Vertebrate Assemblages Associated with Headwater Hydrology in Western Oregon Managed Forests

Deanna H. Olson and George Weaver

Abstract: We characterized headwater stream habitats, fish and amphibian fauna, in and along 106 headwater stream reaches at 12 study sites within managed forest stands 40 to 70 years old in western Oregon. Headwater stream types in our sample included perennial, spatially intermittent, and dry reaches. We captured 454 fish of three species groups and 1,796 amphibians of 12 species. Using canonical correlation, nonmetric multidimensional scaling ordination, and generalized linear models, we identified species and assemblages associated with reach hydrologic type (e.g., perennial, intermittent, dry), stream size, gradient, and substrate composition. Our findings of torrent salamander (*Rhyacotriton* species) occurrences in spatially intermittent streams, and patchy and infrequent occurrences of *Cottus* fish (sculpins) and coastal tailed frogs (*Ascaphus truei* Stejneger) suggests these taxa warrant consideration during headwater management for retention of locally distinct biotic resources. FOR. SCI. 53(2):343–355.

Keywords: spatially intermittent streams, amphibians, trout, streambank, torrent salamanders, cottid fishes, tailed frogs

STREAM RIPARIAN ZONES are delineated ecologically by a suite of biophysical processes and properties that transition both latitudinally and longitudinally into the surrounding watershed (e.g., Gregory et al. 1991, Gregory 1997, Naiman and Decamps 1997, Naiman et al. 2000). In forested ecosystems of the Pacific Northwest, our understanding has grown over the last decade regarding the ecological characterization and functional role of headwater streams and riparian areas in larger ecosystem contexts. This has become a critical management issue in some areas due to the large spatial extent of headwater stream networks (e.g., 95% of stream channels [i.e., reaches], 70% of stream length [Meyer and Wallace 2001], and 70 to 80% of catchment areas (Gomi et al. 2002). The potential consequences for management of these streams are (1) longitudinal effects on downstream populations or processes (e.g., providing prey for fish production [Wipfli and Gregovich 2002], sediment delivery [Benda and Cundy 1990, Benda and Dunne 1997a, b], and wood [Reeves et al. 2003]); (2) the potential role in maintaining latitudinal populations or processes (e.g., reciprocal subsidies, Baxter et al. 2005); and (3) maintenance of populations or processes specific to headwaters (e.g., macroinvertebrates (Progar and Moldenke 2002, Meyer and Wallace 2001) and amphibians (Adams and Bury 2002, Sheridan and Olson 2003)). Nevertheless, our knowledge of the ecology of these systems remains sparse (Gomi et al. 2002) even though they have been characterized as undergoing widespread degradation at alarming rates (Meyer and Wallace 2001).

Furthermore, tying headwater ecological values to forest management practices has lagged, resulting in a wide array of headwater management approaches afforded to these systems (Gregory 1997, Sheridan and Olson 2003). At minimum, no riparian protection is provided, for example along ephemeral streams in British Columbia and in some US state or private lands. At maximum, entire hillslopes (landslide-prone areas, USDA and USDI 1994), headwater subdrainages (due to overlapping interim riparian reserves in highly dendritic stream networks) (USDA and USDI 1994) or location of patch reserves for species concerns (Cissel et al. 1998, 1999) have been proposed for protection on US federal lands. These conflicting approaches have raised the question, what are critical headwater riparian resources warranting mitigation in a managed forest landscape? In particular, the longitudinal transition of headwater streams and riparian zones from zero- to second-order (Strahler 1957) reaches needs refined characterization to better enable informed management decisions based on resource prioritization.

Amphibians have been proposed as potentially key taxa for consideration during headwater stream management in western Pacific Northwest forests (e.g., Bury 1988, Adams and Bury 2002), largely because they dominate vertebrate assemblages in the upper portion of watersheds (see Davic and Welsh 2004), and have documented effects resulting from forest management practices (e.g., site- and stand-level effects (Welsh and Lind 1996, deMaynadier and Hunter

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1995, Steele et al. 2003) and landscape-level effects (Raphael et al. 2002, Willson and Dorcas 2003, Stoddard and Hayes 2005). Several species have known headwater associations. *Ascaphus* (tailed frogs, 2 species), *Rhyacotriton* (torrent salamanders, 4 species), and *Dicamptodon* (Pacific giant salamanders, 4 species) are taxa endemic to the Pacific Northwest, are typically characterized as being found in headwaters (Davic and Welsh 2004, Jones et al. 2005), and are taxa of concern in the region (Blaustein et al. 1995, Corkran and Thoms 1996). Additionally, several woodland salamanders (Plethodontidae) are found in or along headwater streams and similarly have status of concern (e.g., Washington State: *Plethodon dunni* Bishop [Dunn's salamander], *P. vandykei* Van Denburgh [Van Dyke's salamander]; Corkran and Thoms 1996).

Many Pacific Northwest forest fauna have tight associations with vegetation conditions (e.g., Olson et al. 2001), whereas stream amphibians have strong associations with physical habitat features. For example, species-habitat associations are reported for substrate (e.g., coastal tailed frog, *Ascaphus truei* Stejneger: Adams and Bury 2002, Welsh and Lind 2002, Dupuis and Steventon 1999; Columbia torrent salamander, *R. kezeri* Good and Wake: Wilkins and Peterson 2000), gradient (stream: southern torrent salamander, *R. variegatus* Stebbins and Lowe, Diller and Wallace 1996; Olympic torrent salamander, *R. olympicus* Gaige, Adams and Bury 2002; sideslope: *Plethodon dunni*, Wilkins and Peterson 2000), surface geology (*R. variegatus*, Diller and Wallace 1996; *Dicamptodon* spp., *A. truei*, and *P. dunni*, Wilkins and Peterson 2000) northerly aspects (*R. kezeri* and *P. dunni*; Wilkins and Peterson 2000; coastal giant salamander, *Dicamptodon tenebrosus* Baird and Girard, Stoddard and Hayes 2005), and elevation and stream width (Cope's giant salamander, *D. copei* Nussbaum, Adams and Bury 2002; *A. truei*, *D. tenebrosus*, and *Rhyacotriton* spp., Stoddard and Hayes 2005). Interestingly, most studies of headwater amphibians have not specifically considered stream hydrology or the larger drainage network extending downstream from zero-order basins into perennial stream reaches in their habitat assessments, but have located studies on only perennial stream reaches (e.g., Welsh and Lind 2002, Steele et al. 2003, Stoddard and Hayes 2005). However, Welsh et al. (2005) recently reported that coastal giant salamanders and black salamanders (*Aneides flavipuncatus* Strauch) were more abundant along spatially discontinuous intermittent stream reaches than perennial reaches in northern California. Also, Sheridan and Olson (2003) focused on characterizing amphibian distributions in zero-order basins, and reported geomorphic patterns. For headwater-associated species, the relative value of ephemeral or intermittent streams in comparison to downstream perennial reaches is poorly understood. Relative to timber management activities, these uppermost reach types compose a majority of the landscape (Meyer and Wallace 2001, Gomi et al. 2002), may receive less attention and protection due to the absence of fish (e.g., USDA and USDI 1994), typically lack latitudinal vegetation gradients due to "compressed" riparian zones (i.e., narrow strips of riparian conditions alongside streams) (Sheridan and Olson 2003, Sheridan and Spies 2005), and may sometimes not be recognized because they do not appear on all topographic maps (Meyer and Wallace 2001).

With much of the Pacific Northwest forest landscape now consisting of managed forest, having sustained at least one stand-replacement timber harvest, we were interested in advancing knowledge of the biophysical relationships within managed headwater systems. In particular, our overarching objective was to examine associations among headwater habitats and aquatic-dependent vertebrates: instream fish, instream amphibians, and streambank amphibians. Stream reaches we studied represent a gradient of flow regimes, including perennial, intermittent, and headmost reaches or swales with no evidence of surface water flow during spring or summer. Dry channels were included in our sample to further characterize the extent of aquatic amphibian distributions in zero-order basins in managed stands; Sheridan and Olson (2003) provided an initial characterization of these assemblages in the dry portion of headwaters in unmanaged stands. We included wetted reaches with and without fish to examine potential biological and physical-hydrologic associations of species and among groups of species. Such drainage-scale characterization of managed headwater forests is critical to structuring management decisions attempting to ensure that managed landscapes contribute to maintaining biodiversity (e.g., Lindenmeyer and Franklin 2002).

Methods

We conducted our study at 12 headwater forest sites in the western Cascade Range and Coast Range of Oregon, from Mount Hood to Coos Bay (Figure 1, Table 1). Headwater stream reaches ranged from zero-to-second order (Strahler 1957). Most sites were part of the USDI Bureau of Land Management density management and riparian buffer study (site descriptions in Cissel et al. 2004, 2006); however, three sites occurred on lands administered by the USDA Forest Service (Table 1). Site selection was nonrandom (Olson et al. 2002), but typical of young managed stands across nine federal administrative units of the Coast and Cascade Ranges. Study site sizes ranged 47 to 279 ha, but most site areas were <100 ha (Cissel et al. 2006). Site areas were determined from the specific treatment unit boundaries of the study sites within which these study reaches were located, and these boundaries usually extended from stream reaches to their upland ridgelines, inclusive of from one to eight reaches per treatment unit (as shown in Figure 2). Stands were 40 to 80 yrs old, naturally regenerated from previous clearcut harvest without stream buffers, and consisted of homogeneous forest within the western hemlock (*Tsuga heterophylla* [Raf.] Sarg.) vegetation zone (Franklin and Dyrness 1988), dominated by Douglas-fir trees (*Pseudotsuga menziesii* [Mirbel] Franco) with 430 to 600 trees per hectare (tph). A distinct zone of riparian vegetation generally was not evident at these sites and riparian forests were similar to upslope conditions, with a couple of exceptions, such as about a 15 m-wide zone of red alder (*Alnus rubra* Bong.) along portions of one reach at Callahan Creek. Riparian-to-upland vegetation and microsite conditions at these sites are under investigation (P.

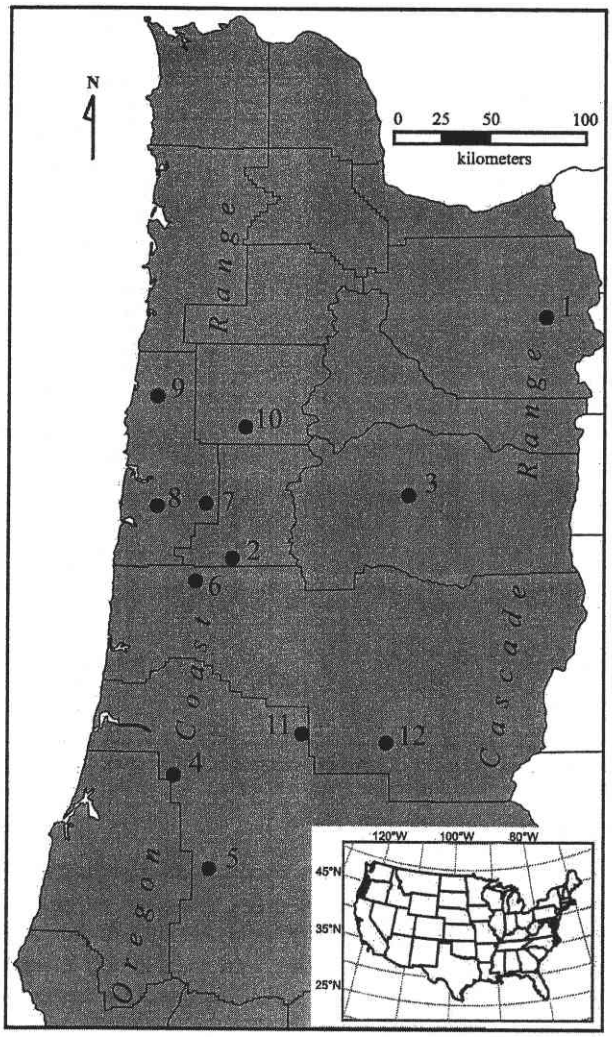

Figure 1. Location of 12 study sites in western Oregon where headwater stream channel fauna and habitats were characterized. Numbers correspond to site descriptions in Table 1.

Anderson and M. Kluber, unpublished data). Portions of two older sites, Perkins and North Ward, were thinned 20 years earlier, at about age 50 years, to 250 tph.

At the 12 sites, 106 headwater reaches were inventoried once for habitat and fauna in 1995 to 1999 (Table 1). Minimum reach length was two site-potential tree heights (110–150 m). Reaches generally were distinguished by tributary junctions, reach length within the study site boundary, or by the upstream end of water flow (Figure 2). Reach inclusion in our survey usually was contingent on the future forest thinning treatment to be conducted in that portion of sites (reference unthinned unit or moderate thinning unit); however, broader inclusion of reaches to characterize the larger basin was conducted opportunistically. Reaches above end-of-water were sampled due to uncertainty of these zero-order basins functioning as streams, or as habitat for stream-dependent amphibians. Some dry reaches had evidence of past scour and deposition. Consequently, within sites, reaches were not independent because a continuous stream thread from dry to perennial streams may have included more than one reach (e.g., Figure 2: tributary flowing into reach B was a sample reach, and the dry channel at its upstream end was another sample reach in the study). Also, relative to amphibian assemblages, animals may have been able to move overland between neighboring subdrainages, even if they were located in different large watersheds such that aquatic connectivity was not an issue (Figure 2, stream A, also streams at lower right of figure).

Stream habitat typing was conducted using a modified Hankin and Reeves (1988) stream survey. Within a year, reaches were typed during both the wet season (March to June) and dry season (July to September) by walking upstream and measuring or visually estimating habitat parameters. Survey timing tracked local weather conditions such that the sites sampled later in a season were at higher elevations and were sampled after snow had melted and temperatures were above freezing. For each reach, we first identified the sequential microhabitat units dominated by no surface flow (dry units) and two types of wet units: slow (pool) or fast water flow (step, cascade, riffle) habitat types. Dry units were variable in length and could have been short sections in-filled with unstable side-slope colluvium or downed wood embedded with substrate or other debris. Surface flow under downed logs not embedded or in-filled by substrate was not considered a dry unit. We collected several habitat measures in wet units (Table 2), including unit size (e.g., average depth, length, and width), dominant and subdominant substrate type (6 categories: bedrock, >300 mm diameter [diam] rock; boulder, 101–300 mm diam; cobble, 30–100 mm diam; large gravel, 11–30 mm diam; small gravel, 3–10 mm diam; fine substrates, <3 mm diam particles; dominant substrate composed the highest proportion of a unit's composition, subdominant substrate was the second highest proportion), downed wood (tally of large pieces by size, large pieces were ≥1 m long and ≥0.1 m diam), and stream gradient for wetted reaches in four categories: flat (0–5%), moderate (6–15%), moderately steep (16–30%), and steep (>30%). These habitat measures were not collected in dry reaches because our initial focus was to characterize habitats of flowing streams; fauna was sampled in both flowing and dry reaches. Units were recorded as being either "sample-able" or not for fauna due to accessibility (e.g., inaccessible due to abundant downed wood).

Stream wetness of reaches was assessed with three measures: "hydrotype," average dry reach length, and percentage of the reach length with discontinuous surface water flow. Hydrotype was a categorical variable related to the continuity (or lack of) water flow in the entire reach. We used a seven-category scale for hydrotypes: (1) perennial reaches, flowing during both spring and summer surveys; (2) summer intermittent, where reaches flowed consistently in spring and became spatially discontinuous in summer; (3) perennial-ephemeral, where reaches flowed in spring but were completely dry in summer; (4) intermittent, where reaches were spatially discontinuous in both spring and summer; (5) intermittent-ephemeral, where reaches had discontinuous flow in spring and were dry in summer; (6) dry reaches that had evidence of scour and deposition but no flow in either spring or summer; and (7) above-end-of-water, dry reaches that did not have evidence of scour and

Table 1. Study sites and reaches characterized in our study of aquatic vertebrates in western Oregon managed forest headwaters

Site No.	Site	Latitude & longitude	Forest stand age (yrs)	No. Reaches			
				Total	P	I	D
1	Delph Creek	N45°15′56″ W122°9′33″	30–50	5	1	2	2
2	Green Peak	N44°22′00″ W123°27′30″	30–50	9	3	2	4
3	Keel Mountain	N44°31′41″ W122°37′55″	30–50	14	3	5	6
4	North Soup Creek	N43°33′57″ W123°46′38″	30–50	8	0	5	3
5	O.M. Hubbard	N43°17′30″ W123°35′00″	30–50	14	3	4	7
6	Ten High	N44°16′50″ W123°31′06″	30–50	13	4	4	5
7	Cougar (USFS)	N44°30′42″ W123°39′49″	30–50	8	4	2	2
8	Grant (USFS)	N44°30′42″ W123°45′51″	30–50	5	1	1	3
9	Schooner (USFS)	N44°56′09″ W123°51′21″	30–50	11	2	5	4
10	Callahan Creek*	N44°50′5″ W123°35′26″	70–80	6	3	1	2
11	North Ward	N43°46′08″ W123°12′05″	70–80	4	1	2	1
12	Perkins	N43°42′51″ W122°54′47″	70–80	9	4	3	2

Older stands included once-thinned and never-thinned (*) areas. Reaches are distinguished by hydrotype: P, perennial (continuous surface flow; hydrotypes 1, 2, and 3; see text or Figure 3 for definitions); I, spatially intermittent (i.e., discontinuous surface flow; hydrotypes 4 and 5); or D, dry swale (non surface flow; hydrotypes 6 and 7).

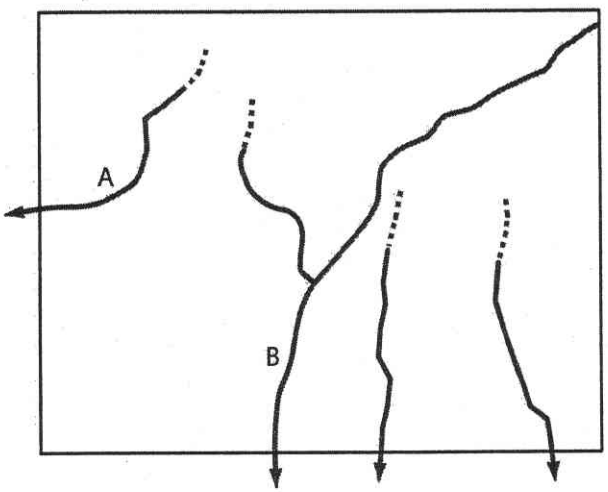

Figure 2. Schematic representation of the layout of our headwater stream reaches within a study site. Stream reaches within a single site occasionally drained into a different watershed (A) or the upstream reach continued outside the site boundary (B), but more usually distinct reaches were distinguished by tributary junctions (e.g., as seen by the joining of two reaches, B). Dry channels (dashed lines) had scour and deposition but no surface flow, and were distinguished as separate reaches to explore the upstream extent of aquatic animal distributions.

deposition and no flow was seen in spring or summer. Average dry length was the average length of all of the dry portions of the stream reach; for a perennial stream reach this would have a value of zero, and it would be greater than zero for other hydrotypes. Percentage discontinuous reach was ratio of total reach length without surface flow to that with surface flow.

Instream vertebrate surveys were conducted after habitat surveys at 10 units per reach using a random systematic approach of eligible units. Units were defined as either pool or riffle as during habitat typing, were sample-able (accessible), and were at least 15 m from downstream or upstream reach boundaries. Units were sampled in proportion to their frequency of occurrence. For example, if fast water habitat composed 80% of the reach, then 8 of 10 survey units were riffles. The first unit was chosen randomly from the first five downstream units. Systematic sampling of every *n*th unit occurred upstream, where n = number of sample-able habitat units by type in the reach divided by 10. This method spaced the remaining upstream units throughout the reaches. Similarly, in reaches above end-of-water, ten 2-m-long units were sampled, with location of units chosen in representative areas along the defined dry channel swale. Widths of those sampled dry units were determined by the downstream wetted reach width within about 20 m of end-of-water flow.

For reaches, one of two instream survey methods was used. Electrofishing was conducted when fish were present. Entire slow-water units were electrofished, and representative 2-m lengths of fast-water units were electrofished. These representative lengths usually had flow conditions similar to those of the majority of the entire fast-water unit. Upper and lower ends of sampled units were blocked with nets, and two or more passes of the electrofisher through the unit were conducted to achieve a 75% reduction in captures of all species from the first pass, or to achieve a pass with no fish or amphibians. If the fifth pass did not achieve this, the survey crew stopped sampling that unit. We recognize

Table 2. Habitat variables (see text for description), the spatial scale at which they were initially collected, and the method used to aggregate smaller-scale variables to reach-level values

Variable	Measurement units	Initial measurement scale	Reach value determination
Average width	Meters	Habitat unit	Average of habitat unit measurements
Average depth	Meters	Habitat unit	Average of habitat unit measurements
Gradient	%	Reach	As measured
Dominant substrate	Categories 1–9 (small to bedrock)	Habitat unit	Mode (most common value) of categories from habitat units
Subdominant substrate	Categories 1–9 (small to bedrock)	Habitat unit	Mode (most common value) of categories from habitat units
Large wood	No. pieces	Reach	Total number of pieces
% discontinuous reach	%	Reach	As measured
Pool riffle ratio	Number	Reach	As measured
Average pool depth	Meters	Habitat unit	Average of habitat unit measurements
Average dry length	Meters	Reach	As measured
Hydrotype	Categories 1–7 (wet to dry)	Reach	Reduced to 3 levels: 1 = continuous flow in spring, 2 = intermittent in spring, 3 = dry or above end of water in spring

that amphibians may not have been sampled completely by this method due their occurring within substrates; however, we assumed that capture rates could be estimated. Hand-sampling was conducted in streams without fish. As above, entire slow-water units and representative 2-m reaches of fast-water and dry units were searched. The surveyor proceeded upstream, first visually searching for animals, then removing moveable cover objects (most cobbles and smaller substrates, and smaller wood pieces), and finally sifting through smaller cover and substrates. Animals were captured with aquarium dipnets and placed in buckets or plastic bags until postsearch taxonomic identification. After sampling, substrate and cover items were replaced, and animals were returned to units.

For each sampling unit, banks on each side of the reach were hand-searched. Due to bank habitat variability (e.g., occasional solid bedrock side slopes or large trees rooted at the stream edge), surveyors used a more practical, timed area search. Each bank was searched for 5 min within 2 m of stream reach edges, with flexibility to concentrate searches in suitable habitat for amphibians, after which the search area was estimated. Cover items including logs, moss, litter, and rocks were peeled away in layers and carefully replaced. Captures were maintained in plastic bags until postsearch species identification, whereupon they were replaced beneath their respective cover. Amphibian handling times were excluded from search times.

Statistical Analyses

We characterized biophysical relationships by analyzing reach-level data. Data collected at a habitat unit level were summarized at a reach level for all variables (Table 2) by calculating either the mean value for each reach (depth, width), the value per meter of reach length (large wood), or mode (dominant substrate, subdominant substrate). Measurements collected directly at the reach scale (i.e., hydrotype, percentage discontinuous reach, average dry length, gradient, and pool/riffle ratio) were used in analyses as measured (Table 2). However, some categories of habitat parameters had few observations, so we combined selected categories to allow more meaningful comparisons. We simplified reach hydrotype into three categories: spring perennial (continuous flow: hydrotypes 1, 2 and 3), spring intermittent (discontinuous flow: hydrotypes 4 and 5), and dry reaches (hydrotypes 6 and 7), and we merged small and large gravel into one category to analyze five substrate categories. We also coded the substrate variable so that numeric values correlated with substrate size.

Reach-level capture rates of amphibians and fish were obtained by dividing the counts by the length of the search area (i.e., no. animals m^{-1} length of stream) for the instream samples. Reaches sampled by each of the two instream sampling methods (electrofishing and hand-sampling) were distinguished during analyses by either adding a survey method parameter into the models to assess their potential effect, or by conducting separate analyses by method (see below). Counts from bank samples were divided by search area (length $\times$ width) of each bank sample (i.e., no. animals m^{-2}). We used only wet-season spring animal survey data in analysis to reduce the noise contributed by seasonal variation. Due to single visits to survey reaches, we cannot address species detectability using our methods (see Hyde and Simons 2001, Bailey et al. 2004a, b), and recognize that habitat associations derived from our surveys may be affected by spatial or temporal detectability issues per species and survey method. Consequently, we do not couch our results in terms of densities or relative abundances, but rather in terms of occurrences, detections, and captures.

We used three statistical methods to characterize headwater reaches. Canonical correlation (SAS-PROC CANCOR, SAS Corp.) examined the relationship between species assemblages and habitat parameters (James and McCulloch 1990). Nonmetric multidimensional scaling (NMS; Splus statistical software, Insightful Corporation, Seattle, WA) was also used to examine species assemblages, but this method better enabled us to determine whether reach-level assemblages were associated with specific reaches or specific sites. Generalized linear models (glm) function, Splus statistical software) examined individual species-specific habitat relationships.

Canonical correlations were calculated separately for combined instream and bank fauna, instream-species assemblages,

and bank amphibians. Canonical correlations work well when the set of predictor variables set is intercorrelated because they create an independent set of canonical variables that are linear combinations of the correlated ones. The modest to strong correlations anticipated between variables such as hydrotype, average dry length, and percentage discontinuous reach made canonical correlation a useful method for these data. Potential existed for autocorrelation among reaches from the same sites. We accounted for this by using an adjusted degrees of freedom for the significance test of the canonical pairs; a sample size of 12 (the number of independent sites) was used for the significance test instead of the number of stream reaches. We accounted for a potential difference in captures from sampling method, electrofishing, and hand sampling, by including an indicator variable for survey "method" in the canonical correlation analysis. The indicator variable for sampling method helps to normalize the number of captures between reaches sampled with different methods, and its role in distinguishing species assemblages can be ascertained by comparison of correlation coefficients.

NMS ordination is a multivariate technique that computes a scaled distance (dissimilarity index) between all pairs of stream reaches, followed by clustering of the stream reaches into similar groups (McCune and Grace 2002). We calculated dissimilarity using the instream and bank species capture rates, with prescaling (division by the capture rate SD) of the variables and a dissimilarity metric calculated as the summation of absolute distances between the relative densities for all vertebrate species. Clusters were created using the dissimilarity matrix and the clustering algorithms in the software (Splus, Insightful Corporation, Seattle, WA). Clusters were interpreted by their vertebrate composition, site locations, and habitat attributes. We analyzed instream data in two sets; one analysis was conducted with electrofishing data and the other with hand-sampling data.

Generalized linear models (McCullagh and Nelder 1989) examined individual species-habitat relationships. Unlike canonical correlation and NMS, habitat variables needed to be uncorrelated for generalized linear models. A subset of the original set of variables was selected that were uncorrelated and still captured the majority of the habitat information. Correlation coefficients and pairwise scatter plots were used to determine the strength of the correlation between the habitat variables and to choose a best subset of independent habitat variables. The set chosen was hydrotype, dominant substrate class, downed wood density, average reach width, and gradient. As in the canonical correlation, we accounted for the difference in captures rates between the electroshock and hand-sampling methods by including an indicator variable for survey method. For the generalized linear model, the model for the logarithm of the average capture rates per reach was a linear function of the habitat attributes. We examined only the more common species in our samples; we included species that were present in at least one reach in at least half of the sites. For most species examined, the data exhibited underdispersion (i.e., the variance of capture rates increased with the average capture rate at less than the 1:1 rate as specified by the standard Poisson model). Underdispersion was detected by examination of the residual plots and estimated by dividing the residual deviance by its degrees of freedom (McCullagh and Nelder 1989). Underdispersion in our case probably represented the modest correlations in species capture rates between reaches from the same site and represents a way to account for this lack of independence. Significance tests and P values for the habitat variables were adjusted for this underdispersion. Model parameters were estimated by maximum likelihood; P values for each coefficient were calculated using drop-in-deviance tests that compare the model with the variable included to the model without the variable. Drop-in-deviance values (difference in residual deviance between the model including the habitat variable and the model excluding it) have an asymptotic chi-squared distribution (McCullagh and Nelder 1989).

In summary, our three analyses represented alternative ways to look at the data, and allowed for comparison of results using different approaches, data subsets, and assumptions. Canonical correlation examined the multivariate species and habitat data sets for significant assemblage-habitat groupings using all habitat attributes, while generalized linear models tested individual species-habitat associations for the most common species with a subset of habitat attributes that were not correlated. Including survey method as a parameter in these two approaches allowed us to examine its influence on the results. NMS ordination also analyzed the species data for significant groupings, but allowed site-specific or reach-specific assemblages to be distinguished, as well as associations with habitat attributes. Analyzing the data separately by survey method in the NMS ordinations allowed a comparison of findings between methods, and concordance with the canonical correlations and generalized linear models could be ascertained.

Results

We inventoried 29 spring-season perennial streams (continuous surface flow; 20 sampled with electrofishing, 9 with hand searches), 36 spring-season spatially intermittent streams (discontinuous surface flow; two sampled with electrofishing and 34 with hand searches), and 41 dry or above end-of-water reaches (Table 1). Three of seven spring-summer hydrotypes were infrequent (hydrotype 3 [perennial-ephemeral], 1 reach; hydrotype 5 [intermittent-ephemeral], 4 reaches; hydrotype 6 [dry channel with scour and deposition in both seasons], 3 reaches). An even distribution of dominant substrate classes was found in perennial streams, and many had gradients between 6 and 15% (15 of 29 stream reaches). Spatially intermittent streams were characterized by fine substrates (25 of 36 streams) and gradients ranging between 6 and 15% (23 of 36 streams). Intermittent streams had average dry reach lengths that were generally short (mean = 12.6 m, SE = 0.4) and percentage discontinuous reach values that were around 25% (mean = 25.2, SE = 0.5). Downed wood density was similar between the perennial and intermittent streams (0.22 pieces m^{-1} and 0.21 pieces m^{-1}, respectively).

Across all 12 sites, 454 fish of three species groups and 1,796 amphibians of 12 species were captured. There were seven more commonly detected species (Table 3), and infrequently captured amphibians included (1) northern red-legged frog, *Rana aurora* Baird and Girard (5 captures, 2 sites); (2) Pacific treefrog, *Pseudacris regilla* Baird and Girard (7 captures, 5 sites); (3) northwestern salamander, *Ambystoma gracile* Baird (4 captures, 4 sites); (4) Cascade torrent salamander, *Rhyacotriton cascadae* Good and Wake (25 captures, 2 sites); (5) rough-skinned newt, *Taricha granulosa* Skilton (25 captures, 7 sites); and (6) Oregon slender salamander, *Batrachoseps wrighti* Bishop (38 captures, 2 sites). Amphibians dominated instream reaches, and banks contributed an additional amphibian diversity component (Figure 3). All fish were found in perennial streams, and banks had the highest overall amphibian species richness (12 species, Figure 3). Relatively few animals were detected in dry reaches, as demonstrated by *Batrachoseps wrighti*, which occurred at only 2 sites with 38 total captures representing about a quarter of the animals found in and along dry channels (Figure 3). Fish taxa detected were *Cottus* (sculpins, 3 sites, 203 of 207 captures from one site) and *Oncorhynchus* (trout, 6 sites) species. Cottids were not identified to species but likely included *Cottus perplexus* Gilbert and Evermann (reticulate sculpin), *C. gulosus* Girard (riffle sculpin), *C. asper* Richardson (prickly sculpin), or *C. aleuticus* Gilbert (Coast Range sculpin; D. Bateman, US Geological Survey, personal communication Oct. 2006; Bond 1973). *Oncorhynchus clarki* Richardson (coastal cutthroat trout, likely resident forms) occurred in our sample, as well as small "0+" year-old *Oncorhynchus* that could not be identified to species, although they were likely *O. clarki* given the occurrence of larger identified individuals in our sample. Three juvenile *Lampetra* (lamprey) species were found at one site, but were not identified to species. Amphibian species included three assemblages, stream (*Ascaphus truei*, *Rhyacotriton variegatus*, *R. cascadae*, and *Dicamptodon tenebrosus*), pond (*Rana aurora*, *Taricha granulosa*, *Pseudacris regilla*, *Ambystoma gracile*), and terrestrial breeders (*Plethodon dunni*, *P. vehiculum* Cooper [western red-backed salamander], *Ensatina eschscholtzii* Gray, and *Batrachoseps wrighti*), but most pond-breeders occurred only incidentally.

Canonical correlation analyses described differences in species composition and habitat attributes between the perennial, low-gradient, woody streams and the discontinuous, steeper streams. For the combined instream and bank analysis, the first canonical correlation was significant (P = 0.0247) with an estimated adjusted canonical correlation of 0.63 (Table 4). Two discrete assemblages emerged. One was dominated by instream taxa, including *Oncorhynchus* species, *Ascaphus truei*, *Dicamptodon tenebrosus*, *Taricha granulosa*, and *Plethodon dunni* (largest positive coefficients). The second group consisted of instream *Plethodon vehiculum* and a bank assemblage of *Rhyacotriton* species and *A. truei* (largest negative canonical coefficients, Table 4). The division of the habitat variables between these groups was indicated by the largest scaled canonical coefficients for habitat. The first assemblage was associated with those variables having larger positive coefficients (average depth and wood density), and the second assemblage was associated with hydrotype, which had the largest negative coefficient. Survey method had a large positive canonical coefficient, indicating a positive association between electrofishing and the instream-dominated assemblage in the perennial reaches.

The analysis of the instream vertebrates separately gave one significant canonical correlation (P = 0.0315) with a canonical correlation of 0.613 (Table 5). The scaled canonical coefficients indicated an assemblage of *Oncorhynchus* species, *Cottus* species, *D. tenebrosus*, and *A. truei* (largest positive scaled canonical coefficients) that were associated with high wood density, and a separate assemblage (largest negative coefficients) of *P. dunni*, *P. vehiculum*, *T. granulosa*, and *Rhyacotriton* species. The habitat attributes seemed to divide between reaches with high wood densities (largest positive coefficient) and low depth, high-gradient, drier hydrotype (intermittent or dry) reaches (largest negative coefficients). Again, survey method was associated with the fish and amphibian assemblage occurring in the perennial reaches with high wood density.

Table 3. Number of captures for the more commonly detected species in and along headwater reaches at 12 western Oregon study sites

Species	Total no.	No. Captures/Study Site											
		1	2	3	4	5	6	7	8	9	10	11	12
Trout species *Oncorhynchus*	244	13	0	104	0	0	0	0	0	26	56	28	17
Coastal giant salamander *Dicamptodon tenebrosus*	909	120	30	536	2	29	15	4	3	10	120	21	19
Southern torrent salamander *Rhyacotriton variegatus*	179	0	46	0	10	26	38	8	22	24	2	3	0
Ensatina *Ensatina eschscholtzii*	88	1	9	54	2	13	6	0	1	1	1	0	0
Western red-backed salamander *Plethodon vehiculum*	201	0	42	4	37	11	19	32	13	18	16	9	0
Dunn's salamander *Plethodon dunni*	315	0	21	70	40	30	13	13	15	2	12	51	48
Coastal tailed frog *Ascaphus truei*	52	0	4	18	0	0	14	0	0	2	14	0	0
Total no. species/site		5	6	7	9	8	8	7	7	7	10	8	6

Total number of species per site includes infrequently detected species (see text). Study site numbers are defined in Table 1.

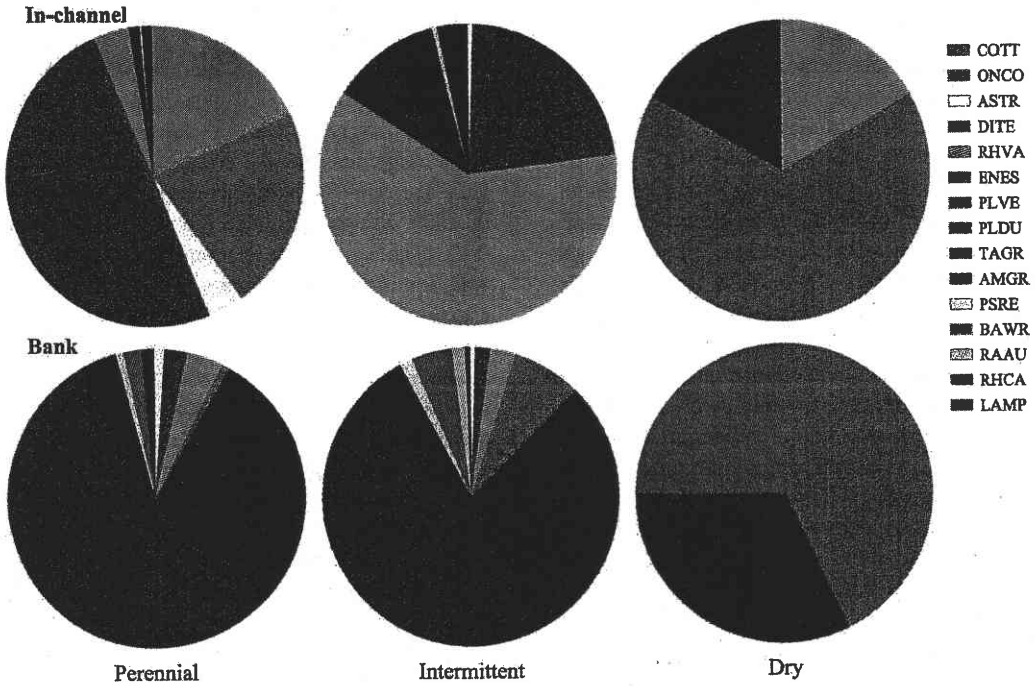

Figure 3. Taxa detected in 106 headwater reaches assorted by instream and bank habitats and streamflow regimes: perennial stream (hydrotypes 1, 2, and 3), spatially intermittent (discontinuous) stream (hydrotypes 4 and 5), and dry channels above end-of-water (hydrotypes 6 and 7). Pie charts indicate relative composition only; see text and Table 3 for total numbers of animals per species detected and number of sites at which they occurred. Species name acronyms: COTT = *Cottus* fishes; ONCO = *Oncorhynchus* fishes; ASTR = *Ascaphus truei*; DITE = *Dicamptodon tenebrosus*; RHVA = *Rhyacotriton variegatus*; ENES = *Ensatina eschscholtzii*; PLVE = *Plethodon vehiculum*; PLDU = *Plethodon dunni*; TAGR = *Taricha granulosa*; AMGR = *Ambystoma gracile*; PSRE = *Pseudacris regilla*; BAWR = *Batrachoseps wrighti*; RAAU = *Rana aurora*; RHCA = *Rhyacotriton cascadae*; LAMP = *Lampetra* species.

Table 4. Canonical correlation results for the combined bank and instream reach characterization of headwater species capture rates and habitat attributes

Species	Canonical Coefficient	Habitat Variable	Canonical Coefficient
Cottus species	0.087	Average width	0.031
Oncorhynchus species	2.30	Average depth	0.963
Dicamptodon tenebrosus	0.146	Gradient	−0.075
Ascaphus truei	1.80	Dominant substrate	0.003
Plethodon dunni	0.996	Subdominant substrate	−0.005
P. vehiculum	−1.04	Wood density	0.250
Taricha granulosa	0.527	% Discontinuous reach	0.006
Rhyacotriton species	−0.258	Pool riffle ratio	0.015
Dicamptodon tenebrosus (B)	0.094	Average pool depth	0.006
Ascaphus truei (B)	−0.250	Average dry length	−0.005
Rhyacotriton species (B)	0.027	Hydrotype	−0.104
Ensatina eschscholtzii (B)	−0.003	Survey method	0.508
Plethodon dunni (B)	0.010		
P. vehiculum (B)	−0.033		
Taricha granulosa (B)	−0.037		
Batrachoseps wrighti (B)	−0.011		

The first canonical correlation was significant ($P = 0.0247$) with an estimated adjusted canonical correlation of 0.63. Scaled canonical coefficients per parameter are provided. (B) indicates animals were found along stream banks.

For the bank vertebrate data, the first canonical correlation was significant ($P = 0.0369$) with a canonical correlation of 0.562 (Table 6). The dominant vertebrates for this bank assemblage were *D. tenebrosus*, *B. wrighti*, and *E. eschscholtzii*, and they were associated with high densities of large wood and average dry length. Negative coefficients reflected *Rhyacotriton* species and *P. vehiculum* occurring along smaller discontinuous streams.

Clusters of five assemblages were constructed with NMS ordination, two groups from the set of reaches sampled by electrofishing, and three from the set of reaches sampled by hand. From hand-sampling, the three clusters can be described as follows: (1) most (84) reaches grouped into a cluster including perennial (18 reaches: *D. tenebrosus* instream, *P. dunni* and *P. vehiculum* on banks), intermittent (30 reaches: instream *D. tenebrosus*, *Rhyacotriton* species, and some *T. granulosa*; bank-dwelling *P. dunni*, *P. vehiculum*, and some *T. granulosa*, *E. eschscholtzii*, and *B.*

Table 5. Canonical correlation results for the instream-only reach characterization of headwater species capture rates and habitat attributes

Species	Canonical coefficient	Habitat variable	Canonical coefficient
Cottus species	0.277	Average width	0.073
Oncorhynchus species	1.265	Average depth	−0.459
Dicamptodon tenebrosus	0.265	Gradient	−0.139
Ascaphus truei	0.882	Dominant substrate	−0.009
Plethodon dunni	−4.889	Subdominant substrate	0.020
P. vehiculum	−6.987	Wood density	0.474
Taricha granulosa	−0.318	% discontinuous reach	−0.006
Rhyacotriton species	−0.236	Pool-riffle ratio	0.021
		Average pool depth	0.015
		Average dry length	0.004
		Hydrotype	−0.203
		Survey method	0.200

One significant canonical correlation ($P = 0.0315$) with a canonical correlation of 0.613 resulted. Scaled canonical coefficients per parameter are provided.

Table 6. Canonical correlation results for the bank-only (B) reach characterization of headwater species capture rates and habitat attributes

Vertebrate variable	Canonical coefficient	Habitat variable	Canonical coefficient
Dicamptodon tenebrosus (B)	0.7174	Average width	−0.0934
Ascaphus truei (B)	0.1044	Average depth	−0.2758
Rhyacotriton species (B)	−0.4709	Gradient	−0.1385
Ensatina eschscholtzii (B)	0.295	Dominant substrate	−0.1192
Plethodon dunni (B)	0.0151	Subdominant substrate	−0.2679
P. vehiculum (B)	−0.288	Wood density	0.9116
Taricha granulosa (B)	0.0861	% Discontinuous reach	−0.3707
Batrachoseps wrighti (B)	0.6556	Pool-riffle ratio	−0.0855
		Average pool length	−0.1662
		Average dry length	0.2772
		Hydrotype	−0.2519

The first canonical correlation was significant ($P = 0.0369$) with a canonical correlation of 0.562. Scaled canonical coefficients for each parameter are provided.

Table 7. Instream species-habitat associations using generalized linear models

	Rhyacotriton variegatus disp = 0.233			*Dicamptodon tenebrosus* disp = 0.195			*Plethodon dunni* disp = 0.025			*Oncorhynchus* species disp = 0.0215		
Model	df	*P*	coef	df	*P*	coef	df	*P*	coef	df	*P*	coef
Null	40	—	−6.1 (1.4)	58	—	−3.1 (0.6)	58	—	−5.4 (1.3)	58	—	−9.97 (597)
Method		0.088	−2.5 (1.9)	57	0.214	0.28 (0.22)	57	0.072	0.78 (0.39)	57	<0.0001	1.2 (0.2)
+Hydrotype	39	0.173	0.65 (0.49)	56	0.409	0.22 (0.27)	56	0.042	−0.87 (0.5)	56	<0.0001	−9.2 (597)
+Gradient	38	<0.001	0.86 (0.22)	55	0.301	−0.21 (0.21)	55	0.044	0.71 (0.34)	55	<0.0001	−1.2 (0.2)
+Downed wood density	37	0.122	4.37 (2.8)	54	0.663	0.71 (1.6)	54	0.58	−1.7 (3.1)	54	0.636	0.7 (1.5)
+Average width	36	0.21	−0.8 (0.66)	53	0.094	0.6 (0.36)	53	0.18	−1.7 (1.4)	53	0.015	0.8 (0.4)
+Dominant substrate	35	0.034	0.16 (0.07)	52	0.187	0.08 (0.08)	52	0.51	0.072 (0.11)	52	0.043	−0.2 (0.1)

Habitat variables were added one at a time, beginning with Method, in the order shown in the table. The *P* values for each variable represent the significance of that variable after the variables in earlier rows in the table were added to the model. df = degrees of freedom, coef = regression coefficient (standard error), + indicates parameter added to model, disp indicates the estimated dispersion parameter per model. Positive coefficients for survey "Method" indicate an association with electrofishing; a negative coefficient indicates an association with hand-sampling. See text for habitat variable descriptions.

wrighti), and dry (36 reaches: some *P. vehiculum*) reaches; (2) a second cluster contained six reaches, three of which were from Green Peak, with instream *Rhyacotriton* species and *D. tenebrosus*, and *P. dunni* and *P. vehiculum* on the banks, where *Rhyacotriton* captures were more frequently greater than *D. tenebrosus*; (3) a third cluster represented a single reach from the O.M. Hubbard site with *D. tenebrosus* instream and *P. dunni* on the banks, but no captures of *Rhyacotriton*. The 14 reaches sampled by electrofishing contained *D. tenebrosus* instream and *P. dunni* on banks, but one cluster (three reaches) contained *Oncorhynchus* and *Cottus* fish from the Callahan Creek and Keel Mountain sites, while the other cluster (11 reaches) did not have *Cottus* and only a few captures of *Oncorhynchus* and *D. tenebrosus*.

For individual species, habitat associations were examined using a generalized linear model for each of the most common taxa using data from sites where they occurred (Tables 7 and 8). Capture rates of *R. variegatus*, both instream and on banks, were greater in higher gradient reaches and reaches dominated by the larger substrate classes. There tended ($P < 0.10$) to be more captures in reaches with hand-sampling for *R. variegatus* (negative coefficient, Table 7). Instream *D. tenebrosus* captures were

Table 8. Bank species habitat associations using generalized linear models

Model	*Rhyacotriton variegatus* disp = 0.01			*Ensatina eschscholtzii* disp = 0.012			*Plethodon vehiculum* disp = 0.026		
	df	*P*	coef	df	*P*	coef	df	*P*	coef
Null	40	—	−9.5 (2.0)	58	—	−6.0 (3.2)	58	—	−5.4 (1.8)
+Hydrotype	39	0.191	−1.04 (0.81)	57	0.682	0.486 (1.2)	56	0.788	0.1 (0.4)
+Gradient	38	0.012	1.04 (0.46)	56	0.077	−1.05 (0.64)	55	0.011	0.43 (0.17)
+Downed wood density	37	0.373	2.9 (3.3)	55	0.068	5.21 (2.7)	54	0.495	−1.0 (1.5)
+Average width	36	0.183	−1.14 (0.91)	54	0.291	0.70 (0.65)	53	0.795	−0.1 (0.4)
+Dominant substrate	35	0.012	0.45 (0.23)	53	0.011	−0.42 (0.21)	52	0.039	0.121 (0.06)

Habitat variables were added one at a time, beginning with Hydrotype, in the order shown in the table. The *P* values for each variable represent the significance of that variable after the variables in earlier rows in the table are added to the model. df = degrees of freedom, coef = regression coefficient (standard error), + indicates parameter added to model, disp indicates the estimated dispersion parameter per model. See text for habitat variable descriptions.

associated with wider streams. For *P. dunni*, instream captures were highest in intermittent streams with higher gradients, and there tended to be higher capture rates in reaches with electrofishing for *P. dunni*. *Oncorhynchus* species were associated with lower-gradient, perennial streams with smaller substrates, and instream sampling method (i.e., electrofishing). On banks (Table 8), *E. eschscholtzii* capture rates increased with smaller substrates and tended ($P < 0.10$) to increase with lower gradients and more down wood. Bank captures *of P. vehiculum* were highest along steep gradient reaches with larger substrates. No clear habitat associations were evident for bank-dwelling *P. dunni*. All fitted models had estimated dispersion parameters less than one, indicating that our data exhibited less variation than expected from a random sample of reaches.

Overall, capture rates were typically higher using electrofishing, creating a bias toward more captures in perennial streams (hydrotypes 1, 2, and 3). Average number of captures per meter of reach length was about threefold greater for electrofishing (0.45 individuals m^{-1}) than for hand-sampling (0.16 individuals m^{-1}). No significant difference existed in the number of species captures per meter between electrofishing (0.038 species m^{-1}) and hand-sampling (0.042 species m^{-1}). The different methods also captured different species, with fish captured by electrofishing (as per design) and *R. variegatus* captured by hand-sampling. This was supported by the results previously discussed, for example where method distinguished different assemblages in the canonical correlations and NMS ordination, and was associated with the different taxa in the glm analyses.

Discussion

Headwaters and amphibians are emerging as important considerations during management of Pacific Northwest forests. Headwaters have become of interest due to their potentially great spatial extent (examples in USDA and USDI 1993, Meyer and Wallace 2001), and variable approaches land managers have toward them (Sheridan and Olson 2003). Amphibians have been highlighted for declining populations globally (e.g., Stuart et al. 2004) and locally (e.g., Blaustein 2005), and "can be the predominant vertebrates in headwaters in Pacific Northwest forests" (Bury et al. 1991). We advance knowledge of these systems and taxa by our identification of amphibian-dominated assemblages in headwater reaches of managed forest stands in western Oregon. These include assemblages that are both longitudinally and latitudinally segregated along reaches, in perennial streams, spatially discontinuous or intermittent streams, dry reaches, and stream banks. Figure 3 shows how the species composition of these different headwater zones shifts significantly, as if a kaleidoscope was being ratcheted to re-assort these taxa among headwater areas. However, whereas a kaleidoscope might re-assort randomly, our results support a largely predictable species assortment with changing physical habitat conditions. Importantly, since our findings stem from 12 case study sites in western Oregon, our inference is consequently limited to these sites. However, our findings suggest hypotheses that need evaluation elsewhere, especially across the ranges of these species, which extend from northern California to British Columbia.

Overall, we found a relatively species-rich headwater community that included known headwater-associated species and several others. Three fish and 12 amphibian species were detected overall, with 5 to 10 species occurring per site (Table 3). Although several of the amphibians we sampled were detected incidentally, some such as *Ensatina eschscholtzii* and *Taricha granulosa* were found at several sites. This shows headwater streams and near-banks are habitat for species not traditionally considered stream or headwater associates; the role of headwaters for their refuge, dispersal, breeding, or foraging warrants further study. Half of the amphibian species we detected are on state or federal lists of concern-species (sensitive or special status species) (see Corkran and Thoms 1996, USDA and USDI 2005). Besides reserved land allocations, managed lands may contribute to their persistence across the forest landscape. With a single harvest in the histories of most of the sites, the fauna was fairly robust. Our characterization of headwater vertebrate assemblages in managed forests adds specificity to previously vague biotic values referenced by the Aquatic Conservation Strategy of the federal Northwest Forest Plan (USDA and USDI 1994, 1996a, b), and provides additional habitat association information for amphibian species of concern in managed forest landscapes (e.g., state sensitive species, Marshall 1992; USDA Forest Service, Region 6 sensitive species and USDI Bureau of Land Management, Oregon special status species, USDA and USDI 2005).

Spatially intermittent streams are of particular interest because these reaches may not be identified for protection during forest management planning in all land ownerships and allocations (e.g., Meyer and Wallace 2001, Sheridan and Olson 2003). For example, many northwestern forest streams and adjoining riparian areas are managed primarily for fisheries objectives, and resulting stream surveys may be limited to reaches with perennial flow and resident fish; upstream reaches may not be further characterized. The prevalence of spatially intermittent stream reaches in our sample (55% of reaches with surface flow in the spring season) suggests they may occur frequently at a managed forest stand scale. A comparison of reach type occurrences in unmanaged headwaters would be interesting; the unmanaged zero-order basins surveyed by Sheridan and Olson (2003) do not specifically characterize these types of reaches. We speculate that the spatial intermittency we found may partly reflect reach in-filling through side-slope failures and erosion, possibly resulting from the previous clearcut harvest at the sites. If that were the case, the fluvial power of water flow in headwaters may not alter such conditions very much in the 40 to 70 years since harvest at the sites; consequently, effects of reach sedimentation may be long-lasting. This hypothesis warrants further study by comparing reach characteristics under different disturbance regimes, while accounting for interacting factors such as slope gradients. Due to its dominance in our sample, the ecology of spatially intermittent reaches for species' habitat and system functions also needs closer examination. Proposed functions of these reaches include production of arthropods that may contribute significantly to downstream food webs (e.g., Wipfli and Gregovich 2002, Progar and Moldenke 2002) and wood inputs for downstream structure (Reeves et al. 2003). Sheridan and Olson (2003) and Sheridan and Spies (2005) suggest that the uppermost headwaters include spatially compressed (i.e., narrow) riparian zones. As in Sheridan and Olson (2003), we also found discrete bank amphibian assemblages close to the stream channel.

Headwater stream hydrology and other physical habitat attributes were associated with distinct assemblages and species. Although the link between survey method (electrofishing and hand-sampling) and species detections clouds these potential relationships; once survey method was accounted for, several of these species-hydrotype associations remained. Fish were found in perennial stream sections, as might be expected, and we found *P. dunni* also were associated with these reaches with continuous water flow as well as reaches with higher gradients. Analyzing the hand-sampled reaches separately (NMS ordination), *Rhyacotriton* species were in assemblages that occurred in spatially intermittent hydrotypes. However, a strong hydrotype relationship did not emerge for *Rhyacotriton* from the glm analyses of species-habitat associations; in that analysis higher gradient and larger substrates were correlated with both instream and bank *Rhyacotriton* capture rates. Correlation of habitat attributes might explain this; for the glm analyses, we removed correlated habitat attributes from the analysis. Gradient and substrate also were associated with bank *P. vehiculum* and inverse relationships were apparent for instream *Oncorhynchus* and bank *E. eschscholtzii* (inverse relations). This supports previous studies highlighting the importance of physical habitat attributes for stream vertebrates, including substrate (e.g., *A. truei*: Adams and Bury 2002, Welsh and Lind 2002, Dupuis and Steventon 1999; *Rhyacotriton kezeri*: Wilkins and Peterson 2000), gradient (e.g., *R. variegatus*: Diller and Wallace 1996; *R. olympicus*: Adams and Bury 2002), and stream hydrology (Welsh et al. 2005).

Interestingly, some species and assemblages were specific to either reaches or sites. In particular, both *Cottus* fish and *A. truei* were patchy in occurrence and did not occur within all reaches within relatively close proximity at a site. Wilkins and Peterson (2000) also found tailed frogs at only a fraction of managed headwaters in their sample, while Stoddard and Hayes (2005) found them in 81% of drainages surveyed. In our study and that conducted by Wilkins and Peterson (2000), these animals may have been affected by prior disturbances, such as the previous timber harvest, and have not yet recovered to populate all available habitat. Closer inspection of species-habitat associations in relation to habitat availability in headwaters might explain patchy patterns. Alternatively, these patterns may be related to species' life histories or behaviors. For example, do *Cottus* and *A. truei* have aggregation tendencies that promote patchiness? In any event, our results suggest that unique assemblages in headwaters may be highly localized such that single reaches within a managed headwater or forest stand could be important for the retention of a species at local scales. Extensively applied surveys to detect presence of species of concern, such as *A. truei*, could be used to prioritize protections to reaches with particular species (Olson et al. 2007). Also, this pattern suggests that at least some reaches within a local area appear to be independent relative to species, supporting use of reach-level studies to characterize headwater streams.

In summary, we identify species and species-assemblages associated with headwaters in selected managed forest stands of western Oregon. Our findings suggest a two-pronged approach can clarify the biota of interest in headwater drainages and lead to management activities consistent with their likely persistence. First, identification of reaches that may function as habitat for unique or sensitive species and species-assemblages can be determined by rapidly applied inventories of stream reaches and banks. Our data suggest *Rhyacotriton* salamanders, *Ascaphus* frogs, and *Cottus* fish may be taxa of specific consideration in our headwater sample: *Rhyacotriton* because of their uppermost headwater tendencies, and *Cottus* and *Ascaphus* because of their patchy occurrences among reaches. Our data suggest that these taxa are not rare within reaches, so that extensively applied reach-level censuses could detect distinct assemblage patterns. Second, retention of headwater stream physical habitat attributes associated with these species may be critical to their persistence. In particular, we found stream hydrology, gradient, and substrate to be predictors of several species and assemblage patterns.

Literature Cited

ADAMS, M.J., AND R.B. BURY. 2002. The endemic headwater stream amphibians of the American Northwest: Associations

with environmental gradients in a large forested preserve. *Global Ecol. Biogeogr.* 11:169–178.

BAILEY, L.L., T.R. SIMONS, AND K.H. POLLOCK. 2004a. Estimating site occupancy and species detection probability parameters for terrestrial salamanders. *Ecol. Applic.* 14:692–702.

BAILEY, L.L., T.R. SIMONS, AND K.H. POLLOCK. 2004b. Spatial and temporal variation in detection probability of Plethodon salamanders using the robust mark-recapture design. *J. Wildl. Manag.* 68:14–24.

BAXTER, C.V., K.D. FAUSCH, AND W.C. SAUNDERS. 2005. Tangled webs: Reciprocal flows of invertebrate prey link streams and riparian zones. *Freshw. Biol.* 50:201–220.

BENDA, L.E., AND T.W. CUNDY. 1990. Predicting deposition of debris flows in mountain channels. *Can. Geotech. J.* 27:409–417.

BENDA, L.E., AND T. DUNNE. 1997a. Stochastic forcing of sediment supply to channel networks from landsliding and debris flows. *Water Resour. Res.* 33:2849–2863.

BENDA, L.E., AND T. DUNNE. 1997b. Stochastic forcing of sediment routing and storage in channel networks. *Water Resour. Res.* 33:2865–2880.

BLAUSTEIN, A.R. 2005. Declining amphibian populations. P. 20–21 in *Amphibians of the Pacific Northwest*, Jones, L.L.C., W.P Leonard, and D.H. Olson (eds.). Seattle Audubon Society, Seattle, WA. 227 p.

BLAUSTEIN, A.R., J.J. BEATTY, D.H. OLSON, AND R.M. STORM. 1995. *The biology of amphibians and reptiles in old-growth forests in the Pacific Northwest.* Gen. Tech. Rep. PNW-GTR-337. USDA Forest Service, Pacific Northwest Research Station, Portland, OR. 98 p.

BOND, C.E. 1973. *Keys to Oregon freshwater fishes.* Technical Bulletin 58, Agricultural Experiment Station, Oregon State University, Corvallis, OR. 42 p.

BURY, R.B. 1988. Habitat relationships and ecological importance of amphibians and reptiles. P. 61–76 in *Streamside management riparian wildlife and forestry interactions*, Raedke, K.J. (ed.). Inst. Resour. Contrib. 59, University of Washington, Seattle, WA.

BURY, R.B., P.S. CORN, K.B. AUBRY, F.F. GILBERT, AND L.L.C. JONES. 1991. Aquatic amphibian communities in Oregon and Washington. P. 353–362 in *Wildlife and vegetation of unmanaged Douglas-fir forests*, Ruggerio, L.F., K.B. Aubry, A.B. Carey, and M.H. Huff (technical coordinators). Gen. Tech. Rep. PNW-GTR-285, USDA Forest Service, Pacific Northwest Research Station, Portland, OR.

CISSEL, J.H., P. ANDERSON, S. CHAN, A. MOLDENKE, D. OLSON, R. PROGAR, K. PUETTMANN, C. THOMPSON, AND S. WESSELL. 2004. *Bureau of Land Management's Density Management Study.* Cooperative Forest Ecosystem Research (CFER) program fact sheet. Oregon State University, Corvallis, OR. 6 p.

CISSEL, J.H., P. ANDERSON, D.H. OLSON, K. PUETTMANN, S. BERRYMAN, S. CHAN, AND C. THOMPSON. 2006. *BLM density management and riparian buffer study: Establishment report and study plan.* USDI, US Geological Survey, Scientific Investigations Report 2006-5087. 144 p.

CISSEL, J.H., F.J. SWANSON, G.E. GRANT, D.H. OLSON, S.V. GREGORY, S.L. GARMAN, L.R. ASHKENAS, M.G. HUNTER, J.A. KERTIS, J.H. MAYO, M.D. MCSWAIN, S.G. SWETLAND, K.A. SWINDLE, AND D.O. WALLIN. 1998. *A landscape plan based on historic fire regimes for a managed forest ecosystem: The Augusta Creek study.* PNW-GTR-422, Forest Service, Pacific Northwest Research Station, Portland, OR. 82 p.

CISSEL, J.H., F.J SWANSON, AND P.J. WEISBERG. 1999. Landscape management using historical fire regimes: Blue River, Oregon. *Ecol. Appl.* 9(4):1217–1231.

CORKRAN, C.C., AND C. THOMS. 1996. *Amphibians of Oregon, Washington and British Columbia.* Lone Pine Publishing, Renton, WA. 175 p.

DAVIC, R.D., AND H.H. WELSH JR. 2004. On the ecological roles of salamanders. *Ann. Rev. Ecol. Evol. Syst.* 35:405–434.

DEMAYNADIER, P.G., AND M.L. HUNTER JR. 1995. The relationship between forest management and amphibian ecology: A review of the North American literature. *Environ. Rev.* 3:230–261.

DILLER, L.V., AND R.L. WALLACE. 1996. Distribution and habitat of *Rhyacotriton variegatus* in managed, young growth forests in north coastal California. *J. Herpetol.* 30(2):184–191.

DUPUIS, L., AND D. STEVENTON. 1999. Riparian management and the tailed frog in northern coastal forests. *For. Ecol. Manag.* 124:35–43.

FRANKLIN, J.F., AND C.T. DYRNESS. 1988. Natural vegetation of Oregon and Washington. Oregon State University Press, Corvallis, OR. 452 p.

GOMI, T., R.C. SIDLE, AND J.S. RICHARDSON. 2002. Understanding processes and downstream linkages of headwater streams. *Bioscience* 52:905–916.

GREGORY, S.V. 1997. Riparian management in the 21st century. P. 69–85 in *Creating a forestry for the 21st century: The science of ecosystem management*, Kohm, K.A., and J.F. Franklin (eds.). Island Press, Washington, DC.

GREGORY, S.V., F.J. SWANSON, AND W.A. MCKEE. 1991. An ecosystem approach to riparian zones. *Bioscience* 40:540–551.

HANKIN, D.G., AND G.H. REEVES. 1988. Estimating total fish abundance and total habitat area in small streams based on visual estimation methods. *Can. J. Fish. Aquat. Sci.* 45:834–844.

HYDE, E.J., AND T.R. SIMONS. 2001. Sampling plethodontid salamanders: Sources of variability. *J. Wildl. Manag.* 65:624–632.

JAMES, F.C., AND C.E. MCCULLOCH. 1990. Multivariate Analysis in ecology and systematics: Panacea or Pandora's box? *Annu. Rev. Ecol. Syst.* 21:129–166.

JONES, L.L.C., W.P. LEONARD, AND D.H. OLSON (EDS.). 2005. *Amphibians of the Pacific Northwest.* Seattle Audubon Society, Seattle, WA. 227 p.

LINDENMAYER, D.B., AND J.F. FRANKLIN. 2002. *Managing forest biodiversity: A comprehensive multiscaled approach.* Island Press, Washington DC. 351 p.

MARSHALL, D.B. 1992. *Sensitive vertebrates of Oregon.* Oregon Department of Fish and Wildlife, Portland.

MCCULLAGH, P., AND J.A. NELDER. 1989. *Generalized linear models.* Chapman and Hall, New York. 511 p.

MCCUNE, B., AND J.B. GRACE. 2002. *Analysis of ecological communities.* MjM, Gleneden Beach, OR. 300 p.

MEYER, J.L., AND J.B. WALLACE. 2001. Lost linkages and lotic ecology: Rediscovering small streams. P. 295–317 in *Ecology: Achievement and challenge*, Press, M.C., N.J. Huntley, and S. Levins (eds.). Blackwell Scientific, Oxford, United Kingdom.

NAIMAN, R.J., R.E. BILBY, AND P.A. BISSON. 2000. Riparian ecology and management in the Pacific coastal rain forest. *Bioscience* 50:996–1011.

NAIMAN, R.J., AND H. DECAMPS. 1997. The ecology of interfaces-riparian zones. *Ann. Rev. Ecol. Syst.* 28:621–658.

OLSON, D.H., P.D. ANDERSON, C.A. FRISSELL, H.H. WELSH JR., AND D.F. BRADFORD. 2007. Biodiversity management approaches for stream-riparian areas: Perspectives for Pacific Northwest headwater forests, microclimates, and amphibians. *For. Ecol. Manag.* In press.

OLSON, D.H., S.S. CHAN, AND C.R. THOMPSON. 2002. Riparian buffers and thinning designs in western Oregon headwaters

accomplish multiple resource objectives. P. 81–92 in *Congruent management of multiple resources: Proceedings from the Wood Compatibility Initiative workshop.* Johnson, A.C., R.W. Haynes, and R.A. Monserud (eds.). Gen. Tech. Rep. PNW-GTR-563. USDA Forest Service, Pacific Northwest Research Station, Portland, OR.

OLSON, D.H., J.C. HAGAR, A.B. CAREY, J.H. CISSEL, AND F.J. SWANSON. 2001. *Wildlife communities in westside and high montane forest.* P. 187–212 in Wildlife-habitat relationships in Oregon and Washington, Johnson, D.H., and T.A. O'Neil (eds.). Oregon State University Press, Corvallis, OR.

PROGAR, R.A., AND A.R. MOLDENKE. 2002. Insect production from temporary and perennially flowing headwater streams in western Oregon. *J. Freshw. Ecol.* 17:391–407.

RAPHAEL, M.G., P.A. BISSON, L.L.C. JONES, AND A.D. FOSTER. 2002. Effects of streamside forest management on the composition and abundance of stream and riparian fauna of the Olympic Peninsula. P. 27–40 in *Congruent management of multiple resources: Proceedings from the Wood Compatibility Initiative workshop*, Johnson, A.C., R.W. Haynes, and R.A. Monserud (eds.). Gen. Tec. Rep. PNW-GTR-563. USDA Forest Service, Pacific Northwest Research Station, Portland, OR.

REEVES, G.H., K.M. BURNETT, AND E.V. MCGARRY. 2003. Sources of large wood in a pristine watershed in coastal Oregon. *Can. J. For. Res.* 33:1363–1370.

SHERIDAN, C.D., AND D.H. OLSON. 2003. Amphibian assemblages in zero-order basins in the Oregon Coast Range. *Can. J. For. Res.* 33:1452–1477.

SHERIDAN, C.D., AND T.A. SPIES. 2005. Vegetation-environment relationships in zero-order basins in coastal Oregon. *Can. J. For. Res.* 35:340–355.

STEELE, C.A., E.D. BRODIE JR., AND J.G. MACCRACKEN. 2003. Relationships between abundance of Cascade torrent salamanders and forest age. *J. Wildl. Manag.* 67:447–453.

STODDARD, M.A., AND J.P. HAYES. 2005. The influence of forest management on headwater stream amphibians at multiple spatial scales. *Ecol. Appl.* 15:811–823.

STRAHLER, A.N. 1957. Quantitative analysis of watershed geomorphology. *Trans. Am. Geophys. Union* 38:913–920.

STUART, S.N., J.S. CHANSON, N.A. COX, B.E. YOUNG, A.S.L. RODRIGUES, D.L. FISCHMAN, AND R.W. WALLER. 2004. Status and trends in amphibian declines and extinctions worldwide. *Science* 306:1783–1786.

USDA AND USDI [US DEPARTMENT OF AGRICULTURE AND US DEPARTMENT OF INTERIOR]. 1993. *Forest ecosystem management assessment team (FEMAT): An ecological, economic, and social assessment.* Portland, OR.

USDA AND USDI [US DEPARTMENT OF AGRICULTURE AND US DEPARTMENT OF INTERIOR]. 1994. *Record of decision on management of habitat for late-successional and old-growth forest related species within the range of the northern spotted owl [Northwest Forest Plan].* Portland, OR.

USDA AND USDI [US DEPARTMENT OF AGRICULTURE AND US DEPARTMENT OF INTERIOR]. 1996a. *Riparian reserve evaluation techniques and synthesis. Module of the guide to watershed analysis.* Riparian Reserve Technical Team, Regional Ecosystem Office, Portland, OR. Interagency publication. 42 p.

USDA AND USDI [US DEPARTMENT OF AGRICULTURE AND US DEPARTMENT OF INTERIOR]. 1996b. *Species information: Addendum to appendix B, riparian reserve evaluation techniques and synthesis. Module of the guide to watershed analysis.* Riparian Reserve Technical Team, Regional Ecosystem Office, Portland, OR. Interagency publication. 342 p.

USDA AND USDI [US DEPARTMENT OF AGRICULTURE AND US DEPARTMENT OF INTERIOR]. 2005. *Bureau of Land Management, Oregon and Washington, and US Forest Service, region 6, interagency special status and sensitive species program: Agency policies and lists.* www.or.blm.gov/ISSSP/index.htm. Accessed Jan. 11, 2006.

WELSH, H.H. JR., G.R. HODGSON, AND A.J. LIND. 2005. Ecogeography of the herpetofauna of a northern California watershed: Linking species patterns to landscape processes. *Ecography* 28:537–551.

WELSH, H.H. JR., AND A.J. LIND. 1996. Habitat correlates of the southern torrent salamander, *Rhyacotriton variegatus* (Caudata rhyacotritonidae), in northwestern California. *J. Herpetol.* 30:385–398.

WELSH, H.H. JR., AND A.J. LIND. 2002. Multiscale habitat relationships of stream amphibians in the Klamath-Siskiyou region of California and Oregon. *J. Wildl. Manag.* 66:581–602.

WILKINS, R.N., AND N.P. PETERSON. 2000. Factors related to amphibian occurrence and abundance in headwater streams draining second-growth Douglas-fir forests in southwestern Washington. *For. Ecol. Manag.* 139:79–91.

WILLSON, J.D., AND M.E. DORCAS. 2003. Effects of habitat disturbance on stream salamanders: Implications for buffer zones and watershed management. *Conserv. Biol.* 17:763–771.

WIPFLI, M.S., AND D.P. GREGOVICH. 2002. Export of invertebrates and detritus from fishless headwater streams in southeast Alaska: Implications for downstream salmonid production. *Freshw. Ecol.* 47:957–969.