

Relation of headwater macroinvertebrate communities to in-stream and adjacent stand characteristics in managed second-growth forests of the Oregon Coast Range mountains¹

Michael B. Cole, Kevin R. Russell, and Todd J. Mabee

Abstract: Although headwater streams constitute a significant portion of stream length within watersheds, their aquatic fauna, contributions to regional biodiversity, and responses to forest management have been understudied. Macroinvertebrate communities, physical habitat, and water chemistry were sampled from 40 headwater streams in managed forests in the Oregon Coast Range mountains. We characterized functional and structural attributes of macroinvertebrate communities in relation to physical, chemical, and biological gradients. Substrate composition, specific conductance, and riparian forest age showed the strongest correlations with resultant ordination patterns in macroinvertebrate community composition. Among individual metrics of community structure and composition, total macroinvertebrate density and dominance by three taxa showed the strongest correlations with forest age. No community measures were related to densities of torrent salamanders (*Rhyacotriton kezeri*) or crayfish (*Pacifastacus leniusculus*), suggesting these potential predators had little influence on overall macroinvertebrate community structure. Rare taxa were sampled from several reaches, including *Rhyacophila* probably *viquaea* for which little information is available, and an *Eobrachycentrus* sp., previously known to occur only in the Cascade mountains. Headwater streams within these managed forests of north-western Oregon appear to be taxa rich, continue to support taxa limited to headwater streams, and harbor taxa about which little is known.

Résumé : Malgré que les ruisseaux de tête constituent une portion significative de la longueur des ruisseaux dans un bassin hydrographique, on a peu étudié leur faune aquatique, leur contribution à la biodiversité régionale et leur réponse à l'aménagement. Les communautés de macroinvertébrés, le milieu physique et la chimie de l'eau ont été échantillonnés dans 40 ruisseaux de tête en forêt aménagée dans la chaîne côtière de l'Oregon. Nous avons caractérisé les attributs fonctionnels et structuraux des communautés de macroinvertébrés en relation avec des gradients physiques, chimiques et biologiques. La composition du substrat, la conductivité spécifique et l'âge de la forêt riveraine ont montré les plus fortes corrélations avec les axes principaux d'ordination des communautés de macroinvertébrés. Parmi les métriques individuelles de structure et de composition des communautés, la densité totale de macroinvertébrés et la dominance de trois taxons ont montré les plus fortes corrélations avec l'âge de la forêt. Aucune mesure de communauté n'était reliée à la densité des salamandres des torrents (*Rhyacotriton kezeri*) ou des écrevisses (*Pacifastacus leniusculus*), ce qui suggère que ces prédateurs potentiels ont peu d'influence sur la structure globale des communautés de macroinvertébrés. Des échantillons de plusieurs biefs contenaient des taxons rares, incluant *Rhyacophila* probably *viquaea*, une espèce peu connue et un individu de *Eobrachycentrus* sp., une espèce auparavant considérée comme inféodée à la chaîne des Cascades. Les ruisseaux de tête dans ces forêts aménagées du Nord-Ouest de l'Oregon semblent être riches en taxons, continuent de supporter des taxons limités aux ruisseaux de tête et abritent des taxons peu connus.

[Traduit par la Rédaction]

Introduction

Headwater streams are important functional components of lotic ecosystems, delivering water, sediment, and organic

material to downstream reaches (Meyer and Wallace 2001; Gomi et al. 2002). Because these small channels constitute a significant proportion of stream length within watersheds (Sidle et al. 2000), headwater streams potentially provide

Received 11 June 2002. Accepted 19 February 2003. Published on the NRC Research Press Web site at <http://cjfr.nrc.ca> on 8 July 2003.

M.B. Cole² and T.J. Mabee. ABR, Inc., Environmental Research and Services, P.O. Box 249, Forest Grove, OR 97116, U.S.A.
K.R. Russell.³ Willamette Industries, Inc., P.O. Box 488, Dallas, OR 97338, U.S.A.

¹This paper was presented at the symposium Small Stream Channels and Riparian Zones: Their Form, Function and Ecological Importance in a Watershed Context, held 19–21 February 2002, The University of British Columbia, Vancouver, B.C., and has undergone the Journal's usual peer review process.

²Corresponding author (e-mail: mcole@abrinc.com)

³Present address: College of Natural Resources, University of Wisconsin, Stevens Point, WI 54481, U.S.A.

important habitats for unique and diverse assemblages of aquatic fauna (Dieterich and Anderson 1995; Muchow and Richardson 2000). Despite their numerical dominance and functional importance, however, headwater streams have received little attention when compared with higher order streams and rivers. Richardson (2000) cites the absence of fish from headwater systems as the primary reason these channels have been understudied by researchers and aquatic resource managers.

Recognition that riparian zones play critical roles in maintenance of biodiversity (Naiman et al. 1993), and specifically maintenance of aquatic biota (Mahoney and Erman 1984; Richardson 1992), has focused increased attention on riparian forest management and effects of timber harvest on these areas (Hibbs and Chan 1991; Pabst and Spies 1999; Brinson et al. 2002). Although studies of forest management effects on aquatic biota historically have focused on fish (Richardson 2000), recent interest in the status of aquatic amphibians considered sensitive to timber harvest in the Pacific Northwest (e.g., Diller and Wallace 1996; Wilkins and Peterson 2000) has highlighted the need to better characterize biota of forested headwater streams. To date, however, few studies have investigated macroinvertebrate communities in coastal Pacific Northwest headwater systems (Haggerty et al. 2002; Wipfli and Gregovich 2002) and we are unaware of any published studies that characterize benthic macroinvertebrate communities or habitats within headwater streams in the Oregon Coast Range mountains.

Maintaining diverse and properly functioning headwater stream macroinvertebrate communities in managed forests first requires characterizing (i) the baseline patterns of community composition in these systems, (ii) the ways in which these communities relate to physical, chemical, and biological conditions, and (iii) the ways in which forest management practices potentially alter these communities. Previous work has shown that both the function and composition of macroinvertebrate communities in larger stream systems are influenced by timber harvest. Timber harvest and related activities (e.g., logging roads) can increase sediment inputs to streams, thereby altering substrate characteristics and channel morphology, which in turn are related to reductions in macroinvertebrate diversity (Lenat et al. 1981; Waters 1995; Quinn et al. 1997). Removal of riparian canopy and attendant increases in solar radiation can increase water temperatures and alter thermal regimes critical to the life history and ecology of macroinvertebrates (Vannote and Sweeney 1980; Murphy et al. 1981; Wallace et al. 1988). The input of nutrients from terrestrial sources may interact with increased light availability and stream temperature to enhance in-stream primary productivity, resulting in changes to the structure of macroinvertebrate and other aquatic communities (Murphy et al. 1981; Hawkins et al. 1983; Murphy 1998). Structural changes in macroinvertebrate communities following removal of riparian vegetation may include reductions in shredder abundance and increases in scraper abundance in response to these shifts in energy and nutrient inputs (Stout et al. 1993). However, we still lack even baseline information regarding headwater stream macroinvertebrate communities in the Pacific Northwest (Muchow and Richardson 2000), including the current status of these com-

munities within managed forests, their relationships with biotic and abiotic habitat attributes, and how these communities respond to forest management practices.

In this study, we investigated the composition and habitat relationships of headwater stream macroinvertebrate communities within managed forests of the Oregon Coast Range mountains. Our primary objectives were to (i) characterize baseline structural and functional attributes of macroinvertebrate communities within these managed headwater stream systems, (ii) determine whether macroinvertebrate community characteristics were related to both biotic and abiotic attributes of streams and adjacent riparian forests, and (iii) examine the influence of predators on community structure relative to other factors. By structural composition of macroinvertebrate communities, we mean richness, density, and relative abundance of taxa or groups of taxa, relative abundance of sensitive and tolerant organisms, and other community attributes that characterize the structure of benthic communities. By functional composition, we mean the relative abundance of the primary functional feeding groups occurring in these headwater systems.

Methods and materials

Study area

Our study was conducted on private second-growth timber lands on the western slopes of the Coast Range mountains in Clatsop and Tillamook counties, northwestern Oregon. Most of this property lies within 39 km of the coast. Two vegetation zones, Sitka spruce (*Picea sitchensis* (Bong.) Carrière) and western hemlock (*Tsuga heterophylla* (Raf.) Sarg.), occur within the study area (Franklin and Dyrness 1973). Sitka spruce dominates the narrow (5–15 km) fog belt along the Pacific Ocean. Inland of the spruce zone lies the western hemlock zone, representing an east–west gradient of western hemlock near the coast to Douglas-fir (*Pseudotsuga menziesii* (Mirb.) Franco) at more inland sites.

Large-scale timber harvesting in the study area began in the early to mid-1900s when entire drainages were clear-cut from the coast inland. The study area currently is composed of 0- to 80-year-old second- and third-growth stands of Douglas-fir, western hemlock, and Sitka spruce regenerated naturally (pre-1950s) or artificially. Conifers of minor abundance include western red cedar (*Thuja plicata* Donn ex D. Don), grand fir (*Abies grandis* (Dougl. ex D. Don) Lindl.), and noble fir (*Abies procera* Rehd.). Hardwoods, including bigleaf maple (*Acer macrophyllum* Pursh) and red alder (*Alnus rubra* Bong.) also are significant stand components. Dominant plants in the shrub layer include ocean spray (*Holodiscus discolor* (Pursh) Maxim.), vine maple (*Acer cirinatum* Pursh), red huckleberry (*Vaccinium parvifolium* Smith), rhododendron (*Rhododendron macrophyllum* D. Don ex G. Don), young red alder, sword fern (*Polystichum munitum* Kaulfuss), and salal (*Gaultheria shallon* Pursh). Historically, headwater streams in the study area received no riparian protection (pre-1972 Oregon Forest Practices Act). Current protection along perennial headwater streams in the study area includes equipment exclusion zones and retention of all understory vegetation and non-

merchantable conifers (<15 cm diameter) within 3 m of the high water level on each side of the stream.

Elevations across the study area range from 5 to 780 m. Geology is dominated by two major divisions of lithology: basalt and marine sediment (Franklin and Dyrness 1973). The area's bedrock is of marine basalt origin overlain with marine sediments. Layers of sandstone, siltstone, and clay vary in thickness from 1 to >30 m. Surficial geology is a complex matrix of uplifted marine sediment with outcroppings of volcanic rock. Outcrops of loose surface basalt are present in many portions of the study area, and bedrock basalt is close to the surface at higher elevations. The Pacific Ocean creates a cool, seasonally wet climate across the study area. Mean annual precipitation ranges from 90 cm at inland sites to 380 cm along the coast (Taylor 1993). Most rain falls between October and May, with significant snow accumulation common above 500 m. Peak flow in the extensive network of rivers and streams across the study area coincides with the winter storm season (November to February). Minimum and maximum temperatures average 0°C in January and 25°C in August, respectively (K.R. Russell et al., in review⁴).

Field sampling

We sampled macroinvertebrates from 40 first-order streams in June and July 2001. Streams were randomly selected from a larger pool of 119 streams randomly selected from across the study area in conjunction with a study of Columbia torrent salamanders (*Rhyacotriton kezeri* (Gage) Good and Wake; K.R. Russell et al., in review⁴). The origin of each stream was first located and then the stream was partitioned into low (0–5°), medium (6–10°), and high gradient (≥15°) segments prior to sampling to control for gradient effects on torrent salamanders (Diller and Wallace 1996; Wilkins and Peterson 2000). If available, two 10-m segments of each of three gradient classes (up to six segments per stream) were randomly selected for physical, chemical, and biological sampling.

Macroinvertebrate samples were collected within each segment prior to sampling for physical conditions, water chemistry, and torrent salamanders. Composites of two Surber samples of macroinvertebrates (total area = 0.18 m², 500-µm mesh) were collected from randomly selected locations within each sample segment to produce a sample representative of the occurrence of macroinvertebrates within the segment. Composite macroinvertebrate samples were placed into 1-L polyethylene bottles and preserved in isopropyl alcohol for later laboratory sorting and identification.

Canopy closure was estimated at the lower and upper ends of each segment with a spherical densiometer read at the four cardinal directions and converted to percent canopy cover. We measured water temperature, dissolved oxygen, and conductivity with a YSI Model 85 water chemistry meter (YSI Incorporated, Yellow Springs, Ohio) and recorded pH (nearest 0.01, Oakton pH Testr 3 (Construction Safety Products Inc., Shreveport, La.). In each segment, we tallied large woody debris (≥10 cm diameter and ≥2 m long) and

small woody debris (<10 cm diameter and <2 m long) that broke the vertical plane of the bank-full channel (Wilkins and Peterson 2000). We established a 100 m² (10 × 10 m) riparian plot immediately adjacent to and centered on both sides of each segment, and visually estimated percent cover of exposed soil, woody and herbaceous ground cover, understory shrubs and trees (conifer and hardwood), and overstory canopy (conifer and hardwood) within each plot (Wilkins and Peterson 2000).

In each segment, we also sampled up to six cross-stream microhabitat transects. Transects were located at 2-m intervals and perpendicular to the flow of water. Each transect was assigned to one of four habitat types: cascade, riffle, run, or pool (modified from Platts et al. 1983; Diller and Wallace 1996). Channel dimensions (wetted width, depth profile, bank-full width, bank-full height) were recorded at each transect. Streambed substrate composition was measured by performing size tallies along each transect ($n \leq 90$ per segment, $n \leq 540$ per reach). At each of 15 equally spaced locations on each transect, the substrate type (bedrock, boulder, cobble, coarse gravel, fine gravel, sand, fines, and wood) first touched by a finger placed into the water was recorded. Torrent salamander and crayfish searches were performed at the same time that physical habitat data were collected. Detailed accounts of torrent salamander and crayfish search techniques employed for this study are provided elsewhere (K.R. Russell et al., in review⁴).

Macroinvertebrate sorting and identification

Samples were sorted to remove a 500-organism subsample from each preserved composite sample using a Caton gridded tray (Caton 1991). Contents of the sample were first emptied onto the gridded tray and then floated with water to evenly distribute the sample material across the tray. Squares of material from the 30-square gridded tray were removed to a Petri dish, which then was placed under a dissecting microscope at ×7–10 magnification to sort aquatic macroinvertebrates from the sample matrix. Macroinvertebrates were removed from each sample until 525–550 organisms were counted, or until the entire sample had been sorted.

After sample sorting, macroinvertebrates other than Chironomidae were identified to the lowest practical level of taxonomic resolution. Aquatic insects were keyed using Merritt and Cummins (1996), Stewart and Stark (1993), Wiggins (1996), and a number of regional and group-specific keys. Non-insect taxa were keyed using Pennak (1989) and a number of regional treatments of particular macroinvertebrate groups.

Data analysis

Macroinvertebrate communities were examined using two approaches: (i) multivariate pattern analysis followed by indirect gradient analysis (Gauch 1982), and (ii) an array of metrics that describe the structural and functional composition of the sampled communities (Karr and Chu 1999). These metrics were also correlated with measured environmental variables. Multivariate analysis was performed at

⁴K.R. Russell, T.J. Mabee, and M.B. Cole. In Review. Distribution and habitat of Columbia torrent salamanders at multiple spatial scales in managed forest of northwestern Oregon. *J. Wildl. Manage.*

both stream segment and stream scales (i.e., segment data pooled by stream); metrics were calculated only from stream-scale data. Exploratory data analysis indicated that streams from which only two or three segments were sampled resulted in lower taxa richness than streams from which four or more segments were sampled. Because these differences are likely attributable to effects of unequal sampling effort (Carter and Resh 2001), we included only streams from which four or more segments were sampled in the analyses of stream-scale data ($n = 33$).

An array of metrics was calculated from stream-scale macroinvertebrate data to characterize structural and functional attributes of these communities. We used metrics that appropriately described the major aspects of and range in community structure present in the data. The relative abundance of functional feeding groups was also calculated for each stream. Taxa were classified as disturbance sensitive, sediment sensitive, sediment tolerant, and cold-water obligate using ecological attribute coding from Wisseman (unpublished data⁵). Taxa were classified as rare if no coding was available (i.e., absent from the taxa list) or if the taxon was determined to be rare by another source.

Multivariate analyses were performed in PC-ORD Version 4 statistical software using $\log_{10}(x + 1)$ transformed macroinvertebrate density data to reduce the influence of numerically dominant taxa (Krebs 1989). This type of transformation is useful when there is a high degree of variation within attributes (taxa, in the case of this study) or among attributes within a sample (McCune and Mefford 1999) and has previously been used on macroinvertebrate community data prior to performing multivariate analysis (e.g., Jackson 1993; Reece and Richardson 2000; Rempel et al. 2000; Zimmer et al. 2000). These logarithmic density data served as the raw data for all subsequent multivariate analyses in this study.

Rare taxa may introduce bias into data that prevents ordination techniques from extracting major patterns in community composition (Gauch 1982). For multivariate analyses, we omitted any taxa that occurred at only one site and that represented less than 0.5% of the total abundance in that sample and analyzed data with and without rare taxa. Excluding rare taxa from the data produced ordination patterns similar to those produced from the full data set, but resulted in improved correlation of environmental variables with ordination axes.

Data standardization also can improve multivariate analysis of community data (Jackson 1993). Therefore we analyzed both unstandardized data (e.g., Reece and Richardson 2000) and data standardized to relative abundance (standardized in relation to row totals; e.g., Ford and Rose 2000). Ordinations using data standardized to relative abundance also produced stronger correlations between ordination axes and environmental variables; only results using standardized data are presented here.

Nonmetric multidimensional scaling (NMS) was performed on both stream and segment scale data using the Sorenson (Bray–Curtis) distance measure and a minimum of 400 iterations. NMS, a nonparametric ordination technique,

was used because it assumes no underlying distribution of the data, is robust to data departures from normality, and therefore is suggested for use with ecological data (McCune and Mefford 1999). Environmental variables to be correlated with macroinvertebrate NMS ordinations were first checked for normality using normal probability plots and Kolmogorov–Smirnov normality tests. Data were then log or square-root transformed when necessary to achieve or better approximate normality. Environmental variables were then correlated with the resulting ordination axes to examine whether major patterns in community structure were correlated with measured physical or chemical gradients. The original macroinvertebrate data matrix also was correlated with the ordination axes to determine which taxa were most responsible for producing the major ordination patterns. No measured environmental variables were significantly correlated with the results of segment-scale NMS. Therefore, only results of the stream-scale NMS analysis are reported.

Finally, environmental variables that were significantly related to NMS axes were correlated using Spearman rank correlation coefficients with each of these metrics to examine relationships between environmental conditions and structural and functional attributes of macroinvertebrate communities. For all analyses, p values of correlation coefficients were considered significant at $\alpha < 0.01$. Torrent salamander and crayfish densities also were correlated with both NMS axes and macroinvertebrate community metrics to examine associations among biological components in these headwater systems.

Results

In the 33 streams with four or more sampled segments, gradient ranged from 5.2 to 29°, wetted width ranged from 0.4 to 3.4 m, and substrate composition ranged widely (Table 1). Mean age of riparian forests adjacent to stream reaches was 41.5 years (Table 1). Dissolved oxygen and conductivity in reaches averaged 84.4% and 57.1 $\mu\text{S}/\text{cm}$, respectively. Torrent salamanders averaged 1.3 individuals/ m^2 and ranged from 0.0 to 17.8 individuals/ m^2 . All crayfish collected from both visual searches and Surber samples were signal crayfish (*Pacifastacus leniusculus* Bott). Based on visual searches, *P. leniusculus* averaged 0.2 individuals/ m^2 in sample reaches, ranging from 0.0 to 0.9 individuals/ m^2 .

Macroinvertebrate community composition ranged widely among sampled streams. Taxa richness ranged from 31 to 59 and averaged 45 taxa per stream (Table 2). Across all 40 headwater streams, 83 insect and 18 non-insect taxa were collected. In the 33 streams used for analysis of macroinvertebrate communities, numerically dominant taxa included Sphaeriidae, Gammaridae, Orthocladinae, Tanytarsini, Oligochaeta, Ostracoda, the leuctrid *Moselia infuscata* (Claassen), the peltoperlid *Yoraperla brevis* (Banks), and Chloroperlidae. Total invertebrate densities averaged 2239 individuals/ m^2 and ranged from 190 to 7893 individuals/ m^2 .

Ephemeroptera, Plecoptera, and Trichoptera (EPT) richness ranged from 10 to 29, and averaged 19 taxa per stream (Table 2). Trichoptera exhibited the highest richness, averag-

⁵R.W. Wisseman. 1996. Benthic invertebrate monitoring and bioassessment in western montane streams. Version 1.0 taxa coding parameters. Aquatic Biology Associates, Corvallis, Ore. Unpublished.

Table 1. Mean, standard deviation, and range of environmental variables measured from Oregon Coast Range headwater streams sampled for macroinvertebrates with Surber samplers in June and July 2001 ($n = 33$).

Environmental variable	Mean	SD	Range
Physical			
Stand age (years)	41.5	12.0	3–62
Gradient (degrees)	11.2	4.9	5.2–29.3
Wetted width (m)	1.2	0.7	0.4–3.4
bank-full width (m)	1.6	0.6	0.6–3.4
Large wood tally	6.7	3.7	0.5–19.2
Woody riparian canopy cover (%)	69.5	14.6	2.9–90.8
Overhead canopy cover (%)	92.4	16.9	0.9–99.6
Bedrock (%)	1.3	4.6	0.0–25.0
Boulder (%)	1.0	1.6	0.0–6.7
Cobble (%)	8.8	6.5	0.0–23.7
Coarse gravel (%)	14.8	7.3	0.0–30.5
Fine gravel (%)	18.4	8.0	1.8–42.5
Sand (%)	11.6	7.3	1.2–37.3
Fines (%)	18.5	13.1	0.5–67.2
Hard pan (%)	0.5	1.1	0.0–5.0
Wood (%)	24.8	10.3	2.1–46.5
Sand and fines (%)	30.1	11.6	9.3–68.5
Cobble and coarse gravel (%)	23.7	12.1	0.0–45.5
Pool habitat (%)	5.6	7.2	0.0–28.1
Run habitat (%)	4.1	7.8	0.0–27.8
Riffle habitat (%)	60.8	19.2	30.0–100.0
Cascade habitat (%)	29.4	18.5	0.0–66.7
Temperature (°C)	10.4	1.4	7.5–14.2
Chemical			
DO (% saturation)	84.4	6.6	67.5–97.6
Specific conductance (µS/cm)	57.1	22.5	24.5–134.5
Predators			
<i>Pacifastacus leniusculus</i> (density)	0.24	0.27	0.00–0.94
<i>Rhyacotriton kezeri</i> (density)	1.31	3.55	0.00–17.79

Note: DO, dissolved oxygen.

ing 8.9 and ranging from 4 to 15 taxa per stream. Coldwater obligate taxa were common, averaging 6 and ranging from 3 to 10 taxa per stream (Table 2). Similarly, sensitive taxa also were common in sampled streams, averaging 6 and ranging from 2 to 12 taxa per stream. Rare taxa collected included *Rhyacophila viquaea* (Milne) and *Eobrachycentrus* spp.; only one individual of each of these taxa was collected and identified from the study (Table 3).

Gatherers were the most abundant functional feeding group, averaging 45.0% of the sampled communities across all streams and ranging widely in abundance among sampled streams (Table 3). Shredders (34.0%) and predators (10.6%) were the second and third most abundant functional groups, respectively. Scrapers averaged only 3.4% of the total abundance and filterers only 2.8%.

NMS produced a three-dimensional ordination that explained 86% of the variation in the original sample space. Among measured physical and chemical variables, stream substrate composition, including percent coarse gravel, cobble, and boulder, percent woody substrate, and percent fine substrate were significantly correlated with NMS axis 1,

Table 2. Mean, standard deviation, and range of metric values calculated from Oregon Coast Range headwater streams from which four or more stream segments were sampled for macroinvertebrates with Surber samplers in June and July 2001 ($n = 33$).

Metric	Mean	SD	Range
Taxa richness	45.2	7.1	31–59
EPT richness	18.8	4.8	10–29
Mayfly richness	4.7	1.5	2–7
Stonefly richness	5.2	1.5	2–8
Caddisfly richness	8.9	2.9	4–15
No. of sensitive taxa*	6.4	2.3	2–12
No. of sediment sensitive taxa*	1.6	0.8	1–3
% tolerant individuals*	8.7	5.9	1.5–22.0
% sediment tolerant individuals*	7.9	4.9	1.2–19.3
% dominance by 1 taxon	30.0	14.4	13–77
% dominance by 3 taxa	51.5	13.2	21–86
Total density (individuals/m ²)	2239	2073	190.4–7893
% scrapers*	3.3	3.2	0.2–12.3
% predators*	10.6	5.7	2.9–25.5
% filterers*	2.8	2.4	0.1–8.9
% gatherers*	45.0	18.4	20.6–90.1
% shredders*	34.0	16.8	3.9–64.7
% omnivores*†	2.5	2.1	0.2–7.6

Note: EPT, Ephemeroptera, Plecoptera, and Trichoptera.

*Attribute coding is unpublished information from the Oregon Department of Environmental Quality.

†Omnivorous classification is based on a taxon’s ability to feed on either plant or animal material at a given stage of the organism’s life history (later instars, generally), rather than on a shift in feeding strategy as the organism develops.

whereas specific conductance and stand age were significantly correlated with axis 2 (Fig. 1 and Table 4). No environmental variables were significantly correlated with NMS axis 3 (Table 4). A number of macroinvertebrate taxa were significantly correlated with NMS axes 1 and 2 (Table 5); these taxa were largely responsible for the resulting ordination patterns produced along these axes.

Among environmental variables found to be significantly correlated with NMS axes, stand age and specific conductance were significantly correlated with several structural and functional metrics. Total density and dominance by both one and three taxa decreased with increasing stand age (Fig. 2). Both percent gatherers ($r = -0.606$, $p = 0.0002$) and percent shredders ($r = 0.671$, $p < 0.0001$) were significantly correlated with specific conductance (Fig. 3); further correlation analysis of individual taxa with specific conductance revealed a significant correlation between Gammaridae density and specific conductance ($r = 0.630$, $p < 0.001$). The relationship appeared to show a threshold of approximately 47 µS/cm, below which Gammaridae did not occur (Fig. 3).

Among measures of substrate composition significantly correlated with NMS axis 1, only percent woody substrate was correlated with any metric: percent scrapers ($r = -0.487$, $p = 0.004$). Despite the apparent importance of inorganic substrate in shaping these headwater communities, as determined by indirect gradient analysis, no individual community metrics were significantly correlated with measures of substrate composition.

Table 3. Occurrence of sensitive, cold-water obligate, and rare macroinvertebrate taxa in 40 headwater streams in managed forests of the Oregon Coast Range mountains.

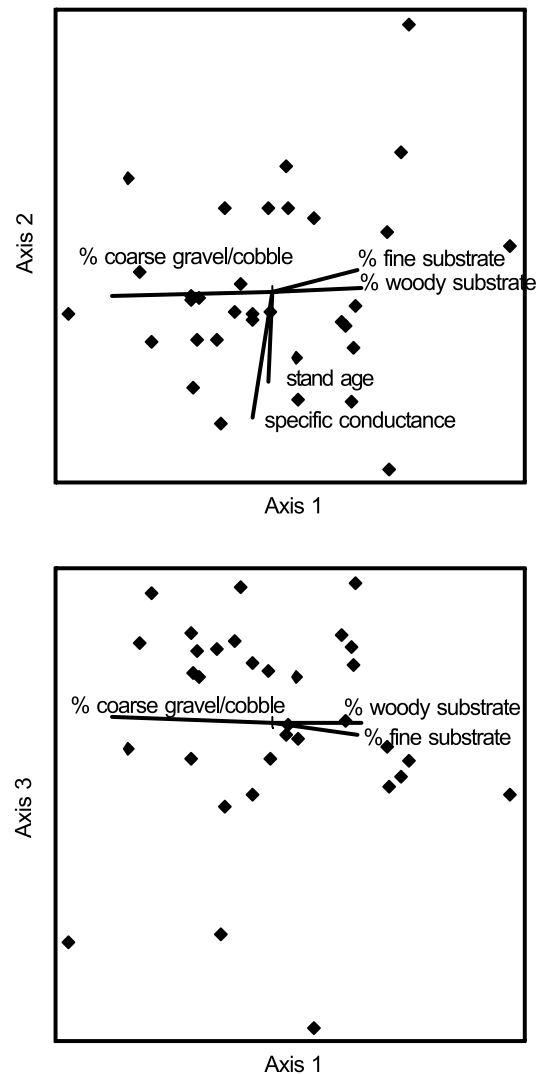
Taxon	Description	No. (%) of streams where taxon was present
Ephemeroptera		
<i>Drunella coloradensis</i>	S	8 (20.0)
Plecoptera		
<i>Doroneuria</i>	S, C	20 (50.0)
<i>Moselia infuscata</i>	S, C	39 (97.5)
<i>Perlomyia</i>	S, C	38 (95.0)
<i>Yoraperla brevis</i>	S, C	37 (92.5)
<i>Zapada columbiana</i>	S, C	35 (87.5)
Trichoptera		
<i>Anagapetus</i>	S, C	10 (25.0)
<i>Chyranda centralis</i>	S, C	11 (27.5)
<i>Cryptochia</i>	S, C	9 (22.5)
<i>Ecclisocosmoecus scylla</i>	S, C	6 (15.0)
<i>Eobrachycentrus</i> sp.	R	1 (2.5)
<i>Eocosmoescus frontalis</i>	R	3 (7.5)
<i>Farula</i>	S, C	11 (27.5)
<i>Goeracea</i>	S	16 (40.0)
<i>Palaeagapetus</i>	C	3 (7.5)
<i>Psychoglypha</i>	C	31 (77.5)
<i>Rhyacophila viquaea</i>	R	1 (2.5)

Note: Taxa were classified as rare (R) when absent from the Oregon Department of Environmental Quality's taxa coding list and, in the case of *Eobrachycentrus* sp., because the species was not known to occur in the Oregon Coast Range mountains before this study (R. Wisseman, personal communication). S, sensitive; C, coldwater.

Discussion

Macroinvertebrate communities have only recently been studied in headwater streams of the coastal mountain ranges of the Pacific Northwest. Recent work documenting macroinvertebrate communities in headwater streams in the Willapa Hills of southwestern Washington State indicated that these communities generally exhibited low richness and density (Haggerty et al. 2002), and perhaps represented a subset of organisms found also in higher-order streams. In contrast, our work, conducted in similar managed headwater forests ≤ 150 km from sites sampled by Haggerty et al. (2002), suggests that headwater communities are relatively taxa rich and support a number of species about which little is known. Data collected by Muchow and Richardson (2000) in British Columbia also suggest that headwater reaches may support a diverse aquatic fauna comparable to those of downstream reaches. Additionally, our study indicates that densities of headwater macroinvertebrates may be much higher than previously reported. Mean invertebrate density reported here (2283 individuals/m²) averaged an order of magnitude higher than the mean density (134 individuals/m²) reported from southwestern Washington by Haggerty et al. (2002). In contrast, our density estimates from the Oregon Coast Range are within the range of stream macroinvertebrate densities (2000–5750 individuals/m²) previously reported from the Cascade Range mountains of Oregon (Murphy et al. 1981; Hawkins et al. 1982).

Fig. 1. Nonmetric multidimensional scaling (NMS) bi-plots of macroinvertebrate communities sampled from 33 headwater streams on managed second-growth forests in northwestern Oregon. Plots include vector overlays of environmental variables significantly correlated with NMS axes.



We believe differences in sampling methods may help explain discrepancies between our results and those of Haggerty et al. (2002). While we used an active net-based (Surber) sampling technique, Haggerty et al. (2002) used passive substrate basket samplers to attract macroinvertebrates because they determined that net-based sampling would not be effective in their slash-covered study streams. These different sampling approaches, as well as differences in adjacent riparian forests (see below) likely produced the large differences in both richness and density between the two studies.

Macroinvertebrate communities are known to respond to timber harvest and subsequent forest regeneration (Gregory et al. 1987), and many of the streams in our study have no history of riparian protection (pre-1972 state timber harvest regulations). Our results indicate that macroinvertebrate communities varied even in relation to the relatively narrow range of forest ages associated with our study streams. Correlation of stand age with both ordination axes and metrics

Table 4. Correlation coefficients (*r*) of measured physical, chemical, and biological variables correlated with resultant ordination axes from nonmetric multidimensional scaling (NMS) of macroinvertebrate data collected from 33 headwater streams in the Oregon Coast Range in June and July 2001.

Variable	Correlation with NMS axis		
	1	2	3
Stand age (years)*	-0.118	-0.518 [§]	0.304
Gradient (degrees)	-0.030	0.006	0.050
Wetted width (m)	-0.279	-0.084	0.226
Bank-full width (m)	-0.274	-0.041	0.340
Large wood tally	0.150	-0.162	-0.256
Bedrock (%) [†]	-0.325	0.235	-0.110
Boulder (%) [†]	-0.227	0.091	-0.118
Fines (%) ^{*†}	0.505 [‡]	0.259	-0.192
Hardpan (%) [†]	-0.071	0.097	-0.164
Wood (%) [*]	0.522 [§]	0.112	0.005
Sand and fines (%) [*]	0.461 [‡]	0.210	-0.082
Cobble and coarse gravel (%) [*]	-0.697 [§]	-0.132	0.123
DO (% saturation)	-0.400	-0.380	0.367
Specific conductance (µS/cm) ^{*†}	-0.248	-0.618 [§]	0.228
<i>Pacifasticus lenisculus</i> (density)	-0.164	-0.031	-0.261
<i>Rhyacotriton kezeri</i> (density)	-0.136	-0.260	0.070

Note: DO, dissolved oxygen.

*Variables were significantly correlated with one of the three ordination axes.

[†]Variables were square-root transformed prior to correlation analysis.

[‡]*p* < 0.01.

[§]*p* < 0.001.

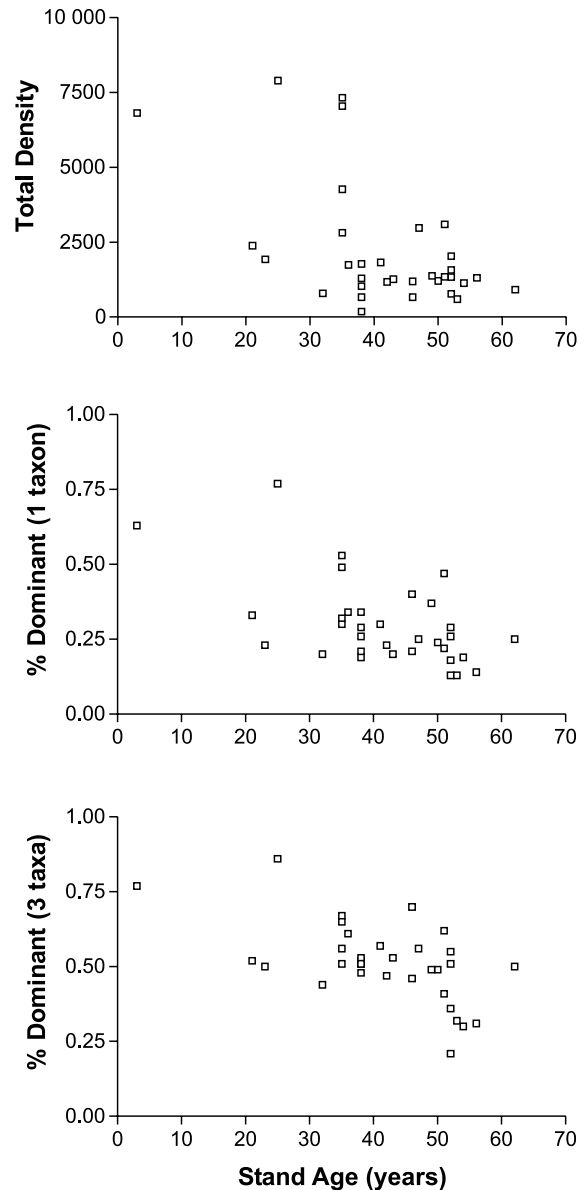
Table 5. Macroinvertebrate taxa that were significantly correlated (*p* < 0.01) with resultant ordination axes from nonmetric multidimensional scaling (NMS) of macroinvertebrate data collected from 33 headwater streams in the Oregon Coast Range in June and July 2001.

Axis 1	Axis 2	Axis 3
Acari	<i>Ramellogammarus</i>	<i>Ecclicosmoecus scylla</i>
<i>Ceratopsyche</i>	<i>Gammarus</i>	<i>Moselia infuscata</i>
<i>Molophilus</i>	<i>Cinygma</i>	<i>Ameletus</i>
Oligochaeta	<i>Meringodixa</i>	Chloroperlidae
Sphaeriidae	Acari*	<i>Eucorethra</i>
<i>Ulomorpha</i>	<i>Bittacomorpha</i> *	<i>Pedicia</i>
<i>Cinygmula</i> *	Hydra*	<i>Perlomyia</i>
<i>Doroneuria</i> *	Ostracoda*	<i>Ramellogammarus</i> *
<i>Farula</i> *	Planorbidae*	Empididae*
<i>Cinygma</i> *	<i>Zapada cinctipes</i> *	<i>Gammarus</i> *
<i>Ironodes</i> *	<i>Zapada columbiana</i> *	<i>Goeracea</i> *
<i>Polycentropus</i> *		<i>Juga</i> *
<i>Yoraperla brevis</i> *		Chironomidae*

*Taxon positively correlated with the axis indicated.

indicated significant correlation with major patterns in macroinvertebrate community density and structure. We note that these relationships are only correlative, but they provide a good foundation for suggesting plausible relationships and testable hypotheses, and underscore the need to further study effects of forest management on headwater communities above the limits of fish distribution (Muchow and Richardson 2000; Richardson 2000).

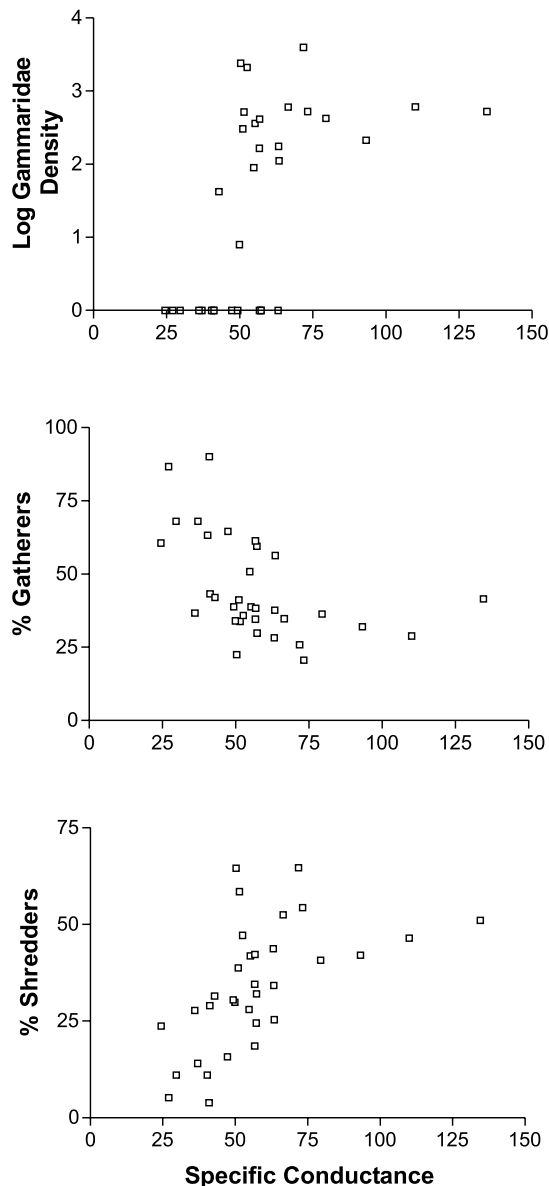
Fig. 2. Relationships between forest stand ages and macroinvertebrate community metrics significantly correlated with stand age from 33 headwater streams on managed second-growth forests in northwestern Oregon.



We found that total macroinvertebrate densities were inversely correlated with stand age. Younger stands showed higher but also greater variation in densities, whereas older stands consistently supported lower densities of organisms. Small streams in Pacific Northwest forests are light-limited and exhibit relatively low primary production (Murphy et al. 1981; Bisson and Bilby 1998). The lower richness and density of macroinvertebrates reported by Haggerty et al. (2002) when compared with our data may reflect the fact that riparian stands in her study were ≥50 years old.

Previous work has shown that streams in clearcuts may initially support higher densities of invertebrates because increased solar radiation results in increased primary production (Murphy et al. 1981; Hawkins et al. 1983; Murphy 1998), but in our study, only one stand was young enough to allow full solar exposure. This may explain why although

Fig. 3. Relationships between specific conductance and macroinvertebrate community attributes significantly correlated with specific conductance measured from 33 headwater streams on managed second-growth forests in northwestern Oregon.



we observed higher densities in younger stands, we did not find the high scraper densities often associated with dramatic increases in insolation (Murphy et al. 1981; Wallace et al. 1988). Instead, the functional composition of our headwater reaches was heavily dominated by detritivorous taxa, with the combined abundance of shredders and gatherers averaging 77% of each sample but scrapers averaging only 8%. Murphy (1998) suggested that optimal levels of stream productivity may actually occur at less than full exposure to sunlight. Perhaps the post-clearcut to mid-successional stages (e.g., 25–45 years old) occurring in the riparian stands adjacent to many of our study streams are providing such conditions that are favorable to optimizing production by benthic communities.

It is also plausible that the large amounts of post-harvest slash historically left within or adjacent to headwater stream channels across the study area retained detritus (Benke and Wallace 1990) or directly contributed to the food base for the large number of detritivores we observed (Anderson et al. 1978; Haggerty et al. 2002). With the heavy shading created by these large inputs of slash after logging, large increases in autotrophic primary production and related shifts in assemblage structure may not be expected to occur (Haggerty et al. 2002). Gregory et al. (1987) suggested that post-harvest woody debris may persist in streams for some time, thereby favoring increased production by detritivores. Over extended periods (e.g., decades), loading of debris would decrease, resulting in reductions in detritivore abundance. Our data suggest that a net loss in the amount or quality of allochthonous food resources, likely woody debris, may be occurring in these headwater streams several decades following timber harvest. Presumably, woody debris inputs would begin to increase again after a century or more of forest succession and result in greater storage of organic matter and increased heterotrophic production (Gregory et al. 1987). However, in the interim between the initial increase in primary production and the much later loading of large wood from the death of mature trees, secondary production of stream communities should tend to decrease (Gregory et al. 1987), as perhaps is occurring in our study reaches bordered by older stands (e.g., 50–60 years old).

Headwater stream reaches bordered by younger stands also exhibited higher dominance by a few taxa. Organisms that occurred in the highest densities are generally regarded as tolerant to disturbance, including Sphaeriidae, Gammaridae, and Chironomidae (Oregon Department of Environmental Quality, unpublished data). Higher macroinvertebrate densities in reaches in younger forest stands appeared to be largely composed of these less sensitive taxa, as total density was highly correlated with percent dominance by the three most abundant taxa. Our results indicate that much of the increased production in stream reaches occurring within younger stands is limited to a few taxa that are less sensitive to disturbance. In contrast, reaches in older stands showed lower dominance by these organisms, presumably because physical stream conditions, on average, were more stable and less favorable to increased dominance by tolerant organisms such as chironomids and sphaeriid clams.

Substrate composition also appeared to be important in shaping macroinvertebrate communities, as percent fine sediment was correlated with macroinvertebrate community structure gradients along NMS axis 1. We found that oligochaetes and sphaeriid clams increased in abundance with increasing levels of fine sediment, as indicated by correlation with NMS axis 1 (Table 5). In contrast, a number of mayflies, caddisflies, and stoneflies were strongly negatively correlated with NMS axis one (Table 5), indicating that these taxa were associated primarily with stream reaches with relatively low levels of deposited sediment. These observed patterns are consistent with what Waters (1995) reports to be the “classic” sediment-induced change in community composition from one of Ephemeroptera, Plecoptera, and Trichoptera (EPT) taxa to one that includes dominance by oligochaetes.

Significant correlation occurred between specific conductance and percent gatherers, percent shredders, and Gammaridae density. The relationship between Gammaridae density and specific conductance appeared to be particularly strong, with a threshold of 47 $\mu\text{S}/\text{cm}$, below which Gammaridae were not found. Because Gammaridae were among the dominant taxa in our study streams, it is likely that variation in their abundance was, in large part, contributing to the observed correlations between specific conductance and percent shredders and gatherers. Although the relationship suggests that some dissolved element may limit Gammaridae abundance in some coastal headwater systems, the result may simply represent an intercorrelation of specific conductance with some other unmeasured variable that co-varies with Gammaridae abundance. Working with Isopoda crustaceans, Reynoldson (1961) found a positive relationship between the occurrence of *Asellus* and the concentration of calcium and dissolved solids, but to our knowledge, no such similar relationships have been reported with Amphipoda taxa.

Haggerty et al. (2002) suggested that predation by amphibians and crayfish might explain the low densities of macroinvertebrates she observed in coastal Washington headwater streams. Although both torrent salamanders and crayfish are known to feed on many of the invertebrate species we found (Bury and Martin 1967; Hershey and Lamberti 1998), we found no significant relationships between macroinvertebrate community attributes and densities of either of these predators.

A number of sensitive and rare species were recorded in our study reaches. For example, several caddisfly taxa known to be rare and limited to cold headwater streams were collected. Perhaps the most significant taxon collected in this study was *Eobrachycentrus*, previously known to occur only in the Cascade Range mountains. *Eobrachycentrus gelidae* (Wiggins), the Mount Hood brachycentrid caddisfly, is currently listed by the U.S. Fish and Wildlife Service as a species of special concern. We are in the process of determining whether our sample represents *E. gelidae* or a previously unknown species. Another rare caddisfly larva we documented, *Rhyacophila* probably *viquaea*, has yet to be described in the published literature. The larva we collected is currently thought to be that of *R. viquaea* (previously described as that of *R. ecosa* by Wold 1972; R. Wisseman, personal communication), but examination of pupal characters of this species is still needed for confirmation.

The high taxa richness, abundance of sensitive species, and presence of rare and poorly known taxa in our study reaches highlight the need to better characterize the biota of forest headwater streams, and specifically those within managed forests (Muchow and Richardson 2000). Richardson (2000) suggests that many of these species may not necessarily be at risk or particularly rare, but are so poorly known simply because headwater streams and associated aquatic fauna have largely been ignored. For example, *Eocosmoescus frontalis* (Banks), found in three of our study reaches, has been reported to occur only in a handful of locations in the Pacific Northwest (Wiggins and Richardson 1989), yet more recent information indicates that this taxon is more abundant across its range than previously thought (R. Wisseman, personal communication). As additional data

describing the distribution and abundance of headwater stream fauna are gathered, we will be able to better assess the status of organisms occurring in these areas.

Headwater streams within managed forests of the Oregon Coast Range appear to be species rich, continue to support taxa that are restricted to cold headwater habitats, and still harbor taxa about which very little is known. Clearly, headwater streams in the Pacific Northwest and those within managed forests make a more important contribution to regional aquatic biodiversity than has been previously realized. Our results also suggest that macroinvertebrate communities in headwater streams may respond to changes in forest succession for decades following harvest, and further underscore our current lack of understanding regarding the ways in which forest practices affect headwater stream biota. To conserve the biodiversity of headwater streams while continuing to manage forests for timber production, we need to increase our efforts to characterize macroinvertebrate communities and habitat relationships within these important habitats. Only then can we begin to understand the consequences of riparian management for headwater biota (Muchow and Richardson 2000).

Acknowledgements

We are grateful to Willamette Industries, Inc. for providing funding and study sites. P. Penttila, T. Holt, G. Stevens, M. Morgans, and M.J. Rochelle provided important support to this work. A. Gonyaw and J. Strom provided both field work and laboratory support for this project. K. Diemer and K. Murk also performed field work for this study. R. Wisseman performed confirmatory identification of rare macroinvertebrate taxa and other voucher specimens. We are grateful to R.J. Danehy, M.A. Melchior, and K. Godbout for critical reviews of the manuscript.

References

- Anderson, N.H., Sedell, J.R., Roberts, L.M., and Triska, F.J. 1978. The role of aquatic invertebrates in processing of wood debris in coniferous forest streams. *Am. Midl. Nat.* **100**: 64–81.
- Benke, A.C., and Wallace, J.B. 1990. Wood dynamics in Coastal Plain blackwater streams. *Can. J. Fish. Aquat. Sci.* **47**: 92–99.
- Bisson, P.A., and Bilby, R.E. 1998. Organic matter and trophic dynamics. *In River ecology and management: lessons from the Pacific Coastal Ecoregion. Edited by R.J. Naiman and R.E. Bilby. Springer-Verlag, New York. pp. 373–398.*
- Brinson, M.M., MacDonnell, L.J., Austen, D.J., Beschta, R.L., Dillaha, T.A., Donahue, D.L., et al. 2002. Riparian areas: functions and strategies for management. National Research Council, National Academy of Sciences, Washington, D.C.
- Bury, R.B., and Martin, M. 1967. The food of the salamander *Rhyacotriton olympicus*. *Copeia*, **1967**: 487.
- Carter, J.L., and Resh, V.H. 2001. After site selection and before data analysis: sampling, sorting, and laboratory procedures used in stream benthic macroinvertebrate monitoring programs by USA state agencies. *J. North Am. Benthol. Soc.* **20**: 658–682.
- Caton, L. 1991. Improved subsampling methods for the EPA "Rapid Bioassessment" benthic protocols. *Bull. North Am. Benthol. Soc.* **8**: 317–319.

- Dieterich, M., and Anderson, N.H. 1995. Lifecycles and food habits of mayflies and stoneflies from temporary streams in western Oregon. *Freshw. Biol.* **34**: 47–60.
- Diller, L.V., and Wallace, R.L. 1996. Distribution and habitat of *Rhyacotriton variegatus* in managed, young growth forests in north coastal California. *J. Herpetol.* **30**: 184–191.
- Ford, J., and Rose, C.E. 2000. Characterizing small subbasins: a case study from coastal Oregon. *Environ. Monit. Assess.* **64**: 359–377.
- Franklin, J.F., and Dyrness, C.T. 1973. Natural vegetation of Oregon and Washington. U.S. For. Serv. Gen. Tech. Rep. PNW-8.
- Gauch, H.G. 1982. Multivariate analysis in community ecology. Cambridge University Press, New York.
- Gomi, T., Sidle, R.C., and Richardson, J.S. 2002. Understanding processes and downstream linkages of headwater systems. *BioScience*, **52**: 905–916.
- Gregory, S.V., Lamberti, G.A., Erman, D.C., Koski, K.V., Murphy, M.L., and Sedell, J.R. 1987. Influence of forest practices on aquatic production. In *Streamside management: forestry and fishery interactions*. Edited by E.O. Salo and T.W. Cundy. Univ. Wash. Inst. For. Resour. Contrib. 57. pp. 233–255.
- Haggerty, S.M., Batzer, D.P., and Jackson, C.R. 2002. Macroinvertebrates assemblages in perennial headwater streams of the Coastal Mountain range of Washington, U.S.A. *Hydrobiologia*, **479**: 143–154.
- Hawkins, C.P., Murphy, M.L., and Anderson, N.H. 1982. Effects of canopy, substrate composition, and gradient on the structure of macroinvertebrate communities in Cascade range streams of Oregon. *Ecology*, **63**: 1840–1856.
- Hawkins, C.P., Murphy, M.L., Anderson, N.H., and Wilzbach, M.A. 1983. Density of fish and salamanders in relation to riparian canopy and physical habitat in streams of the northwestern United States. *Can. J. Fish. Aquat. Sci.* **40**: 1173–1185.
- Hershey, A.E., and Lamberti, G.A. 1998. Stream macroinvertebrate assemblages. In *River ecology and management: lessons from the Pacific Coastal Ecoregion*. Edited by R.J. Naiman and R.E. Bilby. Springer-Verlag, New York. pp. 169–199.
- Hibbs, D.E., and Chan, S. 2001. Developing management strategies for riparian areas. In *Water, Aquatic Resources, and Vegetation Management: Proceedings of the 22nd Forest Vegetation Management Conference, 16–18 January 2001, Redding, Calif.* University of California Cooperative Extension Forestry Program, Redding, Calif. pp. 89–96.
- Jackson, D.A. 1993. Multivariate analysis of benthic invertebrate communities: the implication of choosing particular data standardizations, measures of association, and ordination methods. *Hydrobiologia*, **268**: 9–26.
- Karr, J.R., and Chu, E.W. 1999. Restoring life in running waters. Better biological monitoring. Island Press, Washington, D.C.
- Krebs, C.J. 1989. Ecological methodology. Harper Collins, New York.
- Lenat, D.R., Penrose, D.L., and Eagleson, K.W. 1981. Variable effects of sediment addition on stream benthos. *Hydrobiologia*, **79**: 187–199.
- Mahoney, D.L., and Erman, D.C. 1984. The role of stream-side buffer strips in the ecology of aquatic biota. In *California riparian systems: ecology, conservation, and production management*. Edited by R.E. Warner and K. Hendrix. U.C.L.A. Press, Los Angeles, Calif. pp. 168–176.
- McCune, B., and Mefford, M.J. 1999. PC-ORD. Multivariate analysis of ecological data, version 4. MJM Software Design, Gleneden Beach, Ore.
- Merritt, R.W., and Cummins, K.W. (Editors). 1996. An introduction to the aquatic insects of North America. 3rd ed. Kendall/Hunt, Dubuque, Iowa.
- Meyer, J.L., and Wallace, J.B. 2001. Lost linkages and lotic ecology: rediscovering small streams. In *Ecology: achievement and challenge*. Edited by M.C. Press, N.J. Huntly, and S. Levin. Blackwell Scientific, Oxford, U.K. pp. 295–317.
- Muchow, C.L., and Richardson, J.S. 2000. Unexplored diversity: macroinvertebrates in coastal British Columbia headwater streams. In *Proceedings of a Conference on the Biology and Management of Species and Habitats at Risk, Kamloops, B.C., 15–19 February 1999. Vol. 2*. Edited by L.M. Darling. B.C. Ministry of Environment, Lands and Parks, Victoria, B.C., and University College of the Cariboo, Kamloops, B.C. pp. 503–506.
- Murphy, M.L. 1998. Primary production. In *River ecology and management: lessons from the Pacific Coastal Ecoregion*. Edited by R.J. Naiman and R.E. Bilby. Springer-Verlag, New York. pp. 144–168.
- Murphy, M.L., Hawkins, C.P., and Anderson, N.H. 1981. Effects of canopy modification and accumulated sediment on stream communities. *Trans. Am. Fish. Soc.* **110**: 469–478.
- Naiman, R.J., DeCamps, H., and Pollack, M. 1993. The role of riparian corridors in maintaining regional biodiversity. *Ecol. Appl.* **3**: 209–212.
- Pabst, R.J., and Spies, T.A. 1999. Structure and composition of unmanaged riparian forests in the coastal mountains of Oregon, U.S.A. *Can. J. For. Res.* **29**: 1557–1573.
- Pennak, R.W. 1989. Freshwater invertebrates of the United States. 3rd ed. J. Wiley & Sons, New York.
- Platts, W.S., Megahan, W.F., and Minshall, G.W. 1983. Methods for evaluating stream, riparian, and biotic conditions. USDA For. Serv. Gen. Tech. Rep. INT-138.
- Quinn, J.M., Cooper, A.B., Davies-Colley, R.J., Rutherford, J.C., and Williamson, R.B. 1997. Land use effects on habitat, water quality, periphyton, and benthic invertebrates in Waikato, New Zealand hill country streams. *N.Z. J. Mar. Freshw. Res.* **31**: 569–577.
- Reece, P.F., and Richardson, J.S. 2000. Benthic macroinvertebrate assemblages of coastal and continental streams and large rivers of southwestern British Columbia, Canada. *Hydrobiologia*, **439**: 77–89.
- Rempel, L.L., Richardson, J.S., and Healey, M.C. 2000. Macroinvertebrate community structure along gradients of hydraulic and sedimentary conditions in a large gravel-bed river. *Freshw. Biol.* **45**: 57–73.
- Reynoldson, T.B. 1961. Observations on the occurrence of Asellus (Isopoda, Crustacea) in some lakes of northern Britain. *Proc. Int. Assoc. Theor. Appl. Limnol.* **14**: 988–994.
- Richardson, J.S. 1992. Food, microhabitat, or both? Macroinvertebrate use of leaf accumulations in a montane stream. *Freshw. Biol.* **27**: 169–176.
- Richardson, J.S. 2000. Life beyond salmon streams: communities of headwaters and their role in drainage networks. In *Proceedings of a Conference on the Biology and Management of Species and Habitats at Risk, Kamloops, B.C., 15–19 February 1999. Vol. 2*. Edited by L.M. Darling. B.C. Ministry of Environment, Lands and Parks, Victoria, B.C., and University College of the Cariboo, Kamloops, B.C. pp. 473–476.
- Sidle, R.C., Tsuboyama, Y., Noguchi, S., Hosoda, I., Fujieda, M., and Shimizu, T. 2000. Stormflow generation in steep forested headwaters: a linked hydrogeomorphic paradigm. *Hydrol. Process.* **14**: 369–385.
- Stewart, K.W., and Stark, B.P. 1993. Nymphs of North America

- stonefly genera (Plecoptera). University of North Texas Press, Denton, Tex.
- Stout, B.M., Benfield, E.F., and Webster, J.R. 1993. Effects of forest disturbance on shredder production in southern Appalachian headwater streams. *Freshw. Biol.* **29**: 59–69.
- Taylor, G.H. 1993. Normal annual precipitation, state of Oregon [map]. Oregon Climate Service, Oregon State University, Corvallis, Ore.
- Vannote, R.L., Minshall, G.W., Cummins, K.W., Sedell, J.R., and Cushing, C.E. 1980. The river continuum concept. *Can. J. Fish. Aquat. Sci.* **37**: 130–137.
- Wallace, J.B., Gurtz, M.E., and Smith-Cuffney, F. 1988. Long-term comparisons of insect abundances in disturbed and undisturbed headwater streams. *Verh. Int. Ver. Theor. Angew. Limnol.* **23**: 1224–1231.
- Waters, T.F. 1995. Sediment in streams: sources, biological effects, and control. American Fisheries Society Monograph 7. American Fisheries Society, Bethesda, Md.
- Wiggins, G.B. 1996. Larvae of the North American caddisfly genera (Trichoptera). 2nd ed. University of Toronto Press, Toronto, Ont.
- Wiggins, G.B., and Richardson, J.S. 1989. Biosystematics of *eocosmoecus*, a new nearctic caddisfly genus (Trichoptera: Limnephilidae, Dicosmoecinae). *J. North Am. Benthol. Soc.* **8**: 355–369.
- Wilkins, R.N., and Peterson, N.P. 2000. Factors related to amphibian occurrence and abundance in headwater streams draining second-growth Douglas-fir forests in southwestern Washington. *For. Ecol. Manage.* **139**: 79–91.
- Wipfli, M.S., and Gregovich, D.P. 2002. Invertebrates and detritus export from fishless headwater streams in southeastern Alaska: implications for downstream salmonid production. *Freshw. Biol.* **47**: 957–970.
- Wold, J. 1972. Systematics of the genus *Rhyacophila* (Trichoptera: Rhyacophilidae) in western North America with special reference to the immature stages. M.Sc. thesis, Oregon State University, Corvallis, Ore.
- Zimmer, K.D., Hanson, M.A., and Butler, M.G. 2000. Factors influencing invertebrate communities in prairie wetlands: a multivariate approach. *Can. J. Fish. Aquat. Sci.* **57**: 76–85.