Influence of Wood on Aquatic Biodiversity

STEVEN M. WONDZELL AND PETER A. BISSON
USDA Forest Service, Pacific Northwest Research Station, Olympia Forestry Sciences Laboratory
3625 93rd Avenue SW, Olympia, Washington 98512-9193, USA

Abstract.—We review published literature examining the role of wood in mediating biodiversity in aquatic ecosystems, identifying the components of biodiversity, taxonomic groups, and scales that have been studied, and highlight gaps in existing knowledge. The components of biodiversity most frequently studied include species diversity (or richness) of macroinvertebrates and fishes, structural complexity within habitat units, and the diversity of habitats found in a stream reach. Many of these studies show that large wood increases biodiversity by providing stable, hard substrates for colonization by periphyton and macroinvertebrates; by increasing microhabitat complexity; and by shaping channel morphology by controlling patterns of erosion and deposition in stream reaches. The abundance of wood in channels, as well as its functional role, varies greatly in longitudinal, lateral, and vertical dimensions along the river corridor. The influence of wood on community structure and ecosystem processes also varies across these dimensions and from stream headwaters to river mouths and nearshore marine environments. Thus, wood can influence biodiversity at all of these scales. Numerous studies, however, have failed to show an effect of wood on biodiversity. These conflicting results illustrate that wood abundance, its functional role in streams, and its influence on biodiversity depend on a variety of factors, and it is the total effect of all these factors, not simply the presence of large wood, that determines patterns of biodiversity.

Introduction

The objective of this paper is to review published literature examining the role of wood in mediating biodiversity in aquatic ecosystems. We take a broad view of biodiversity, one that considers the multiple components of biodiversity that might be important in aquatic and riparian ecosystems, including genetic, age-class, and life history diversity of individual species; species richness or diversity; life-form or functional-group diversity; habitat diversity (or habitat complexity); ecosystem diversity; and landscape diversity.

A review of aquatic and riparian literature in a recently compiled bibliography of papers (http://riverwood.oregonstate.edu/html/intro.html v. 1) examining the role of large wood in the world’s rivers turned up 54 papers that examined some component of biodiversity or species richness. These 54 papers comprise less than 5% of the publications cited. Further, none of these 54 studies focused solely on the relation between large wood (logs or snags) and species diversity or species richness in lakes, streams, or riparian zones. We realize that our literature search was limited or may have missed references. Even so, our examination identified several clear areas of past research emphasis and highlighted gaps in existing knowledge. First, the importance of wood as an element of physical habitat and its role in shaping channel morphology are the most widely studied aspects of the relation between biodiversity and large wood, accounting for the greater part of all the published literature (Table 1). Second, most studies examine only species diversity as it relates to the abundance of large wood or the role of wood in creating habitat or microhabitat diversity. Relatively few studies link the role of wood in creating habitat diversity to species diversity or species richness (Table 2). Third, we found no studies linking large wood to any of the other components of biodiversity (Table 2). Fourth, of the studies examining species diversity, the most commonly studied taxa are invertebrates, followed closely by fishes (Table 3). By comparison, studies of the role of large wood and biodiversity in riparian zones or of other types of organisms are quite rare. Finally, studies of large wood and biodiversity largely focus on individual channel-units (for example, pools or riffles) or short reaches (less than
TABLE 1. The 54 (of 1,192) literature citations examining the role of large wood in biodiversity of aquatic ecosystems, categorized by the topic of biodiversity studied; some citations fall into more than one category.

<table>
<thead>
<tr>
<th>Topic</th>
<th>Number</th>
<th>Percentage</th>
</tr>
</thead>
<tbody>
<tr>
<td>Source of food, energy, or nutrients</td>
<td>1</td>
<td>2</td>
</tr>
<tr>
<td>Wood as habitat</td>
<td></td>
<td></td>
</tr>
<tr>
<td>Wood provides a substrate</td>
<td>20</td>
<td>37</td>
</tr>
<tr>
<td>Wood adds complexity to habitat unit</td>
<td>25</td>
<td>46</td>
</tr>
<tr>
<td>Added cover (predation)</td>
<td>4</td>
<td>7</td>
</tr>
<tr>
<td>Visual screening (competition)</td>
<td>1</td>
<td>2</td>
</tr>
<tr>
<td>Current velocity (refuge)</td>
<td>5</td>
<td>9</td>
</tr>
<tr>
<td>Disturbance (refuge)</td>
<td>2</td>
<td>4</td>
</tr>
<tr>
<td>Wood provides a unique habitat</td>
<td>8</td>
<td>15</td>
</tr>
<tr>
<td>Wood as a factor in habitat formation</td>
<td>21</td>
<td>39</td>
</tr>
</tbody>
</table>


500 m). Although large wood can influence migratory species in different ways and in different parts of the stream network depending on age-class and life form, we failed to find studies examining the influence of wood on biodiversity at the scale of an entire river network (Table 4). Clearly, the narrowly focused topic of large wood and biodiversity has received comparatively little attention from aquatic and riparian ecologists. Instead, most effort has been devoted to understanding the functional significance of large wood in aquatic ecosystems.

The Role of Large Wood Relative to Biodiversity

Large wood potentially influences biodiversity in aquatic ecosystems in many ways and at multiple spatial scales. Large wood is a source of organic matter and nutrients for aquatic insects (Benke and Wallace 2003, this volume). Thus, wood influences both the trophic structure and productivity of aquatic food webs and thereby influences both species composition and diversity. Wood also serves as habitat, for example, for wood-boring or mining invertebrates and for salamanders nesting in rotten logs. More typically, however, wood is viewed as an element of physical habitat, either providing a specific substrate, especially for biofilms and macroinvertebrates, or by adding complexity to existing habitats, such as pools. Also, large wood can control patterns of erosion and deposition of sediment, thus helping shape channel morphology and helping determine the types and relative abundance of physical habitats present in a stream reach. The role of wood in streams varies with location along the stream network. Wood recruitment to streams is often episodic, with

TABLE 2. The 54 (of 1,192) literature citations examining the role of large wood in biodiversity of aquatic ecosystems, categorized by the component of biodiversity examined.

<table>
<thead>
<tr>
<th>Diversity component</th>
<th>Number</th>
<th>Percentage</th>
</tr>
</thead>
<tbody>
<tr>
<td>Genetic</td>
<td>0</td>
<td></td>
</tr>
<tr>
<td>Age-class</td>
<td>0</td>
<td></td>
</tr>
<tr>
<td>Life-form</td>
<td>0</td>
<td></td>
</tr>
<tr>
<td>Dietary</td>
<td>1</td>
<td>2</td>
</tr>
<tr>
<td>Species</td>
<td>29</td>
<td>54</td>
</tr>
<tr>
<td>Habitat</td>
<td>33</td>
<td>61</td>
</tr>
<tr>
<td>Ecosystem</td>
<td>0</td>
<td></td>
</tr>
<tr>
<td>Landscape or network</td>
<td>0</td>
<td></td>
</tr>
</tbody>
</table>

Table 3. The 54 (of 1,192) literature citations examining the role of large wood in biodiversity of aquatic ecosystems, categorized by the taxon of interest; some citations fall into more than one category.

<table>
<thead>
<tr>
<th>Topic</th>
<th>Number</th>
<th>Percentage</th>
</tr>
</thead>
<tbody>
<tr>
<td>Physical habitat studies (no other taxon)</td>
<td>9</td>
<td>17</td>
</tr>
<tr>
<td>Aquatic studies</td>
<td>44</td>
<td>81</td>
</tr>
<tr>
<td>Fungi</td>
<td>2</td>
<td>4</td>
</tr>
<tr>
<td>Macrophytes</td>
<td>1</td>
<td>2</td>
</tr>
<tr>
<td>Invertebrates</td>
<td>21</td>
<td>39</td>
</tr>
<tr>
<td>Crustaceans</td>
<td>1</td>
<td>2</td>
</tr>
<tr>
<td>Amphibians</td>
<td>2</td>
<td>4</td>
</tr>
<tr>
<td>Fish</td>
<td>17</td>
<td>31</td>
</tr>
<tr>
<td>Riparian studies</td>
<td>6</td>
<td>11</td>
</tr>
<tr>
<td>Moss</td>
<td>15</td>
<td>2</td>
</tr>
<tr>
<td>Plants</td>
<td>3</td>
<td>6</td>
</tr>
<tr>
<td>Other vertebrates</td>
<td>2</td>
<td>4</td>
</tr>
</tbody>
</table>


large pulses of wood entering streams during, or shortly after, major disturbances. Further, floods and debris flows can significantly restructure a stream’s wood load. This high spatial and temporal variability in wood loading is likely to result in changes in biodiversity at multiple spatial and temporal scales.

Wood as a unique substrate or habitat

Several studies showed that wood provides a unique habitat to which some species are specially adapted or provides habitat critical for some aspect of a species’ life history. Examples of wood specialists include the wood-boring isopods called gribbles Limnoria spp. and the wood-boring mollusks called shipworms (naval shipworm Teredo navalis and feathery shipworm Bankia setacea) that occupy bays and estuaries (Maser and Sedell 1994). Some freshwater macroinvertebrates are also obligate wood specialists, including the functional groups of miners and tunnelers, such as the larval crane fly Lipsothrix spp., the larval riffle beetle Lara avara, and species of caddisflies that gauge attachment sites on wood (Anderson et al. 1978; Wallace and Anderson 1996; Wallace et al. 1996; Benke and Wallace 2003). Although relatively few species require wood, many are facultative wood-using species. These include many aquatic macroinvertebrates that use wood as an attachment site when it is available (Anderson et al. 1978; Benke and Wallace 2003) and species like the Van Dyke’s salamander Plethodon vandykei, a species that can nest in moderately decayed stumps and logs (Blessing et al. 1999).

Wood also provides important basking habitat for several species of turtles in the southeastern United States, in environments where other basking habitats are not available (Lindeman 1999). Clearly, the

Table 4. The 54 (of 1,192) literature citations examining the role of large wood in biodiversity of aquatic ecosystems, categorized by the spatial scale of the study; some citations fall into more than one category.

<table>
<thead>
<tr>
<th>Scale</th>
<th>Number</th>
<th>Percentage</th>
</tr>
</thead>
<tbody>
<tr>
<td>Particle (or piece)</td>
<td>13</td>
<td>24</td>
</tr>
<tr>
<td>Subunit</td>
<td>25</td>
<td>46</td>
</tr>
<tr>
<td>Channel unit</td>
<td>21</td>
<td>39</td>
</tr>
<tr>
<td>Stream reach</td>
<td>31</td>
<td>57</td>
</tr>
<tr>
<td>Stream section</td>
<td>0</td>
<td>0</td>
</tr>
<tr>
<td>Stream network</td>
<td>0</td>
<td>0</td>
</tr>
</tbody>
</table>

presence of highly specialized, wood-obligate species depends on the presence of wood; similarly, the abundance of many facultative wood-using species is also dependent on wood, especially in environments that lack alternative hard substrates. Thus, wood contributes directly to the richness of species in these communities (Wallace et al. 1996; Benke and Wallace 2003).

**Wood as a source of nutrients or energy**

In general, wood does not provide a readily available form of energy for stream ecosystems. It is difficult to decompose, in part because lignin and cellulose are inherently resistant to decomposition, but also because lignin breakdown is dominantly an aerobic process (Suberkropp 1998; Bilby 2003, this volume). Water-saturated logs in streams and rivers become anaerobic, except near the wood surface where oxygen can diffuse into the log. Consequently, only the surface layers of the logs decompose readily (Harmon et al. 1986; Bilby et al. 1999). Because wood is more resistant to decomposition than leaves and other organic matter, it does not represent a significant energy source to most temperate stream food webs. Although many species of miners, gougers, scrapers, shredders, and collectors are abundant on wood, it is often the biofilm on the wood surface, not the wood substrate itself, that is the primary food for these macroinvertebrates (Bowen et al. 1998; Bisson and Bilby 1998). More recent studies do indicate, however, the use of wood as a primary food source for several aquatic insect taxa (Hoffman and Hering 2000). Although wood is a poor source of energy and nutrients, wood is often a key feature trapping other organic materials, forming what are commonly called “debris dams” (Angermeier and Karr 1984; Smock et al. 1989; Wallace et al. 1995; Murphy and Meehan 1991; Diez et al. 2000). Organic matter collected on or around large wood is an important substrate for heterotrophic organisms (Anderson and Sedell 1979; Triska et al. 1982; Gregory et al. 1987; Smock et al. 1989; Casas 1997). Thus, wood can strongly influence trophic structure, helping to determine the composition of macroinvertebrate communities and the relative abundance of functional-feeding groups in stream ecosystems (Anderson and Sedell 1979; Benke et al. 1985; Smock et al. 1989; Wallace et al. 1995; Wallace et al. 1996).

**Wood as a substrate**

One of the most studied aspects of wood and biodiversity is its influence as a substrate (Table 1). Studies have examined the importance of wood in providing a relatively stable, hard substrate in a variety of aquatic ecosystems, where it can support more species-rich communities of periphyton and benthic invertebrates (Benke et al. 1985). Research results on the role of large wood in biodiversity are often conflicting, however. The clearest evidence for increased biodiversity comes from studies of low-gradient streams, estuaries, and lakes with soft-textured bed sediments where wood is the only hard, stable substrate (Benke et al. 1985; Benke and Wallace 2003). If wood pieces are large or securely imbedded in the stream channel (including tree roots exposed in streambanks), they are less likely than the streambed sediment to be disturbed or moved during high flows (Wallace and Benke 1984; Benke and Wallace 2003). Similarly, because wood breaks down slowly, it lasts longer than leaves or other organic substrates (Wallace and Benke 1984; Wallace et al. 1996). Thus, in many low gradient sand or fine-sediment bedded streams, wood-dwelling macroinvertebrates comprise a substantial proportion of the total macroinvertebrate biomass and are an important food source for fish and other consumers (Angermeier and Karr 1984; Benke et al. 1985; Smock et al. 1989; Benke and Wallace 2003). Clearly, wood, when present, provides an important substrate for a variety of aquatic organisms, although its functional importance in stream ecosystems and its influence on biodiversity may depend on the availability of alternative, hard, stable substrates (also see Benke and Wallace 2003).

Wood surfaces also provide diverse microhabitats. Greater species richness of macroinvertebrates has been observed on rough-conditioned wood than on either unconditioned or smooth wood (Magoulick 1998). Wood properties change with exposure to water, physical abrasion, and decomposition; thus, surface complexity tends to increase with time. The complex microhabitats of decayed wood appear to contribute to increased biodiversity of macroinvertebrate communities (Hax and Golladay 1993). O’Connor (1991) found that rough-textured wood supported greater macroinvertebrate species richness, which was attributed to increased habitat complexity. Similarly, differences in bark texture among tree species can also contribute to microhabitat variation, apparently increasing microhabitat diversity and po-
tentially leading to changes in species diversity of macroinvertebrates in aquatic ecosystems (Bowen et al. 1998). However, not all studies have shown relations between species and microhabitat diversity (France 1997; Magoullick 1998). In some cases, macroinvertebrates may simply be opportunistic colonizers of available hard substrates (France 1997). In other cases, analyses focused on species diversity—habitat complexity relations may miss more complex functional relations between macroinvertebrates and woody substrates (O’Connor 1991) or the effects of recent disturbances (Anderson 1992) that also affect community composition.

**Wood creates complexity in habitat units**

A second commonly studied aspect of wood and biodiversity is its influence in creating complexity in a habitat unit, such as a pool, riffle, or rapid (Table 1). A large body of research documents that wood-created habitat complexity serves important functions in many aquatic ecosystems. Wood can visually isolate individuals and thereby reduce competition (Doloff and Reeves 1990; Crook and Robertson 1999; Doloff and Warren, Jr. 2003, this volume); wood also provides a variety of refugia (Sedell et al. 1990; Crook and Robertson 1999), including hiding cover (Angermeier and Karr 1984; Everett and Ruiz 1993; Inoue and Nakano 1998). Log accumulations may also be good foraging sites for predatory macroinvertebrates and for fish feeding on macroinvertebrates (Benke et al. 1985; Wallace et al. 1996; Crook and Robertson 1999; Benke and Wallace 2003). Wood in pools also creates microhabitat patches (channel-subunit scale) with varying depths and flow velocities, which can contribute to microhabitat partitioning of co-occurring species (Reeves et al. 1997; Reeves et al. 1998; Thévenet and Statzner 1999) and can result in increased diversity of fish species and age-classes (Bisson et al. 1992). During floods, structural complexity created by wood provides refugia that can reduce disturbance to benthic macroinvertebrates (Borchardt 1993; Palmer et al. 1996) and contribute to the overwinter persistence of salmonids in a stream reach (McMahon and Hartman 1989; Quinn and Peterson 1996; Harvey et al. 1999). Wood is especially important in areas where alternative sources of structural complexity are not available, for example, in rivers and estuaries where streambed sediment is soft and rock, emergent vegetation, and reefs or reef-like structures are lacking (Everett and Ruiz 1993; Wallace et al. 1996; Benke and Wallace 2003) or in soft-bottomed lakes lacking macrophytes and other physical structures (France 1997).

We know of no examples in which wood decreases measures of diversity in habitat units. Linking the effects of increased habitat diversity to other components of biodiversity, however, is problematic. Some studies have shown that increased habitat diversity was correlated to increased diversity of fishes (Reeves et al. 1993; Thévenet and Statzner 1999). Other studies have failed to show this relationship. For example, the amount of wood in pools did not influence salmonid diversity in Oregon Coast Range streams (Chen 1999); coastal cutthroat trout *Oncorhynchus clarki clarki* density did not differ between simple pools and pools with wood-formed habitat diversity, which was attributed to a lack of interspecific competition (Simondet 1997). Also, adding wood to a tropical forest stream had little influence on populations of freshwater shrimp, probably because habitat structure was provided by cobbles and boulders (Pyron et al. 1999). Clearly, diversity at the microhabitat and habitat-unit scale can be functionally important, at least to some species and life forms, especially where wood-related habitat diversity contributes to functional processes in aquatic ecosystems that would otherwise be lacking (Doloff and Warren 2003). However, separating the influence of diversity from other confounding effects or isolating the effect of diversity at the microhabitat scale from diversity at larger scales can be difficult.

**Wood as a geomorphic element creating a diversity of habitats**

A third commonly studied aspect of wood and biodiversity is its influence in creating a diversity of habitat units in a stream reach (Table 1). Wood-forced patterns of scour and deposition are often important in determining the type and number of channel units in alluvial reaches of streams. This relation between wood and channel morphology has been widely studied in streams of the northern Pacific coast of North America and in a wide variety of streams throughout the world (Heede 1972; Bilby 1981; Mosley 1981; Trotter 1990; Ebert et al. 1991; Shields and Smith 1992; Dose and Roper 1994; Assani and Petit 1995; Fetherston et al. 1995; Wallace et al. 1995; Abbe and Montgomery 1996; Doloff 1996; Wood-Smith and Buffington 1996; Hilderbrand et al. 1997; Gurnell and Sweet 1998; Ward et al. 1999b; Gerhard and Reich 2000; Gurnell
The relation between wood and channel morphology is not present in all streams and rivers, however (Inoue and Nakano 1998).

Effects of large wood on channel morphology depend on the amount of wood, its size and orientation in the stream channel, and the size and type of stream (Keller and Swanson 1979; Swanson et al. 1982; Bilby and Bisson 1998; Montgomery and Buffington 1998; Beechie et al. 2000; Gurnell et al. 2002). These relations are well described for mountain stream networks. In small streams, single logs, as well as logjams, frequently form channel-spanning blockages and can alter channel morphology by obstructing the flow of water, forming pools, and storing sediment (Bilby 1981; Andrus et al. 1988; Bilby and Ward 1989; Nakamura and Swanson 1993; Richmond and Fausch 1995; Wallace et al. 1995; Gurnell et al. 2002). If logs are oriented parallel to the stream, or only partially block the stream, they tend to create scour pools.

In large streams and rivers, single logs are not large enough to control channel-forming processes. Instead, large logjams are required. These jams can block channels during floods, driving channel avulsions (Gottesfeld and Johnson-Gottesfeld 1990; Wondzell and Swanson 1999), helping form secondary channels and other off-channel habit, which is important for many aquatic species (Sedell et al. 1984; Bryant et al. 1991; Crispin et al. 1993). Wood is also deposited on stream banks, gravel bars, and floodplains during floods, influencing channel morphology by stabilizing streambanks, creating scour pools, or helping form gravel bars (Malanson and Butler 1990; Fetherston et al. 1995; Richmond and Fausch 1995; Abbe and Montgomery 1996; Bilby and Bisson 1998; Montgomery and Buffington 1998; Edwards et al. 1999; Braudrick and Grant 2001; Gurnell et al. 2002). Large logjams can be long-lasting, protecting and stabilizing gravel bars in the active channel of braided rivers, initiating a successional sequence that will give rise to vegetated mid-channel islands (Fetherston et al. 1995; Abbe and Montgomery 1996; Edwards et al. 1999). All these processes help form complex, multiple-channel floodplains in large rivers, areas widely recognized for high biodiversity (Brown 1997; Ward et al. 1999a, 1999b). Because of the functional relations between wood and channel morphology, wood is widely recognized as contributing to habitat diversity in streams (Bisson 1987).

Several studies have shown that the amounts of wood present in a stream reach are correlated to the number of pools and sometimes to either the area or volume of pool habitats in those streams (Murphy et al. 1986; House and Boehne 1987; Andrus et al. 1988; Carlson et al. 1990; Crispin et al. 1993; Richmond and Fausch 1995; Dollof 1996; Gurnell and Sweet 1998). Management practices that reduce the amounts of wood in streams often lead to reductions in pool volume and area (Murphy et al. 1986; McIntosh et al. 1994) and reduce habitat diversity (Shields and Smith 1992). Changes in the relative abundance of different habitat units, especially pools and riffles, can have marked influence on the diversity of fish species and age-classes in streams. For example, comparing a wood-rich stream with a wood-poor stream in western Washington showed that the wood-poor stream was dominated by riffle habitats and the age-0 and age-1 steelhead trout O. mykiss, which prefer riffle environments. The wood-rich stream, however, was dominated by pools, and fish biomass was more evenly distributed among the three species present and among multiple age-classes of these species (Hicks et al. 1991). Studies of sand-bedded streams have shown similar results, with greater richness of fish communities in streams with more abundant wood and more pools (Ebert et al. 1991; Shields et al. 1994).

Several studies have compared composition and productivity of macroinvertebrate communities between forested and clear-cut reaches of streams (Murphy and Hall 1981; Anderson 1992) and among forest, plantation, and pasture reaches (Quinn et al. 1997), where the nonforest reaches have reduced amounts of instream large wood or wood is entirely lacking. Several of these studies found that the overall richness of macroinvertebrates differed little among reaches (Anderson 1992; Quinn et al. 1997) or was greater in nonforested reaches lacking large wood (Murphy and Hall 1981). Stream productivity, however, was limited by available light in the examples cited, so that forest removal increased primary production and resulted in large changes in macroinvertebrate community composition.

Many of the studies that have examined the role of large wood in streams have compared areas with different land uses. In the Pacific Northwest of the United States and Pacific coastal regions of Canada and Alaska, comparisons between clear-cut and unharvested areas dominate much of the published literature. Many of these studies focus on large wood, relating the amounts of large wood present in the stream to the attributes of interest, for example, numbers
of pools, abundance of fish, or diversity of macroinvertebrate communities. However, wood abundance is only one of several stream attributes affected by land use patterns (Gregory et al. 1987; Hanchet 1990). For example, a study in New Zealand comparing native forest with pasture to examine effects of land use on native fish communities could not isolate the effect of wood abundance from the effects of shade, cover provided by instream vegetation, water temperature, and substrate coarseness (Hanchet 1990). Similarly, Quinn et al. (1997) concluded that several factors, including light, temperature, productivity, water quality, fine sediment, current velocity, and channel morphology—in addition to the presence and abundance of wood—may have contributed to differences in macroinvertebrate communities among native forest, plantations, and pasture. Collectively, the studies cited above show that the effect of wood on biodiversity depends strongly on the functional role of large wood in stream ecosystems. In some cases, wood strongly influences biodiversity; in other cases, wood appears to have little influence on biodiversity. In all cases, however, isolating the influence of wood from other confounding factors is difficult.

Organic-matter retention and sediment storage

Large wood effectively traps small pieces of wood and other organic materials, such as leaves, needles, and twigs (Angermeyer and Karr 1984; Smock et al. 1989; Gregory et al. 1993; Wallace et al. 1995; Murphy and Meehan 1991; Diez et al. 2000) and even carcasses of dead fish such as salmon (Cederholm and Peterson 1985). Further, the abrasion or erosion of the surface of large wood can be a significant source of fine particulate organic matter (Ward and Aumen 1986). Wood thus influences the retention of organic matter in stream reaches (Bilby 1981; Harmon et al. 1986; Bisson and Bilby 1998). Because the organic matter collected on or around large wood is an important substrate for heterotrophic organisms and the primary consumers that feed on them, large wood can help determine stream trophic relations (Anderson and Sedell 1979; Triska et al. 1982; Gregory et al. 1987; Smock et al. 1989; Casas 1997), the diversity and composition of the macroinvertebrate communities, and the relative abundance of functional-feeding groups present in a stream reach (Anderson and Sedell 1979; Benke et al. 1985; Smock et al. 1989; Wallace et al. 1995; Wallace et al. 1996).

Large wood influences patterns of erosion, transport, and deposition of sediment at many different scales in stream networks (Palmer et al. 1996; Wallace et al. 1996; Buffington and Montgomery 1999; Lancaster et al. 2001). Wood can create low streamflow-velocity environments, characterized by deposition of fine-textured sediment that function as refugia for some macroinvertebrates during floods (Palmer et al. 1996). Also, patterns of sediment deposition create “textural patches” characterized by different grain-size distributions and can provide greater diversity of aquatic habitats than otherwise might be present (Gerhard and Reich 2000). For example, wood can create patches of sediment with grain-sizes suitable for fish that must spawn in substrates of a specific size (Buffington and Montgomery 1999). Large wood can also control sediment storage, especially in small mountain streams (Nakamura and Swanson 1993; Montgomery et al. 1996), where it forms pool-step sequences. The change in the longitudinal gradient of streams across pool-step sequences is the primary factor driving hyporheic exchange flow in small mountain streams (Harvey and Bencala 1993; Kasahara and Wondzell, in press), which creates unique physical, chemical, and hydrologic environments in streams and riparian zones that provide a diversity of habitats for many specially adapted macroinvertebrates (Stanford and Ward 1988). Similarly, large wood can control deposition of sediment in active stream channels, initiating formation of sand or gravel bars that can eventually become vegetated islands in a braided channel (Edwards et al. 1999; Ward et al. 1999b). Thus, wood controls sediment and organic matter storage in streams at scales ranging from the particle and microhabitat up to entire stream reaches, and it contributes to habitat diversity at these scales.

Wood and Biodiversity over Scales of Space and Time

Spatial scales

Spatial scale in streams has been defined geomorphologically, starting from the particle through the sub-unit, channel geomorphic unit, stream reach, river section, and up to the network scale (Frissell et al. 1986; Grant et al. 1990; Sedell et al. 1990; Gregory et al. 1991). We have examined the role of large wood in mediating biodiversity, organizing our discussion around the functional role of wood,
and we have shown that the functional role of large wood and its effects on biodiversity have been studied at spatial scales ranging from the particle through the stream reach (Table 4). At larger spatial scales, however, the role of wood and its importance to maintaining biodiversity have received comparatively little attention, despite research showing that large wood influences habitat complexity from the headwater reaches of small streams through low-land sections of large rivers, in tidal reaches and estuaries, on ocean beaches, and even on the floor of the ocean (Maser and Sedell 1994). Further, the role of large wood, the way it is distributed in streams (Swanson et al. 1982; Gregory et al. 1993; Bilby and Bisson 1998; Martin and Benda 2001; Gurnell et al. 2002), and the way it influences streams and their biological communities changes with location in the stream network (Sedell et al. 1982; Bisson et al. 1987; Bilby and Ward 1989; Crook and Robertson 1999).

We draw from a study of fall chinook salmon *O. tshawytscha* in the Sixes River, Oregon (Reimers 1971) to illustrate the possible influence of large wood at the network scale. The life histories of anadromous salmonids include exposure to a sequence of habitats, from small tributary streams to the ocean and back again. Populations must evolve adaptations to the diversity of aquatic habitats available in the stream network, and often, this evolution leads to a strategy of spreading risk among different life history alternatives. Fall chinook salmon in the Sixes River, Oregon display five life history strategies (Table 5) defined by differences in rearing times in tributary streams, the mainstem river, and the estuary (Reimers 1971). The importance of wood in determining salmonid habitat quality in tributary and mainstem rivers has been widely studied (Bisson et al. 1987; McMahon and Hartman 1989; Bilby and Bisson 1998), and even in estuaries, most juvenile chinook were associated with wood (Reimers 1971). Presumably, the relative success of different life history strategies, each spending different lengths of time in tributary, mainstem, and estuary habitat, would be related, at least in part, to the abundance of large wood. Reimers (1971) examined this question in the Sixes River, finding that more than 90% of returning adults were of lifehistory type 3. Reimers (1971) also hypothesized that improved tributary and mainstem habitat could lead to increased numbers of life history types 4 and 5. Despite the importance of large wood in streams and rivers of the north Pacific Coast of North America and the documented importance of wood to the habitat of salmon that inhabit those rivers, we know of no studies that have examined the role of large wood and habitat complexity in maintaining the relative abundance and long-term viability of alternative life histories of salmon at the scale of an entire stream network.

Schlosser and Angermeier (1995) pointed out that the lack of understanding of the links between the diversity of habitats available at a network scale and metapopulation dynamics are a critical gap in knowledge for fish conservation. An important topic for future conservation research will be to understand the importance of habitat diversity across scales in maintaining both genetic and life history diversity of individual species as well as species diversity. Further, there is a need to understand the role of biophysical processes in maintaining that habitat diversity and to understand how the spatial distribution and connectivity of habitat patches at river network, or larger scales, influences biodiversity.

### Temporal scale

Wood abundance changes naturally over time at both site and watershed scales. Wood enters chan-

---

**Table 5.** Five different types of life-history strategies of fall chinook salmon in the Sixes River, Oregon for 1 year after emergence (em) of salmon fry from streambed gravels. Emergence occurs between March and May; peak emergence is in mid to late April, with some protracted emergence into June. Length of juvenile residence in tributary (T), mainstem river (R), and estuary habitat (E), and timing of out-migration to the ocean (O) are shown. Capital letters, above columns, denote months. Data from Reimers (1971).

<table>
<thead>
<tr>
<th>Life history</th>
<th>M</th>
<th>A</th>
<th>M</th>
<th>J</th>
<th>J</th>
<th>A</th>
<th>S</th>
<th>O</th>
<th>N</th>
<th>D</th>
<th>J</th>
<th>F</th>
<th>M</th>
<th>A</th>
</tr>
</thead>
<tbody>
<tr>
<td>Type 1</td>
<td>em</td>
<td>em</td>
<td>T</td>
<td>O</td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Type 2</td>
<td>em</td>
<td>em</td>
<td>T</td>
<td>R</td>
<td>E</td>
<td>E</td>
<td>E</td>
<td>E</td>
<td>E</td>
<td>O</td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Type 3</td>
<td>em</td>
<td>em</td>
<td>T</td>
<td>R</td>
<td>E</td>
<td>E</td>
<td>E</td>
<td>E</td>
<td>E</td>
<td>O</td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Type 4</td>
<td>em</td>
<td>em</td>
<td>T</td>
<td>R</td>
<td>R</td>
<td>R</td>
<td>R</td>
<td>R</td>
<td>R</td>
<td>R</td>
<td>R</td>
<td>R</td>
<td>R</td>
<td>R</td>
</tr>
<tr>
<td>Type 5</td>
<td>em</td>
<td>em</td>
<td>T</td>
<td>R</td>
<td>R</td>
<td>R</td>
<td>R</td>
<td>R</td>
<td>R</td>
<td>R</td>
<td>R</td>
<td>R</td>
<td>R</td>
<td>R</td>
</tr>
</tbody>
</table>
nels as the result of streambank erosion during major floods, from tree mortality caused by windstorms, fires, insects or disease, and from other disturbances, such as landslides (Harmon et al. 1986; Lienkaemper and Swanson 1987; Naiman et al. 1992; Dolloff et al. 1994; Reeves et al. 1995; Dolloff 1996; Wallace et al. 1996; Bragg 2000; Martin and Benda 2001; Benda et al. 2002, 2003, this volume; Gurnell et al. 2002; Gurnell 2003; Montgomery et al. 2003; Nakamura and Swanson 2003; all this volume). Once in the stream, mobilization of in-channel wood by fluvial transport during floods, or by debris flows, can cause significant restructuring of a stream's wood load. Reeves et al. (1995) hypothesized that centuries-long cycles of episodic inputs followed by long-term loss of wood and coarse sediment after wildfires drive long-term changes in both the composition and productivity of fish communities in Oregon Coast Range streams. Many of these changes are related to the abundance and physical characteristics of pools anchored by large wood; as wood disappears from stream channels—and in the absence of fresh inputs of wood and coarse sediment—the stream becomes dominated by shallow-water habitats that favor riffle-dwelling species (Hicks et al. 1991). Thus, patterns in wood-controlled biodiversity would be expected to change through time. Some recent studies have begun to examine long-term dynamics of large wood in streams and rivers at landscape scales (Lancaster et al. 2001; Martin and Benda 2001), but these dynamics have yet to be linked to long-term patterns of biodiversity.

Conclusions

Many studies have shown that wood in rivers and streams increases biodiversity, especially species diversity and richness of macroinvertebrates and fishes, structural complexity in habitat units, and the diversity of habitats in a stream reach. Many other studies, however, failed to show an effect of wood on biodiversity. These contrasting results highlight the importance of the functional role of wood in aquatic ecosystems. In some streams, wood provides unique functions: (1) providing the only hard and stable substrate available, (2) creating microhabitat complexity within channel units not provided by other structural elements such as large cobbles and boulders, and (3) controlling the morphology of large alluvial rivers or the number and type of channel units present in a smaller stream. In these cases, large wood often contributes significantly to biodiversity at multiple spatial scales. However, the relationships between large wood and biodiversity can be confounded by many factors (for example, number of fish species present, presence or absence of alternative hard substrates, availability of alternative cover, amounts of light and primary productivity). Further, both land use history and natural disturbances influence the amount of wood present in a stream both because natural disturbance is often related to patterns of wood delivery to streams and because the type of disturbance, time since disturbance, and the land use history are related to the successional age and species composition of the adjacent riparian forests. Further, the relative importance of all of these factors can vary with location within a stream network. Thus, the abundance of wood and its functional significance in a variety of biotic and abiotic processes depend on a variety of factors. It is the combined effect of all these factors, in addition to the presence of large wood, which determines patterns of biodiversity.

Acknowledgments

We thank two anonymous reviewers, Stan Gregory, and Deanna Stouder, for helpful comments. Support for this work was provided by the Interior Columbia Basin Ecosystem Management Project. Additional support was provided by the USDA Forest Service’s Pacific Northwest Research Station and both the Aquatic and Land Interactions Program and the Managing Disturbance Regimes Program.

References


Harvey, B. C., R. J. Nakamoto, and J. L. White. 1999. Influence of large woody debris and a bankfull flood on movement of adult resident coastal cutthroat trout (Oncorhynchus clarki clarki) during fall and winter. Canadian Journal of Fisheries and Aquatic Sciences 56:2161–2166.


Wood and Biodiversity


Ward, J. V., K. Tockner, and F. Schiemer. 1999a. Biodiversity of floodplain river ecosystems: eco-