

**Assemblage Structure of Riparian and Drifting Invertebrates Along
Environmental Gradients in Two Streams of
Southern British Columbia**

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Abstract

Assemblages of riparian and drifting invertebrates in two streams of the Thompson River drainage, British Columbia, were examined using multivariate statistical techniques, to assess potential effects of deforestation and other perturbations. Comprehensive sampling for macrofaunal and meiofaunal invertebrates was carried out in the fall of 1994. Diversity and ecological guilds were determined; factors considered included pollution tolerance, trophic type and microhabitat use of the taxa. Data from drift samples were used to calculate biotic (pollution) indices. Although longitudinal trends were apparent for invertebrate assemblages, spatial patterns were inconsistent between drift and riparian datasets, with the exception of terrestrial invertebrates. Terrestrial biota were more abundant downstream in both datasets, despite increases in stream width and canopy opening, perhaps reflecting downstream increases in air temperature and terrestrial productivity. Riparian (terrestrial and emergent) invertebrates were more abundant in the surface drift, whereas aquatic invertebrates dominated the demersal drift. Riparian deforestation appeared to effect drift- and riparian - invertebrate assemblages. Deforested reaches had higher drift densities and lower drift and riparian diversities than did treed reaches, reflecting greater dominance by cladocerans, chironomids, homopterans and/or adult dipterans in deforested reaches. Predatory and pollution-sensitive taxa were generally more abundant in treed habitats, although pollution indices were often contradictory in depicting land-use (floral) trends. Overall, findings suggest that semi-forested stream habitats are conducive to ecological integrity and, thus, fisheries and wildlife in the southern interior of British Columbia.

Résumé

Les communautés d'invertébrés riverains et dérivants de deux cours d'eau du bassin versant de la rivière Thompson (Colombie-Britannique) ont été examinées par les méthodes de l'analyse statistique multivariées afin d'évaluer les effets potentiels du déboisement et d'autres perturbations. On a effectué à l'automne de 1994 un échantillonnage détaillé des invertébrés macrofauniques et méiofauniques. La diversité et la composition des guildes écologiques ont été déterminées; les facteurs pris en considération étaient la tolérance à la pollution, le type trophique des taxons et leur utilisation du microhabitat. Les données sur les échantillons de matériaux entraînés ont été utilisées pour calculer des indices biotiques (pollution). Bien que des tendances longitudinales soient apparentes pour les communautés d'invertébrés, les configurations spatiales tirées des ensembles de données sur les dérivants et les riverains n'étaient pas cohérentes, sauf dans le cas des invertébrés terrestres. Le biote terrestre était plus abondant vers l'aval dans le cas des deux ensembles de données, malgré des accroissements de la largeur des cours d'eau et de l'ouverture dans la voûte forestière, ce qui reflète peut-être des accroissements vers l'aval de la température de l'air et de la productivité terrestre. Les invertébrés riverains (terrestres et émergents) étaient plus abondants dans les matériaux entraînés en surface alors que les invertébrés aquatiques dominaient dans les matériaux entraînés au fond. Le déboisement riverain semble influencer les communautés riveraines et dérivantes d'invertébrés. Les tronçons déboisés présentaient des densités de dérivants plus élevées et de moins grandes diversités des dérivants et des riverains que les tronçons boisés, ce qui reflète une plus grande domination des cladocères, des chironomidés, des homoptères et/ou des diptères adultes dans les tronçons boisés. Les taxons sensibles aux prédateurs et à la pollution étaient généralement plus abondants dans les habitats boisés, bien que les indices de pollution représentaient souvent de manière contradictoire les tendances de l'utilisation des terres (par la flore). Dans l'ensemble, les résultats suggèrent que les

habitats des cours d'eau semi-boisés sont favorables à l'intégrité écologique et ainsi pour la pêche et la faune dans l'intérieur méridional de la Colombie-Britannique.

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1.0 Introduction

Riparian invertebrates (terrestrial taxa and adults of aquatic insects) and drifting invertebrates (aquatic and fallen-terrestrial taxa) are important in stream and riparian ecosystems as food for various predators, including salmonids and other fishes in temperate streams (Waters 1969; Hunt 1975; Mason and MacDonald 1982; Allan 1983). Insectivorous, riparian birds, frogs, and invertebrates often feed heavily on aquatic-derived ('semi-aquatic') flying insects (Jackson and Fisher 1986) and respond to declines in food abundance caused by natural (e.g., hydrologic) and human disturbances (Blancher and McNicol 1986; Gray 1993).

Drift-invertebrate sampling is useful for assessing food availability for fishes and stream-habitat quality, by examining the abundance and diversity of invertebrate taxa. Drift samples of aquatic invertebrates can be used to generate indices of water quality, given the good concordance of these indices with the more-commonly used benthic-invertebrate indices (Larimore 1974). Drift samples of terrestrial invertebrates can provide indices of riparian-habitat quality, because fallen-terrestrial taxa differ with tree species and canopy cover (Bailey 1966; Mason and MacDonald 1982; Jackson and Fisher 1986; Angermeier and Karr 1983). Drift sampling has advantages over benthic and riparian sampling because both aquatic and terrestrial taxa are collected and taxa come from various habitats (Larimore 1974; O'Connell 1978). In addition, benthic samples are more difficult and less cost-effective to collect than drift samples (Larimore 1974; Allan and Russek 1985) because of sediment accumulation in benthic collections, whereas terrestrial-sampling methods preferentially collect ground and/or flying insects (Hooper and Savard 1991) and riparian-sweep nets may collect adult aquatic insects after they have migrated away from the sites where they emerged from (Hinterleitner-Anderson et al. 1992).

Although sampling of emerging aquatic insects is also more efficient than benthic sampling, particularly for contaminant analyses (Ciborowski and Corkum 1988; Kovats and Ciborowski 1989; Dunnigan 1994), different trap types are known to differ in catch efficiency and preferentially collect different taxa (Flannagan and Cobb 1994). In addition, emergent samples may yield low numbers of adult insects if air temperatures are too low ($< 20\text{-}25^{\circ}\text{C}$), if conditions are windy and dry, and if no aquatic-insect taxa are emerging during sampling (Kovats and Ciborowski 1989; Dunnigan 1994).

Indicator taxa and ecological guilds of invertebrates are often used to assess human impact on aquatic and terrestrial ecosystems (Cummins and Wilzbach 1985; Hawkins and MacMahon 1989; Kremen 1992). The relative abundance of zoobenthic guilds have been examined in British Columbia (BC) streams to assess logging, sewage-outfall, and other impacts, including functional (trophic) (Culp and Davies 1983) and pollution-tolerance guilds (Derksen and Kelso 1976). Multivariate statistics and diversity analyses have been used to examine zoobenthic assemblages across pollution gradients, to develop biotic indices of pollution (Wilhm 1972; Dickson et al. 1978; Washington 1984; Gerritsen 1995). Because agricultural (Omernik 1977; Osborne and Kovacic 1993), logging, and other riparian impacts (Lynch et al. 1977; Petersen et al. 1987; Smith et al. 1987; Brewin 1992) adversely alter substrata (via sedimentation), temperature regimes, nutrient levels, algal abundance, and organic- and inorganic-toxin levels in aquatic ecosystems, biotic (pollution) indices are appropriate to assess deforestation impacts on stream ecosystems. Certain non-insect invertebrates, notably aquatic mites and benthic meiofauna, are expected to be good pollution indicators, because they are usually in contact with the substratum and lack adult flying stages that could enhance recolonization of impacted stream reaches (Wagener and LaPerriere 1985; Morrell 1995).

Deforestation is known to affect food availability for lotic invertebrates and fishes in British Columbia (BC) and southeastern Alaska. Logging of coastal streams

alters the relative abundance of terrestrial vs. aquatic foods, because riparian vegetation and stream stability (via erosion and sedimentation) are lost (Chamberlin et al. 1974; Culp and Davies 1983; Hartman and Scrivener 1990; Wipfli 1994). These impacts include relative decreases of terrestrial detritus and aquatic invertebrates and increases of terrestrial invertebrates and periphyton (benthic algae). However, interior streams in BC might be expected to show different trophic patterns, because flow levels are more stable and allow greater retention of detritus in pools (Richardson 1994); Johnston and Slaney (1996) hypothesized that logging should decrease both terrestrial invertebrates and detritus inputs to BC streams, as supported by day (but not night) drift densities in a comparison of a logged and a control stream in inland BC (Slaney et al. 1977). If diet data for salmonids found in inland rivers is used as a measure of invertebrate abundance, these data suggest that riparian deforestation enhances aquatic invertebrates and reduces terrestrial taxa (Hunt 1975). Similarly, Jackson and Fisher (1986) found relatively low inputs of terrestrial invertebrates and emerging-aquatic insects into an inland-desert stream in Arizona, apparently because the stream was open-canopied.

The present study, which encompasses two river valleys of BC's southern interior, is a rapid bioassessment of riparian (aerial) and drift assemblages of invertebrates along three environmental gradients: riparian intactness, longitudinal (up- to downstream) position, and (for drift samples) vertical position in the water column. These trends were assessed with multivariate analyses and diversity indices on relative-abundance data for individual taxa and ecological guilds. Four hypotheses were tested. First, treed and deforested reaches should show spatially consistent differences in assemblage structure; deforested sites should show lower biodiversity, relative increases in aquatic taxa that are pollution-tolerant, and (possibly) changes in abundance of terrestrial and aquatic-herbivorous taxa. Second, the streams should have relatively low abundances of terrestrial taxa in downstream riparian and drift samples, because of increases in stream width and decreases in percent canopy cover

(Vannote et al. 1980). Third, terrestrial and emergent invertebrates should be relatively more abundant in surface-drift samples, whereas aquatic invertebrates should be more important in demersal samples. Fourth, invertebrate taxa were expected to form habitat-use guilds along the riparian-floral gradient because of differing needs for riparian vegetation (by terrestrial invertebrates), pollution tolerances (by aquatic invertebrates), or potentially both factors (by emerging adults of aquatic insects).

2.0 Materials and Methods

2.1 Study Watersheds

The two streams studied, the Salmon (SR) and Nicola (NR) river mainstems, are in the Thompson River drainage in the southern-interior (Kamloops) region of BC (Fraser River basin) (Figures 1 and 2). Because of the semi-arid climate in this region (Clark and Brady 1981), valley vegetation is 'dry forest'; dominant taxa include sagebrush (*Artemisia* spp.) in the Nicola valley and bunchgrass (erect-stemmed, perennial Poaceae), ponderosa pine (*Pinus ponderosa*), and cottonwoods (*Populus* spp.) in both valleys (Thomson 1986; Anon. 1993). Human impacts include mining and logging in headwater tributaries, whereas mainstem areas are subject to riparian deforestation, water withdrawals, and pollution from agricultural activities and localized urbanization (Kerr 1975; Clark and Brady 1981; Woodward and Healey 1993). Agrarian activities in the two valleys include haying and cattle ranching, whereas food-crop farming is prominent in SR and ginseng farming in NR (MOE 1983; MOEP 1987; Millar et al. 1994).

All study reaches were in the middle and lower river zones between 350 and 600 m in elevation, the streams being moderate in size and gradient. Slopes for SR were 4.0 m/km for both stream zones, whereas slopes for NR were respectively 3.2 and 6.4 m/km in the middle and lower (canyon) zones. Average stream

widths ranged from 9 to 14 m in the SR reaches and 12 to 36.5 m in the NR reaches.

2.2 Field and Laboratory Sampling

Sampling was conducted during the fall of 1994 for SR (August 28 to September 12) and NR (September 24 to October 8). In both rivers, three reaches (A, B, and C) of differing riparian intactness (see below) were studied at two sites: middle (#1) and lower (#2) mainstems (Figures 1 and 2). The reaches, which were usually 300 to 400 m in stream length (Appendix 1), were separated by at least 300 m to make the reaches independent sampling units and to minimize sampling of transitional zones. Some reaches within sites were separated by townships, confluences of major tributaries, and/or large distances (≥ 1 km) because of the limited number of lengthy stretches with homogeneous vegetation (Figures 1 and 2). Only reaches 1A and B in the middle SR, 2B and C in the lower SR, and 2A to C in the lower NR were relatively close together. Three vegetation types were categorized in each river valley (Figures 1 and 2). *Forested* (SR only) and *semi-forested* reaches had intact buffer strips (width ≥ 50 m) on both vs. one side(s) of the river, respectively. *Shrubby* reaches (NR only) had sagebrush-dominated buffer strips on both sides of the river, whereas *grassy* reaches were dominated by low and/or high herbs.

Several habitat variables were measured in each reach during invertebrate sampling (Appendix 1). Water temperatures were taken with a hand-held thermometer in the morning (~900 h), noon (~1200 h), and afternoon (~1530 h) over one or two days in each study reach. Surface velocity at drift-net locations were measured before nets were positioned, by timing the movement of a rubber ball over 1 m.

Drifting invertebrates were collected during daylight hours with drift nets, to avoid catching young salmonids. Nets were positioned at the head of each study reach in moderately deep and fast water for 2 to 6 h during morning (usually) or

afternoon; sampling was usually in transitional ('run') zones between pools and riffles (see Appendix 1). The tapered Nitex nets, which were each attached to plastic, bottomless jars at the mouth and tail (collection) ends, had 300-um mesh, mouth openings of 10.2 cm, and total lengths of 1 m (Vadas 1988); the plastic mouths were made narrower than Nitex-net diameters to minimize turbulent backwash and loss of invertebrates (Waters 1969). Four nets were attached to stakes in two nearby rows facing the current, two nets at the surface and two on bottom (cf. Wefring and Hopwood 1981), the top nets breaching the water surface to sample terrestrial drift (Clark and Shera 1985; Cavanagh et al. 1994) and the bottom nets with their mouths 2 to 3 cm above the substratum to avoid sampling benthic invertebrates (O'Connell 1978). Hence, the total surface area of top and bottom drift sampled was $(2 \times 77 \text{ cm}) + (2 \times 82 \text{ cm}) = 318 \text{ cm}^2$. Nets were shaken periodically to prevent silt and leaf buildup.

During drift sampling, water temperatures averaged from 14 to 16°C for all SR reaches and the first two NR reaches, but was cooler (8-12°C in average value) for the last four NR reaches (Appendix 1). This trend was parallel to that for air temperature, which was especially low during mornings when the last four NR reaches were sampled (Vadas and Newman 1997).

Riparian invertebrates were collected during daylight hours in a riffle-pool sequence downstream of the drift nets, using an aerial sweep net at water's edge (Hershey et al. 1993) and/or floating emergent traps (Rosenberg 1978). The sweep net, which was used in both river valleys, was continually swept back-and-forth through riparian vegetation along one or both shores. Total sample time per reach was 15 to 20 minutes. This method was used because air conditions were often windy and cool (usually < 20°C) during the fall sampling (Vadas and Newman 1997) and thus not conducive to emergent-trap sampling (see above).

Four emergent traps were tied to stakes over pools and (usually) pool-head runs during drift-sampling operations, and occasionally overnight when day catches were nil. The aluminum-frame, pyramidal traps, which were similar to the 'day' model of LeSage and Harrison (1979), were each 84 cm tall with a base (0.55 m²) fitted with buoys to allow flotation (Whitehouse et al. 1993). Each trap had a 202-um mesh Nitex net attached to the collector jar at the pyramid's apex. Plastic covers were placed over the traps during rainy periods to prevent insect loss (LeSage and Harrison 1979). Traps were only used in SR because they collected less insects and were more laborious to use than sweep-net samples.

All invertebrate samples were preserved in 75% ethanol and stained with rose bengal to facilitate laboratory sorting (Mason and Yevitch 1967). Samples containing >> 50 large, visible invertebrates were subsampled using the vial technique of Mundie et al. (1983). Namely, each invertebrate sample was flushed of its coarse organic matter (usually leaves) and washed through a 250-um mesh sieve to remove fine sediments. The sample was then poured and stirred into a half-filled bucket containing 11 vials, 5 cm below water level. After 30 minutes, vials were randomly chosen until 100 to 300 invertebrates were collected (cf. Jones et al. 1981). In other samples, however, sample sizes of invertebrates were small (N < 100); for these samples, bottom and top drift nets were often combined, as were sweep-net and emergent-trap samples.

Invertebrates were identified to order, suborder, or family using a dissecting microscope. Nymphal, larval, pupal, and adult life stages of aquatic invertebrates were tabulated separately. This taxonomic resolution allowed categorization of taxa by macrohabitat use (all taxa), pollution tolerance (aquatic and semi-aquatic taxa), and trophic status (aquatic taxa) for guild analyses. Macrohabitat categories were aquatic, semi-aquatic, and terrestrial) (Pennak 1978; Merritt and Cummins 1984); semi-aquatic insects lived at the water's edge or were the aerial adults of aquatic nymphs or larvae. Pollution-tolerance categories included sensitive, moderate, and tolerant, as well as intermediate

categories for ambiguous taxa (Mylinski and Ginsburg 1977; Pennak 1978; Palmer 1984; Kellogg 1991; McDonald et al. 1991); sensitive taxa were generally restricted to clean-flowing waters and tolerant taxa were most abundant in stagnant, heavily polluted waters. Trophic categories were herbivore, predominately herbivore, herbivore-predator (omnivore), predominately predator, and predator (Vadas 1990), based on information provided by Pennak (1978), Merritt and Cummins (1984), and Cummins and Wilzbach (1985); herbivores included taxa that are known to eat algae and/or riparian detritus (e.g., leaves). These categories are cruder than the functional groups used by Cummins and colleagues (based on whether invertebrates feed on algae vs. coarse or fine detritus, solid vs. liquid foods, and benthic vs. water-column foods), because of the limited taxonomic resolution in the present study.

2.3 Data Analysis

The riparian-invertebrate samples were analyzed by calculating relative abundances of taxa. Sample sizes were adequate for only one pairwise comparison between sweep-net and emergent-trap samples.

Relative abundance and density (number/m³) were both used to analyze drift-invertebrate samples. Although top and bottom drift nets were often analyzed separately to characterize invertebrate-assemblage patterns (see below), total drift density was calculated for the four nets (pooled) as number / (average velocity X sample time X mouth-surface area). Average velocity was used because the mouths of the top and bottom nets were near 20% and 80% depth, respectively (cf. Platts et al. 1983); average velocity was estimated as 90% vs. 80% of surface velocity over fine (muddy-sandy) vs. coarse (rocky) substrata, respectively (cf. Vadas 1994). Relative-abundance data were used to assess the similarity of invertebrate assemblages across sample reaches, whereas habitat associations among invertebrate taxa were assessed with density data.

Varimax-factor analysis and/or the Simpson-Levins diversity index were used to examine assemblage patterns for invertebrate taxa, factor analysis being used to define clusters (factor axes) of sites or reaches (cf. Vadas 1991, 1994). I undertook three riparian-invertebrate analyses to examine assemblage patterns along longitudinal and riparian-floral gradients. (1) An overall comparison of samples for the two river valleys was done, based on the seven SR and six NR samples taken. That is, there were 13 variables (samples) and 20 observations (taxa) in the factor analysis. (2) Reaches of the same vegetation type were pooled (within and across rivers) to more specifically assess riparian-floral patterns. Hence, there were four variables: forested, semi-forested, shrubby, or grassy sites. (3) Percent abundance of terrestrial (vs. semi-aquatic) taxa were calculated across longitudinal and riparian-floral gradients. Reaches within sites were pooled to assess longitudinal patterns, so that there were four variables: middle and lower SR and NR. The two rivers were analyzed separately for the riparian-floral analysis, such that there were six variables: forested, semi-forested, and grassy sites in SR and semi-forested, shrubby, and grassy sites in NR.

I undertook eight drift-invertebrate analyses to examine assemblage patterns along longitudinal, riparian-floral, and water-column (vertical) gradients. These included two analyses analogous to that for riparian invertebrates: overall and riparian-floral comparisons across a sample size of 38 observations (taxa). The overall analysis consisted of 11 SR and seven NR samples (18 variables) to be compared, whereas the floral analysis contained four variables.

Based on the overall analysis, pairwise comparisons of bottom vs. top nets were done to establish vertical guilds of drift taxa. The guilds were determined by summing points for the six paired-net comparisons, -1 vs. 1 point being assigned for greater relative abundance in bottom vs. top nets, respectively; the guilds were bottom (≤ -2 points), top (≥ 2 points), or generalized (-1 to 1 points for ≥ 4 comparisons).

I undertook six longitudinal-floral analyses when taxa were pooled into pollution-tolerance, macrohabitat, and trophic guilds; the two rivers were analyzed separately for the riparian-floral comparisons. These analyses involved examination of percentage and diversity data; multivariate analysis was unnecessary because interpretation was facilitated by the small number of observations (guilds) and summation of data into diversity and other indices (see below). Overall herbivore-predator ratios (Table 7) were calculated based on the methodology of Vadas (1990). Alternative pollution indices included two EPT and two sensitivity indices, lower values being suggestive of pollution. Percent EPT is the relative abundance of large-bodied, pollution-sensitive taxa, namely ephemeropterans, plecopterans, and trichopterans (Munro and Taccogna 1994). The EPT:D ratio was a similar index, the abundance of EPT insects being divided by that of a prominent pollution-tolerant taxon, i.e., dipterans (Cash 1995). Sensitivity indices were based on assignment of points for each taxon, namely 3, 2.5, 2, 1.5, and 1 point(s) for sensitive, sensitive-moderate, moderate, moderate-tolerant, and tolerant taxa, respectively (cf. Kellogg 1991; McDonald et al. 1991). Index I was based on percent-abundance data, in that a weighted average was calculated for sensitivity points. In contrast, index II was based on presence-absence data, in that a sensitivity sum was calculated for all taxa present (Kellogg 1991; McDonald et al. 1991).

I undertook varimax-factor and average-ranks analyses on density data to assess habitat associations among the abundant invertebrate taxa, factor analysis being used to define clusters of taxa (cf. Vadas 1991, 1994). There were 16 variables (taxa) and 12 observations (sample reaches) in the factor analysis. The average-ranks analysis was a triplet-wise comparison of reaches within sites. For each taxon, reaches were ranked, and average ranks for each riparian-floral category were calculated. These multi- and univariate analyses were useful for defining riparian-floral habitat-use guilds of invertebrate taxa.

2.4 Graphical Presentation

Because of the complexity of factor-analytic results, multivariate-similarity tables were formulated to show the important factor axes (clusters) and their important observations (cf. Vadas 1991, 1994). 'Important' factor axes were those containing highest or moderately high loadings for at least one variable, whereas 'important' observations included abundant taxa (assemblage analyses) or high-density sites (habitat-association analyses). Variables (sample sites or taxa) showing highest loadings on the same factor axis were considered completely similar, and were stacked vertically in the table. Variables showing only moderately high loadings (within 0.10 Pearson units of the highest loading) on the same axis were considered moderately similar, the variables being placed horizontally with a similarity bar connecting them. Other variables, which loaded on different axes because they were independent, were not connected by similarity bars.

3.0 Results

3.1 Riparian-Invertebrate Assemblages

Based on the data of Appendix 2, multivariate analysis revealed that study reaches clustered into four important factors (Table 1). There was no obvious clustering of sample reaches by river, as SR and NR reaches often clustered (loaded) together because of similar invertebrate assemblages. Up- and downstream reaches often loaded highest on factors 3 vs. 1, respectively. Treed reaches, which were often highest in faunal diversity, usually loaded highly on factor 1, whereas most unforested reaches loaded on the next three factors. The only sweep-net vs. emergent-trap comparison revealed that the two techniques gave similar assemblage (composition and diversity) patterns; oddly, two terrestrial taxa (spiders and homopterans) were collected in emergence

traps. Nematoceran adults were more common in upstream samples and homopterans and hymenopterans were more abundant downstream.

Based on the pooled riparian-floral analysis, treed sites were distinctive from shrubby and grassy sites in invertebrate composition but not in faunal diversity (Table 2). The pooled and unpooled analyses together suggest that longitudinal position and riparian-floral characteristics were both important determinants of riparian-invertebrate composition.

3.2 Drift-Invertebrate Assemblages

Based on the data of Appendices 3-4, multivariate analysis revealed that study reaches clustered into five important factors (Table 3). Again, there were no obvious clustering of sample reaches by river. Longitudinal trends were partially distinct, as some up- and downstream reaches loaded highest on factors 4 vs. 5, respectively. There were no obvious clusters of samples reaches by riparian-floral characteristics. Nevertheless, semi-forested reaches generally had the highest faunal diversities in both rivers, and forested reaches were more diverse than grassy reaches in SR. Whereas meiofaunal taxa (cladocerans and hydroids) were more common in upstream samples, sand-cased trichopteran larvae and homopterans were more abundant downstream.

The six bottom- vs. top-net comparisons revealed that the two techniques often gave similar results (see factor 4), with neither sample systematically higher in faunal diversity (Table 3 and Appendix 4). However, there was some clustering of bottom- vs. top-net samples on the other four factors, revealing that terrestrial and semi-aquatic insects (e.g., homopterans and nematoceran adults) were relatively more important in the upper water column and aquatic insects (e.g., chironomid larvae and mayfly nymphs) showed demersal tendencies (Appendix 4). Exceptions to the vertical trend were three aquatic, non-insect taxa that were common in top and bottom nets (cladocerans, ostracods, and oligochaetes) and

two aquatic-insect taxa that were more important in top nets (legged beetle larvae and stonefly nymphs).

Based on the pooled riparian-floral analysis, forested and shrubby sites were distinct from semi-forested and grassy sites in invertebrate composition,

faunal diversity being high to intermediate at semi-forested (8.5) and forested (6.9) sites (Table 4). Unforested reaches generally showed higher drift densities than treed reaches within sites, because of the influence of cladocerans, chironomids, and/or homopterans (Appendix 5). The uppermost two reaches in SR had the highest drift densities, which included a grassy-muddy (1A) and forested-rocky reach (1B). The third-highest drift density occurred at the uppermost reach in NR (1A), a grassy-muddy reach. These three reaches contained high cladoceran populations despite being far away from lakes (Figures 1 and 2).

In summary, the pooled and unpooled analyses suggest that longitudinal-position and riparian-floral characteristics were both important determinants of drift-invertebrate composition. Together with the riparian-invertebrate analysis, the results suggest that deforestation reduces the diversity of aquatic and riparian invertebrates and enhances the drift of aquatic and/or terrestrial invertebrates. In addition, some vertical stratification of invertebrate taxa were seen in the drift, reflecting the greater abundance of terrestrial and semi-aquatic taxa near the surface and aquatic taxa near the bottom.

3.3 Ecological Guilds

Based on the drift-density data of Appendix 5, multi- and univariate analyses were used to formulate riparian-floral habitat-use guilds. Factor analysis revealed seven important factors, which were indicative of five floral guilds (Table 5). Sand-cased trichopteran larvae and nematoceran pupae were highly dissimilar in distribution because they were abundant in different suites of

reaches. Average-ranks analysis showed that invertebrate taxa were most abundant in forested, semi-forested, shrubby, and/or grassy habitats; several taxa appeared to be generalized (Table 6).

Based on the above percent-abundance and density analyses for drift and riparian invertebrates, habitat-use guilds along the riparian-floral gradient are indicated in Table 6. There were three major floral guilds: treed (four taxa), generalized (seven taxa), and unforested (six taxa). Whereas sensitive and moderately sensitive taxa dominated the treed (forested/semi-forested) guild, generalized and unforested (shrubby-grassy) guilds contained taxa of various tolerances (Appendix 4); pollution-sensitive taxa were only somewhat more abundant at sites with intact, treed riparian zones.

The pooling of data into pollution-tolerance, macrohabitat, and/or trophic guilds further clarified trends along longitudinal and riparian-floral gradients for the drift and riparian data sets (Table 7). Drift-tolerance variables yielded conflicting results. Whereas sensitivity sums, % EPT, and diversity were higher downstream, the EPT:D ratio and sensitivity averages were highest in the middle SR and lower NR. SR semi-forested and NR shrubby sites appeared to be degraded based on sensitivity summation. In contrast, semi-forested sites showed the highest EPT values, partially wooded (SF and SH) sites yielded the highest EPT:D ratios, grassy sites had the lowest sensitivity averages, and treed sites showed the highest guild diversities, collectively suggesting that woody sites were less degraded.

Other guild analyses yielded clearer longitudinal and riparian-floral trends (Table 7). For the macrohabitat analysis, both the drift and riparian data sets showed higher abundances of terrestrial taxa downstream (i.e., higher guild diversity in the downstream drift). Although riparian-floral trends were not apparent among riparian invertebrates, deforestation appeared to favor terrestrial over aquatic invertebrate taxa in the drift (i.e., higher guild diversity in the grassy-site drift).

For the drift-trophic analysis, herbivorous guilds dominated all four longitudinal sites, guild diversity being somewhat higher downstream in SR because of lesser dominance by purely herbivorous taxa. Treed sites were more diverse because of lesser dominance by herbivorous guilds and increased abundance of predatory taxa.

4.0 Discussion

4.1 Riparian-Invertebrate Assemblages

Terrestrial invertebrates were more common downstream in SR and NR, where the streams were wider and canopy cover was lower, in contrast to expectations of the river-continuum concept (Vannote et al. 1980). Nevertheless, Angermeier and Karr (1983) found similar results to mine in tropical (Panamanian) streams and suggested that air turbulence may contribute to this ecological pattern. In contrast, Bailey's (1966) results better conform to the river-continuum concept, in that relatively more terrestrial invertebrates (in contrast to aquatic and emergent taxa) were found in an English tributary, which had more overhanging cover than the mainstem. The pattern evident in SR and NR may indicate downstream increases in terrestrial productivity; warmer air temperatures at lower elevations may have counteracted longitudinal declines in canopy cover. The hypothesis could be evaluated by quantitatively sampling invertebrates throughout the riparian zone, rather than just near the stream as is commonly done with bucket (Mason and MacDonald 1982; Angermeier and Karr 1983) and emergent-trap sampling.

Terrestrial (arachnid spiders and homopterans) and emergent insects (nematoceran and brachyceran dipterans) were dominant in riparian SR-NR samples, and terrestrial hymenopterans were consistently present (Tables 1 and 2). These taxa were generalized or grassy in floral habitat use (Table 6). Mason and MacDonald (1982) found arachnids, homopterans, and dipterans to be the

dominant fallen invertebrates (along with beetles and lepidopterans) in an English stream with a riparian zone of deciduous trees, whereas dipterans dominated sticky-trap samples taken above and along a U.K. moorland stream subjected to livestock grazing (Nelson 1965). Jackson and Fisher (1986) found that adult chironomids and mayflies were the dominant fallen-insect taxa in an open-canopy desert stream in Arizona. Hooper and Savard (1991) found dipterans and hymenopterans (ants) to dominate grassland habitats in the central interior of BC. Both dipteran suborders were dominant in emergent-trap samples taken in the lower Fraser River and other BC estuaries (Whitehouse et al. 1993). Thus, dipterans are common elements of riparian-invertebrate faunas, reflecting the abundance of chironomids and other dipterans in treed and unforested habitats.

Although treed reaches had higher taxonomic diversity than did unforested reaches, invertebrate diversity was similar when reaches were pooled by riparian-vegetation type. That is, unforested sites were generally lower in alpha (small-scale) but not beta (medium-scale) diversity (sensu Cody and Diamond 1975) because invertebrate assemblages were more heterogeneous among stream reaches for unforested than treed sites.

4.2 Drift-Invertebrate Assemblages--Longitudinal and Vertical Patterns

Longitudinal patterns for invertebrate taxa were inconsistent for drift vs. riparian samples, and there were no obvious trends for the trophic guilds. The lack of pattern may reflect the limited longitudinal extent of sampling and use of crude trophic guilds rather than functional groups. For example, Hawkins and Sedell (1981) found that benthic macrodetritivores (shredders) decreased downstream and were replaced by benthic algivores (scrapers) in midsized streams and benthic microdetritivores (collectors) in large rivers, such that herbivore:predator ratios were similar longitudinally for aquatic macroinvertebrates (chironomids excluded).

Vertical-drift patterns were apparent; winged taxa were generally found near the surface and aquatic taxa were usually found near the bottom as also found by O'Connell (1978) in an Alberta river. Nevertheless, terrestrial and aquatic invertebrates were both important in my surface nets, as with Graessner's (1988) drift samples in New Zealand streams. Other researchers have also found vertical stratification in the drift, but patterns often differed from mine. First, SR-NR samples showed planktonic microcrustaceans to be generalized or demersal in drift behavior (Appendix 4), whereas Matter et al. (1983) found escaped-reservoir taxa (zooplankton and chaoborids) especially in surface nets in the downstream tailwater. Second, although active aquatic insects (e.g., baetid-mayfly nymphs) often characterize the upper water column, in contrast to heavier and/or otherwise-attached taxa (e.g., caddisfly larvae) that only enter the bottom drift or rarely drift (Waters 1965; Bailey 1966; Matter and Hopwood 1980; Dudgeon 1983; Matter et al. 1983), percent-abundance data for SR-NR samples and Wefring and Hopwood's (1981) density data show that mayfly nymphs and other aquatic taxa were more common in the demersal drift. O'Connell (1978) found that baetid nymphs were more dense in the bottom drift than in the near-surface drift and benthos, whereas chironomid larvae and pupae showed similar abundance in all three samples and most other EPT taxa were most dense in the benthos; this corresponds to Bailey's (1966) finding that burrowing and/or clinging mayfly nymphs are more demersal than baetid nymphs. These results collectively suggest that winged taxa are more surface-oriented than aquatic invertebrates, especially inactive benthic taxa.

4.3 Drift-Invertebrate Assemblages--Floral Patterns

Invertebrate drift was higher but less diverse in unforested reaches than in treed reaches within the same SR-NR site, because of enhanced drift by cladocerans. The highest drift densities were found in the upper SR, in grassy and forested reaches; the high drift in the latter reach may reflect residual influences of the extensive agricultural zone at and upstream of the nearby grassy reach.

Logging and other human activity often enhance invertebrate drift, in association with increased stream productivity (Larimore 1974; Hunt 1975; Angermeier and Carlson 1985; Wilzbach et al. 1986; Salo and Cundy 1987) and zoobenthic densities at the expense of aquatic-invertebrate diversity (Wilhm 1972; Mylinski and Ginsburg 1977; Washington 1984); all of these trends were apparent in SR-NR samples (Vadas 1997a). On the other hand, if agricultural damage to aquatic habitat is extensive, as in the case of channelization, invertebrate drift may be lower than in unimpacted streams with more intact (woodland) riparian zones (Zimmer and Bachman 1978). In Schlosser's (1982) study of two Illinois streams, the woodland stream had higher invertebrate-drift densities than did the agriculturally impacted, channelized stream in the spring, opposite of summer patterns, whereas the two streams showed similar drift densities in June.

Other researchers have also obtained conflicting results. Narver (1972) and de Leeuw (1982) found that logging had little effect on drift densities in coastal BC watersheds. Slaney et al. (1977) found lower drift densities at sites logged to the streambank in a northern BC watershed. Dance and Hynes (1979) found higher biomass-drift rates (biomass/unit time) of invertebrates in downstream, wooded sites for two Ontario streams, as compared to sites in treeless pastures. Hershey and colleagues (Hinterleitner-Anderson et al. 1992; Hershey et al. 1993) found higher invertebrate drift densities in a fertilized (vs. unfertilized) reach of an Alaskan river, presumably because food availability was adequate to minimize nymphal migrations (cf. Brittain and Eikeland 1988). However, other U.S. (Waters 1969; Larimore 1974; Shiozawa 1986; Allan 1987) and European workers (Bailey 1966; Ghetti and Ravanetti 1984) have found drift densities of aquatic taxa to be positively correlated with zoobenthic densities, although drift was not necessarily density-dependent. Indeed, drift intensity is likely to vary ontogenetically, with increased drift for newly hatched and/or late instars (Brittain and Eikeland 1988), such that O'Connell (1978) only found a positive drift-benthic correlation for baetid-mayfly nymphs in western Canada. Because the SR-NR results suggest that only certain invertebrate taxa increase with riparian

deforestation (Table 6 and Appendix 5), the relationship between drift and benthic densities deserves further study in relation to human impacts.

Along with the SR-NR results, available data suggest that agricultural and other human impacts increase the abundance of cladocerans and/or copepods. Several North American researchers have found these microcrustaceans and other non-insect invertebrates to be more common drifters in streams impacted by agriculture, urbanization, or channelization, relative to undamaged streams with more-forested riparian zones and better instream habitat (e.g., cleaner water, coarser substrata, and/or more-permanent flow) (Northcote et al. 1976; Huish and Pardue 1978; Dance and Hynes 1979; Angermeier and Carlson 1985). Palmer (1990b) reviewed literature showing that benthic meiofauna were common in sandy streams in the eastern U.S. and Canada. The data set included a forested section of a Virginia stream (Goose Creek) with upstream agricultural impacts; cladocerans, copepods, and other meiofauna were important components of drift and benthic samples and fish diets (Vadas 1988, 1990; Palmer 1990a,b, 1992; Palmer et al. 1992).

In contrast, ostracods were more abundant at forested sites in SR and NR and hydroids were generalists (Table 6), corroborating drift studies in Ontario streams. First, ostracods showed higher percent abundance and species richness in the cleaner, permanent stream studied by Hynes and colleagues in Ontario (Dance and Hynes 1979; Victor et al. 1981). These dominant microcrustaceans consisted only of stagnant-pool species in the agriculturally impacted, intermittent stream, whereas the permanent stream also contained riffle species. Second, Fraikin and Anderson (in Anderson et al. 1996) found hydroids to be generalists in another Ontario stream, as these cnidarians were abundant up- and downstream of sedimentation (pipeline) impacts. Hence, agricultural and related activities may decrease the abundance of drifting ostracods via changes in physicochemical characteristics that benefit cladocerans and copepods but have little effect on hydroids.

Dominant macroinvertebrates in the SR-NR drift samples included terrestrial (homopterans), emergent (nematoceran adults), and aquatic insects (chironomids and sand-cased caddisfly larvae) (Tables 3-4). These taxa used forested to grassy habitats (Table 6). Chironomids and terrestrial invertebrates were more abundant at deforested sites than mayflies and caddisflies, particularly sand-cased caddis larvae (Table 6). In contrast to streams with extensive agrarian damage from channelization or loss of permanent flow (Dance and Hynes 1979; Marsh 1980), grassy sites in SR and NR did not show enhanced drift of gastropods (Appendices 3-4). Light levels and water temperatures are probably not high enough in my study streams to stimulate blooms of algae, aquatic-vascular plants, and thus herbivorous gastropods (Marsh 1980; Petersen et al. 1987). Indeed, stream temperatures during sampling were adequate (≤ 18 to 20°C) for large-bodied, sensitive aquatic insects, i.e., EPT taxa (Ross 1963; Gaufin 1973; Hynes 1976; Biggs et al. 1990).

Other drift data sets and information largely corroborate the riparian-floral patterns in the SR-NR samples. Logged streams in BC have shown enhanced drift of dipterans (mostly chironomids) at the expense of mayflies (Slaney et al. 1977; de Leeuw 1982), although other BC and U.S. researchers have found both taxa to be abundant drifters regardless of deforestation impacts (Narver 1972; Schlosser 1982). De Leeuw (1982) also found that the species richness of drift invertebrates decreased with logging, particularly for caddisflies. Dance and Hynes (1979) found relatively more terrestrial insects and less caddisflies drifting at agriculturally impacted (intermittent) sites in an Ontario watershed. Pollution-sensitive invertebrate taxa (caddis- and mayflies) were more prevalent in the drift and benthos of natural, woodland streams in the U.S., whereas chironomids and oligochaetes were usually more important in the drift and benthos of streams subjected to riparian deforestation and instream-habitat impacts (Griswold et al. 1978, 1982; Huish and Pardue 1978; Zimmer and Bachman 1978). Sand-cased caddisflies are considered to be especially intolerant of pollution in North Carolina, whereas aquatic mites are especially

sensitive to sedimentation in Alaska (Wagener and LaPerriere 1985). However, the relative abundance of aquatic vs. terrestrial invertebrates requires further study, given that aquatic and terrestrial drift may both decrease (Slaney et al. 1977) or increase with riparian logging (Sharpe 1975).

The SR-NR drift results also suggest that deforestation causes an increase in herbivorous taxa at the expense of predatory invertebrates, as supported by zoobenthic for these streams (Vadas 1997a). These results conflict with U.S. Pacific Northwest data, because scrapers (algivores) and predators generally increase at the expense of detritivores after logging of small streams in this region (Hawkins et al. 1982; Salo and Cundy 1987). Perhaps the situation is different for BC streams, where logging favors terrestrial over aquatic invertebrates (Chamberlin et al. 1974; Culp and Davies 1983; Hartman and Scrivener 1990; given that riparian taxa are generally not eaten by aquatic invertebrates (Pennak 1978; Merritt and Cummins 1984; Cummins and Wilzbach 1985), deforestation should favor herbivorous over predatory aquatic taxa. Culp and Davies (1983), however, found no significant effects of logging on functional-group composition of benthic macroinvertebrates in a coastal BC watershed; collectors, scrapers, and predators were consistently predominant.

Zoobenthic data from other locations also provide partial corroboration of my H:P results. In a warmwater Michigan stream, King and Ball (1967) found that benthic herbivores (oligochaetes and herbivorous insects) were relatively more abundant at degraded sites, i.e., those with greater sewage-outfall inputs and riparian deforestation; the two woodland sites were the only ones to have H:P production ratios below unity for aquatic insects. All five sites, however, showed uniform decreases in all three groups of aquatic invertebrates when siltation from highway construction was severe, reflecting the opposing effects of sewage enrichment vs. sedimentation impacts on periphyton (benthic algae). Rounick et al. (1982) found that aquatic invertebrates ate relatively more autochthonous foods (e.g., algae) in grassland and older-clearcut streams than in forested

creeks of New Zealand, even though zoobenthic species compositions were similar across all streams. Hence, H:P ratios based on taxonomic status, rather than dietary data, may sometimes be unrealistic for showing increased herbivory in moderately impacted streams. The differences among studies suggests that further deforestation research with small net meshes is necessary to examine drift and benthic samples; inclusion of meiofauna and chironomids in the SR-NR study (contra Hawkins and Sedell 1981; Hawkins et al. 1982) heightened the dominance of herbivorous guilds.

4.4 Drift-Invertebrate Sampling - Caveats

The quantitative values of pollution indices for SR-NR drift (Table 7) and zoobenthic samples (Vadas 1997a) did not match literature expectations, probably due to methodological differences between our results and those of other researchers. EPT percentages were much less than Munro and Taccogna's (1994) criterion of 50% for 'excellent' streams, probably because the criterion was developed for benthic (rather than drift) samples. Indeed, benthic samples often showed higher EPT values, although not always for more-forested sites (Vadas 1997a). And although the EPT:D ratio was higher for partially wooded sites in the drift, the ratio showed highest values at less-forested sites for my benthic samples (Vadas 1997b). Sensitivity sums and averages also yielded ambiguous results for drift (Table 7) and benthic samples (Vadas 1997a), especially since all sums greatly exceeded the 'excellent' criterion (i.e., 23) of Kellogg (1991) and McDonald et al. (1991); the latter result may reflect the larger net-mesh size and less taxonomic splitting for these latter, layperson techniques. Perhaps the ambiguity of these various pollution indices for drift reflects the fact that spatiotemporal heterogeneity in the relative abundance of EPT vs. dipteran taxa can be large in drift samples (Waters 1969; Larimore 1974; Muller 1974; Allan et al. 1988; Brittain and Eikeland 1988), which would clearly affect pollution indices; the SR-NR drift samples were only collected during daylight hours in the autumn (in different months for the two rivers), most

of the samples being taken in run habitats. Nevertheless, benthic samples also did not show expected trends (Vadas 1997a,b), suggesting that the H:P ratio is a better ecological indicator of deforestation than these pollution indices. Although the usefulness of the EPT index to assess pollution impacts may result from the index being applied as taxonomic richness (Lenat and Penrose 1996) rather than percent abundance as I have done, both indices are sensitive to natural factors; smaller substratum and stream sizes often yield lower EPT values (as richness and/or percent of total production), and EPT may increase with clearcutting or nutrient enrichment if periphyton is enhanced (Eaton and Lenat 1991; Lowell and Culp 1996; Wallace et al. 1996).

Two other important factors controlling drift density are flow rate and mesh size (Clifford 1972; Graesser 1988; Brittain and Eikeland 1988), the latter particularly relevant for microcrustaceans and other meiofauna (Clifford 1972). Hence, nets of different mesh size are likely to differ in the relative abundance of invertebrate taxa and thus yield different values for pollution indices. Given that meiofauna appear to be good indicators of human impacts (present study; Morell 1995), use of smaller mesh sizes can improve drift- and benthic-invertebrate monitoring of deforestation and other habitat damage. The present results suggest that microcrustaceans and other non-insect invertebrates vary in their sensitivity to human impacts, even though they all lack adult flying stages.

A final caveat is that the riparian-floral guilds formulated from the riparian and drift data did not completely match that for benthic data (Vadas 1997b), such that Vadas (1997a) should be consulted for guild formulations based on all three invertebrate data sets.

4.5 Management Implications

Considerations of spatiotemporal scales is important for research and management activities in aquatic and terrestrial ecosystems via hierarchical analysis (Marmorek et al. 1993; Woodley et al. 1993; Vadas and Vadas 1995).

In the present paper, examination of unpooled and aggregated data were used to distinguish invertebrate-assemblage patterns along a riparian-floral gradient. Analyses of sites pooled by floral characteristics helped clarify general ecological patterns that might not have been forthcoming from unaggregated analyses because of "noise", i.e., urbanization, mining, and other human impacts unrelated to *in situ* deforestation impacts. Factor analysis is amenable to hierarchical analysis, and presentation of results via multivariate-similarity tabulation (as done here) addresses the criticism (Gerritsen 1995; Fore et al. 1996) that multivariate-statistical methods (despite their reliability) are abstruse, not easily standardized, and do not incorporate biological information into the presentation of results.

Because efforts to control pollution in North America have traditionally focused on point (end-of-pipe) sources rather than on agricultural and other nonpoint (diffuse) sources of pollution (Harvey 1976; Smith et al. 1987; Wentworth 1993), maintenance of riparian-buffer strips to protect water quality and quantity, and thus aquatic biota, has received attention only recently. Riparian trees and tall grasses can retain 80 to 90% of the sediments and nutrients that would otherwise enter streams, as long as the buffer strips are 10 to 50 m in width (Mahoney and Erman 1984; Decamps et al. 1988; Chauvet and Decamps 1989; Gresswell et al. 1989; Welsch 1991; Brewin 1992; Osborne and Kovacic 1993) and preferably 60 to 300 m wide (Tippett and Guglielmo 1993). Forested buffer strips of these dimensions also retain toxins such as pesticides and heavy metals (Winger 1986), protect on-site and downstream thermal regimes (Sharpe 1975; Osborne and Kovacic 1993), and in some cases minimize evaporation losses (from sun exposure) that make permanent streams intermittent (Graf 1980; Bosch and Hewlett 1982; Elmore and Beschta 1987; Petersen et al. 1987). Buffer strips wider than 50 m are needed to maintain inputs of riparian-detrital foods to streams (Petersen et al. 1987) and biodiversity of riparian vertebrates (Vadas and Newman 1997). Clearly, interdisciplinary coordination among management agencies is critical for protecting watershed ecosystems vs.

deforestation impacts (Mackenzie 1980; Allan and Flecker 1993; King et al. 1993).

As emphasized by Rounick and Winterbourn (1982), the presence of riparian vegetation is probably more influential than longitudinal position and floral-species composition for determining zoobenthic-assemblage patterns in temperate streams; riparian forests, plantations, and grasslands all allow proliferation of EPT (sensitive-insect) taxa. Apparently, stream stability is the main determinant of macroinvertebrate patterns, because of increased stability of habitat and food resources (Rounick and Winterbourn 1982). Because Pacific Northwest studies of riparian deforestation are contradictory in showing little (Narver 1972; Culp and Davies 1983) or significant effects on aquatic-invertebrate composition (present study; Hawkins et al. 1982; de Leeuw 1982), future deforestation studies should establish the relations between habitat stability and assemblage structure of drift and benthic invertebrates. The present study and examination of other plant and animal assemblages in the SR and NR watersheds suggest that semi-forested habitats are conducive to ecosystem integrity and thus protection of fisheries and wildlife resources in the southern interior of BC (Michel 1997; Vadas 1997a).

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TABLES

Table 1. Multivariate-similarity table to assess similarity of riparian-invertebrate assemblages across study reaches, based on varimax-factor analyses with the data of Table 1. There were four important factors; these clusters are indicated by similarity bars (). SM, SL, NM, and NL respectively represent the middle and lower Salmon and Nicola valleys, whereas FO = forested, SF = semi-forested, SH = shrubby, and GR = grassy. Sample sites stacked vertically in the diagram loaded highly on the same factor axis, whereas those placed horizontally and connected by a similarity bar were moderately similar. DM = dominant, S = subdominant, and '.' = other (rarer) species.

	SM-SF	SL-SF	SL-FO	NL-SF	NL-GR	NM-SF	SL-GR	NM-GR	SM-GR-E	SM-GR-S	NM-SH	SM-FO	NL-SH
Spiders (Araneida)	S	S	S	S	S	S	S	S	S	DM	DM	DM	DM
Homoptera	DM	DM	DM	DM	DM	DM	DM	DM	DM	S	S	S	S
Nematoceran adults	S	S	S	S	S	S	S	S	S	DM	DM	DM	DM
Brachyceran adults	S	DM	DM	DM	DM	DM	DM	DM	DM	S	S	S	S
Hymenoptera	S	S	S	S	S	S	S	S	S	S	S	S	S
S-L diversity	2.1-4.5	4.4	3.4-4.0	1.5-3.0	5.1	2.2							

Table 2. Multivariate-similarity tables to assess similarity of riparian-invertebrate assemblages across a riparian-floral gradient, based on varimax-factor analysis. The pooled data represent average percentages for each vegetation type across rivers, based on the data of Appendix 2. Dominant (DM), subdominant (S), and common (c) species ($\geq 4\%$) are shown. See Table 1 for format.

	FO		
	SF	SH	GR
Spiders (Araneida)	S	DM	S
Homopterans	DM	C	DM
Nematoceran adults	C	S	DM
Brachyceran adults	C	C	DM
Hymenopterans	C	-	C
S-L diversity	4.2-4.4	3.7	4.9

Table 3 Multivariate-similarity table to assess similarity of drift-invertebrate assemblages across study reaches, based on varimax-factor analyses with the data of Appendices 3-4. Dominant (DM) and subdominant (S) species are shown. NM = nymphs, LV = larvae, AD = adults, and TRIC = trichopterans.

	NM-SF NL-SH	SM-SF-B SL-SF SL-GR-B SL-FO-B NM-GR	SM-SF-T	NM-SH-B NL-SF	SM-GR-B SM-GR-T SM-FO-B SM-FO-T SL-FO-T NM-SH-T	SL-GR-T NL-GR
Chironomid LV	DM	DM	DM	.	.	S
Nematoceran AD	S	.	DM	DM	.	S
Sand-cased TRIC LV	DM	.	S	S	.	.
Homopterans	S	.	S	.	.	DM
Cladocerans	DM	.
Ephemeropteran NM	.	S	S	.	.	.
Hydroid cnidarians	S	.
Diversity	5.9	2.3-7.3	8.5	8.9	1.2-3.1	2.3-5.1

Table 4. Multivariate-similarity tables to assess similarity of drift-invertebrate assemblages across a riparian-floral gradients, based on varimax-factor analyses. The pooled data represent average percentages for each vegetation type across rivers, based on the data of Appendices 3-4. Dominant (DM), subdominant (S), and common (c) species (> 4%) are shown.

	FO		
	SH	SF	GR
Chironomid larvae	S	DM	DM
Cladocerans	DM	.	DM
Homopterans	c	c	DM
Nematoceran adults	c	S	S
Sand-cased trichopteran larvae	c	c	.
Ephemeropteran nymphs	.	S	c
Hydroid cnidarians	c	c	.
Uncased trichopteran larvae	.	c	.
Nematoceran pupae	.	c	.
Oligochaetes	.	.	c
Ostracods & plecopteran nymphs	.	c	.
S-L diversity	5.5-6.9	8.5	6.7

Table 5. Multivariate-similarity table to assess habitat-use (guild) associations among drift-invertebrate taxa across stream reaches, based on varimax-factor analyses with the data of Appendix 5. Reaches where taxa were highly or moderately abundant (relatively), as well as floral-guild classifications, are shown; GEN = generalized on the riparian-floral gradient. Positive and negative signs are shown for taxa that loaded highest on the same axis with opposite signs. See Table 1 for format and Appendix 5 for taxon abbreviations.

	EPHE	MITE	OLIG	CHIR ^a	NEMA ^b	HOMO	(+)	(-)		
	HYDR	UNCA	COLL	BRAC	SAND	NEMP	PLEC	LEPI		
Highly abundant	S1B	S1A	S2B	N2B	S1C&N2C	S2B	N1B	N2C		
Moderately abund.	S1A	S1B	S1C	--	N2A&N2B	S2C&N1A	S1A-S2A ^c	--		
Floral guild	GEN-FO	GEN-GR	GEN-GR	GR	GEN	GEN-GR	GEN	SH		

^aThis taxon was also highly abundant in reach S2B.

^bThis taxon was also moderately abundant in reaches S1B and N1C.

^cModerately abundant in reaches S1A to S2A.

Table 6. Floral-guild classifications of abundant riparian (RIP) and drift-invertebrate taxa, based on Tables 2 and 4-5 and Appendix 5. Data types include percentage (%) and density (DENS) data, as well as average ranks for the comparisons of invertebrate density among vegetation-type triplets within stream sites (middle and lower sites for each river): ranks of 1 and 3 represent highest vs. lowest density, respectively. GEN = generalized and UF = unforested (shrubby-grassy) in habitat use.

Data type &/or vegetation category	Sampling Location		DENS	Average rank				OVERALL COVER GUILD	
	RIP %	Drift %		FO	SF	SH	GR		
Mites (Hydracarina)	.	.	GEN-FO	<u>1</u> ^a	2.2 5	1.5	2.5	FO	FO
Ostracods	.	SF	GEN-FO	<u>1</u>	1.7 5	2.7 5	2.4	FO	FO
Sand-cased trich. LV	.	GEN-FO	GEN	2.2 5	1.7 5	<u>1</u>	2.6	SH	GEN-FO
Plecopteran nymphs	.	SF	GEN	2	<u>1.7</u> 5	2	2.2 5	GEN-SF	SF
Ephemeropteran nymphs	.	SF	GEN-FO	2	2	3	<u>1.5</u>	GEN-GR	GEN
Uncased trich. LV	.	SF	GEN-GR	<u>1.5</u>	2	2.5	2	GEN-FO	GEN
Nematoceran adults	GR	GEN	GEN-GR	<u>1.5</u>	2.2 5	2.5 5	1.7 5	GEN-FO	GEN
Collembolans	.	.	GEN-GR	2.5	<u>1.2</u> 5	2	2.5	SF	GEN
Hymenopterans & spiders	GEN	GEN
Hydroid cnidarians	.	GEN-FO	GEN-FO	2	2.4	<u>1.7</u> 5	1.7 5	GEN-UF	GEN
Oligochaetes	.	GR	GEN-FO	2	2	<u>1.5</u>	2.2 5	GEN-SH	GEN
Aquatic lepidopt. LV	.	.	SH	2	2.1	<u>1.5</u>	2.1	GEN-SH	SH
Chironomid larvae	.	GEN	GEN-GR	2	2.7 5	<u>1</u> 5	1.7 5	SH	GEN-GR
Nematoceran PP	.	SF	GEN-GR	2	2.2 5	2	<u>1.7</u> 5	GEN-GR	GEN-GR
Homopterans	GEN	GR	GR	<u>1.5</u>	2.7 5	2.0	<u>1.5</u>	GEN	GEN-GR
Cladocerans	.	GEN	GEN-GR	<u>1.5</u>	2.5	<u>1.5</u>	2	GEN	GEN-GR
Brachyceran AD	GR	.	GR	2	2.2 5	2	<u>1.7</u> 5	GEN-GR	GR

^aThe riparian-vegetation type with the lowest average rank is underlined for each taxon, to indicate where the taxon was most abundant.

Table 7. Relative (percent) abundance of riparian- and drift-invertebrate guilds across longitudinal and riparian-floral gradients, based on the data of Appendices 2-4. MID = middle and LOW = lower river. Sensitivity indices were based on assignment of points for each taxon, as defined in the text and Appendices 2-4; indices I and II were respectively based on percent-abundance vs. presence-absence data. Percent EPT is the relative abundance of large-bodied, pollution-sensitive taxa, i.e., ephemeroptera, plecoptera, and trichoptera. EPT:D is the numerical ratio of EPT taxa vs. diptera, whereas H:P = overall herbivore:predator ratio.

	Floral						Longitudinal			
	Salmon R.			Nicola R			Salmon R.		Nicola R.	
	FO	SF	GR	SF	SH	GR	MID	LOW	MID	LOW
RIPARIAN SAMPLES										
Habitat guilds										
Terrestrial ^a	72	74	31	68	58	68	48	70	50	79
DRIFT SAMPLES										
Pollution-tolerance guilds										
Sensitive	22	41	13	33	22	23	28	24	20	35
Sensitive-moderate	+	+	1	0	0	0	0	1	0	0
Moderate	41	11	47	17	41	8	49	14	33	11
Moderate-tolerant	10	13	10	19	10	31	5	19	12	28
Tolerant	27	34	29	30	27	38	18	43	34	26
Sensitivity index I (average)	1.9	2.0	1.8	1.9	1.9	1.7	2.1	1.7	1.8	1.95
Sensitivity index II (sum)	50.5	41	53	36.5	34.5	36.5	40	58.5	37	38.5
% EPT	9	32	8	32	17	21	15	19	18	32
EPT:D ratio	0.3	0.8	0.25	0.7	0.6	0.5	0.9	0.4	0.4	0.9
S-L diversity	3.4	3.2	3.0	3.7	3.3	3.4	2.8	3.4	3.5	3.6
Macrohabitat guilds										
Aquatic	86	84	81	77	86	48	92	76	89	51
Semi-aquatic	4	10	7	17	9	19	5	9	10	20
Terrestrial	9	6	11	6	5	33	3	14	1	29
S-L diversity	1.3	1.4	1.5	1.6	1.3	2.7	1.2	1.7	1.2	2.6

Table 7 (Continued)

	Floral						Longitudinal			
	Salmon R.			Nicola R			Salmon R.		Nicola R.	
	FO	SF	GR	SF	SH	GR	MID	LOW	MID	LOW
Trophic guilds (and assumed H:P ratios)										
Herbivorous (H only)	48	41	60	39	65	44	64	30	50	52
Predominately herbivorous (2:1)	26	35	30	33	26	48	15	52	35	30
Herbivorous-predatory (1:1)	3	8	32	18	5	5	5	4	8	12
Predominately predatory (1:2)	1	0	+	5	0	0	0	1	2	1
Predatory (P only)	21	16	7	5	5	4	16	12	5	4
Overall H:P ratio	2.1	2.2	4.3	2.5	5.2	3.5	3.3	2.1	3.5	3.8
S-L diversity	2.9	3.1	2.2	3.4	2.0	2.4	2.2	2.7	2.6	2.6

^aDoes not include the semi-aquatic guild.

FIGURES

Figure 1. Map of the Salmon River watershed. The study sites (#1 and 2) on the river include three reaches (A, B, and C) of differing riparian intactness (as indicated). The Salmon watershed is northeast of the Nicola watershed (figure 2), originating near 50°10' north and 119°45' west coordinates. Asterisks (*) indicate reaches with obvious cattle damage.

Figure 2. Map of the Nicola River watershed. The study sites (#1 and 2) on the river include three reaches (A, B, and C) of differing riparian intactness (as indicated). The Nicola River originates near 50°10' north and 119°45' west coordinates. Asterisks (*) indicate reaches with obvious cattle damage.

APPENDIX

Appendix 1 Aquatic physicochemical variables measured during invertebrate sampling. Water temperature, which was measured in the morning, noontime, and afternoon (N = 3), was summarized as mean, minimum, and maximum values. Average velocity was calculated as 90% vs. 80% of surface velocity over fine (*) vs. coarse substrata, respectively. Mesohabitat types included runs in the head (HR) or tail of pools (TR) or central locations of pools (PL), runs (RN), or riffles (RF). Reaches were forested (FO), semi-forested (SF), shrubby (SH), or grassy (GR).

	Salmon River						Nicola River					
	Middle			Lower			Middle			Lower		
	GR	FO	SF	SF	GR	FO	SH	SF	GR	SF	GR	SH
Temperature data (°C)												
Mean	15	14	14	16	15	15	15	16	12	10	8	9
Minimum	14	13	11	13	13	12	14	14	10.5	8	5.5	7
Maximum	15	15	16	19	18	17	16	17	14	11	10	11
Drift-net data												
Depth (cm)	31	44	40	31	24	31	61	39	76	49	51	40
Average velocity (cm/s)	15*	19	44	43	34	67*	28*	35	26	36	38	33
Sample time (h)	4.5	4.5	6.0	6.0	2.6	5.4	5.0	3.2	3.0	2.25	2.0	2.3
Mesohabitat type	PL	TR	TR	TR	TR	RN	PL	TR	HR	RF	TR	TR

Appendix 2 Relative (percent) abundance of riparian invertebrates in the Salmon and Nicola valleys. Sampling was spatially stratified by site (middle and lower river) and reach (riparian intactness). Collections were made with emergent traps (E), a sweep net (S), or both techniques (ES). S-L diversity is the Simpson-Levins index, whereas + indicates < 1%. See Appendix 1 for riparian-floral categories.

Vegetation category Sampling technique	Salmon River						Nicola River						
	Middle			Lower			Middle			Lower			
	GR E	FO S	SF ES	SF ES	GR ES	FO ES	SH S	SF S	GR S	SF S	GR S	SH S	
TERRESTRIAL INVERTEBRATES													
Hemipterans													
Homopterans	11	1	16	42	54	13	47	21	34	19	31	65	4
Heteropterans	0	2	2	2	3	1	+	3	1	0	3	1	+
Other insects													
Orthopterans	0	0	0	1	0	0	0	0	0	0	0	0	+
Thysanopterans	0	1	1	0	2	1	0	0	6	3	0	0	0
Hymenopterans	0	1	5	3	0	2	5	3	2	0	13	21	1
Dipteran pupae	0	0	0	0	0	1	0	0	0	0	1	0	0
Coleopterans	0	0	0	0	0	1	0	2	3	0	0	0	0
Lepidopterans	0	0	0	0	0	0	0	0	0	0	0	0	+
Unknown insects	0	2	1	0	4	0	3	0	0	0	0	0	1
Arachnids													
Spiders (Araneida)	1	19	31	19	17	23	31	19	16	16	26	8	60
Mites (Acarina)	0	0	4	0	1	+	0	0	0	0	0	0	0
OTHER INVERTEBRATES													
Roundworms (Nematoda)	0	0	0	0	0	+	0	0	0	0	0	1	0
Oligochaetes	0	0	0	0	0	1	0	0	1	3	0	0	0
Semi-aquatic insects													
Dipterans													
Brachycerans	2	0	11	2	2	41	6	1	27	47	19	1	28
Nematocerans	80	73	24	29	8	9	8	50	12	12.	4	4	4
Unknowns	1	0	0	0	0	0	0	0	0	5	0	0	0
Other insects													
Collembolans	0	1	1	0	5	+	0	0	0	0	0	0	0
Ephemeropterans	5	1	5	2	3	1	1	0	0	0	0	0	0
Dragonflies (Odonata)	0	0	0	0	0		0	0	0	0	0	0	0
Trichopterans	0	1	0	1	0	4	0	0	0	0	1	0	0

	Salmon River						Nicola River						
	Middle			Lower			Middle			Lower			
	GR	FO	SF	SF	GR	FO	SH	SF	GR	SF	GR	SH	
Vegetation category	E	S	ES	ES	ES	ES	S	S	S	S	S	S	
Sampling technique													
Total # of animals	164	172	191	124	118	220	251	125	113	32	68	145	269
S-L diversity	1.5	1.8	5.1	3.4	3.0	4.0	3.1	3.0	4.4	3.4	4.5	2.1	2.2

Appendix 3 Percent abundance of drifting invertebrates in the sites and reaches of the Salmon River. Sampling was done with bottom (B), top (T) nets, or both nets (BT). Sample sizes (N) represent the actual number of invertebrates sampled. See Appendix 2 for format.

Vegetation Category Net Location	Salmon River										
	Middle						Lower				
	GR		FO		SF		SF	GR		FO	
	B	T	B	T	B	T	BT	B	T	B	T
EPHEMEROPTERANS (mayflies)											
Nymphs	3	1	5	5	20	11	15	11	3	7	3
Adults	0	0	0	0	0	0	0	0	2	0	1
COLEOPTERANS (beetles)											
Curculionidae larvae	+	0	0	0	0	0	0	0	0	0	0
Legged larvae ^a	0	0	0	+	0	0	1	0	2	0	0
Elmid adults	0	0	0	0	0	0	0	1	0	0	0
TRICHOPTERANS (caddisflies)											
Sand-cased larvae	0	0	0	0	7	9	9	1	0	3	1
Uncased larvae	5	1	2	1	9	4	1	1	0	4	2
Adults	0	0	0	0	0	0	1	0	1	0	0
DIPTERANS (true flies)											
<u>Brachycerans</u>											
Orthorrhapha larvae	0	0	0	0	0	0	0	0	0	0	1
Adults	0	0	0	0	0	0	0	0	0	0	0
<u>Nematocerans</u>											
Ceratopogonid larvae	0	0	0	0	0	0	0	1	0	0	4
Chaoborid larvae	0	0	0	0	0	0	0	0	0	1	1
Chironomid larvae	11	1	5	2	37	21	28	63	15	45	29
Dixid larvae	0	0	0	0	0	0	1	0	0	1	1
Simuliid larvae	0	0	0	0	1	1	0	0	0	0	0
Tipulid larvae	0	0	0	0	0	0	0	0	3	0	0
Unknown larvae	0	+	0	0	0	0	0	0	0	0	0
Pupae	0	0	0	0	0	0	10	9	6	11	9
Adults	+	+	0	3	2	18	4	2	17	1	12
OTHER INSECTS											
Collembolans	0	+	0	+	0	4	3	0	5	0	0
Dragonfly nymphs (Odonata)	0	0	0	0	0	0	0	0	1	1	0
Plecopteran nymphs	0	+	0	+	3	1	3	0	1	0	0
Aquatic lepidopteran larvae	0	0	0	0	0	0	0	0	0	0	0
Homopterans	0	0	+	1	0	9	3	7	38	7	28
Hymenopterans	0	0	0	0	0	6	0	1	0	0	1
Thysanopterans	0	0	0	0	0	0	0	0	0	0	0
Unknown terrestrials	0	0	0	0	0	1	0	0	0	0	0

Appendix 3 (Continued)

Vegetation Category Net Location	Salmon River										
	Middle						Lower				
	GR		FO		SF		SF	GR		FO	
	B	T	B	T	B	T	BT	B	T	B	T
MOLLUSKS											
Pelecypods	0	0	0	0	0	0	0	0	0	2	0
Gastropods	0	0	+	2	0	1	0	0	0	1	0
ARACHNIDS											
Mites (Hydracarina)	1	+	3	1	4	6	4	1	0	8	8
Spiders (Araneida)	0	0	0	+	0	2	0	0	1	0	0
CRUSTACEANS											
Amphipods	+	+	0	+	0	0	1	0	0	0	0
Cladocerans	60	93	48	55	0	1	0	0	0	3	0
Copepods	2	1	1	+	0	0	0	0	0	2	0
Ostracods	0	+	2	2	1	2	4	1	0	5	0
OTHER INVERTEBRATES											
Hydroid cnidarians	11	1	29	18	12	4	8	1	3	1	0
Roundworms (Nematoda)	+	0	0	0	0	0	0	0	0	0	0
Oligochaetes	6	1	6	7	4	0	5	0	2	0	0
Total # (N)	432	3629	374	469	140	114	178	134	180	119	145
% of sample analyzed^b	100	100	30	61	100	30	100	100	100	34	100
S-L diversity	2.6	1.2	3.1	2.9	4.8	8.5	7.3	2.3	4.9	4.3	5.2

^aElmids and haliplids.

^bAssuming that each subsampled vial was 4.3% of the total sample (R.L. Vadas, Jr., unpubl. data).