreciated. Nonetheless, many streams and rivers have already been seriously damaged, and attempts to restore natural channels and floodplains should consider reintroducing wood to channels. While research in this area is still in its infancy, management and restoration strategies need to balance boating safety and other perceived liability issues with the importance of natural riverine habitats.

Although applied aspects are dealt with elsewhere in this volume, we will briefly mention a few restoration attempts that deal with invertebrates. In an experiment related to the concept of restoration, Wallace et al. (1995) added logs to a small mountain stream in North Carolina and demonstrated that such manipulations can result

in significant functional shifts in the abundance, biomass, and production of the invertebrate assemblages in newly created depositional habitats. The addition of wood to a low-gradient third-order stream in Virginia caused an increase in pool habitat and a subsequent shift in functional group biomass (Hilderbrand et al. 1997; Lemly and Hilderbrand 2000). None of the Virginia streams in these studies were degraded, however, but the researchers were not intending to assess the success of restoration. On the other hand, Gerhard and Reich (2000) studied changes in microhabitats and invertebrates in a regulated and straightened third-order stream in Germany to which wood had been added as an accidental effect of forest management. Although they sampled on only a single date, they found an increase in microhabitats, an increase in invertebrate species, and an almost fivefold increase in invertebrate density in "restored" sections. The paucity of invertebrate assessments in attempts to re-introduce wood for restoration illustrates the clear need for work on this topic. The possibility for the greatest benefits of wood introduction will probably be found in systems where streambed substrate is unsuitable for many invertebrate species (shifting sand, pumice) and where wood has historically provided the only major stable substrate.

Summary

Research on wood-dwelling invertebrates can be divided into three basic approaches. The first deals with wood as a substrate from which invertebrates can obtain food resources and play a role in decomposition. Such studies were in smaller streams in which wood is part of the detrital pool. The second approach treats wood as a major habitat or attachment site for a wide variety of functional feeding groups (rather than just a detrital food source), and such habitats are referred to as snags. Although snags (as habitat) can be important in smaller streams, their relative importance seems to increase as stream size increases, as gradient decreases, and as alternative hard substrates disappear. The third considers the important role of wood in creating lentic habitats for invertebrates along the course of streams, either by enhancing pool and riffle sequences with wood accumulations or by forming major ponds and wetlands from beaver dams. Thus, wood has a profound effect on the diversity, abundance, production, and function of invertebrate assemblages in lotic systems of all sizes. The habitats and food sources created by wood and their associated invertebrates, in turn, form the foundation for higher trophic levels, particularly fishes, but including all vertebrate predators. Although much has been accomplished in understanding the role of invertebrates on wood in streams and rivers, much remains to be learned in quantifying that role and in using this information in bioassessment and restoration protocols for streams and rivers of all sizes.

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