

**ECOLOGICAL LINKAGES BETWEEN HEADWATERS AND
DOWNSTREAM ECOSYSTEMS: TRANSPORT OF ORGANIC MATTER,
INVERTEBRATES, AND WOOD DOWN HEADWATER CHANNELS¹**

Mark S. Wipfli, John S. Richardson, and Robert J. Naiman²

ABSTRACT: Headwater streams make up a large proportion of the total length and watershed area of fluvial networks, and are partially characterized by the large volume of organic matter (large wood, detritus, and dissolved organic matter) and invertebrate inputs from the riparian forest, relative to stream size. Much of those inputs are exported to downstream reaches through time where they potentially subsidize river communities. The relative rates, timing, and conversion processes that carry inputs from small streams to downstream reaches are reasonably well quantified. For example, larger particles are converted to smaller particles, which are more easily exported. Also, dissolved organic matter and surface biofilms are converted to larger particles which can be more easily intercepted by consumers. However, the quality of these materials as it affects biological activity downstream is not well known, nor is the extent to which timing permits biological use of those particles. These ecological unknowns need to be resolved. Further, land uses may disrupt and diminish material transport to downstream reaches by removing sources (e.g., forest harvest), by affecting transport and decomposition processes (e.g., flow regulation, irrigation, changes in biotic communities), and by altering mechanisms of storage within headwaters (e.g., channelization). We present conceptual models of energy and nutrient fluxes that outline small stream processes and pathways important to downstream communities, and we identify informational gaps that, if filled, could significantly advance the understanding of linkages between headwater streams and larger rivers. The models, based on empirical evidence and best professional judgment, suggest that navigable waters are significantly influenced by headwater streams through hydrological and ecological connectivities, and land use can dramatically influence these natural connectivities, impacting downstream riverine ecosystems.

(KEY TERMS: ecosystem services; headwater streams; organic matter; invertebrates; wood; subsidy; transport.)

Wipfli, Mark S., John S. Richardson, and Robert J. Naiman, 2007. Ecological Linkages Between Headwaters and Downstream Ecosystems: Transport of Organic Matter, Invertebrates, and Wood Down Headwater Channels. *Journal of the American Water Resources Association* (JAWRA) 43(1):72-85. DOI: 10.1111/j.1752-1688.2007.00007.x

¹Paper No. J06017 of the *Journal of the American Water Resources Association* (JAWRA). Received February 3, 2006; accepted August 9, 2006. © 2007 American Water Resources Association. No claim to original U.S. government works

²Respectively, Associate Professor, Freshwater Ecology and Fisheries, USGS Alaska Cooperative Fish and Wildlife Research Unit, Institute of Arctic Biology, University of Alaska Fairbanks, Fairbanks, Alaska 99775; Associate Professor, Aquatic and Riparian Ecology, Department of Forest Sciences, University of British Columbia, 3041 – 2424 Main Mall, Vancouver, British Columbia, Canada V6T 1Z4; and Professor, Aquatic and Fishery Sciences, School of Aquatic & Fishery Sciences, University of Washington, Box 355020, Seattle, Washington 98195 (E-Mail/Wipfli: mark.wipfli@uaf.edu).

INTRODUCTION

Ecological linkages between headwater streams and larger order rivers are poorly documented, yet it is believed that headwaters are crucial for sustaining the structure, function, productivity, and biocomplexity of downstream ecosystems (Haigh *et al.*, 1998). Headwater streams provide downstream habitats with a multitude of ecosystem services, including water, nutrients (e.g., nitrogen and phosphorus), food [e.g., organic matter (OM) and invertebrate prey for fishes, salamanders, insectivorous birds], and woody debris (Wipfli and Gregovich, 2002; Compton *et al.*, 2003; Gregory *et al.*, 2003) (Figure 1). Headwater streams also serve as refugia and source areas for biodiversity (Meyer *et al.*, this issue). However, the quality and timing of delivery of these services to downstream communities remain in question.

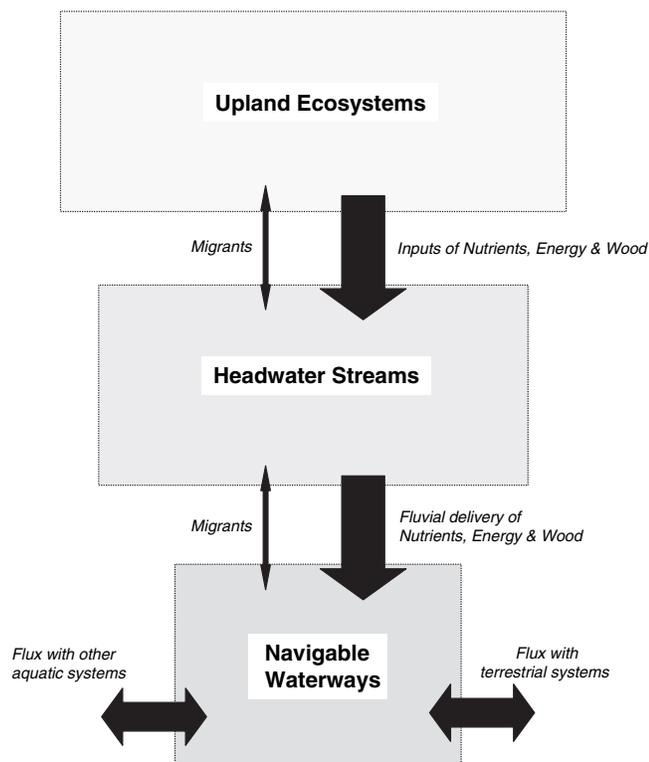


FIGURE 1. Natural Connectivity Model. Headwater streams are sources of energy and serve as conduits for nutrients, energy, and wood, linking upland ecosystems with navigable waters downstream. Natural hydraulic connectivity afforded by headwater streams provides a fluvial avenue for ecological connectivity between upland habitats and navigable waters to exist.

There are several reasons why headwater streams could be important to the ecology and biological integrity of downstream reaches. First, headwater habitats

encompass >80% of stream networks and watershed land areas (Naiman, 1983a; Benda *et al.*, 2005). Second, they are closely tied spatially to larger streams (Figure 2), entering these waters at numerous contact points (tributary junctions) along channel networks (Leopold *et al.*, 1964; Kiffney *et al.*, in press). Third, the water draining from headwater streams provide a continual source of essential products (e.g., nutrients, food, wood), which support aquatic and riparian biota, including those inhabiting navigable waterways (Naiman and Sedell, 1979; Naiman, 1982, 1983b; Meyer and Wallace, 2001; Wipfli and Gregovich, 2002).

Much concern exists regarding the amount of riparian and other protections that should be given to headwater channels. Compared with larger order systems, headwater streams commonly receive far less riparian buffer protection during logging or other land management activities, although protection measures vary across jurisdiction and with objectives (U.S. Dept. of Agriculture Forest Service, 1997, 1999; Blinn and Kilgore, 2001; Moore and Richardson, 2003). If headwater habitats do play key ecological roles in larger streams, inadequate protection may not only harm headwater streams, but would almost certainly impact the integrity and sustainability of downstream habitats. Understanding their ecological importance and how management activities might affect their structure and function will provide better information for managers and policy makers to craft effective guidelines to adequately protect the environmental integrity of navigable waters.

This article focuses on three primary ecological materials: OM in particulate (POM) and dissolved (DOM) forms, invertebrates, and wood – and how these materials enter, behave, change, and are delivered from headwater to downstream habitats. We discuss the potential effects of these materials on downstream communities, and how management activities can affect their delivery. Finally, we suggest future research avenues where essential knowledge is lacking. Although this article often focuses on Pacific Northwest systems, principles and concepts apply to streams throughout North America and beyond. Here, we define headwaters and headwater streams as small (usually <1 m wide) wetted channels, and typically containing no fish, usually because of the lack of suitable habitat or the presence of fish migration barriers, but are fluvially connected to downstream water bodies that do. We acknowledge that larger streams receive resource subsidies from other sources, including marine systems via salmon (*Oncorhynchus* spp.) and other anadromous species. We also acknowledge that biota migrate between headwater and downstream habitats (Richardson *et al.*, 2005b; Meyer *et al.*, this issue), but here we focus entirely on materials entering larger streams from their headwaters.

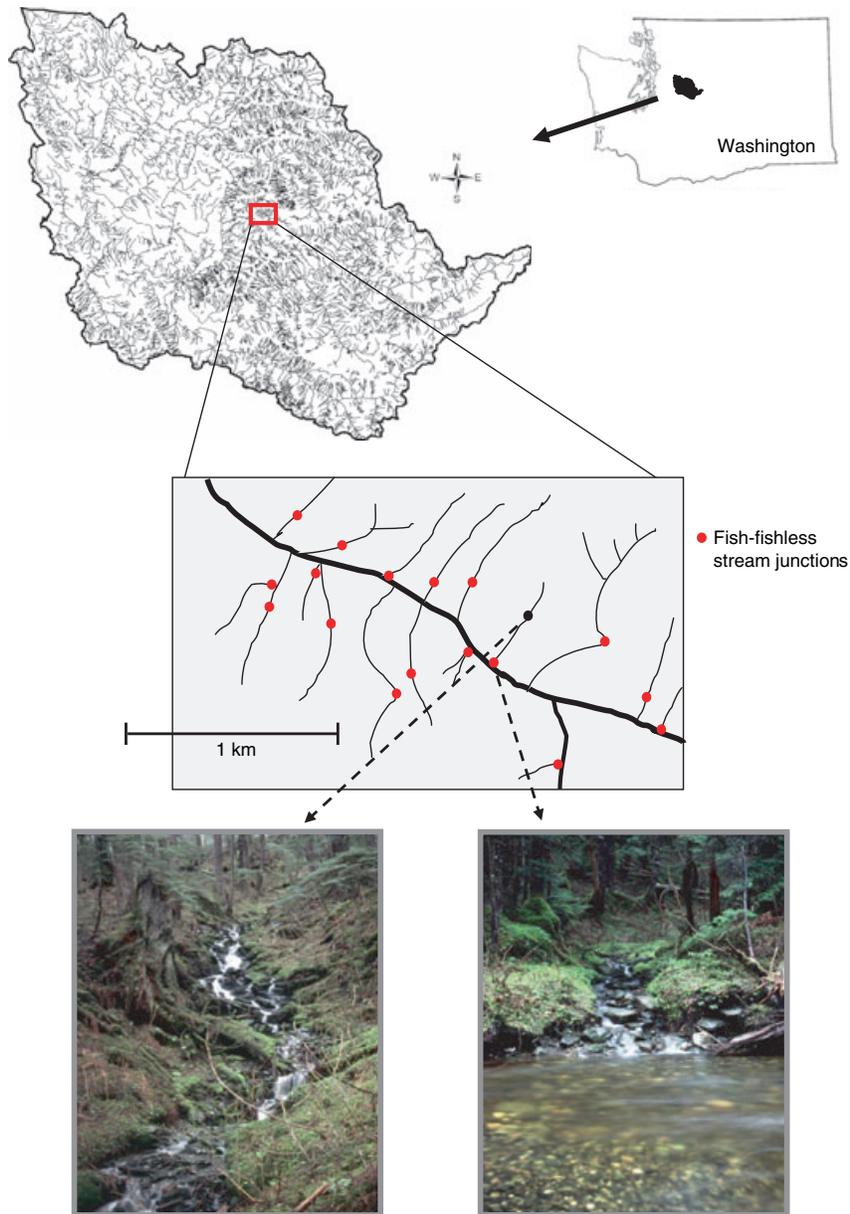


FIGURE 2. Representative Watershed Showing Linkages Between Fishless Headwater Channels and Downstream Fish-Bearing Habitats. Red dots indicate common fish-fishless transition points.

Evidence suggests that headwaters are critically important to downstream ecosystems (Naiman *et al.*, 1987; Meyer and Wallace, 2001; Gomi *et al.*, 2002; Wipfli and Gregovich, 2002; Compton *et al.*, 2003). They dominate channel networks in terms of stream length and watershed area, they transport matter to navigable waterways, and they have intimate and direct connections to these waterways. Collectively, this evidence supports the notion that headwater streams are key drivers in watershed-scale, riverine processes. Understanding which headwater goods and services are important, and the magnitude of their effects on downstream habitats and communities, will

advance management to concurrently consider upland forests, headwater streams, and downstream rivers as an integrated system.

DETRITUS, INVERTEBRATE AND WOOD INPUTS TO HEADWATER STREAMS

Riparian vegetation plays a key role in the ecology and productivity of headwater streams (Richardson, 1991; Naiman and Décamps, 1997; Wallace *et al.*,

1999; Meyer *et al.*, this issue). Riparian plants are especially important to streams and associated aquatic communities through allochthonous inputs that partially drive the energetics and structure of aquatic food webs (Figure 3) (Naiman *et al.*, 2005). DOM (including colloidal matter) leaching from decaying plant litter, particulate matter in the form of plant litter (e.g., leaves and twigs), woody debris, and terrestrial invertebrates all enter headwater streams and play key roles in food web dynamics, production, nutrient or carbon retention, and other processes (Wipfli, 1997; Wallace *et al.*, 1999; Richardson *et al.*, 2005a; Meyer *et al.*, this issue) (Figure 3).

There are three primary input pathways for organic materials: (1) litter fall (i.e., free fall of material from riparian plants into streams) of material which includes plant litter (leaves, twigs), invertebrates, and wood, (2) overland flow of particulate and dissolved organic material from plants and mass wasting, oftentimes during periods of precipitation, and (3) subsurface movement that includes leachate from plant matter in subsurface water, and dispersal of invertebrates such as oligochaete worms and other soilborne fauna from riparian soils to streams (Cummins *et al.*, 1989; Wipfli, 1997; Wallace

et al., 1999; Nakano and Murakami, 2001). Seasonal timing of these inputs varies widely, depending upon type of material, ecological region, and elevation (Richardson *et al.*, 2005a). For example, temperate deciduous trees usually shed leaves in autumn as they senesce (e.g., Benfield, 1997; Webster *et al.*, 1999). Conversely, coniferous trees and angiosperms with typically evergreen leaves (e.g., ericaceous plants such as *Rhododendron*, *Arbutus*, *Gaultheria*, and others) can drop their leaves and needles at other times of year (Richardson, 1992). Other inputs of nutrient-rich plant material include bud scales, seeds, cones, and flowers; all of which are likely to fall into streams at times other than the period of leaf fall.

Dissolved organic matter in headwater streams is highly variable in quantity and quality, both temporally and spatially (Meyer *et al.*, 1998; Kiffney *et al.*, 2000; McArthur and Richardson, 2002). DOM enters streams primarily with ground water, although some may leach directly from leaf litter that drops directly into streams. It is broken down by exposure to UV radiation, digestion by bacteria, and other mechanisms into simpler (e.g., smaller) molecules, which are often more biologically available (e.g., Baker *et al.*, 2000).

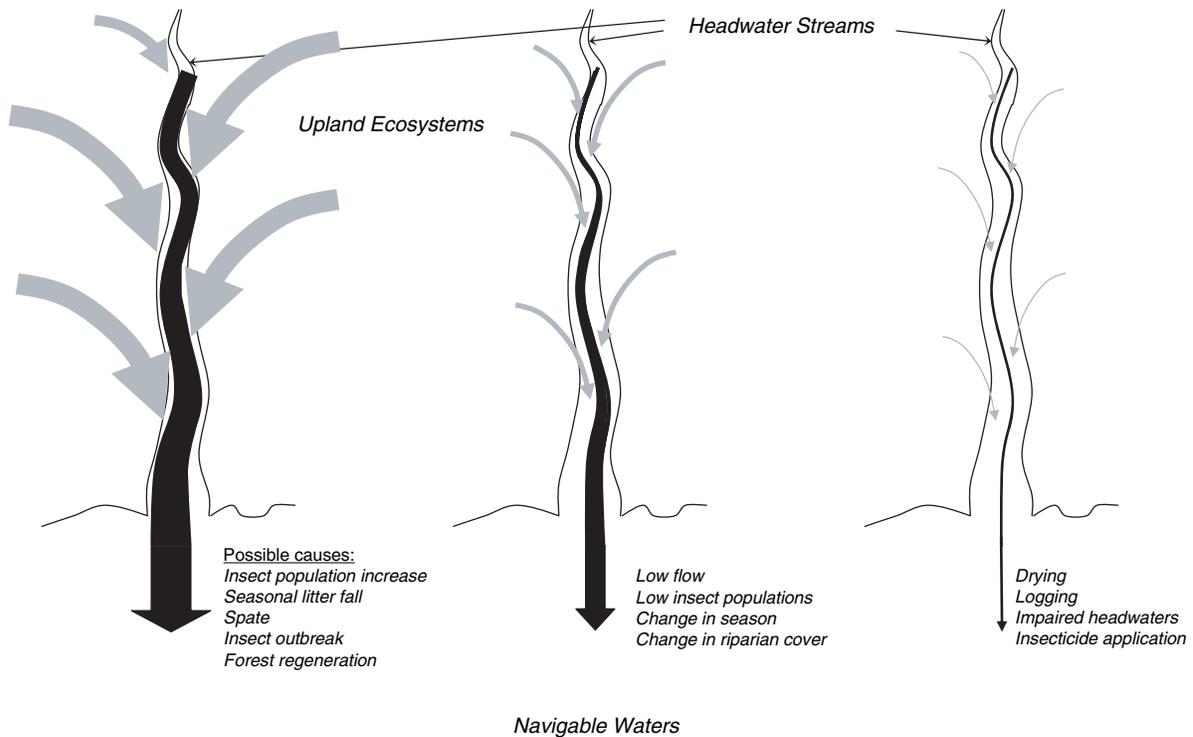


FIGURE 3. Resource Flow Model. Magnitude of nutrient, energy, or wood flow over time as a function of changing insect life history patterns, seasonal temperature changes, rainfall, natural and other physical disturbances, forest pest outbreaks, and other forces. Grey arrows represent terrestrial inputs into headwater streams and black arrows indicate resource flow to downstream habitats. Arrow thickness depicts approximate magnitude of resource flow.

CONVERSION, RETENTION, AND
TRANSPORT IN HEADWATERS

Terrestrial invertebrates occur along riparian corridors and are associated with both deciduous and coniferous plants, leaf litter, and riparian soils (Wipfli, 1997; Allan *et al.*, 2003). Commonly occurring groups include aphids, leafhoppers, beetles, caterpillars, sawflies, spiders, mites, springtails, small wasps, and flies, and all contribute substantially to the diets of consumers in streams (Hynes, 1970; Hunt, 1975; Mason and Macdonald, 1982; Nielsen, 1992; Baxter *et al.*, 2004, 2005). For example, over half of the prey mass ingested by salmonids in southeastern Alaska streams originates from surrounding forest ecosystems (Wipfli, 1997). Similarly, terrestrial invertebrates form a substantial portion of the prey ingested by cutthroat trout (*Oncorhynchus clarki*) in streams along coastal Oregon (Romero *et al.*, 2005) as well as for stream-resident salmonids in Japan (Nakano *et al.*, 1999; Kawaguchi and Nakano, 2001; Nakano and Murakami, 2001). Both overstory and understory plants support and contribute substantial amounts of terrestrial invertebrate biomass to small streams (Allan *et al.*, 2003).

An obvious indication of the intimate association of headwater streams and the terrestrial landscape is the abundance of wood in streams (Naiman and Décamps, 1997; Bisson and Bilby, 1998; Gregory *et al.*, 2003). Large wood (LW, defined as >10 cm diameter and >1 m long) has a variety of controlling influences on headwaters, affecting channel form, providing sites for storage of OM and sediment, and modifying the movement and transformation of nutrients (Bisson *et al.*, 1987). It is well known that LW influences the physical characteristics of headwater streams, affecting the in-channel biological community (Maser and Sedell, 1994; Bilby and Bisson, 1998) as well as the dynamics of the adjacent riparian forest (Naiman *et al.*, 2002).

The distribution of LW in streams largely depends on channel size (Swanson *et al.*, 1982; Bilby and Ward, 1989). In headwater channels, LW exhibits a random distribution reflecting the pattern and rate of LW recruitment as average peak flows cannot normally move the debris (although large flows may). This is in sharp contrast to large channels where LW is distributed in clumps (jams), due to transport and subsequent aggregation (Latterell, 2005). Distribution of LW in headwaters also depends on input processes. If the dominant process is bank undercutting of live trees or direct fall of dead trees, then distribution follows the patterns described above. If the dominant input process is episodic, such as debris flow, wind-throw or flooding, then clumps of LW are larger and less frequent than in streams without such inputs (Bisson *et al.*, 1987).

Upon entering streams, OM may be retained and “processed” – biophysically transformed through consumption and feeding processes – or transported downstream (Webster *et al.*, 1999; Richardson *et al.*, 2005a). Transformations can diminish or increase the size (and quality) of particles, depending upon the process. Generally, large particles of OM are broken down to smaller particles through abrasion and through consumption by various organisms, including microbes and invertebrates (Hynes, 1975; Webster and Benfield, 1986; Bisson and Bilby, 1998). Fungi and bacteria can also decompose large organic particles to smaller sizes, or make them more vulnerable to physical breakdown (Suberkropp, 1998). Larger particles are also known to be physically diminished in size through abrasion and other physical forces (Heard *et al.*, 1999).

Particles consumed by various aquatic invertebrates are effectively repackaged as feces, which can be subsequently ingested by other organisms or entrained in the water column and carried downstream (Wotton and Malmqvist, 2001). In some instances, the fecal particles are in a characteristic size range that can be readily identified (Naiman, 1983b; Wotton and Malmqvist, 2001). DOM also can be converted to larger particles through flocculation, a process that leads to the weak aggregation of colloidal-size particles (Petersen, 1986).

The repackaging of fine particles of OM or DOM into feces by collectors within streams, such as by black fly (Simuliidae) larvae, can yield prodigious amounts of fine particles that flow to downstream reaches (Wotton *et al.*, 1998; Malmqvist and Wotton, 2002). However, specific mechanisms leading to characteristic particle sizes, as in feces, are tied to the seasonal timing of species-specific life cycles. For example, black fly larvae progress through a number of stages during their life cycle, and each stage has a characteristic size (within a species) and therefore a specific fecal particle size. Black flies stop feeding at pupation and thus that source of specific-sized particles ceases. Thus, some of the processes affecting transformation and repackaging of OM may change through the year, and will also depend on available standing stocks.

Organic matter storage and transport are a function of the variable and complex channel geomorphology of these systems. Storage mechanisms (see below) include depositional areas (Negishi and Richardson, 2003), burial in sediments, and entrapment by wood (Speaker *et al.*, 1988; Bilby and Ward, 1991; Ehrman and Lamberti, 1992; Hoover *et al.*, 2006). Larger

particles (e.g., deciduous leaves) are more easily stored than smaller particles (Webster *et al.*, 1999); for instance, deciduous leaves are often more efficiently stored than are smaller conifer needles. Coupled with differences in sizes is the hardness of leaves, e.g., conifer *vs.* deciduous, which affects how they conform to intercepting structures, and hence their storage probabilities within the headwater channel (T. Hoover, University of British Columbia, personal communication, 2006). The inverse of storage is that as particles diminish in size they are more easily transported, thus nearly all transport of OM is as fine particulate organic matter (FPOM, 0.63 μm to 1.0 mm diameter) and DOM (Wallace *et al.*, 1995; Kiffney *et al.*, 2000). Although a large fraction of OM inputs occur as leaf litter and other coarse particulate OM (>1 mm diameter), only a small amount is exported annually as large particles, e.g., <1-4% (Naiman and Sedell, 1979; Wallace *et al.*, 1995; Kiffney *et al.*, 2000). Thus, these small particles (FPOM and DOM) together account for >95% of the export of OM from headwaters (Naiman, 1982; Wallace *et al.*, 1995; Kiffney *et al.*, 2000).

Large wood through its impacts on channel morphology and hydraulics affects the accumulation of mineral and organic particles. Woody debris increases pool frequency and size (Robison and Beschta, 1990), forms and stabilizes gravel bars (Lisle, 1986; Fetherston *et al.*, 1995; Abbe and Montgomery, 1996), and in larger streams increases channel width by adding roughness and complexity by increasing the number of meanders and backchannels (Latterell *et al.*, 2006). The higher hydraulic roughness associated with LW reduces flow velocities (Maser *et al.*, 1988). The influence of LW on channel networks and material retention depends on stream size and gradient, flow regimes, LW residence time, and the relative size and morphology of dominant riparian vegetation. The greatest impacts occur on headwater streams at low flow and immediately after wood emplacement as channel dimensions adjust to the new hydraulic conditions (Nanson *et al.*, 1995).

DELIVERY TO DOWNSTREAM SYSTEMS

Headwater streams deliver a wide range of materials produced or otherwise derived from headwater habitats, including products from both above and below ground. Water is one of the most obvious of those materials. But there are numerous others, including nutrients, dissolved organic and inorganic carbon, particulate carbon, aquatic and terrestrial invertebrates, and wood (Figure 3). While these materials play key roles in the structure, function, productivity,

and biodiversity of riverine ecosystems, the relative importance of headwater contributions of these products to the integrity of downstream ecosystems is not well understood, and subsequently often not considered in resource management negotiations.

A disproportionate amount of OM transport occurs during relatively high flows (Bormann and Likens, 1979; Naiman, 1982; Wallace *et al.*, 1995; Kiffney *et al.*, 2000). Total fluxes of particulate organic materials follow a power function of discharge rates (e.g., Wallace *et al.*, 1995; Kiffney *et al.*, 2000). As discharge increases, the tractive force to entrain particles increases nonlinearly and total fluxes of OM increase. Wallace *et al.* (1995) showed that 63-77% of OM export occurred in the largest 20 floods over a 9-year period. Thus, supply of OM to downstream reaches is highly pulsed. However, export rates are also a function of OM supply stored in the stream channel and adjacent riparian zone. During autumn and winter periods when there is more OM available for transport, the absolute rates of export are higher for a given discharge than when that supply is lower (Wallace *et al.*, 1995).

Concentrations of organic particles may increase only slightly, or not at all, with increased flow (e.g., Naiman, 1982; Kiffney *et al.*, 2000); however, the total flux from headwaters will be at least proportional to discharge. In streams with snowmelt-dominated hydrographs, the largest annual peaks in flow are in spring. Additionally, amounts of OM available for export are also high after being retained in stream reaches under ice at relatively low flows, resulting in large fluxes of OM during snowmelt. Likewise, in streams with rain-dominated hydrographs, total export is highest during peak flows.

Relative to OM, much less is known about the fate of terrestrial invertebrates upon entering headwater streams. Undoubtedly, some are eaten by consumers – salamanders, shrews, dippers, waterstriders, and other species. Those not immediately consumed probably drown and are likely retained and decomposed similarly to other allochthonous inputs (i.e., twigs and leaf litter). A substantial amount of terrestrial invertebrates is transported downstream to habitats occupied by fishes or other consumers, and may be especially important prey items in food-limited aquatic environments (Boss and Richardson, 2002; Wipfli and Gregovich, 2002). Piccolo and Wipfli (2002) showed that both terrestrial and aquatic invertebrates are transported downstream from headwater ecosystems to salmonid-rearing habitats and that riparian cover and riparian forest management affect the amount of prey biomass delivered downstream. Deciduous tree species and their understory associates in headwaters lead to higher delivery rates of invertebrates and OM downstream than coniferous-dominated forests,

apparently from greater allochthonous inputs and higher instream productivity in headwater channels (Wipfli and Musslewhite, 2004).

Both terrestrial and aquatic invertebrates from headwater streams are transported to aquatic habitats lower in the drainage, with timing and magnitude of transport varying by month, season, and year. During October-December, invertebrate transport from headwaters can be $<0.5 \text{ mg/m}^3$ of streamflow, rebounding to $>10 \text{ mg/m}^3$ in spring in headwater streams in southeastern Alaska (Wipfli and Gregovich, 2002). A massive amount of year-to-year variation in downstream transport also exists, with delivery rates of invertebrate mass ranging $<0.5\text{-}12 \text{ mg/m}^3$ streamflow among years during the same season. In spite of this large variability, this material transport can support up to 2,000 juvenile fish per kilometer of stream length in downstream habitats (Wipfli and Gregovich, 2002). The calculations incorporate invertebrate and detritus transport $>250 \mu\text{m}$ but do not account for smaller invertebrates or OM $<250 \mu\text{m}$, which comprises most OM transport in streams (Naiman and Sedell, 1979; Wallace *et al.*, 1995; Wotton *et al.*, 1998; Malmqvist and Wotton, 2002). Including the smaller size fractions, depending upon extent of utilization by food webs, would bring the number of fish potentially supported above 2000/km of stream. Further, riparian vegetation cover type effects on stream productivity additionally influence the amount of material transported to fish habitats, ultimately boosting fish production downstream (Piccolo and Wipfli, 2002). Recent evidence from the North Cascade Range of the Pacific Northwest indicated that fish densities are higher in downstream habitats receiving greater headwater subsidies (invertebrates) than habitats receiving lower levels of prey inputs (C. Binckley and M.S. Wipfli, unpublished data).

Timing of delivery of OM and invertebrates influences the effects of these materials on the receiving community. Timing is important both in terms of the actual delivery of material to consumers occupying downstream habitats and in terms of relationships to the physiological or biological state of consumers at the time of delivery. In effect, can consumers immediately take advantage of this headwater subsidy or are effects manifested later or further downstream? If products are delivered during times when consumers cannot sequester them, such as at night when drift feeding fishes are not feeding, or during the winter when physiological processes have slowed, the effects would be much less than those during periods of active feeding. Magnitude of material delivery is also critically important, both in terms of the absolute amount of material delivered, including quality, and in terms of relative quantity and quality compared

with other sources (such as instream or hyporheic production within the respective mainstem habitats or from marine sources delivered from spawning salmon in places like the Pacific Northwest).

Unlike OM and invertebrates, LW, once in the channel, often resides for decades to centuries – or moves unhindered downstream. Several regional studies have shown that LW exposed to wetting and drying normally remains in the channel for 70-100 years, but some pieces appear to remain for several centuries to millennia (Swanson and Lienkaemper, 1978; Swanson *et al.*, 1982). Residence time of a particular piece of wood is likely influenced by many of the same environmental factors affecting LW abundance and distribution: wood decay rate, lateral channel stability, channel morphology, flood intensity, and riparian forest composition (Naiman *et al.*, 2002; Latterell, 2005).

Mechanisms of wood delivery to streams range from processes that provide wood predictably through time to relatively rare, episodic events that generate large quantities of wood in a short period. Perhaps the most predictable wood input mechanism is tree mortality related to stand development and succession. Rate of LW input to the channel due to mortality varies as a function of tree species and successional stage of the riparian stand (Meleason *et al.*, 2003).

Relatively rare, severe disturbances, including windstorms, fire, or flood, can add massive amounts of wood to the channel network (Harmon *et al.*, 1986; May and Gresswell, 2003). Avalanches, landslides, and debris torrents transport wood from hillslopes through headwater tributary channels and deposit the wood and associated sediment in downstream reaches (May and Gresswell, 2003). For example, from 10 to $>50\%$ of the wood in fish-bearing stream reaches in several watersheds of the Oregon Coast Range is generated by landslides that initiate debris torrents in headwater channels (Harmon *et al.*, 1986; Reeves *et al.*, 2003). Likewise, severe windstorms can deliver large amounts of wood to headwaters, the amount delivered depending on wind direction relative to the channel, soil moisture, tree species, and a number of other interrelated factors. Fire occurrence varies as a function of aspect, elevation, and other factors. However, fires recur in most western forests at intervals ranging from decades to $>1,000$ years (Agee, 1988). Wood abundance in headwaters increases rapidly following a fire (as well as disease and insect outbreaks) as the standing-dead trees fall (Benda *et al.*, 1998).

It is difficult to make quantitative comparisons of LW abundance across headwater streams. In general though, LW abundance peaks in the southern end of the Pacific Coastal Ecoregion and decreases toward

the north (Harmon *et al.*, 1986). At one extreme, the LW biomass in redwood-forested streams of California averages 74.2 kg/m², with highs of 180 kg/m² in certain reaches. At the other extreme, biomass in Sitka spruce-lined streams of southeast Alaska averages only 6.6 kg/m². As a whole, headwater streams in the Pacific Coastal Ecoregion have a higher abundance of LW than other forested areas in North America (Harmon *et al.*, 1986). Nevertheless, in every case examined, LW comprises >90% of the standing stock of OM.

Within channels, the abundance of LW depends, in part, on the scale of examination. Most comparative studies have limited their focus to the wetted channel. However, nearly half of the river-deposited wood in the Queets River, Washington, lies abandoned in the forested floodplain (Latterell, 2005). When these are counted, the density of LW is much more similar to that found in headwater streams. Also, jam densities per kilometer are identical in the mainstem and tributaries. The wetted areas of headwater channels tend to have more abundant LW (by volume) than large channels, as large channels have a greater capacity to transport wood (Swanson *et al.*, 1982; Bilby and Ward, 1989). For example, LW in first- and second-order streams may cover 50% of the channel, while the percentage declines by half or more in higher order streams (Swanson and Lienkaemper, 1978; Anderson and Sedell, 1979; Triska *et al.*, 1982). Abundance is influenced by channel stability as well as by size. LW is reported to be twice as abundant in unconstrained channels with fine substrate as in constrained channels with bedrock and boulder substrate (Bilby and Wasserman, 1989).

The abundance of LW also depends on the surrounding riparian forest. Its biomass is positively related to tree density in eastern Washington streams (Bilby and Wasserman, 1989). Streams in coniferous forests have more LW than streams in hardwood forests because conifers are usually larger, less easily transported, and more decay resistant (Harmon *et al.*, 1986). Similarly, streams in mature stands tend to have more LW than those in young stands where the riparian forest often is composed of smaller hardwood trees (Grette, 1985; Bilby and Ward, 1991).

A contemporary perspective is that the average size of LW, measured in length, volume, or diameter, increases with channel size (Bilby and Ward, 1989). However, this is not always the case. In the Queets River, small diameter logs were more common in the mainstem river (Latterell, 2005), for two reasons. First, most small logs are alder, which are far more abundant along the mainstem. Second, high densities of logjams prevent the loss of smaller pieces. Even though larger channels have a greater capacity to

transport wood, small pieces flushed downstream can be concentrated where jams are abundant. This is a topic that requires reexamination, incorporating data from floodplains of medium- to large-sized rivers to reveal the true pattern.

EFFECTS OF RESOURCE MANAGEMENT

Much of the North American landscape has been modified by human activities – forest harvest and management, agricultural development, and urbanization. Land use and natural disturbances dramatically affect the flow of OM, invertebrates, and wood into headwater streams and the subsequent movement of this material to downstream fish habitats. Collectively, this potentially impacts or even obliterates the hydrological connectivity and subsequent ecological connectivity between upland ecosystems and downstream navigable waters (Figures 3 and 4).

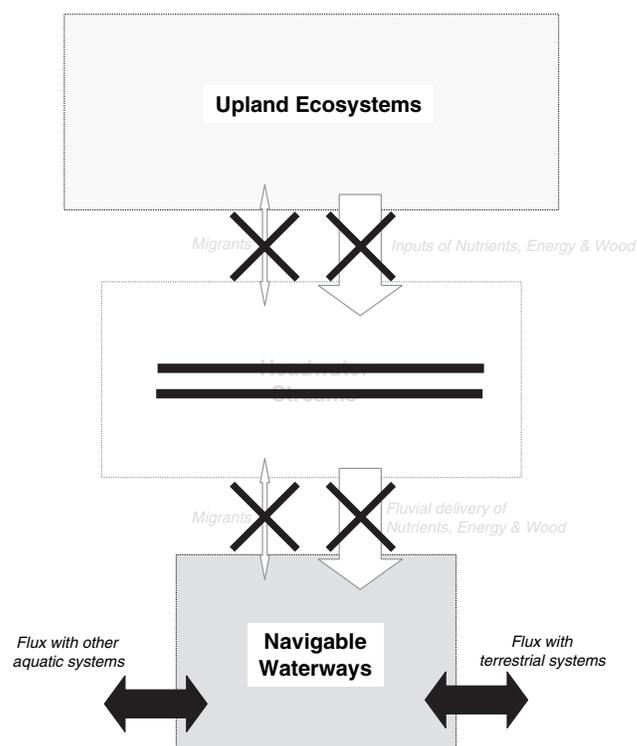


FIGURE 4. Impaired Connectivity Model. Impacts to headwater streams that result in degraded or lost hydrological connectivity will dramatically impact the ecological connectivity among upland ecosystems, headwater streams, and downstream navigable waters. This disconnect means food webs and communities in those receiving waters would not receive the nutrients, energy, and wood they would under more natural conditions.

Most examples given below relate to forest harvesting effects, but the alterations to headwater systems from agriculture, urban development, mining, and other land uses contribute in similar ways to changes in processes that affect supplies of organic materials to downstream environments.

Dynamics of OM are altered by forest harvesting, especially around headwaters where many jurisdictions provide for no mandatory treed reserves or provide limited protection (e.g., Blinn and Kilgore, 2001). Changes in input rates in the short term (removal of forest canopy) give way to compositional changes in the quality of inputs from riparian forests as the forest goes through succession. Often the fast-growing trees associated with regenerating forest provide higher quality leaf litter (e.g., Benfield *et al.*, 2001). Breakdown rates of OM have generally been found to be faster following harvesting as a result of higher quality leaf litter, higher nutrient concentrations in water, and the consumer response to improved resource conditions (Benfield *et al.*, 2001). These changes putatively lead to faster reduction of particle size and more efficient transport to downstream reaches, but perhaps at the expense of the slow release of finer particles. Reduced storage of OM within headwaters following logging may also be a long-term product of reduced wood inputs and the complexity they provide for storage.

Land use can dramatically affect the mass of terrestrial invertebrates entering streams, and the subsequent flow of invertebrate mass from headwater channels to downstream habitats. Clearcutting or other disturbances that expose mineral soils often lead to substantial alder regeneration, especially along headwater channels. The net effect often converts conifer-dominated forests to deciduous-dominated forests (Harrington *et al.*, 1994; Orlikowska *et al.*, 2004). While this process leads to short-lived, less stable deciduous LW for streams and their riparian zones (Bilby and Bisson, 1998), the subsequent alder regrowth apparently increases productivity of lower trophic levels in streams, increasing the prey resources for fishes and other consumers (Piccolo and Wipfli, 2002; Wipfli and Musslewhite, 2004; Romero *et al.*, 2005). However, the ecological implications of this change in forest cover, and its effects on food resources for fishes and other consumers, have not been measured.

The net effect of landscape modifications by human activities on LW in headwater streams has been a drastic decline in standing stocks as the wood has either been actively removed, or the recruitment curtailed by severe modifications to the surrounding forest and riparian zone, or both (Maser and Sedell, 1994; Elozegi and Johnson, 2003). These reductions can be directly linked to younger riparian forests,

artificially stabilized banks (in headwater and larger streams), and consequently greater LW mobility – and many regions of the world provide stark examples of how land conversion influences LW abundance in streams (reviewed by Elozegi and Johnson, 2003). In one example for small streams in the rapidly urbanizing Puget Sound region of Washington, the volume of LW decreased from $\sim 1,200 \text{ m}^3/\text{km}$ to near zero, and the number of pieces declined by 75% as the proportion of the basin with impervious surfaces increased from near zero (undeveloped) to $\sim 60\%$ (urban) (May *et al.*, 1997). Substantial amounts of LW were found only in stream reaches with substantial riparian cover. Similar examples exist for the eastern United States, the United Kingdom, Germany, and other developed countries.

IMPLICATIONS OF IMPACTS

Regenerating forests following harvesting can take several trajectories depending on environmental conditions during the initiation process and any management of the stand initiation, e.g., planting or brush control. For example, as noted above, under some conditions riparian forests regenerate with deciduous trees such as alder, while under other conditions the same site could regenerate to conifer trees. Additionally, early seral-stage species differ in quality as a food resource to aquatic consumers. As forests regenerate, inputs slowly recover. For instance, following harvesting to the streambank, or with small reserves, input rates of OM can be diminished by >10-fold (P.M. Kiffney and J.S. Richardson, unpublished data), but inputs of litter may recover within a decade.

As is the case with OM, the implications of altering native forests on prey flow to streams and subsequent aquatic productivity could be substantial, especially because consumers in streams are likely, in part, to be food limited (Hunt, 1975; Wipfli *et al.*, 1998, 2003; Boss and Richardson, 2002). A reduction in food supplies (quantity or quality) would likely affect consumers in many ways, including reduced growth, production, and survival, as well as body condition and fat reserves (Gerking, 1994; Adams, 1998; Heintz *et al.*, 2004). Clearly, more food or food with greater nutritional value would benefit consumers, but less food or lower quality could be problematic. If food is not a limiting factor, changes in forest cover, regardless of how it affects food resources for consumers, likely would have less impact on those consumers via direct trophic pathways, but may affect them through changes in temperature or predation pressure.

Similarly, as with OM and invertebrates, the implications of altering native forests and LW are significant. Wood in streams was historically viewed as an unaesthetic nuisance, either as obstacles to migration or as potential hazards. However, it is now recognized that LW is so essential for the long-term integrity of stream and river corridors in many Western states that measures assuring a continued supply of LW of appropriate size, volume, and species composition need to be maintained (Naiman *et al.*, 2002; Gregory *et al.*, 2003). So far, management actions have included larger and more widespread riparian buffers, regulations preventing LW removal from headwater streams as well as the removal of dead and dying trees in riparian zones, and additions of LW to channels previously cleaned. However, in general, the status of headwater streams and the LW contained therein have remained problematic for management, largely because the streams are viewed as nonessential fish habitat and because they are intimately embedded in the upland forest – thereby hindering forest harvest and development.

KNOWLEDGE GAPS, CURRENT CHALLENGES, AND FUTURE RESEARCH DIRECTIONS

There remain many questions regarding the values of subsidies from headwaters to downstream reaches and the extent to which those river reaches rely on upstream ecosystem goods and services. OM is often considered as a single resource type, but there are large qualitative differences amongst particles, and not just by size (Naiman, 1982, 1983b; Richardson, 1984; McArthur and Richardson, 2002; Richardson *et al.*, 2004). These qualitative differences may vary depending on source, time of year, and degree of processing. For instance, particles of wood have different nutritional values to downstream consumers than do small invertebrates or bacteria. Assays of the quality of various materials are relatively rare. Where dissolved organic carbon was once considered to be largely refractory and of low nutritional value, it is becoming clearer that colloidal-sized materials may be more bioavailable than previously thought. In addition, photo-degradation of DOM contributes to production of short-chained molecules that are more easily metabolized by bacteria (e.g., Baker *et al.*, 2000). Understanding the quality of this downstream transport and associated effects on receiving food webs is essential for more effective river management and maintaining long-term ecological integrity.

In addition to how quality might vary, the timing of delivery of material subsidies to downstream may

be equally important. For instance, if major fluxes occur at a time of year when cold temperatures and high flows reduce consumption by downstream consumers, then materials may not contribute as much to the environmental basis of production in recipient reaches. It has been asserted that coevolution of the timing of resource inputs and consumer use of those inputs may be important, but this is difficult to demonstrate. If land use in headwaters alters timing and the nature of subsidies, then it is possible that any coevolved consumer-resource timing could be decoupled by changes to the fluxes. These coevolutionary questions require elucidation.

Knowing the extent to which food webs in downstream habitats are receiving subsidies of OM and invertebrates from headwaters, and are utilizing and depending on them, is crucial to understanding how uplands and their associated streams and riparian zones should be managed. We know, for example, that invertebrates transported from headwaters enter fish-bearing habitats, and we have estimates on the potential fish biomass this subsidy can support, but empirical data on actual consumer effects remain unknown (Wipfli and Gregovich, 2002). Knowing both quantity and quality relations are crucial; empirical data will shed much light on the ecological connectedness of headwaters with valley bottom habitats.

Despite the worldwide importance of human modifications to landscapes, there are relatively few quantitative investigations of LW in headwater streams impacted by agriculture and urbanization – and a surprising paucity of studies in forested landscapes. Further, there are virtually no quantitative data linking LW in headwaters to downstream communities despite knowing that LW exerts strong controls on water hydraulics, sediment routing, nutrient and OM fluxes, and community composition (but see Valett *et al.*, 2002).

Comprehensive studies are needed on the ways by which various forms of land use affect the standing stocks, size distribution, species composition, and mobility of LW. Further, as management strategies and actions vary by region, it is imperative that investigations account for the variety of consequences – in intensity as well as in terms of ecological effects – to understand how the various management regimes interact with natural disturbance regimes (e.g., floods, fire). The way the public perceives LW, and headwater streams in general, will be key in any successful management strategy. Thoughtful management actions can ensure the continued supply and abundance of LW and, by doing so, maintain the long-term productivity of stream and river corridors. However, this cannot be ultimately successful without strong public understanding and support. The grand challenge will be to demonstrate

to the broader public that headwater streams with their detritus and invertebrates are integral to the vitality of entire river networks. In effect, that headwater streams are inseparable from fish-bearing rivers downstream (Naiman and Latterell, 2005). Nevertheless, the search for answers as to how the quality, magnitude, and timing of headwater materials provide subsidies to downstream still requires direct testing of consumer use of, and responses to, those materials – a fertile area for experimental investigations.

ACKNOWLEDGMENTS

We thank Joshua J. Latterell for preparing the GIS portion of Figure 2, for providing insightful comments on earlier drafts, and for thoughtful discussions on the roles of large wood in headwaters. Dave Gregovich graciously supplied the tributary junction picture for Figure 2. Thanks also to Mark Rains and Tracie Nadeau for their feedback and comments, and for giving us the opportunity to contribute to this special issue.

LITERATURE CITED

- Abbe, T.B. and D.R. Montgomery, 1996. Large Woody Debris Jams, Channel Hydraulics, and Habitat Formation in Large Rivers. *Regulated Rivers* 12:201-222.
- Adams, S.M., 1998. Ecological Role of Lipids in the Health and Success of Fish Populations. In: *Lipids in Freshwater Ecosystems*, M.T. Arts and B.C. Wainman (Editors). Springer-Verlag, New York, pp. 132-160.
- Agee, J.K., 1988. Successional Dynamics of Forest Riparian Zones. In: *Streamside Management: Riparian Wildlife and Forestry Interactions*. Contribution No. 59, K.J. Raedeke (Editor). Institute of Forest Resources, University of Washington, Seattle, Washington, pp. 31-43.
- Allan, J.D., M.S. Wipfli, J.P. Caouette, A. Prussian, and J. Rodgers, 2003. Influence of Streamside Vegetation on Terrestrial Invertebrate Inputs to Salmonid Food Webs. *Canadian Journal of Fisheries and Aquatic Sciences* 60:309-320.
- Anderson, N.H. and J.R. Sedell, 1979. Detritus Processing by Macroinvertebrates in Stream Ecosystems. *Annual Review of Entomology* 24:351-377.
- Baker, M.A., H.M. Valett, and C.N. Dahm, 2000. Organic Carbon Supply and Metabolism in a Shallow Groundwater Ecosystem. *Ecology* 81:3133-3148.
- Baxter, C.V., K.D. Fausch, M. Murakami, and P.L. Chapman, 2004. Non-native Stream Fish Invasion Restructures Stream and Riparian Forest Food Webs by Interrupting Reciprocal Prey Subsidies. *Ecology* 85:2656-2663.
- Baxter, C.V., K.D. Fausch, and W.C. Saunders, 2005. Tangled Webs: Reciprocal Flows of Invertebrate Prey Link Streams and Riparian Zones. *Freshwater Biology* 51:201-220.
- Benda, L.E., D.L. Miller, T. Dunne, G.H. Reeves, and J.K. Agee, 1998. Dynamic Landscape Systems. In: *River Ecology and Management*, R.J. Naiman and R.E. Bilby (Editors). Springer-Verlag, New York, pp. 261-288.
- Benda, L.E., M.A. Hassan, M. Church, and C.L. May, 2005. Geomorphology of Steepland Headwaters: The Transition From Hillslopes to Channels. *Journal of the American Water Resources Association* 41:835-851.
- Benfield, E.F., 1997. Comparison of Litterfall Input to Streams. *Journal of the North American Benthological Society* 16:104-108.
- Benfield, E.F., J.R. Webster, J.L. Tank, and J.J. Hutchens, 2001. Long-Term Patterns in Leaf Breakdown in Streams in Response to Watershed Logging. *International Review of Hydrobiology* 86:467-474.
- Bilby, R.E. and P.A. Bisson, 1998. Function and Distribution of Large Woody Debris. In: *River Ecology and Management*, R.J. Naiman and R.E. Bilby (Editors). Springer-Verlag, New York, pp. 324-346.
- Bilby, R.E. and J.W. Ward, 1989. Changes in Characteristics and Function of Woody Debris With Increasing Size of Streams in Western Washington. *Transactions of the American Fisheries Society* 118:368-378.
- Bilby, R.E. and J.W. Ward, 1991. Characteristics and Function of Large Woody Debris in Streams Draining Old-Growth, Clear-cut, and Second-Growth Forests in Southwestern Washington. *Canadian Journal of Fisheries and Aquatic Sciences* 48:2499-2508.
- Bilby, R.E. and L.J. Wasserman, 1989. Forest Practices and Riparian Management in Washington State: Data Based Regulation Development. In: *Practical Approaches to Riparian Resource Management*, R.E. Gresswell, B.A. Barton, and J.L. Kershner (Editors). U.S. Bureau of Land Management, Billings, Montana, pp. 87-94.
- Bisson, P.A. and R.E. Bilby, 1998. Organic Matter and Trophic Dynamics. In: *River Ecology and Management*, R.J. Naiman and R.E. Bilby (Editors). Springer-Verlag, New York, pp. 373-398.
- Bisson, P.A., R.E. Bilby, M.D. Bryant, C.A. Dolloff, G.B. Grette, R.A. House, M.L. Murphy, K.V. Koski and J.R. Sedell, 1987. Large Woody Debris in the Pacific Northwest: Past, Present, and Future. In: *Proceedings, Streamside Management: Forestry and Fishery Interactions*, E.O. Salo and T.W. Cundy (Editors). University of Washington, Seattle, Washington, pp. 143-190.
- Blinn, C.R. and M.A. Kilgore, 2001. Riparian Management Practices: A Summary of State Guidelines. *Journal of Forestry* 99:11-17.
- Bormann, F.H. and G.E. Likens, 1979. *Pattern and Process in a Forested Ecosystem*. Springer-Verlag, New York.
- Boss, S.M. and J.S. Richardson, 2002. The Effects of Food and Cover on the Growth, Survival and Movement of Cutthroat Trout in Coastal Streams. *Canadian Journal of Fisheries and Aquatic Sciences* 59:1044-1053.
- Compton, J.E., M.R. Church, S.T. Larned, and W.E. Hogsett, 2003. Nitrogen Export From Forested Watersheds in the Oregon Coast Range: The Role of N₂-Fixing Red Alder. *Ecosystems* 6:773-785.
- Cummins, K.W., M.A. Wilzbach, D.M. Gates, J.B. Perry, and W.B. Talliafero, 1989. Shredders and Riparian Vegetation. *BioScience* 39:24-30.
- Ehrman, T.P. and G.A. Lamberti, 1992. Hydraulic and Particulate Matter Retention in a 3rd-Order Indiana Stream. *Journal of the North American Benthological Society* 11:341-349.
- Elosegi, A. and L.B. Johnson, 2003. Wood in Streams and Rivers in Developed Landscapes. *American Fisheries Society Symposium* 37:337-353.
- Fetherston, K.L., R.J. Naiman, and R.E. Bilby, 1995. Large Woody Debris, Physical Processes and Riparian Forest Development in Montane River Networks of the Pacific Northwest. *Geomorphology* 13:133-144.
- Gerking, S.D., 1994. *Feeding Ecology of Fish*. Academic Press, San Diego, California.
- Gomi, T., R.C. Sidle, and J.S. Richardson, 2002. Headwater and Channel Network – Understanding Processes and Downstream Linkages of Headwater Systems. *BioScience* 52:905-916.
- Gregory, S.V., K.L. Boyer, and A.M. Gurnell (Editors), 2003. *The Ecology and Management of Wood in World Rivers*. American Fisheries Society Symposium 37, Bethesda, Maryland.

- Grette, G.B., 1985. *The Abundance and Role of Large Organic Debris in Juvenile Salmonid Habitat in Streams in Second Growth and Unlogged Forests*. M.S. Thesis, School of Fisheries, University of Washington, Seattle, Washington.
- Haigh, M.J., R.B. Singh, and J. Krecek, 1998. Headwater Control: Matters Arising. In: *Headwaters: Water Resources and Soil Conservation*, M.J. Haigh, J. Krecek, G.S. Rajwar, and M.P. Kilmartin (Editors). A.A. Balkema, Rotterdam, the Netherlands, pp. 3-24.
- Harmon, M.E., J.F. Franklin, F.J. Swanson, P. Sollins, S.V. Gregory, J.D. Lattin, N.H. Anderson, S.P. Cline, N.G. Aumen, J.R. Sedell, G.W. Lienkaemper, K. Cromack and K.W. Cummins, 1986. Ecology of Coarse Woody Debris in Temperate Ecosystems. *Advances in Ecological Research* 15:133-302.
- Harrington, C.A., J.C. Zasada, and E.A. Allen, 1994. Biology of Red Alder (*Alnus rubra* Bong.). In: *The Biology and Management of Red Alder*, D.E. Hibbs, D.S. DeBell, and R.F. Tarrant (Editors). Oregon State University Press, Corvallis, Oregon, pp. 3-22.
- Heard, S.B., G.A. Schultz, C.B. Ogden, and T.C. Griesel, 1999. Mechanical Abrasion and Organic Matter Processing in an Iowa Stream. *Hydrobiologia* 400:179-186.
- Heintz, R.A., B.D. Nelson, J.P. Hudson, M. Larsen, L. Holland, and M.S. Wipfli, 2004. Marine Subsidies in Freshwater: Effects of Salmon Carcasses on the Lipid Class and Fatty Acid Composition of Juvenile Coho Salmon. *Transactions of the American Fisheries Society* 133:559-567.
- Hoover, T., J.S. Richardson, and N. Yonemitsu, 2006. Flow-Substrate Interactions Create and Mediate Leaf Litter Resource Patches in Streams. *Freshwater Biology* 51:435-447.
- Hunt, R.L., 1975. Food Relations and Behavior of Salmonid Fishes. Use of Terrestrial Invertebrates as Food by Salmonids. In: *Coupling of Land and Water Systems*, Vol. 10, A.D. Hassler (Editor). Springer-Verlag, New York, pp. 137-151.
- Hynes, H.B.N., 1970. *The Ecology of Running Waters*. University of Toronto Press, Toronto, Ontario, 555 pp.
- Hynes, H.B.N., 1975. The Stream and Its Valley. *Verhandlungen der Internationalen Vereinigung für Theoretische und Angewandte Limnologie* 19:1-15.
- Kawaguchi, Y. and S. Nakano, 2001. Contribution of Terrestrial Invertebrates to the Annual Resource Budget for Salmonids in Forest and Grassland Reaches of a Headwater Stream. *Freshwater Biology* 46:303-316.
- Kiffney, P.M., J.S. Richardson, and M.C. Feller, 2000. Fluvial and Epilithic Organic Matter Dynamics in Headwater Streams of Southwestern British Columbia, Canada. *Archiv für Hydrobiologia* 149:109-129.
- Kiffney, P.M., C.M. Greene, J.E. Hall, and J.R. Davies, 2006. Tributary Streams Create Spatial Discontinuities in Habitat, Biological Productivity, and Diversity in Mainstem Rivers. *Canadian Journal of Fisheries and Aquatic Sciences* 63:2518-2530.
- Latterell, J.J., 2005. *The Natural History and Dynamics of Large Wood in the Queets River, Washington*. Ph.D. Dissertation, University of Washington, Seattle, Washington.
- Latterell, J.J., J.S. Bechtold, R.J. Naiman, T.C. O'Keefe, and R. Van Pelt, 2006. Dynamic Patch Mosaics and Channel Movement in an Unconfined River Valley of the Olympic Mountains. *Freshwater Biology* 51:523-544.
- Leopold, L.B., M.G. Wolman, and J.P. Miller, 1964. *Fluvial Processes in Geomorphology*. W.H. Freeman, San Francisco, California.
- Lisle, T.E., 1986. Stabilization of a Gravel Channel by Large Streamside Obstructions and Bedrock Bends, Jacoby Creek, Northwestern California. *Geological Society of America Bulletin* 97:999-1011.
- Malmqvist, B. and R.S. Wotton, 2002. Do Tributary Streams Contribute Significantly to the Transport of Faecal Pellets in Large Rivers? *Aquatic Science* 64:156-162.
- Maser, C. and J.R. Sedell, 1994. *From the Forest to the Sea: The Ecology of Wood in Streams, Rivers, Estuaries and Oceans*. St. Lucie Press, Delray Beach, Florida.
- Maser, C., R.F. Tarrant, J.M. Trappe, and J.F. Franklin (Editors), 1988. *From the Forest to the Sea: A Story of Fallen Trees*. USDA Forest Service General Technical Report PNW-GTR-229. Pacific Northwest Research Station, Portland, Oregon.
- Mason, C.F. and S.M. Macdonald, 1982. The Input of Terrestrial Invertebrates From Tree Canopies to a Stream. *Freshwater Biology* 12:305-311.
- May, C.L. and R.E. Gresswell, 2003. Large Wood Recruitment and Redistribution in Headwater Streams in the Southern Oregon Coast Range, U.S.A. *Canadian Journal of Forest Research* 33:1352-1362.
- May, C.W., E.B. Welch, R.R. Horner, J.R. Karr, and B.W. Mar, 1997. Quality Indices for Urbanization Effects on Puget Sound Lowland Streams. University of Washington, Civil Engineering Dept., Water Resources Series, Tech Report 154, Seattle, Washington.
- McArthur, M.D. and J.S. Richardson, 2002. Microbial Utilization of Dissolved Organic Carbon Leached From Riparian Litterfall. *Canadian Journal of Fisheries and Aquatic Sciences* 59:1668-1676.
- Meleason, M.A., S.V. Gregory, and J.P. Bolte, 2003. Implications of Riparian Management Strategies on Wood in Streams of the Pacific Northwest. *Ecological Applications* 13:1212-1221.
- Meyer, J.L. and J.B. Wallace, 2001. Lost Linkages and Lotic Ecology: Rediscovering Small Streams. In: *Ecology: Achievement and Challenge*, M.C. Press, N.J. Huntly, and S. Levin (Editors). Blackwell Science, Malden, Massachusetts, pp. 295-317.
- Meyer, J.L., J.B. Wallace, and S.L. Eggert, 1998. Leaf Litter as a Source of Dissolved Organic Carbon in Streams. *Ecosystems* 1:240-249.
- Meyer, J.L., D.L. Strayer, J.B. Wallace, S.L. Eggert, and G.S. Helfman, 2007. The Contribution of Headwater Streams to Biodiversity in River Networks. *Journal of the American Water Resources Association*. 43, DOI: 10.1111/j.1752-1688.2007.00008.x
- Moore, R.D. and J.S. Richardson, 2003. Progress Towards Understanding the Structure, Function, and Ecological Significance of Small Stream Channels and Their Riparian Zones. *Canadian Journal of Forest Research* 33:1349-1351.
- Naiman, R.J., 1982. Characteristics of Sediment and Organic Carbon Export From Pristine Boreal Forest Watersheds. *Canadian Journal of Fisheries and Aquatic Sciences* 39:1699-1718.
- Naiman, R.J., 1983a. The Annual Pattern and Spatial Distribution of Aquatic Oxygen Metabolism in Boreal Forest Watersheds. *Ecological Monographs* 53:73-94.
- Naiman, R.J., 1983b. The Influence of Stream Size on the Food Quality of Seston. *Canadian Journal of Zoology* 61:1195-2010.
- Naiman, R.J. and H. Décamps, 1997. The Ecology of Interfaces: Riparian Zones. *Annual Review of Ecology and Systematics* 28:621-658.
- Naiman, R.J. and J.J. Latterell, 2005. Principles for Linking Fish Habitat to Fisheries Management and Conservation. *Journal of Fish Biology* 67:166-185.
- Naiman, R.J. and J.R. Sedell, 1979. Characterization of Particulate Organic Matter Transported by Some Cascade Mountain Streams. *Journal of the Fisheries Research Board of Canada* 36:17-31.
- Naiman, R.J., J.M. Melillo, M.A. Lock, T.E. Ford, and S.R. Reice, 1987. Longitudinal Patterns of Ecosystem Processes and Community Structure in a Subarctic River Continuum. *Ecology* 68:1139-1156.
- Naiman, R.J., E.V. Balian, K.K. Bartz, R.E. Bilby, and J.J. Latterell, 2002. Dead Wood Dynamics in Stream Ecosystems. In: *Proceedings of the Symposium on the Ecology and Management of Dead Wood in Western Forests*. General Technical Report

- GTR-PSW-181, W.F. Laudenslayer Jr., P.J. Shea, B. Valentine, C.P. Weatherspoon, and T.E. Lisle (Editors). U.S. Department of Agriculture, Forest Service, Pacific Southwest Research Station, Albany, California, pp. 23-48.
- Naiman, R.J., H. Décamps, and M.E. McClain, 2005. *Riparia: Ecology, Conservation and Management of Streamside Communities*. Elsevier/Academic Press, San Diego, California.
- Nakano, S. and M. Murakami, 2001. Reciprocal Subsidies: Dynamic Interdependence Between Terrestrial and Aquatic Food Webs. *Proceedings of the National Academy of Sciences* 98:166-170.
- Nakano, S., Y. Kawaguchi, Y. Taniguchi, H. Miyasaka, Y. Shibata, H. Urabe, and N. Kuhara, 1999. Selective Foraging on Terrestrial Invertebrates by Rainbow Trout in a Forested Headwater Stream in Northern Japan. *Ecological Research* 14:351-360.
- Nanson, G.C., M. Barbetti, and G. Taylor, 1995. River Stabilization due to Changing Climate and Vegetation During the Late Quaternary in Western Tasmania, Australia. *Geomorphology* 13:145-158.
- Negishi, J.N. and J.S. Richardson, 2003. Responses of Organic Matter and Macroinvertebrates to Placements of Boulder Clusters in a Small Stream of Southwestern British Columbia, Canada. *Canadian Journal of Fisheries and Aquatic Sciences* 60:247-258.
- Nielsen, J.L., 1992. Microhabitat-Specific Foraging Behavior, Diet, and Growth of Juvenile Coho Salmon. *Transactions of the American Fisheries Society* 121:617-634.
- Orlikowska, E.H., R.L. Deal, P.H. Hennon, and M.S. Wipfli, 2004. Role of Red Alder in Riparian Forest Structure Along Headwater Streams in Southeastern Alaska. *Northwest Science* 78:111-123.
- Petersen, R.C., 1986. *In situ* Particle Generation in a Southern Swedish Stream. *Limnology and Oceanography* 31:432-437.
- Piccolo, J.J. and M.S. Wipfli, 2002. Does Red Alder (*Alnus rubra*) in Upland Riparian Forests Elevate Macroinvertebrate and Detritus Export From Headwater Streams to Downstream Habitats in Southeastern Alaska? *Canadian Journal of Fisheries and Aquatic Sciences* 59:503-513.
- Reeves, G.H., K.M. Burnett, and E.V. McGarry, 2003. Sources of Large Wood in the Main Stem of a Fourth-Order Watershed in Coastal Oregon. *Canadian Journal of Forest Research* 33:1363-1370.
- Richardson, J.S., 1984. Effects of Seston Quality on the Growth of a Lake-Outlet Filter Feeder. *Oikos* 43:386-390.
- Richardson, J.S., 1991. Seasonal Food Limitation of Detritivores in a Montane Stream: An Experimental Test. *Ecology* 72:873-887.
- Richardson, J.S., 1992. Coarse Particulate Detritus Dynamics in Small, Montane Streams of Southwestern British Columbia. *Canadian Journal of Fisheries and Aquatic Sciences* 49:337-346.
- Richardson, J.S., C.R. Shaughnessy, and P.G. Harrison, 2004. Litter Breakdown and Invertebrate Association With Three Types of Leaves in a Temperate Rainforest Stream. *Archiv für Hydrobiologie* 159:309-325.
- Richardson, J.S., R.E. Bilby, and C.A. Bondar, 2005a. Organic Matter Dynamics in Small Streams of the Pacific Northwest. *Journal of the American Water Resources Association* 41:921-934.
- Richardson, J.S., R.J. Naiman, F.J. Swanson, and D.E. Hibbs, 2005b. Riparian Communities Associated With Pacific Northwest Headwater Streams: Assemblages, Processes, and Uniqueness. *Journal of the American Water Resources Association* 41:935-947.
- Robison, E.G. and R.L. Beschta, 1990. Characteristics of Coarse Woody Debris for Several Coastal Streams of Southwest Alaska, USA. *Canadian Journal of Fisheries and Aquatic Sciences* 47:1684-1693.
- Romero, N., R.E. Gresswell, and J.L. Li, 2005. Changing Patterns in Coastal Cutthroat Trout (*Oncorhynchus clarki clarki*) Diet and Prey in a Gradient of Deciduous Canopies. *Canadian Journal of Fisheries and Aquatic Sciences* 62:1797-1807.
- Speaker, R.W., K.J. Luchessa, J.F. Franklin, and S.V. Gregory, 1988. The Use of Plastic Strips to Measure Leaf Retention by Riparian Vegetation in a Coastal Oregon Stream. *American Midland Naturalist* 120:22-31.
- Suberkropp, K.F., 1998. Microorganisms and Organic Matter Processing. In: *River Ecology and Management*, R.J. Naiman and R.E. Bilby (Editors). Springer-Verlag, New York, pp. 120-143.
- Swanson, F.J. and G.W. Lienkaemper, 1978. Physical Consequences of Large Organic Debris in Pacific Northwest Streams. USDA Forest Service General Technical Report PNW-69. Pacific Northwest Forest and Range Experiment Station, Portland, Oregon.
- Swanson, F.J., S.V. Gregory, J.R. Sedell, and A.G. Campbell, 1982. Land-Water Interactions: The Riparian Zone. In: *Analysis of Coniferous Forest Ecosystems in the Western United States*, R.L. Edmonds (Editor). Hutchinson Ross, Stroudsburg, Pennsylvania, pp. 267-291.
- Triska, F.J., J.R. Sedell, and S.V. Gregory, 1982. Coniferous Forest Streams. In: *Analysis of Coniferous Forest Ecosystems in the Western United States*, R.L. Edmonds (Editor), Hutchinson Ross, Stroudsburg, Pennsylvania, pp. 292-332.
- U.S. Dept. of Agriculture Forest Service, 1997. *Tongass Land Management Plan Revision: Final Environmental Impact Statement*, Appendix, Vol. 1. USDA For. Serv. R10-MB-388e.
- U.S. Dept. of Agriculture Forest Service, 1999. *Record of Decision. Tongass National Forest Land and Resource Management Plan*. USDA For. Serv. FS-639.
- Valett, H.M., C.L. Crenshaw, and P.F. Wagner, 2002. Stream Nutrient Uptake, Forest Succession, and Biogeochemical Theory. *Ecology* 83:2888-2901.
- Wallace, J.B., M.R. Whiles, S. Eggert, T.F. Cuffney, G.H. Lugthart, and K. Chung, 1995. Long-Term Dynamics of Coarse Particulate Organic Matter in Three Appalachian Mountain Streams. *Journal of the North American Benthological Society* 14:217-232.
- Wallace, J.B., S.L. Eggert, J.L. Meyer, and J.R. Webster, 1999. Effects of Resource Limitation on a Detrital-Based Ecosystem. *Ecological Monographs* 69:409-442.
- Webster, J.R. and E.F. Benfield, 1986. Vascular Plant Breakdown in Fresh-Water Ecosystems. *Annual Review of Ecology and Systematics* 17:567-594.
- Webster, J.R., E.F. Benfield, T.P. Ehrman, M.A. Schaeffer, J.L. Tank, J.J. Hutchens, and D.J. D'Angelo, 1999. What Happens to Allochthonous Material That Falls Into Streams. A Synthesis of New and Published Information From Coweeta. *Freshwater Biology* 41:687-705.
- Wipfli, M.S., 1997. Terrestrial Invertebrates as Salmonid Prey and Nitrogen Sources in Streams: Contrasting Old-Growth and Young-Growth Riparian Forests in Southeastern Alaska, USA. *Canadian Journal of Fisheries and Aquatic Sciences* 54:1259-1269.
- Wipfli, M.S. and D.P. Gregovich, 2002. Export of Invertebrates and Detritus From Fishless Headwater Streams in Southeastern Alaska: Implications for Downstream Salmonid Production. *Freshwater Biology* 47:957-969.
- Wipfli, M.S. and J. Musslewhite, 2004. Density of Red Alder (*Alnus rubra*) in Headwaters Influences Invertebrate and Detritus Subsidies to Downstream Fish Habitats in Alaska. *Hydrobiologia* 520:153-163.
- Wipfli, M.S., J.P. Hudson, and J.P. Caouette, 1998. Influence of Salmon Carcasses on Stream Productivity: Response of Biofilm and Benthic Macroinvertebrates in Southeastern Alaska, USA. *Canadian Journal of Fisheries and Aquatic Sciences* 55:1503-1511.
- Wipfli, M.S., J.P. Hudson, J.P. Caouette, and D.T. Chaloner, 2003. Marine Subsidies in Freshwater Ecosystems: Salmon Carcasses

Increase the Growth Rates of Stream-Resident Salmonids. *Transactions of the American Fisheries Society* 132:371-381.

Wotton, R.S. and B. Malmqvist, 2001. Feces in Aquatic Ecosystems. *BioScience* 51:537-544.

Wotton, R.S., B. Malmqvist, T. Muotka, and K. Larsson, 1998. Fecal Pellets From a Dense Aggregation of Suspension Feeders in a Stream: An Example of Ecosystem Engineering. *Limnology and Oceanography* 43:719-725.