A SURVEY OF INVERTEBRATES ASSOCIATED WITH WOOD DEBRIS IN AQUATIC HABITATS[1]

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[1]Technical Paper No. 6419, Oregon Agricultural Experiment Station.

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ABSTRACT

A field survey was undertaken to examine the community of invertebrates associated with wood debris in freshwater systems, with an emphasis on forested streams of the western states. Fifty-six taxa representing 5 orders of insects and other invertebrates are identified as closely associated with wood, while 129 taxa are listed as facultative users. The methods of utilization range from the opportunistic use of the wood surface for refuge, resting and feeding, to ingestion of wood tissue, including sub-surface boring. Wood debris is found most abundantly in headwater streams, where the low streamflows cause less abrasion and displacement of the material, and allow more extensive conditioning by decomposers. Obligate xylophages occurred predominantly in these low order streams.

INTRODUCTION

This study is part of a long-term project on the role of wood in aquatic habitats and the relation of invertebrates to the degradation and mineralization of wood debris. In a previous paper, Anderson *et al.* (1978) recorded about 40 species of invertebrates associated with woody debris in Oregon streams, though the biomass was 2 orders of magnitude less than that on leaf debris. The differences were attributed to the refractory nature of wood. Wood decay in streams requires decades, or longer, whereas leaves are processed by microbes and invertebrates in months or a few years (Petersen and Cummins, 1974; Anderson and Sedell, 1979).

Wood debris constitutes the major organic input to the headwater streams of the Pacific Northwest. Swanson *et al.* (1976) estimated that the standing crop of large wood debris (> 10 cm dia) was over 40 kg/m^2 in headwater streams flowing through old-growth Douglas fir *Pseudotsuga menziesii* (Franco) stands in the Oregon Cascades. In view of the quantities in these streams it is apparent that wood has a significant role in energy flow, nutrient dynamics, stream morphology, and in shaping the biotic community structure of these lotic ecosystems (Swanson *et al.*, 1976; Keller and Swanson, 1979; Anderson and Sedell, 1979; Triska and Cromack, 1980).

Anderson *et al.* (1978) identified some aquatic invertebrates that were intimately associated with wood. Their preliminary estimates suggested that invertebrate feeding could account for 15-20% of the wood loss over the entire degradation cycle. Except for the above, literature on aquatic invertebrate communities inhabiting logs or inundated trees has emphasized the exploitation of these sites as habitats for attachment and filter feeding, or surfaces where the periphyton film is grazed (McLachlan, 1970; Nilsen and Larimore, 1973; Benke *et al.*, 1979).

The purpose of this project was to examine the wood-associated aquatic community from several biogeographic regions, in streams of various sizes and in lentic habitats. Extensive field surveys were undertaken in 1978 and 1979 to identify those organisms in some way associated with wood. The basic survey criterion for determining an association is simply the consistent occurrence of a taxon on this substrate. It encompasses invertebrates restricted to feeding solely on or in wood; those which have a preference for woody debris as habitat for some life stage; and animals with casual utilization of wood as simply another available substrate.

METHODS

Invertebrates were collected in several regions in order to include various ecosystem types. However, we concentrated our efforts in the Pacific Coast and northern Rocky Mountain states. The emphasis has been on the lower order headwater streams because they tend to be forested and do not have the power to flush out most of the wood. These streams are also generally less impacted by agriculture or other management practices. Where practical, larger streams were also sampled, as were some lakes, ponds and reservoirs.

Field collecting consisted primarily of picking the animals from logs or branches with forceps. Internal organisms were collected by scraping or slicing the wood with a knife. An improved method for obtaining the surface organisms was to use a back-pack pressure tank and sprayer to wash the insects into a bucket. This "flushing" technique was a significant improvement over the time-consuming and tedious process of handpicking. Also, it tends to dislodge individuals from the crevices or rough surfaces. The collected material was concentrated by pouring it through a fine mesh net and transferred to a sample jar. Specimens were preserved in the field in 70% ethyl alcohol. Some wood samples were brought to the laboratory in a cooler for washing and examination. In some cases the pieces of wood were submerged or kept damp in screen cages to rear adults for identification.

Collecting from wood was primarily qualitative as the availability of this substrate varied greatly and the time required for quantitative sampling would have been prohibitive. Field notes included habitat characteristics (current speed, stream size, substrate, surrounding vegetation, etc.) and wood qualities (size, species, texture, rot class, degree of submergence, etc.).

We found it useful to adopt an inclusive definition of aquatic habitat because the zone of greatest activity is at the land-water interface. In sites where wood extends from the bank into the water, species richness (especially of burrowing forms) is greater than on completely submerged wood. It seems justifiable to include this semi-aquatic component in the analysis because the area would be submerged at high water and, because of the capillary properties of wood, it remains waterlogged or moist through most of the year. In some instances where the wood was not completely saturated, the records are listed as "semi-terrestrial."

Gut analysis was done to determine which species ingested wood and thereby contributed to degradation by decreasing the particle size. These results are reported in the accompanying paper (Pereiera *et al.*, 1982).

COLLECTION AREAS

The collecting areas are arranged in Tables 1 and 2 generally north to south along the Pacific Coast and then from the crest of the Cascade Range, from west to east. The locations and approximate number of sites visited are: Olympic Peninsula rain forest (Hoh River drainage) 20 sites, mid-September; Western Oregon (Coast Range and Willamette Valley) 50+ sites, all seasons; Oregon (western slopes of Cascade Range) 50+ sites, all seasons; Southern Oregon - Northern California (Siskiyous and northern Sierra Nevada) 40 sites, December-March; California (coastal redwood zone) 12 sites, January-February; Southern California (coastal region and Channel Islands) 20 sites, December and February; Eastern Oregon (east slope of the Cascade, Ochoco, Strawberry, Wallowa and Blue Mountains), 50 sites, August; Idaho, Colorado, Wyoming (western slope, Rocky Mountains) 50 sites, July-August.

Sampling of streams northeast of Mt. St. Helens, Washington, was conducted in 1980 to assess the role of wood debris as habitat for invertebrate recolonization in areas devastated by the May 18, 1980 eruption. Streams were selected along a range of impacts from Ape Canyon on the flanks of the mountain, through the Clearwater drainage, where blowdown was severe and along the direction of the ash plume to Elk Creek. Lake Creek, near Packwood, Cowlitz Co., was lightly dusted with ash but served as a control site. Small debris was collected and washed to sample the invertebrates. Large logs were abundant in the Clearwater Creek sites but it was not practical to collect from these surfaces so most collections were from small wood debris.

Some collections were made from wood debris east of the Rocky Mountains. Though not definitive, the data are useful for comparison with the western material so the locations are given. Wisconsin: a collection by D. Krueger in June from Otter Creek, Sauk Co., a well-oxygenated medium-sized cobble substrate stream in a mature mixed deciduous-coniferous second-growth forest (Peckarsky, 1979). Pennsylvania: about 20 collections in April from 10 streams along a transect in the eastern deciduous forest from Erie Co. to Chester Co. These included a first-order stream at Heart's Content, Warren Co., a remnant stand of old-growth beech-hemlock forest with stream debris loading similar to that in streams of the Pacific Northwest. Streams near the Stroud Water Research Lab were included because of other research conducted there (Minshall *et al.*, in press). North Carolina: five streams in the Coweeta Forest, Macon Co., in March. These watersheds have received considerable study (Webster, 1977; Woodall and Wallace, 1972) and include both mature southern hardwood stands and recent clearcuts.

DATA PRESENTATION AND INTERPRETATION

The data from the survey are presented in Tables 1 and 2, partitioning the fauna into 2 categories: (a) those that are largely dependent upon wood at some life stage or that have a significant effect on wood degradation through feeding, or using wood in case building, and (b) those that are more opportunistically associated. While some taxa that are listed as "closely associated" may not as a whole be endemic to wood, the individuals collected appeared to be restricted to this habitat.

Occurrence of taxa on wood within each area is coded as: A = abundant, LA = locally abundant, C = common, O = occasional, and R = rare. These categories are not based on absolute numbers but on subjective relative frequencies. *Abundant* taxa are ubiquitous in wood collections from streams throughout a given region (e.g. *Baetis*), while the local designation implies that a taxon may occur at high densities but its distribution is constrained by some factor. For example, the tipulid *Lipsothrix* is restricted to boring in logs of a specific texture but may be numerous in a particular log. Local populations may also be those found in certain types of streams such as very small or very slow streams. *Common* indicates that the taxon is likely to be found, at least in low densities, in most collections from its predominant habitat. *Occasional* occurrence means that an organism was collected in $< 10\%$ of the sites sampled. In the *rare* category we list species where $<$ 10 specimens were collected. These are included either because they were in wood (i.e. burrowing), or they are taxa known only from exceptional records.

Habitat types are distinguished as: H = headwaters (1st - 2nd order streams) (Strahler, 1957); M = mid-sized streams (3rd - 5th order); L = large streams and rivers. Underlining indicates dominance in a category, whereas ( ) indicates limited occurrence. As was indicated previously, the collecting was biased towards headwater streams because both wood and the xylophilous fauna was more abundant there. However, wood in larger streams was frequently examined and we believe we have an adequate sample of the fauna from larger streams. Lentic habitats, including beaver ponds, were markedly unproductive for wood associated taxa; thus records of lentic species are only noted under "Comments."

Wood type is based on texture: 1 = firm smooth wood; 2 = firm, but grooved or textured wood, often including some bark; 3 = soft, rotted wood, some of which could be broken open by hand.

Associations are functional classifications of how wood substrates are used: 1 = boring or tunnelling; 2 = ingestion of wood by gouging, scraping, or rasping; 3 = scraping of associated aufwuchs; 4 = use as physical habitat such as concealment in grooves, attachment for feeding (e.g. *Simulium)* or for net attachments and retreats (e.g. Hydropsychidae); 5 = predation, but apparently common on wood compared with other substrates.

The taxa listed in the tables are those collected during this survey and in Anderson *et al.* (1978) and do not include other literature records. Also excluded are the Odonata, Megaloptera, most Coleoptera (especially Hydrophilidae and Dytiscidae), and some families of Diptera because, while often occurring on wood, their association appeared very non-specific and their feeding activities would have minimal impact on wood degradation. Many of these organisms are predatory, and use the wood as a temporary resting place or feeding substrate.

RESULTS

Where Anderson *et al.*, (1978) listed about 40 taxa associated with wood debris in 7 streams in the Oregon Coast and Cascade Ranges, there are 45 given here as closely associated (Table 1) and over 80 (excluding Chironomidae) in the facultatively associated group (Table 2). Although the list of xylophilous taxa is trebeled, the dominant groups were largely identified in the earlier study.

As a basis for discussing geographic and habitat relations of the wood-associated fauna, the insect orders and other invertebrate groups are considered first.

EPHEMEROPTERA. Of the genera collected, only *Cinygma* is considered closely associated with wood. However, in collections from tethered grooved sticks from the Cascade Range stream, Mack Creek, the mayflies are frequently the numerically dominant order (N. H. Anderson, unpublished). *Ephemerella (Drunella) coloradensis* (Dodds) (= *Ephemerella flavilinea* in Anderson *et al.*, 1978) and *Ephemerella infrequens* McDunnough are abundant species on wood at this site. Taxa with wood in the guts included *Cinygma, Epeorus, Paraleptophlebia,* and to a lesser extent *Ameletus* and some *Ephemerella.* Mayfly feeding is largely by scraping or collecting, and where wood is ingested it is mostly secondary to ingestion of the aufwuchs layer (Pereira *et al.*, 1982). For several heptageniids, *Ephemerella* and the ubiquitous *Baetis,* the primary use of wood substrates is classified as habitat. In lentic situations *Callibaetis* and *Siphlonurus* were commonly found resting on submerged wood. In backwaters or alcoves of streams, both

Ameletus and *Paraleptophlebia* were common on wood. As the physical abrasion tends to be less in these sites, the superficial layers may be soft and reticulated, providing both concealment and a microbially enriched food source.

PLECOPTERA. All families of stoneflies were collected on wood debris, but they occurred in the substrates or leaf debris in similar abundance so the associations are listed as facultative. The families of detritivores, Pteronarcidae, Peltoperlidae, Capniidae, Leuctridae, Taeniopterygidae and Nemouridae, are often collected on wood, or in the leaf debris that accumulates on wood. In autumn or early winter, when many stoneflies are abundant, it is difficult to distinguish the substrate utilized because of the leaf packs on wood. However, gut analysis indicated a significant amount of wood fibers in many genera, including *Yoraperla, Pteronarcys, Pteronarcella,* and some genera of Nemouridae. The Leuctridae and Capniidae were not distinguished due to taxonomic difficulties, especially as most larvae were quite immature. Their elongate body form enables the larvae to utilize cracks in bark and wood for concealment, but our limited data on gut analysis indicated only small quantities of ingested wood. Though listed as shredders by Merritt and Cummins (1978), it may be that the early and mid-instars of leuctrids and capniids are fine particle collector-gatherers.

Predacious stoneflies, Chloroperlidae, Perlodidae and Perlidae, frequently utilize wood substrates as habitat. Chloroperlids of the genera previously grouped under *Alloperla* (see Jewett, 1959) were common predaceous stoneflies on wood; their slender bodies are well adapted for penetrating into cracks and crevices. Emergent wood appeared to be a favored substrate for adult emergence of this group. Perlids were also frequently found in burrows gouged by terrestrial beetles and under loosened bark.

TRICHOPTERA. Caddisfly larvae were the most conspicuous insects on wood surfaces. They are relatively large and easily seen because of their cases and retreats. Free-living larvae, net spinners and case makers all occur on wood debris. There are about twice as many taxa listed in Tables 1 and 2 as were reported by Anderson *et al.* (1978). We have documented wood ingestion by about 20 species, confirming the earlier suggestion that many of the leaf shredders also feed to some degree on wood and associated microbes. The Calamoceratidae, Lepidostomatidae, and several genera of Limnephilidae are the taxa most closely associated with wood, in feeding, case-making, and utilization for pupation.

COLEOPTERA. The diverse assemblage of beetles listed would probably be doubled if genera of Dytiscidae and Hydrophilidae had been included but, as was indicated previously, their occurrence was considered to be transitory. The elmid, *Lara avara* LeConte, was the most common beetle associated with wood and is an important wood gouger (Anderson *et al.,* 1978). Larvae and adults of the wharf borer, *Ditylus quadricollis* LeConte (Oedemeridae) were collected in large numbers in a few submerged logs in Oregon and Washington; where they occurred the wood was riddled by their tunnels. The other families are primarily borers in waterlogged wood. Many are considered terrestrial (Lucanidae, Melasidae, Tenebrionidae), but the larvae collected were in wood that was either submerged, or largely saturated. All of these taxa are listed as rare or occasional; their scarcity indicates minimal importance in wood degradation in water. Taxa listed in Table 2 demonstrated some affinity for wood substrates but based on our current knowledge, they are not implicated in wood degradation.

DIPTERA. Fly larvae are the major wood decomposers in aquatic habitats because of their burrowing habits. Though a few were recorded from firm wood (e.g. *Brillia* and *Axymyia),* the majority occurred in decayed or soft wood. Several of the borers are fully aquatic (e.g. some Chironomidae, Stratiomyidae, Syrphidae, some Tipulidae, Xylophagidae), but a major zone of occurrence is at the interface between land and water. Several of the tipulids, especially *Lipsothrix,* occur in partially submerged logs (Rogers and Byers, 1957; Dudley, 1982).

Over 50 genera of larval Chironomidae were collected from wood substrates (Table 3). The list includes many common genera and those with a large number of species, so it largely reflects the ubiquity of chironomids in freshwater habitats. Tabulation of geographic distributions is unwarranted as most of these genera are widely distributed. Also, the functional classification or associations of all genera are not listed as these are largely redundant with the habit and trophic relations given by Coffman (1978). Though most of the chironomids were surface associates that used the wood as habitat, several genera that ingest wood were identified. Most of these are probably boring or mining taxa (e.g. *Brillia, Stenochironomus)* but considerably more study is required to identify and elucidate the habits and relative importance of xylophilous midges.

Of the 12 most common genera of midge larvae collected from tethered sticks placed in western Oregon streams, only *Brillia* and a new genus of Orthocladiinae were xylophagous. The functional group of the other dominant taxa was: collector-gatherers—*Corynoneura, Paratendipes;* collector-filterers—*Rheotanytarsus, Tanytarsus;* collector-scraper—*Eukiefferiella;* shredder-collector—*Rheocricotopus;* and predator—*Thienemannimyia.* Further data on gut contents of wood-associated chironomids is given in Pereira *et al.* (1982).

Some notable records of Diptera larvae boring in wood were obtained during this study. An undescribed species of Axymyiidae *(Axymyia n. sp.)* was collected from a firm cedar log *(Thuja plicata* Donn.) in the western Cascades (Lane Co., OR), while larval exuviae were found in a soft alder log in the Coast Range (Benton Co., OR). The larvae bore long galleries which are oriented vertically to the log surface. They have a long, extensible respiratory siphon in addition to two long coiled gill filaments, and reside at the base of the gallery in a manner similar to that described for the only other North American member of the family (Krogstad, 1959). The pachyneurid *Cramptonomyia spenceri* Alexander inhabited very punky alder at the margin of a small, densely canopied Cascade foothill stream (Linn Co., OR). The only other record of larvae of this species was from alder wood at another mesic site near Vancouver, B.C. (Vockeroth, 1974).

Highly decayed alder logs associated with the margins of low-order streams were also utilized by several other uncommon dipterans. These were not identified to the species level because no associations could be made with adults. Included were three genera of Syrphidae of the subfamily Milesiinae. *Sphegina sp.* was collected once (Linn Co., OR) and *Pocota sp.* at three sites (Lincoln Co., Benton Co., OR). *Xylota sp.* was found in several low-gradient streams (Lincoln Co., Benton Co., OR), and was also associated with sodden Douglas fir. *Glutops sp.* (Pelecorhynchidae) was also found boring into alder in a very small Cascade Range stream (Linn Co., OR). A fly belonging to the Stratiomyidae, *Myxosargus sp.,* was collected from unidentified punky wood from similar streams, but in more arid regions. One specimen came from a high-desert meadow stream with mixed conifers upstream (Crook Co., OR), while the other was from a coastal stream in southern California (Santa Barbara Co.). Both bored shallowly into the wood, and were atypical for soldier fly larvae in that the cuticle is soft and not leathery. The last two taxa were not listed in the excellent work on wood-associated Diptera by Teskey (1976).

The flies listed as facultatively associated with wood (Table 2) are mostly common nematocerous families that exploit the substrate as habitat and would have minimal impact in wood degradation.

OTHER INVERTEBRATES. A range of invertebrates other than insects were recorded on wood debris in both lentic and lotic habitats. In backwaters of streams, annelid worms are common in wood that is in the final stages of decay (Table 1). According to William Fender (personal communication), the dominant species in our material was the holarctic species *Dendrodrilus rubidus* (Savigny). The taxa listed in Table 2 include predators (Acarina), scavengers (planarians, amphipods), detritivores (isopods), filter feeders (sphaerids) and scrapers (snails). The snail, *Juga plicifera* (Lea) (as *Oxytrema silicula)* has been previously implicated as important in wood degradation due to its abundance on wood debris (Anderson *et al.,* 1978).

DISCUSSION

RELATION OF HABITAT TO INVERTEBRATE COLONIZATION OF DEBRIS

Comparisons of habitats in the South Fork Hoh River drainage of the Olympic rain forest provide some insights on factors limiting the occurrence of xylophilous taxa where wood debris is abundant. Four fairly discrete habitats were examined: main stream (6th-order), isolated side braids, low-gradient terrace tributaries, and higher gradient tributaries above the terraces. Only the latter streams had a reasonably good fauna of wood-associated insects. These included borers *(Lipsothrix),* gougers *(Lara avara),* scrapers *(Cinygma)* and several other groups on the surface and within the wood crevices (Chironomidae, Heptageneidae, Baetidae, Nemouridae, Peltoperlidae, Perlodidae, Limnephilidae, Rhyacophilidae). Where these streams levelled out into the terraced area, siltation and accumulation of organic fine particles excluded many of the gougers and scrapers. A few collectors (Chironomidae, Baetidae) and predators (Rhyacophilidae) were found. Wood-boring tipulids were uncommon and only occurred where wood was partially emergent and well decomposed. Much of the wood in the terraced streams was buried in sediment where dissolved oxygen is low or absent and fungal activity is inhibited.

In the main stream of the Hoh, abrasion, rather than siltation or low dissolved oxygen, diminished the role of invertebrates in wood degradation. The superficial layers colonized by microbes were physically removed, displacing the food supply and possibly the invertebrates. Most of the wood occurred in large debris jams, or was deposited on shore during floods where it became unavailable to the aquatic forms. The most common usage was as an emergence substrate. The intermittent channels and pools in the braided side-channels had only a small fauna of wood associates. The temporal instability, lentic nature, and siltation are apparently factors that limited the fauna largely to chironomids and a few tipulids. The variation in patterns of use between the habitats present in the Hoh drainage indicates that the invertebrate community and its impact on wood are dependent on the physical regime.

No invertebrates were found restricted to wood in lentic situations, though adults of the dryopid beetle, *Helichus striatus* LeConte, seemed to have a strong preference for wood. However, many diverse groups including *Callibaetis* and *Siphlonurus* mayflies, amphipods, chironomids, several snails and families of predaceous insects commonly use this for feeding, refuge or rest. Invertebrates were sometimes more abundant on wood than on silty substrates in ponds. Beaver dams had a remarkably low density and diversity of invertebrates, possibly because the fresh wood takes a considerable period for microbial colonization, and also because of the level of siltation in these ponds. Wood in reservoirs was also depauperate whereas in natural lakes there was a number of wood-surface associates. No internal colonizers were collected in lakes, which possibly could be associated with oxygen exchange problems.

WOOD DEBRIS AS HABITAT IN MT. ST. HELENS STREAMS

The catastrophic effects of the May 18, 1980 eruption of Mt. St. Helens on stream systems afforded a unique opportunity to monitor the role of wood debris as a habitat for the stream fauna. In some areas the channels were sluiced by mudflows, removing in-channel wood and the riparian vegetation, whereas in the path of blast, the forests were flattened and stream channels filled with logs and wood debris. During 1980, the large wood was particularly important in shaping channels, trapping sediments and in some sites it was the only stable substrate in a shifting bed of ash and pumice.

Table 4 compares the number of taxa collected from wood and from mineral substrates in September 1980 in streams experiencing a range of impacts. Five benthos samples were taken in each stream on riffles with a Hess-type sampler (0.05 m^2). Wood was collected from debris jams, back-water areas, and as individual pieces that were hung up in riffle areas.

In Ape Canyon and Muddy River the fauna was eliminated by the eruption but a few individuals, primarily dipterans and *Baetis,* had recolonized by September. There was no large wood or other stable substrates in these channels and density of invertebrates was extremely low ($< 1/m^2$).

The importance of wood as habitat in streams with otherwise unstable substrates was evident at the Clearwater Creek sites, especially in Upper Clearwater. Several taxa survived the eruption at this site but densities were very low (benthos density $= 7/m^2$). Twice as many taxa were collected from wood debris as from the Hess samples and densities also seemed to be higher on wood. The fauna was composed of typical benthic taxa, without a significant component of xylophilous species, so the wood basically served as a refuge. At Middle Clearwater there was a small area where the channel had cut through the ash exposing the original cobble bed and this supported a fairly diverse fauna, including more taxa than were collected from wood. Only 4 taxa were collected from the wood samples that were not recorded from the benthos and none of these was considered to be restricted to this habitat.

Lower Clearwater contained a lower number of taxa than the control site. This is attributed to the scouring effects of transported sediments as there were no direct blast effects in this area. Several taxa of closely-associated wood fauna (c.f. Table 1) survived at this site: *Lara, Cinygma, Heteroplectron,* limnephilid caddisflies, and nemourid stoneflies.

The heavy ashfall at Elk Creek had no effect on diversity of taxa although densities were markedly lower than at Lake Creek ($97/m^2$ vs. $616/m^2$). The wood samples increased the taxa pool by 13 at Elk, probably due to the undersampling of the low-density benthos populations. Wood debris was probably important in Elk Creek in maintenance of diversity by affording a refuge above the ash deposits. When the current re-exposed areas of original streambed it could then be recolonized by individuals from wood substrates.

FAUNAL COMPARISONS IN BIOGEOGRAPHIC AREAS

The collections from various regions do not disclose discrete wood-associated communities in different areas but instead indicate trends related to physical parameters. Continuous moisture appears to be by far the most important factor. The greatest diversity of wood-related species occurs in mesic forested streams west of the Cascade divide. Debris loading of these streams is also highest. All trophic levels and many functional feeding groups are represented. Wood-restricted forms decrease as one moves from west to east or from north to south, although facultative associates may remain quite abundant.

Chironomids, which probably play a relatively small role in wood decomposition in wet regions, became the dominant fauna in streams of sagebrush country or xeric forests. Midges were found boring under the bark of willow, and up to 5 mm into soft deciduous and conifer wood. Some of the larger xylophages, such as *Lara* and *Lipsothrix* were only found at higher elevations in the Rockies, Sierra Nevada and the intermountain region. The elevation gradient would correspond with an increasing moisture gradient. The importance of chironomids, and decrease in other xylophages, may be related to lack of constancy of the habitat. Both flood disturbance and risk of desiccation are greater in the arid regions, and the short life cycle and high dispersal ability of midges may better enable them to exploit these temporally fluctuating habitats. Despite the fact that the riparian zone is generally more wooded than the surrounding area, there is much less wood entering dryland streams than in dense forest situations. Physical abrasion in these flashy streams will serve to further reduce and disrupt the suitable habitat.

Limited collections from streams in the eastern deciduous forest region provide some comparisons with northwest streams. In most streams, the amount of wood debris was considerably less than that found in the northwest but the wood-associated fauna was well represented and the taxa included functional analogues of the xylophilous fauna listed in Tables 1 and 2. Many of the sites were low-gradient, silty streams in second-growth forests but the first-order creek at Heart's Content, PA, flowed through a remnant stand of beech-hemlock old growth and contained considerable wood debris. The diverse wood-associated fauna of this stream is likely typical of conditions prior to the extensive land clearing in the east. Shredders collected from wood debris included *Lepidostoma, Pycnopsyche, Pseudostenophylax,* Leuctridae, *Peltoperla, Amphinemura* and the cranefly, *Epiphragma.* The scrapers and collectors included many of the same genera as in the northwest: *Baetis, Ephemerella, Glossosoma* and *Hydropsyche.* Small tributaries to Doe and Buck Run (Chester Co., PA), and other first-order streams had a good complement of wood borers. These were mostly flies, as was typical of other areas: *Lipsothrix sylvia* (Alexander), *Limonia, Epiphragma, Brillia* and other Chironomidae and Sciaridae. Lumbricid worms occurred along with flies in very rotten wood. The melasid beetle *Fornax* was found here as well as in Oregon.

In larger Pennsylvania streams (2nd-4th order) where siltation was greater, the fauna of strict wood associates was reduced. However, where a log or stick afforded the most stable substrate for attachment or where it trapped fine particles, the fauna was more diverse: *Ephemerella (Serratella* and *Eurylophella), Heptagenia, Stenonema,* the net-spinning caddis *Lype diversa* (Banks), glossosomatids, elmid and psephenid beetles, *Dixa,* several chironomids and other collector-scrapers. In riffle areas where siltation was decreased by the current, hydropsychid caddisflies, blackflies, filipalpian and setipalpian stoneflies were common.

Collections from Otter Creek, WI and from streams in the Coweeta Forest, NC, also indicated that most of the common benthic invertebrates utilized wood debris primarily as a habitat. Surface associates were scrapers (e.g. *Stenonema, Neophylax,* planorbid snails), shredders (e.g. *Pycnopsyche, Lepidostoma, Amphinemura,* and the isopod *Asellus),* and collectors (e.g. *Hydropsyche, Lype,* and chironomids). While tunneling tipulids and midges were collected, we did not find gougers such as *Lara* or *Heteroplectron* in our limited survey.

UTILIZATION OF WOOD SUBSTRATES BY INVERTEBRATES

Wood quality or texture is important in determining the kinds of species that will colonize it. The species of wood, degree of waterlogging, and the soundness or decay class all affect wood quality. The extent of mycological invasion and attack by wood-borers in the terrestrial habitat may have considerable influence on its attractiveness in water because texture is frequently related to the condition of the wood when it entered the water.

The three broad categories used to characterize wood type are inadequate to define precise microhabitat preferences, especially since conifer woods were not distinguished from deciduous. However, the classification is a rough indication of differences beween the taxa in Tables 1 and 2. The "closely associated" groups were largely found in soft rotten wood (66%), while about one third preferred grooved, textured wood, and less than 10% were found primarily on firm substrates. By contrast, the facultatively associated taxa (Table 2) are listed as 20% on firm wood, 70% on grooved wood and only 20% on, or in, soft rotted wood.

Functional feeding classifications are also interrelated with wood texture. In part, this explains the higher incidence of facultatively associated taxa with smooth firm wood and of xylophagous species with soft wood. Smooth surfaces are suitable for attachment (e.g. *Brachycentrus, Simulium, Rheocricotopus),* or for grazing the aufwuchs film *(Baetis, Ephemerella, Epeorus, Dicosmoecus, Eubrianax,* snails). Soft wood is not only more easily penetrated by borers, but also contains fungal mycelia as a nutrient source.

Many of the surface-associated invertebrates are more opportunistic in habitat or feeding-site selection than are the internal associates. Thus, the listing in Table 2 as facultative wood associates is our subjective judgment of preference for wood. This requires more work to accurately verify. As has been indicated previously, all functional feeding groups are represented in the wood associates but it is doubtful whether feeding is the primary basis for association of most taxa listed in Table 2. Instead, wood offers a refuge from predation and/or the abiotic environment. The many grooves, crevices, cracks and pieces of loose bark on a well-conditioned log hold the majority of animals collected. Predators, such as perlid, perlodid and chloroperlid stoneflies, hydrophilid beetle larvae, and the *acropedes* groups of rhyacophilid caddisflies, sometimes comprise the largest biomass in this microhabitat. Wood in the guts of predators may represent utilization or may be from prey gut contents.

Borers include some families of semi-terrestrial or semi-aquatic beetles, some caddisflies which hollow out twigs for cases *(Heteroplectron, Amphicosmoecus)* and those that tunnel into soft wood for pupation *(Heteroplectrcn, Micrasema, Lepidostoma).* However, Diptera larvae are the dominant borers, both in abundance and diversity. Oxygen diffusion into submerged wood is rapidly attenuated with the result that microbial colonization in the matrix can be oxygen limited. Xylophagous species are at least partially dependent on the microbes for nutrition as well as requiring oxygen for respiration. Thus, depth of penetration is probably restricted by oxygen gradients, accounting for galleries being located just under the wood surface. Burrowing species predominantly occur in shallow headwaters or in partially submerged wood. Some species have special respiratory adaptations such as haemoglobin in *Stenochironomus,* or the extensible respiratory siphons of *Axymyia* and syrphids.

Boring activity will expose new surfaces for microbial colonization and also spread the inoculum for invasion of sound wood. There is often a zone visibly stained with fungi radiating from *Lipsothrix* galleries. It is not known whether this is caused by a symbiont carried by the larvae, or is a less tightly linked relationship. The galleries of terrestrial beetles will also increase fungal activity after the wood is in the water. Some tipulid larvae have been collected from these preconditioned galleries.

The feeding activities of taxa listed under categories 1 (borers) and 2 (ingestion by gouging, scraping or rasping) result in wood utilization and degradation. The amount of wood ingested will depend not only on method of feeding and consumption rate, but also on the firmness and amount of fungal penetration in the superficial layer of wood. Wood in category 2 (firm, but grooved or textured) generally has a soft, stained layer at least a few mm deep that has been invaded by mycelia. Gougers *(Lara, Heteroplectron)* shredders (many limnephilids, *Lepidostoma, Yoraperla,* pteronarcids, nemourids) will exploit this fungal-enriched area which contains about 5 times higher nitrogen content than the wood matrix (Anderson *et al.,* in prep.). Scrapers (eg. *Cinygma, Epeorus, Acneus, Glossosoma),* and raspers (snails) will ingest this soft layer along with periphyton. It is quite probable, in light of the abovementioned nitrogen content, that this hyphal-wood film is assimilated by scrapers and possibly also by the largely predaceous forms such as *Rhyacophila* and setipalpian stoneflies.

Many of the species associated with the extremely decomposed material are most accurately cast as detritivores which happen to be in wood instead of some other soft organic material. The rationale for inclusion of these taxa in the tables is that their feeding and burrowing activities will result in particle-size reduction and mineralization of the substrates. Included in this group of detritivores would be some of the Syrphidae, Mycetophilidae, Sciaridae, Tipulidae, Ptilodactylidae and annelid worms. Also, some of the predators (Empididae, Rhagionidae, some Tipulidae, tanypodine midges) are only facultatively associated with rotten wood, while the Xylophagidae are known primarily from rotting wood and beneath bark in terrestrial habitats (Teskey, 1976).

The net-spinning caddisflies frequently use wood substrates for net attachment and conceal themselves within the grooves. Fallen logs may channel the flow in a manner that provides ideal sites with respect to flow rates for maximum filtering efficiency. Densities of *Hydropsyche* nets of 120 per 100 cm^2 were obtained on wood substrates during this survey. The eastern psychomyiid, *Lype diversa* is largely restricted to building retreats on, or in branches and submerged logs. In river channels with unstable substrates, the logs and snags provide the primary site for hydropsychid nets (Benke *et al.,* 1979).

Another mode of association with wood is its utilization as a substrate for attachment or emergence. Many Trichoptera pupate on the surface or bore into the wood. Several taxa, as noted, were abundant enough to exhibit a clear preference for this habitat. For example *Neothremma* pupae were collected in densities of 10 per cm^2 and *Lepidostoma quercina* Ross utilized grooved wood for pupation at densities up to 10 per 100 cm^2. Several families of Diptera, especially Tipulidae will also bore into punky, saturated wood for pupation. A wide variety of species use emergent wood as a substrate for crawling out of the water to emerge as terrestrial adults. Chloroperlid stoneflies and *Ameletus* mayflies are examples of taxa that appear to favor wood over mineral substrates.

CONCLUSIONS

In aquatic habitats there is a continuum of faunal associations on wood debris ranging from obligate restriction to purely opportunistic use of wood as a substrate. There is also a sequence of colonists that parallel the stage of wood decay. New wood entering a stream will be used primarily as habitat, although species such as the midge *Brillia* will mine the cambial and phloem tissue. Wood is then colonized by an algal-microbial community, providing food for collectors and grazers, but this feeding will not significantly affect the wood structure. Fungal invasion of the superficial layer softens the wood to the extent that it may be abraded and ingested by scrapers. More important though, at this stage it becomes suitable for obligate wood gougers and the more generalized shredders, such as limnephilid caddisflies and filipalpian stoneflies, which ingest wood and mycelia. This activity partly results in a more sculptured surface texture providing habitat for many taxa. Continued fungal invasion (over years or decades) into the wood matrix will soften wood tissue and allow some oxygen percolation. Borers that colonize the internal matrix speed the degradation process both by feeding and transport of microbial inocules. In the final phases of decay, detritivores, such as annelid worms, penetrate the material and continued decomposition is then very similar to that occurring in soil or damp terrestrial habitats.

The above scenario will apply to sound wood entering small streams with minimal disturbance. Much of the material is conditioned by fungi and by terrestrial organisms prior to the entry of wood into water. This may shorten the degradation process by allowing more rapid internal colonization by aquatic microbes and invertebrates. During periods of high water, and in larger streams, this process may be attenuated. Physical abrasion will remove soft tissue and stream power will convey wood downstream or deposit it out of the stream channel. Except in small headwater streams or backwater regions, rotting wood will not maintain enough structural integrity to provide a substrate for aquatic invertebrates during the final stages of decomposition. Consequently, the community of invertebrates associated with woody debris, and in turn their role in processing this material, is dependent on these factors which define habitat suitability.

ACKNOWLEDGEMENTS

We gratefully acknowledge the insect identifications provided by H. P. Brown, University of Oklahoma; G. W. Byers, University of Kansas; W. P. Coffman, University of Pittsburgh; D. R. Oliver, M. E. Roussel, and H. J. Teskey, Biosystematics Research Institute, Ottawa; G. L. Peters and L. K. Russell, Oregon State University; and G. B. Wiggins, Royal Ontario Museum, Toronto.

For field and laboratory assistance in sorting material we thank Preston Newman, Christine Pereira, Lin Roberts, and Bill Rosen. Don Krueger provided material from Wisconsin that was very useful to the survey. Editorial comments from Carla D'Antonio were appreciated. Acknowledgement is given to the Santa Cruz Island Company and the University of California for access to the Santa Cruz Island Reserve.

This study was supported by the National Science Foundation, Grant No. DEB 78-10594 and 80-22190. Research on the fauna of Mt. St. Helens streams was conducted under a Cooperative Agreement with the U.S. Forest Service, No. PNW-80-277.

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Table 1. Taxa of invertebrates classed as CLOSELY ASSOCIATED with wood debris in aquatic habitats.

	WA Olym	OR CoRa	OR WeCA	OR-CA SiSr	CA Redw	CA SoCo	OR EaOR	I-W-C RoMt	Habitat	Wood Type	Assoc.	Comments
Number of Sites	20	50+	50+	40	12	20	50	50				
EPHEMEROPTERA												
Heptageniidae												
Cinygma (integrum)	0	C,LA	C	0	C,LA	---	LC	LC	H,M,(L)	1,2,3	2,3	
TRICHOPTERA												
Brachycentridae												
Micrasema	0	C,LA	C,LA	LC	LA	LC	LC	---	H,M	2,3	(2)3,4	Pupation in soft wood; feeding?
Calamoceratidae												
Heteroplectron californicum	---	C,LA	C	0	C,LA	---	LA	---	H,M(L)	2,3	1,2,3,4	Larvae in twig case; late instars and pupae sometimes in logs
Lepidostomatidae												
Lepidostoma unicolor	---	C	C	---	0	C	0	LC	H,M	2,3	2(3)4	Case; pupation in grooves
L. quercina	---	C,LA	---	---	---	---	---	---	---	2,3	2(3)4	Pupation in soft wood
L. roafi	---	---	C	C	---	---	0	---	H	2,3	2(3)4	Pupation
Limnephilidae												
Amphicosmoecus canax	---	---	---	---	---	---	R	0	H	2,3	1,2,4	In twig case; also in logs
Cryptochia	---	C	0	---	---	---	---	0	H	2(3)	(2)3	Case
Glyphopsyche (irrorata)	---	---	---	0	---	---	---	---	H	2	2,3	Case
Halesochila taylori	---	0	0	---	---	---	---	---	H	2(3)	?	Case
Homophylax	---	---	---	---	---	---	---	LC	H	2	2	Case
Hydatophylax hesperus	---	C,LA	0	0	---	---	0	---	H,M	2,3	2	Case
Onocosmoecus	---	C	0	---	---	---	0	---	---	2,3	2	Case
Psychoglypha	---	C	C	---	---	---	C	C	H,M,L	1,2,3	2	Case; prob. gouging
Neothremma	---	C	C	---	LA	0	0	LC	M	1,2,3	(3)4	Pupate in aggregations, pupae bore into soft wood.
Polycentropodidae												
Polycentropus	---	0	0	---	---	---	0	---	H,M,L	2,3	(2)4,5	Net attachment in grooves; also lentic

Table 1. Continued (pg 2)

	WA Olym	OR CoRa	OR WeCA	OR-CA SiSr	CA Redw	CA SoCo	OR EaOR	I-W-C RoMt	Habitat	Wood Type	Assoc.	Comments
Rhyacophilidae												
Rhyacophila acropedes group	C	C	C	C	0	---	LC	LA	H,M	(1),2,3 1,2,3	(2)4,5	Under bark and in crevices
COLEOPTERA												
Elmidae												
Lara avara	LC	C,LA	C,LA	LC	0	---	LC	0	H,M(L)	(1),2,3	2	Gouging; larvae
Psephenidae												
Acneus	0	C	0	---	---	---	---	---	H	1,2	3,4	Scraping, larvae
Lucanidae Sinadendron	---	0	---	---	---	---	---	---	H	3	1	Semiterrestrial; larv.(+ad.?)
Melasidae Fornax	---	---	R	---	---	---	---	---	H	3	1	Semiterrestrial; larvae
Oedemeridae Ditylus quadricollis	---	0	0	---	---	---	---	---	H	3	1	Semiaquatic; larvae, adults
Ptilodactylidae Anchycteis	---	0	0	---	---	---	---	---	H	3	1	Boring in soft wood; larvae
DIPTERA												
Axymyiidae Axymyia	---	R	R	---	---	---	---	---	H	2,3	1	Deep in alder and red cedar

Chironomidae - Incomplete; identified genera with wood in gut include: Brillia, Limnophyes*, "Orthocladius B"**, Eukiefferiella, Paraphaenocladius, Phaenopsectra, Glyptotendipes, Polypedilum (Polypedilum), Polypedilum (Pentapedilum), Stenochironomus (see Table 3).

* - Orthocladiinae nr. Limnophyes or Tokunagaia; ** - Orthocladiinae n.gen. cf. acutilabis.

	WA Olym	OR CoRa	OR WeCA	OR-CA SiSr	CA Redw	CA SoCo	OR EaOR	I-W-C RoMt	Habitat	Wood Type	Assoc.	Comments
Empididae Hemerodromia	0	0	0	---	---	---	---	---	H	(2)3	4,5	Pupation
Weidemannia	---	---	0	---	---	---	---	0	H,M	(2)3	4,5	larvae in alder

Table 1. Continued (pg. 3)

	WA Olym	OR CoRa	OR WeCA	OR-CA SiSr	CA Redw	CA SoCo	OR EaOR	I-W-C RoMt	Habitat	Wood Type	Assoc.	Comments
Mycetophilidae												
Symmerus	LC	LC	LC	---	---	---	LC	---	H,M	3	1	Semi-aquatic; bore in alder & maple
Unknown genera	---	0	---	---	---	---	---	---	H	3	1(?)	
Pachyneuridae												
Cramptonomyia spenceri	---	---	R	---	---	---	---	---	H	3	1	Semi-terrestrial; bore in alder
Pelecorhynchidae												
Glutops	---	---	R	---	---	---	---	---	H	3	1,4	Semi-aquatic, bore in alder
Sciaridae												
Unknown genus	---	LC	LC	---	---	LC	---	---	H	3	1	Semi-aquatic
Stratiomyidae												
Myxosargus	---	---	---	---	---	R	R	---	H	3	1	Bore just under surface
Syrphidae												
Pocota	---	0	---	---	---	---	---	---	H,M	3	1	Bore in very soft wood
Sphegina	---	---	R	---	---	---	---	---	H	3	1	
Xylota	---	0	---	---	---	---	---	---	H	3	1	
Tipulidae												
Austrolimnophila	---	C	C	LC	---	---	LC	---	H	2,3	1	Semi-aquatic
Limonia prob. defuncta	---	---	---	---	---	---	R	---	H	2,3	1	Mainly in alder
Lipsothrix fenderi	C	C	C	---	---	---	---	---	H	3	1	
L. hynesiana	---	---	---	---	0	---	---	---	H	3	1	
L. nigrilinea	---	C	C	---	---	---	R,LC	---	H,M	3	1	Mainly in alder, to ca. 2 cm
L. shasta	---	---	---	0	---	---	---	---	H	3	1	
Tipula spp.	---	C	C	---	---	---	0	0	H,M	3	1,4	Boring, pupation
Xylophagidae												
Xylophagus	LC	LC	LC	---	---	---	---	---	H,M	3	1,5	Larvae and pupae in wood
ANNELIDA												
OLIGOCHAETA												
Lumbricidae												
Dendrodrilus rubidus	?	C	C	?	---	---	---	---	H,M	3	1	In very decayed wood

Table 2. Taxa of invertebrates classed as FACULTATIVELY ASSOCIATED with wood debris in aquatic habitats.

	WA Olym	OR CoRa	OR WeCA	OR-CA SiSr	Ca Redw	Ca SoCo	OR EaOR	I-W-C RoMt	Habitat	Wood Type	Assoc.	Comments
EPHEMEROPTERA												
Baetidae												
Baetis spp.	A	A	A	LA	C	LA	LA	LA	H,M,L	1,2	3,4	
Callibaetis	---	C	LA	---	---	C	LC	---	---	1,2	(3),4	Lentic
Ephemerellidae												
Ephemerella spp.	0	C	A	0	0	LA	C	C	H,M,L	1,2	(2),3,4	
E. doddsi	C	0	C	---	---	---	---	0	H,M	1	(2),3	
E. hecuba	---	---	---	---	---	---	0	0	H,M,L	2	3,4	
E. spinifera	0	0	0	---	---	---	---	---	H,M	1	4,5	
Heptageniidae												
Epeorus spp.	C	C	C	0	---	---	0	C	H,M,L	1,2	2,3	
Heptagenia	---	---	---	---	---	---	LC	C	H,M	1,2	3	
Cinygmula	0	C	C	0	C	---	---	C	H,M	1,2	3	
Rhithrogena	---	0	0	---	---	---	---	---	H,M	1	3	
Leptophlebiidae												
Paraleptophlebia	0	C	C	0	LC	0	C	C	H	1,2,3	2,3,4	
Siphlonuridae												
Ameletus	0	C	LA	---	---	---	0	C	H	1,2	(2),3,(4)	Lentic, emergence
Siphlonurus	---	0	---	---	---	---	0	---	---	1,2	(3),4	Lentic
PLECOPTERA												
Capniidae and Leuctridae	0	C	C	C	0	LC	LC	0	H,M	1,2	(2),4	
Chloroperlidae	LA	C	LA	0	0	LC	0	C	H,M,L	1,2,(3)	4,5	*Alloperla* (s.l.)
Perlidae	C	C	C	C	C	LC	C	C	H,M,L	2,3	4,5	
Perlodidae	0	0	C	0	0	---	LC	0	H,M	2(3)	5	
Nemouridae	LA	?	?	LC	0	LA	LC	C	H,M,L	1,2,3	2,3,4	
Nemoura spp.	LA	?	?	LC	0	LA	LC	C	H,M,L	1,2,3	2,3,4	Sensu latu
Zapada	C	C	C	---	---	---	---	---	H,M	1,2,3	2,3,4	
Malenka	C	C	C	---	---	---	---	---	H,M	1,2,3	2,3,4	
Soyedina	---	?	?	LA	---	---	---	---	H	2	---	Also temporary streams
Peltoperliidae												
Soliperla	---	---	0	0	---	---	---	---	H	2	2,4	
Yoraperla	C	C	C	0	0	---	LC	LC	H	2,3	2,4	
Pteronarcidae												
Pteronarcella	---	0	0	0	---	---	---	0	H,M	2,3	2,4	
Pteronarcys	---	0	0	---	---	---	0	---	M	2,3	2,4	
TRICHOPTERA												
Brachycentridae												
Brachycentrus	---	---	LC	---	---	---	0	LC	M,L	1,2	(3),4	Pupation
Glossosomatidae	0	C	C	0	0	---	---	LC	S,M,L	1	(2),3	Pupation

Table 2. Continued (pg. 2)

	WA Olym	OR CoRa	OR WeCA	OR-CA SiSr	Ca Redw	Ca SoCo	OR EaOR	O-W-C RoMt	Habitat	Wood Type	Assoc.	Comments
TRICHOPTERA (Cont.)												
Helicopsychidae												
Helicopsyche	---	---	---	---	---	---	LA	LA	S,M	1,2	3	Pupation
Hydropsychidae												
Arctopsyche grandis	---	0	0	---	---	---	---	LC	S,M	2	4	Retreat Net attachment
Homoplectra	---	---	R	---	---	---	---	---	S	2	4	" "
Hydropsyche	C	LA	LA	LC	LC	LA	LA	LC	S,M,L	1,2,3	4	" " Oviposition
Parapsyche	---	---	---	---	---	---	---	0	S	2	4	
Hydroptilidae												
Hydroptila	---	---	---	---	---	---	0	---	S	1,2	3,4	Pupation
Ochrotrichia	---	---	---	---	---	---	LC	0	S,M	2	3,4	Pupation
Paleagapetus	---	---	R	---	R	---	---	---	S	2	3,4	In moss
Lepidostomatidae	---	---	---	---	LC	---	0	0	S,M	2	2,4	Species un- determined
Leptoceridae												
Oecetis	---	---	---	---	---	LA	---	---	S,M	1,2	4,5	
Limnephilidae												
Apatania	---	LC	0	LA	LA	---	LC	LC	S,M	2	(3),4	Pupation
Asynarchus	---	---	---	---	---	---	---	0	S	2	2,4	Pupation
Chyranda	---	0	---	---	---	---	0	0	S	2	2,(3)	
Dicosmoecus	---	LC	C	---	---	---	0	---	(S),M,L	1,2	(3),4	Pupation in aggregations
Ecclisocosmoecus	0	0	---	---	---	---	---	---	S,M	1,2	2	
Ecclisomyia	LA	C	0	---	---	---	0	LC	S,M,L	1,2	2,3	
Goeracea	0	0	0	---	---	---	---	---	S	2	3	
Neophylax	---	C	0	---	---	---	0	0	S,M	1,2,3	2,3,4	Pupation
Philopotamidae	---	C	C	---	---	---	---	0	S,M	2	4	Net attachment
Psychomyiidae												
Tinodes	---	---	---	---	---	LC	---	---	S,M	2	3,4,5	Tubes built in grooves
Rhyacophilidae												
Rhyacophila spp.	0	0	C	0	0	0	0	C	S,M	1,2,3	(2),4,5	grandis, hyalinata gr, rotunda gr., betteni gr. arnaudi; verrula
Sericostomatidae												
Gumaga	---	---	---	---	---	LA	---	---	S,M	2	(3),4	Pupation

Table 2. Continued (Pg. 3)

	WA Olym	OR CoRa	OR WeCA	OR-CA SiSr	CA Redw	CA SoCo	OR EaOR	I-W-C RoMt	Habitat	Wood Type	Assoc.	Comments
COLEOPTERA												
Amphizoidae												
Amphizoa	0	---	0	---	---	---	LC	0	H,M	2,3	4,5	Larvae & adults
Dryopidae												
Helichus striatus	---	---	---	---	---	---	0	0	Lentic	2	3,4	Adults in beaver ponds
Elmidae												
Cleptelmis ornata	---	0	---	---	---	---	LC	0	H,M,L	2	3,4	Adults
Heterolimnius	---	0	0	LA	---	---	LC	LA	H,M	2,3	3,4	Larvae & adults
Optioservus	---	C	---	---	0	---	LC	LC	H,M	1,2,3	3,4	Larvae & adults
Helodidae	---	0	---	---	0	LC	---	---	H	?	?	Also tree holes
Hydraenidae												
Hydraena vandykei	---	0	0	0	---	---	LC	---	H,M	2	3,4	Adults
Psephenidae												
Eubrianax edwardsi	---	---	---	0	---	0	0	---	H,M	1,2	2,3,4	Larvae
Tenebrionidae	---	R	---	---	---	---	---	---	H	2	1	Larvae, semi-terr.
DIPTERA												
Cecidomyiidae	LC	LC	LC	---	---	---	---	0	H	2,3	4	
Ceratopogonidae												
Bezzia	---	C	C	---	---	---	0	---	H	3	4,5	
Chironomidae - (currently 50+ genera from wood substrates; see Table 3)												
Dixidae												
Dixa	C	C	C	C	C	C	C	C	H,M	1,2,3	4	Wood-water interface
Empididae	---	0	0	---	---	---	---	0	H	2,3	4,5	In soft wood
Psychodidae												
Pericoma	---	C	0	---	---	---	C	C	H,M	2,3	2,3,4	Also lentic Pupation
Simuliidae	C	C	C	C	C	C	C	C	H,M,(L)	1,2,(3)	(3),4	Attachment for feeding; pupation
Stratiomyiidae	---	---	R	---	---	---	---	R	H	2	3,4	In crevices
Thaumaleidae												
Thaumalea	---	---	---	---	---	---	0	0	H	2	3,4	Wood-water interface
Tipulidae												
Antocha	0	C	C	---	---	---	0	0	H,M	2	3,4	
Dicranota	---	C	C	---	---	---	0	0	H,M	2,3	(2),5	In crevices
Limonia	0	C	C	---	---	---	0	---	H	3	1,4	Also semi-aquatic and lentic
Limnophila	---	0	---	---	---	---	---	---	H	3	(1),4	Semi-aquatic
Molophilus	---	0	---	---	---	---	---	---	H	3	(1),4	Semi-aquatic
Ormosia	---	C	C	---	---	---	---	0	H	3	(1),4	Semi-aquatic

Table 2. Continued (pg. 4)

	WA Olym	OR CoRa	OR WeCA	OR-CA SiSr	CA Redw	CA SoCo	OR EaOR	I-W-C RoMt	Habitat	Wood Type	Assoc.	Comments
Tipulidae (Cont.)												
Pedicia	---	C	C	---	---	---	---	---	H,M	3	4,5	
Ulomorpha	---	---	O	---	---	---	---	---	H	3	(1),4	
ACARINA	C	C	C	C	C	C	C	C	H,M	1,2,3	3,4,5	Includes both aquatic and semi-aquatic
ISOPODA												
Ligidium	O	C	C	C	C	O	---	---	H	2,3	2,3,4	
AMPHIPODA												
Hyallela	---	---	LA	LC	---	---	LA	LA	---	2	3,4	Lentic
Gammarus	---	---	---	---	LC	---	---	---	H	2	(2),3,4	
TURBELLARIA												
Dugesia	C	C	C	C	C	C	C	C	H	1,2,3	4,5	
PELECYPODA												
Sphaeriidae	---	O	O	---	---	---	---	---	H	2,3	4	
GASTROPODA												
Ancylidae-Ferrissia	---	O	---	---	---	---	---	---	H	1	3	
Limnaeidae-Lymnaea	---	---	---	LC	---	---	---	LC	---	1,2	3	Lentic
Physidae-Physa	---	O	O	LC	---	C	LA	LC	H	1,2	3	Also lentic
Planorbidae	---	---	O	---	---	---	O	LC	H,M	1,2	3	Also lentic
Pleuroceridae-Juga	---	A	C	C	O	---	---	---	H,M	1,2,3	2,3	

Table 3. Genera of Chironomidae collected from wood debris in the western States.

Tanypodinae

- *Macropelopia*
- *Procladius*
- *Labrundinia*
- *Larsia*
- *Paramerina*
- *Pentaneura*
- *Thienemannimyia* gr.
- *Zavrelimyia*

Podonominae

- *Boreochlus*

Diamesinae

- *Diamesa*
- *Pagastia*
- *Pseudodiamesa*

Orthocladiinae

- *Brillia*
- *Chaetocladius*

Orthocladiinae (cont.)

- *Corynoneura*
- *Cricotopus* (*Isocladius*)
- *Eukiefferiella*
- *Heterotrissocladius*
- *Hydrobaenus*
- *Limnophyes*
- *Metriocnemus*
- *Microcricotopus*
- *Nanocladius*
- *Orthocladius* (*Euorthocladius*)
- cf. nr. *Paracladius*
- *Parakiefferiella*
- *Parametriocnemus*
- *Paraphaenocladius*
- *Paratrichocladius*
- *Parorthocladius*
- *Psectrocladius*
- *Rheocricoptopus*

Orthocladiinae (cont.)

- *Synorthocladius*
- *Thienemanniella*
- *Tvetenia*
- Unk. gen. (nr. *Limnophyes* or *Tokunagaia*)
- New gen. (nr. *O.* *acutilabis*)

Chironominae

- *Chironomus*
- *Cryptochironomus*
- *Dicrotendipes*
- *Microtendipes*
- *Parachironomus*
- *Paratendipes*
- *Phaenopsectra*
- *Polypedilum*
- *Stenochironomus*
- *Cladotanytarsus*
- *Micropsectra*

Table 3. Continued (Pg. 2)

Chironominae (cont.)
Rheotanytarsus
Stempellinella
Tanytarsus

Table 4. Comparison of faunal diversity in benthos samples and on wood substrates in streams near Mt. St. Helens four months after the May, 1980 eruption. Chironomidae, the dominant group, are only identified at the Family level.

	No. of Invertebrate Taxa			
	Benthos	Wood	Total	Channel Condition
Ape Canyon	5	<5	5	Sluiced by mudflow; heavy deposit of ash and pumice; minimal wood debris.
Muddy River	4	2	5	Sluiced by mudflow; unstable, shifting channel; minimal wood debris.
Upper Clearwater Cr.	11	23	25	Heavy imput of blast deposits; channel with 30-70 cm of ash, and large amount of downed timber.
Middle Clearwater Cr.	26	15	30	Heavy ashfall plus blast deposits transported from upstream; several debris dams formed by downed logs.
Lower Clearwater Cr.	28	29	45	Moderate amount of organic debris and mineral sediments transported from upstream; typical component of in-stream wood debris.
Elk Creek	55	46	68	Heavy ashfall (15-25 cm); typical component of in-stream wood debris.
Lake Creek	65	40	71	Control site (light ashfall); boulder-cobble substrate and normal component of wood debris.