INFLUENCE OF SITE AND LANDSCAPE FEATURES ON VERTEBRATE ASSEMBLAGES IN SMALL STREAMS

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ABSTRACT

The relative influence of site- and landscape-level habitat features on fishes and stream-dwelling amphibians was evaluated at 62 headwater streams on the Olympic Peninsula in Washington state. Watershed areas at the study sites ranged from 16 to 2,817 ha (average 265 ha) and the catchments had varied geologic, land use, and natural disturbance histories. Site-level features included stream habitat type, channel substrate, and riparian forest condition. Landscape-level features included forest age, drainage characteristics, elevation, road density, and landslide frequency. There were important differences in habitat associations among species within the two major headwater vertebrate groups (fishes and amphibians) as well as between the two groups themselves. In general, fishes were more strongly influenced by in-stream habitat parameters than by riparian or watershed variables. Stream-dwelling amphibians, however, were influenced by riparian and watershed features and were less affected by in-stream habitats. Thus, fishes may be the best overall indicators of site-scale stream conditions; amphibians seem to be more sensitive indicators of landscape-scale riparian and upland features. Preliminary comparison of the information value of different landscape-level variables (their importance to stream-dwelling vertebrates relative to the cost of obtaining them) showed that certain variables had much greater utility for landscape-scale assessments than others.

KEY WORDS: Streams, fish, amphibians, riparian, watersheds.

INTRODUCTION

Riparian zones are recognized as fundamentally important interfaces between aquatic and terrestrial ecosystems (Agee 1988; Gregory et al. 1991; FEMAT 1993; Naiman et al. 2000). In addition to mediating the transfer of materials between land and water, riparian zones provide key habitat elements for many species of fish and wildlife. Virtually all aquatic species and many terrestrial plant and animal species closely associated with riparian zones are sensitive to management-induced changes in riparian condition (Thomas et al. 1979; Naiman et al. 1995). The way in which these species respond to anthropogenic disturbance is usually complex and strongly influenced by ecological processes at a particular site (Hayes et al. 1996); therefore, it is often difficult to predict how a particular aquatic-riparian ecosystem will change following a management activity. Recent studies have demonstrated a reduction in aquatic and terrestrial biodiversity in watersheds containing primarily young, managed forests (Reeves et al. 1993; Thomas et al. 1993), and the emerging application of ecosystem-based forestry in the Pacific Northwest has embraced deliberate attempts to restore riparian areas to conditions more like those produced by natural processes (FEMAT 1993; Quigley et al. 1996).

Despite the acknowledged importance of riparian zones to fish and wildlife, relatively few studies have examined the response of riparian systems to management alternatives for commodity production, riparian protection, or

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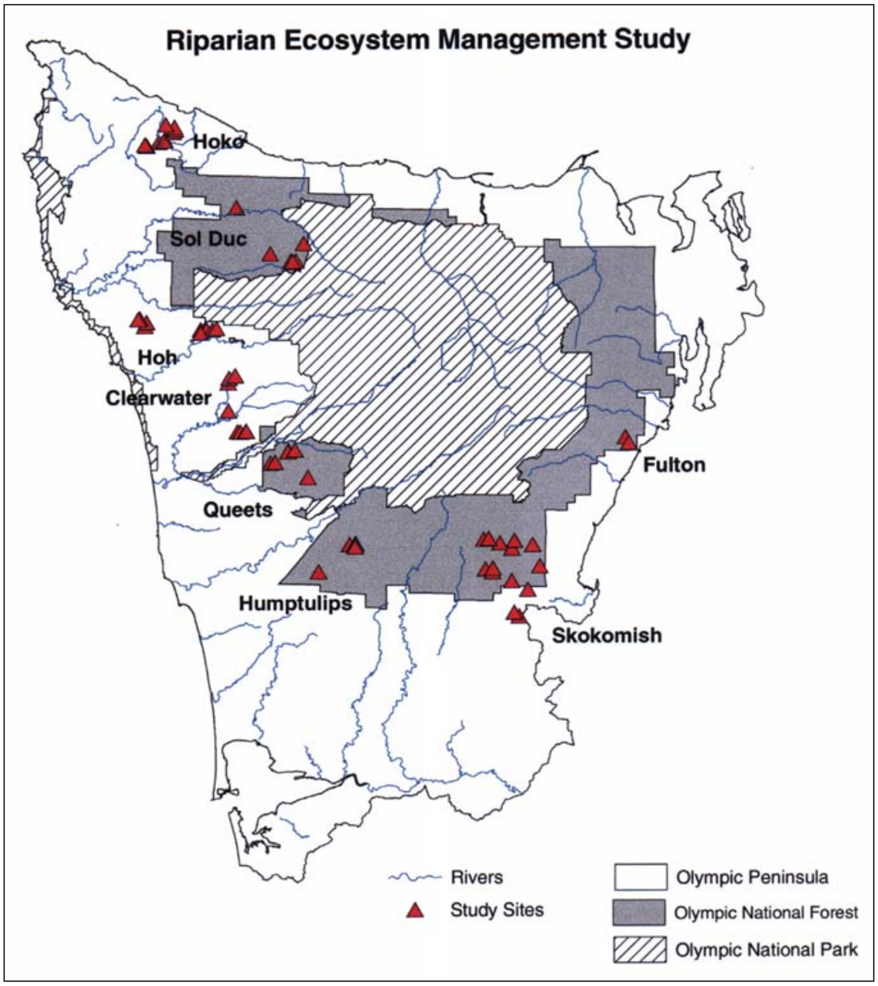

Figure 1—Location of study sites on the Olympic Peninsula, Washington state. Names of major river basins in which study sites occurred are given. The crosshatched area bounds Olympic National Forest and Olympic National Park.

restoration. The Coastal Oregon Productivity Enhancement (COPE) program in Oregon sponsored investigations of riparian rehabilitation, chiefly involving the re-establishment of conifers in alder- and brush-dominated riparian zones[1], and similar research programs have begun in coastal areas of Washington (Berg 1995). In addition to the challenge of re-establishing conifers in riparian zones dominated by deciduous trees or herbaceous vegetation, a number of other important questions exist pertaining to riparian management, e.g., what buffer widths and configurations are needed to protect fish and wildlife habitat along different stream types, what proportion of riparian zones should remain in different seral stages over broad landscapes, whether acceleration of mature forest and old-growth conditions can be achieved through thinning and other silvicultural treatments in a cost-effective manner, and whether riparian vegetation can be deliberately managed for the benefit of aquatic or terrestrial wildlife.

The Riparian Ecosystem Management Study (REMS) examined the effect of different streamside buffers on the major aquatic- and riparian-associated vertebrates, i.e., fishes, amphibians, birds, and small mammals. A total of 62 streams and associated riparian zones were examined on Washington's Olympic Peninsula from 1996 to 1999. Most of our study sites were located in small watersheds, and in fact, about one-third of the streams were too small or too steep to support fishes. Nevertheless, such small streams comprise a majority of the stream network and their riparian zones can occupy a significant portion of the landscape in areas with high drainage densities. The fundamental question we asked was: *Does the structure of managed riparian zones in small streams influence the presence and/or abundance of aquatic and riparian-associated vertebrates?*

[1] COPE Report, Vol. 9, No. 3, Aug. 1996.

Table 1—Top: common names of headwater stream vertebrates[a]. Bottom: site- and landscape-scale variables examined in this study.

	Taxa	
Fishes	**Amphibians**	**Assemblages**
Cutthroat trout	Tailed fiog	All fish species
Torrent sculpin	Cope's giant salamander	All stream-dwelling
Coastrange sculpin	Torrent salamander	amphibian species
	Environmental variables	
	Site	*Landscape*
In-stream	**Riparian**	**Watershed**
Stream channel gradient	Canopy density	% watershed in early-seral forest
% channel in scour pools	% riparian early-seral forest	
% channel in fast-water habitats (riffles, cascades)	% riparian mid-seral forest	% watershed in mid-seral forest
	% riparian late-seral forest	
% channel in glides		% watershed in late-seral forest
% channel in silt and sand substrate		Road density
% channel in gravel and pebble substrate		Drainage density
		Watershed area
% channel in large and small cobble substrate		Elevation at base
		% watershed area in recently active landslides
% channel in boulder and bedrock substrate		% watershed area in southerly aspect
		% watershed area with steep slopes (>60%)

[a] Other taxa (e.g., coho salmon, western redback salamander) were occasionally sampled in the streams, but their frequencies were too low to be included in the analyses.

Although REMS was designed to evaluate vertebrate responses to riparian conditions at the site level (typically, 300 m reaches), we could not ignore the possibility that fishes and amphibians may have been influenced by broad-scale characteristics of the watersheds they inhabited, irrespective of the condition of the immediately adjacent riparian zone. Because our initial analysis of the relationship between different vertebrates and site-level features left many unanswered questions regarding what environmental factors were most influential, we expanded the assessment to include landscape-scale features such as forest age, drainage characteristics, elevation, road density, and disturbance history. This paper reports on the relative influence of site- and landscape-level habitat characteristics on headwater stream vertebrates. Correlation analysis was used to determine the association between abundance of different organisms and site- and landscape-level parameters. We further compared the information value of different parameters (i.e., their overall importance to stream-dwelling vertebrates) to the relative cost of estimating those parameters, in order to identify cost-effective landscape-level indicators of environmental suitability for these organisms. Additional information about the study is found in a companion paper (Raphael et al. 2002, in this proceedings).

STUDY LOCATION AND METHODS

Study Sites

A total of 62 sites consisting of 300-m reaches of stream channel and adjacent riparian zone were selected in first- to third-order, forested streams on Washington's Olympic Peninsula (Figure 1). Most streams were small, 1 to 7 m wide; a few slightly larger streams were 7 to 11 m wide. Elevations of study sites ranged from 120 to 720 m. Riparian conditions at each site were assigned to six different classes depending on whether they were (1) unmanaged with intact forest on both sides of the stream, (2) old forest buffers 16 to 150 m wide (mean = 65 m) within adjacent clear-cuts, (3) second-growth forest 35 to 100 years old with no adjacent harvest, (4) intact second-growth forest

Table 2—Description of site- and landscape-scale (watershed) parameters used in the analysis.

Variable	Variable Type	Description
Site variables		
Stream gradient	In-stream	An average of five or more clinometer measurements along the study reach.
% channel in scour pools	In-stream	Ratio of scour pools (eddy, lateral, mid-channel, plunge) to the total of all habitat units along the study reach.
% channel in fast water habitats	In-stream	Ratio of fast water habitats (rapids, riffles, cascades, chutes and falls) to the total of all habitat units along the study reach.
% channel in glides	In-stream	As above, includes other non-turbulent, fast water habitats such as sheets and runs as well as glides.
% channel in silt and sand substrate	In-stream	Visually estimated % of the wetted substrate in particle sizes <1 to 2mm.
% channel in gravel and pebble substrate	In-stream	Visually estimated % of the wetted substrate in particle sizes 3 to 64mm.
% channel in large and small cobble substrate	In-stream	Visually estimated % of the wetted substrate in particle sizes 65 to 256mm.
% channel in boulder and bedrock substrate	In-stream	Visually estimated % of the wetted substrate in particle sizes >256mm.
Canopy density	Riparian	An average of five or more measurements taken along the channel of each study reach with a canopy densiometer.
% riparian early-seral forest	Riparian	The percentage of the riparian zone adjacent to the study reach in early-seral forest <30 years old.
% riparian mid-seral forest	Riparian	The percentage of the riparian zone adjacent to the study reach in mid-seral forest 31 to 100 years old.
% riparian late-seral forest	Riparian	The percentage of the riparian zone adjacent to the study reach in late-seral forest greater than 100 years old.
Landscape variables		
% watershed early-seral forest	Watershed	A ratio of area of the watershed occupied by early-seral forests less than 30 years old to the total watershed area.
% watershed mid-seral forest	Watershed	A ratio of area of the watershed occupied by mid-seral forests 31 to 100 years old to the total watershed area.
% watershed late-seral forest	Watershed	A ratio of area of the watershed occupied by late-seral forests greater than 100 years old to the total watershed area.
Road density	Watershed	Ratio of road length to watershed area expressed as km/km^2.
Drainage density	Watershed	Ratio of the length of streams to the total watershed area, expressed as km/km^2.
Watershed area	Watershed	The two-dimensional area of the catchment, as measured from the down stream end of each study reach.
Elevation	Watershed	Elevation at the downstream end of each study reach
Recently active landslides	Watershed	A ratio of the area of recently active landslides to the total watershed area, as estimated from aerial photos up to 30 years old.
% watershed in southerly aspect	Watershed	Derived from DEM, a ratio of area of watershed slope aspects between 90° and 270°, to the total watershed area.
% watershed in slopes greater than 60%	Watershed	Derived from DEM, a ratio of area of watershed slopes steeper than 60%, to the total watershed area.

with commercial thinning, (5) second-growth buffers 14 to 32 m wide (mean = 22 m) within adjacent clearcuts, and (6) logged sites up to 35 years old, lacking riparian buffers.

Channel unit surveys (Hawkins et al. 1993) were conducted along the entire length of each stream reach and the dominant streambed substrate was estimated visually. Sites were located on lands administered by the Olympic National Forest, Washington State Department of Natural Resources, and private industrial forest landowners. We studied 3 fish species, 3 amphibian species, 2 vertebrate assemblages (fishes, amphibians), 8 in-stream habitat variables, 4 riparian forest variables, and 10 landscape variables (Table 1). An explanation of the environmental variables is presented in Table 2.

Within the context of this investigation we found no streams that had large Northwest Forest Plan buffers (either 1- or 2-site potential tree heights wide), so we were unable to evaluate that particular buffer treatment. Virtually all study sites were in unmanaged watersheds or areas previously logged according to older buffer strip guidelines that permitted timber harvesting to within 10 to 30 m of the channel. Furthermore, we found that even riparian buffers of mature or old forest had often experienced considerable windthrow. Most of the riparian zones we examined, even those on National Forest, had been managed with a heavy emphasis on wood production.

Vertebrate samples

Fish were sampled by electrofishing using a complete removal summation method. Several randomly selected channel units of each type (Hawkins et al. 1993) present in the reach were repeatedly sampled until no more fish were captured; the combined number of captures represented the estimate for the channel unit. The average density of each fish species in a particular type of channel unit was then extrapolated to the reach as a whole based on the areal percentage of that channel unit type in the stream. Estimated fish densities for each channel unit type, weighted according to the frequency of that type in the overall reach, were combined to produce a stratified estimate of the average fish density throughout the reach. Approximately 40% of the 62 sites we examined possessed no fish, either because they were upstream from an impassable barrier that prevented fish colonization or because they were intermittent and did not provide sufficient surface flow for fish habitation during summer.

Amphibian surveys utilized a randomized transect sampling design. Transects or belts, located perpendicular to the stream channel, were located at 10 m intervals along each study reach. Belts were 1 m wide with variable lengths depending on the wetted width of the stream at that specific location along the channel. Transects were extended beyond the wetted channel for short distances where there were springs or seeps along the channel edge.

Environmental parameters

GIS data layers were used to characterize environmental parameters at the landscape level. Catchment areas were delineated from 10-m digital elevation models (DEMs) obtained from the Olympic National Forest (ONF). Road data were from transportation system maps developed by the ONF in 1990, then updated with 1997 digital ortho-imagery. Forest stand age was derived from a combination of stand data from several watershed analyses conducted on the Olympic Peninsula from 1994 to 1997, and all stand maps were combined and updated with 1997 digital ortho-imagery. Stream networks were derived from a hydrography cover created in 1992 by the ONF and updated with 1997 ortho-imagery at 10-m DEMs. Landslide coverages were also derived from recent watershed analyses on the Olympic Peninsula. Landslide locations were verified with low elevation aerial photographs taken between 1970 and 1999.

Analyses

We utilized a retrospective approach involving comparisons of many sites with different times since logging and different buffer characteristics, instead of long-term analyses of a few sites before and after logging (i.e., the "substituting space for time" approach). The null hypothesis was that there would be no association between the abundance of small stream vertebrates and the characteristics of the adjacent riparian zone assessed in this study. Rejection of the null hypothesis would indicate that certain types of riparian stand conditions affect the composition of some vertebrates.

We used a non-parametric correlation coefficient, Spearman's *rho*, to measure the strength of association between rank-ordered data. The more commonly used parametric correlation coefficient, Pearson's coefficient, was not used because it assumed a linear relationship between two variables, and it was clear from initial scatter plots that associations between vertebrate densities and many variables in the REMS data set were not linear. We normalized all species and assemblage densities to the number of organisms per 100 square m of the wetted stream channel. Tests were two-tailed, and we identified as significant those variables whose association with vertebrate abundance resulted in a Type 1 error of less than 10%. Zero captures

Table 3—Association between headwater stream vertebrates and site- and landscape-scale variables[a] (continued)

Species/sample size	In-stream	Riparian	Watershed
Cutthroat trout, n = 27	Stream gradient (+) % scour pools (+) % glides (-) % small/large cobble (-)		Watershed area (-)
Torrent sculpin, n = 15	% scour pools (+) % fast water habitats (-) % glides (-) % gravel and pebble substrate (-)	% of riparian zone in mid-seral forest (+) % of riparian zone in late-seral forest (-)	% of watershed in late-seral forest(-) Watershed area (-) Recently active landslides (-)
Coastrange sculpin, n = 17	% scour pools (+) % fast water habitats (-) % glides (-) % silt and sand substrate (+) % pebble and gravel substrate (-)	% of riparian zone in late-seral forest (-)	% of watershed in late-seral forest (-) Elevation (-) Drainage density (-)
Tailed frog, n = 20	% boulder and bedrock substrate (+)	% of riparian in late-seral forest (+)	Elevation (+) Watershed area (+) % of watershed with steep slopes (+)
Cope's giant salamander, n = 24	% silt and sand substrate (+)		Road density (-) Recently active landslides (+) Drainage density (-)
Torrent salamander, n = 16	Stream gradient (+) % small and large cobble substrate (-) % boulder and bedrock substrate (-)		% of watershed with steep slopes (+) Elevation (+)
All fishes combined, n = 37	% scour pools (+) % fast water habitats (-) % glides (-) % silt and sand substrate (+) % pebble and gravel substrate (-)	% of riparian zone in late-seral forest (-)	% of watershed in late-seral forest (-) Elevation (-) Recent landslide activity (-) Southerly aspect (+)

Table 3—Association between headwater stream vertebrates and site- and landscape-scale variables[a]

Species/sample size	In-stream	Riparian	Watershed
All stream-dwelling amphibians combined, n = 29	% silt and sand substrate (+)	% riparian in early-seral forest (+)	% of watershed in seral forest(-)
	Stream gradient (+)	% riparian in late-seral forest (+)	% of watershed in late-seral forest (+)
			Road density (-)
			Elevation (+)

[a] Only variables with Spearman's *rho* correlation coefficients having a probability less than 0.10 are shown; all other associations were considered non-significant. Plus signs in parentheses indicate a positive correlation between organism density and a variable. Minus signs indicate a negative correlation. Sample sizes refer to the number of sites in which taxa occurred.

were included in the analyses and all independent variables (Table 1) were included in the model. Statistical tests were performed using SPSS[1] software.

Some of the landscape-scale parameters in the analysis were expensive and time consuming to quantify, often requiring hours of map reading and digitizing. Furthermore, field surveys required many hours of labor, data transcription, and analysis. Because some parameters turned out to have more influence on headwater vertebrates than others, we also compared the "information value" of the variables that were studied, i.e., their weighted average value in correlation analysis of all taxa (irrespective of sign) to the relative cost of obtaining quantitative values for them. Equipment costs were not included; we based our estimates solely on the number of hours required to measure or otherwise quantify each parameter. The goal was to assess the relative cost and benefit of including different site- and landscape-scale features in the analysis of vertebrate abundance.

RESULTS

Fishes

There were important differences in habitat associations between species within major groups (fish and amphibians) as well as between species themselves. In general, fishes were more closely associated with in-stream habitat parameters than with adjacent riparian or watershed variables (Table 3). Cutthroat trout (*Oncorhynchus clarki clarki*) preferred small watersheds and streams with abundant pool habitat. Their lower densities in streams with glides, habitats with cobble substrate, and larger watersheds may have been indicative of reduced abundance in low-gradient, alluvial streams. Cutthroat trout were not sensitive indicators of riparian forest condition.

Torrent sculpins (*Cottus rhotheus*) preferred streams in small watersheds with abundant pool habitat, mid-seral riparian forests (*not* late-seral riparian forests), and watersheds in which there was little mass wasting (landslides). Like cutthroat trout, torrent sculpins were less abundant in low-gradient streams dominated by glide habitat and substrates of moderate size (Table 3). The negative association between torrent sculpins and fast-water habitats could not be explained and may have been caused by factors that were not examined, including interactions with native amphibians.

Coastrange sculpins (*C. aleuticus*) primarily inhabited low elevation alluvial streams with abundant pool habitat. They preferred habitats with fine-grained substrates to those with coarse-grained substrates. Coastrange sculpin densities were reduced in streams with late-seral riparian forests and old-growth dominated watersheds.

Amphibians

Tailed frogs (*Ascaphus truei*) were associated with boulder-dominated streams in high-elevation watersheds with steep gradients and riparian zones dominated by late-seral forests (Table 3). If elevation was associated with cooler stream temperatures, tailed frogs may have been responding to colder waters in high-elevation streams, as this species is known to prefer cold water (Corkran and Thoms 1996).

[1] The use of trade or firm names in this publication is for reader information and does not imply endorsement by the U.S. Department of Agriculture of any product or service.

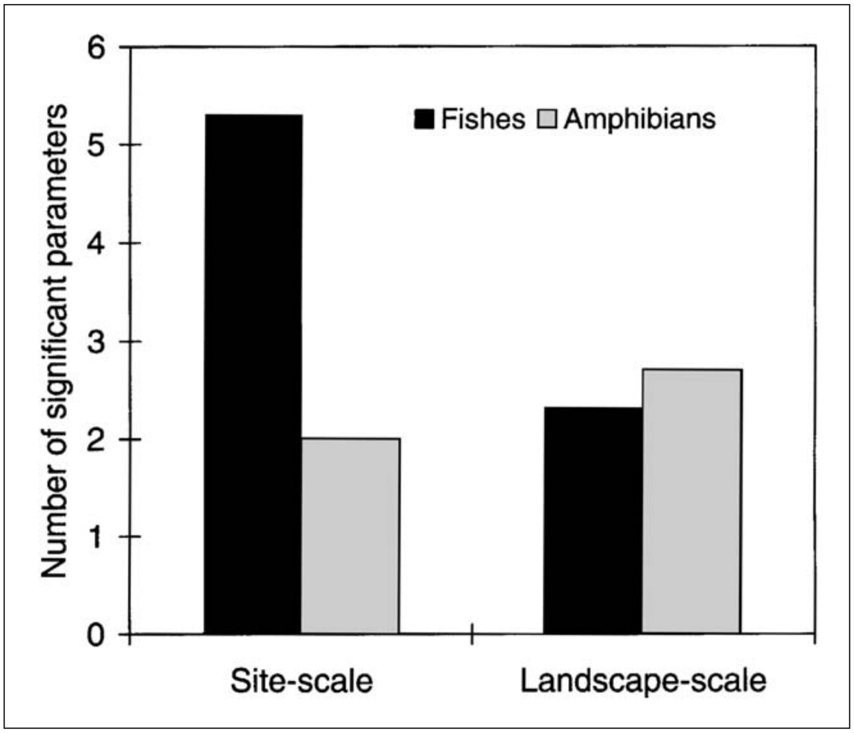

Figure 2—Comparison of the average number of site-scale and landscape-scale variables (Table 1) significantly influencing fish and amphibian species in headwater streams on the Olympic Peninsula.

There was no apparent relationship between the stream-dwelling Cope's giant salamander (*Dicamptodon copei*) and forest age within either the riparian zone or the entire watershed. There was reduced giant salamander abundance in watersheds with high road density and high drainage density. Greater Cope's giant salamander densities in watersheds with recent landslides and in habitats with fine-grained substrate suggest this species responds positively to both fine and coarse sediment inputs, but the reason for this apparent response could not be determined with the data at hand.

Olympic torrent salamanders (*Rhyacotriton olympicus*) preferred high-elevation watersheds with steep topography and high gradient stream channels. They appeared to avoid habitats with coarse-grained substrates (Table 3). There was no correlation between the abundance of torrent salamanders and the composition of riparian or upland forests.

Vertebrate assemblages

Abundance of all fishes combined was greater in streams with frequent pools and fewer riffles and glides (Table 3). The positive association between fish assemblages and sand and silt substrate was probably also related to pools since pool habitat possessed deeper, slowly moving water where fine particles settled out. Overall fish density was reduced in coarse-grained, fast water and glide habitats, suggesting that riffles and cascades were less favorable habitats than pools. Fishes were also generally less abundant in streams with late-seral riparian and upland forests, as well as in high-elevation watersheds and those with recent landslide activity. The somewhat weak but significant correlation between fish abundance and watersheds with southern aspect (which would receive greater solar input) is consistent with the hypothesis that fish populations in headwater streams respond positively to increased solar radiation, resulting in elevated primary and secondary production (Gregory et al. 1987).

Amphibians as a group were more abundant in steep, montane streams than in low gradient coastal streams. Their positive association with sand and silt substrate suggested that most amphibians selected depositional habitats away from swift, turbulent areas of flow. Tailed frog tadpoles were an exception; they preferred turbulent cascade habitat with coarse substrate. Overall, amphibians favored streams with late-seral riparian and upland forests and avoided those with early-seral forests (Table 3). Abundance was greater in high-elevation watersheds but reduced where road densities were above average. The apparent preference of stream-dwelling amphibians for watersheds with late-seral forests and low road density is consistent with the hypothesis that they prosper in landscapes where human disturbance is minimized.

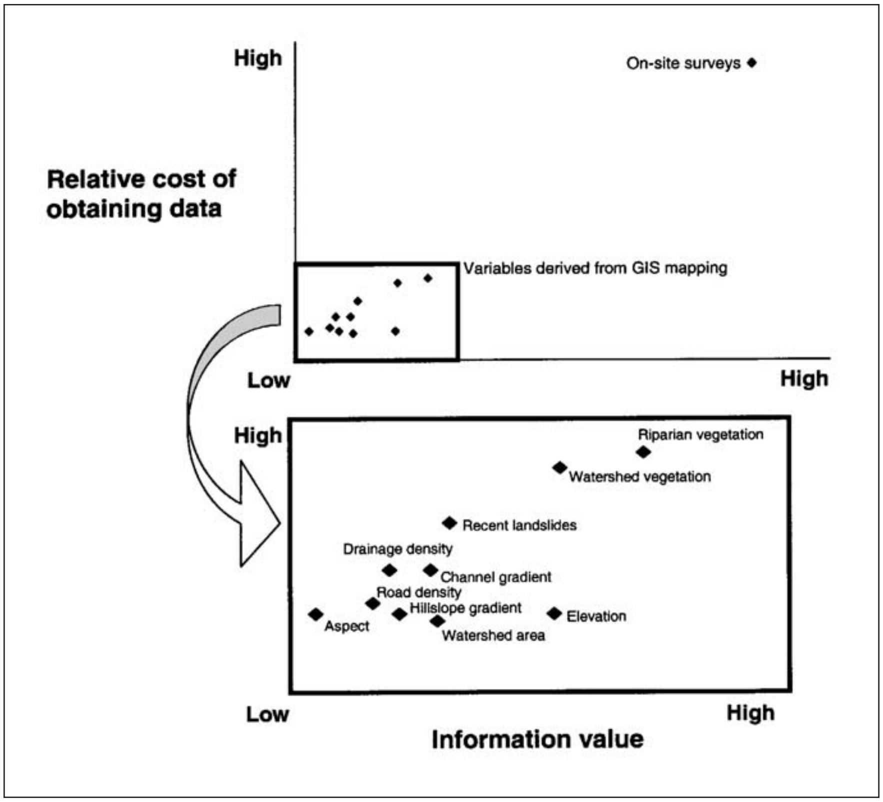

Figure 3—Cost-benefit comparison of various landscape-scale parameters. Information value is the relative influence of each parameter on head-water vertebrates.

Fishes appeared to be more responsive to local conditions than to landscape-scale features, while amphibians were less sensitive to site conditions and were more influenced by the characteristics of the landscape (Figure 2). On average, about five in-stream and riparian site parameters significantly influenced each species, although the parameters themselves differed from species to species. At the watershed scale only about two features, on average, influenced fishes. Amphibians, however, appeared to be more sensitive to landscape-scale parameters than to local conditions. While the reasons for this difference in sensitivity to site and landscape features between fishes and amphibians is not entirely clear, it may have been related to the strict dependence of fish on aquatic habitats, while some amphibians also rely on terrestrial habitats and their movements may have included some upland areas. Thus, amphibians as a group may better integrate overall watershed condition.

Some landscape-scale parameters had greater influence for vertebrate abundance than others, and some were considerably more costly to estimate. The relative cost of obtaining the estimates for landscape-scale parameters was plotted against the information value, i.e., their average score in correlation analysis, of these estimates for headwater vertebrates in our study (Figure 3). We also included two site-level parameters–riparian vegetation and channel gradient–that could have been estimated from air photos or DEM analysis instead of the ground-based methods used in this study, and thus included in landscape assessments. As expected, on-site surveys provided very useful information. However, on-site data were far more expensive to obtain that remote-sensed or map data (Figure 3). Age of riparian vegetation, watershed elevation, and the forest age distribution within the watershed had moderate to high information value. The importance of elevation tended to be high for fishes, and forest characteristics were often valuable for interpreting amphibian abundance. However, the seral age of forest stands was relatively expensive to quantify, both from ground-based surveys and from GIS analyses. The frequency of recent landslides, watershed area, hillslope gradient, drainage density, and road density all had low to moderate average information value, with mass wasting (landslides) being the most expensive to quantify because landslide coverage must be estimated from air photos. Watershed aspect was relatively inexpensive to measure but yielded little information about environmental suitability for headwater vertebrates.

We do not wish to infer that only the parameters scoring high in correlation analysis are worth pursuing, or that those parameters of low information content should not be investigated. Rather, we suggest that this crude cost-benefit analysis may help planners prioritize environmental parameters in landscape assessments of the effects of forest management on headwater vertebrates, and provide hypotheses for other investigators attempting to understand the abundance of fishes and amphibians in small watersheds.

DISCUSSION AND SUMMARY

Results of the study were not consistent across different types of organisms. For fishes, there was little association between species abundance and riparian forest age or the percentage of late-seral forest in the watershed; however, fishes tended to be strongly influenced by the condition of in-stream habitat. Although the riparian forest probably influenced in-stream habitat, our results suggested that the number and size of pools and other habitat parameters important to fishes was likely controlled by a number of other factors, including recruitment of logs and large boulders to the channels by landslides, debris flows, and other disturbance mechanisms. Other parameters associated with the local abundance of fishes in these headwater systems included the elevation of the watershed, gradient of the channel, and the amount of primary production (aquatic plant production as controlled by light and nutrients). Overall, headwater fish populations were highly variable from site to site, which was expected in these disturbance-prone environments (Zalewski and Naiman 1985). Thus, *at the site-level*, we did not reject the hypothesis that the characteristics of the riparian forest had no influence on fish abundance in Olympic Peninsula streams.

Amphibians, however, proved to be more responsive than fishes to riparian forest condition and the amount of late-seral forest in their watersheds. Some amphibians were found to be adaptable generalists, while others were more sensitive to forest management in or near the riparian zone (see Raphael et al. 2002, in this proceedings). Our study suggested that stream-dwelling amphibians were negatively affected by timber removal near small streams. Riparian areas composed of young, early-successional forests did not support amphibian populations at the densities observed in late-seral sites. Buffers of old-growth trees apparently provided habitat refugia for some species and were valuable source areas for recolonization. On the whole, results support the hypothesis that the characteristics of riparian buffers do influence amphibian abundance in Olympic Peninsula streams.

It was clear from our study that the relationship between forest management and the integrity of aquatic and riparian ecosystems was complex. We doubt that it is possible to produce a model or series of models that would predict, quantitatively and with a high level of certainty, the response of headwater aquatic- and riparian-associated vertebrates to management actions at the landscape scale, unless those management actions involved such drastic changes that there would be significant and irreversible alteration of the environment. Likewise, our research suggests that it would be difficult to tailor management actions *at the site level* to produce desired changes in small stream vertebrates at *the population level*. In other words, it seems unlikely that varying the age of riparian buffers at the scale of an operational unit (e.g., 20-100 ha) will predictably and measurably affect the distribution or abundance of most stream-dwelling vertebrate populations within the management area. This is because there will be a spatial mismatch between the distributional boundaries of vertebrate populations and the boundaries of stand-level operations, and because most organisms are free to move from unfavorable to favorable habitats (Schlosser and Angermeier 1995). Local reductions or increases in suitable habitat resulting from stand-level operations may be too small to affect overall population abundance within remaining patches of habitat.

On the other hand, consistent changes in riparian forest properties across large areas may be sufficient to influence population change. If changes in riparian forest structure and composition are pervasive enough to eliminate habitat refugia, populations of headwater vertebrates could decline because suitable habitat is not present throughout their native range and there are insufficient travel corridors to allow for recolonization (Fausch and Young 1995). Because of the unique habitat requirements of different species, linkages between management actions and species' abundance requires understanding at the local population level. For certain species, e.g., resident headwater trout or amphibians with limited distributions, breeding populations can be confined to relatively small areas. For others, e.g., anadromous salmon or neotropical migrant birds, population boundaries are very large. Our study suggests that predictable relationships between species abundance and management activities will require calibration with locally derived data.

A single broadscale measure of ecological performance probably does not exist for headwater vertebrates. Landscape-scale measures of ecosystem condition and performance such as the percentage of a watershed in late-successional forest, the time since the last major disturbance, or the density of roads in an area, may be important to aquatic- and riparian-associated vertebrates but they are insufficient, by themselves, to explain changes in populations over time.

Most headwater organisms are controlled by multiple biotic and abiotic factors, each of which can be more or less important during different periods of the life cycle or over different years (Reeves et al. 1998). Significant associations between some organisms and certain landscape measures were detected in our study, but it is incorrect to assume that a quantitative shift in a single landscape variable (e.g., % old-growth forest, buffer width, density of logging roads) will produce a predictable shift in a species of interest.

Although we conducted correlation analyses between populations and watershed characteristics, none of the watersheds in which sites were located possessed buffers of uniform width and stand age throughout the drainage network. Therefore, we do not have a real basis for assessing the compatibility or tradeoffs between riparian buffer characteristics and vertebrate communities at the ecoregion level. The Olympic Peninsula, where this study was carried out, contains a large inner core of unmanaged, pristine forest (Olympic National Park) surrounded by lands that have been intensely managed for wood production. We found comparatively few *major* differences among the vertebrate populations of headwater streams regardless of buffer properties, but results might have been different if the large, central refuge area of Olympic National Park had not been present.

Our failure to detect consistent differences among riparian treatments was influenced by the limited size of our study sites, usually about 300 linear meters of stream and riparian zone. In spite of our efforts to locate watersheds in which riparian treatments were applied more uniformly across the landscape, or to arrange for deliberate riparian management experiments involving manipulation at a much larger scale, we were unable to locate any study areas that possessed uniform buffers throughout the stream system. Complex patterns of land ownership on the Olympic Peninsula involving public, state, private industrial, small private, and tribal forest lands, each with different riparian management prescriptions, further exacerbated the problem of finding study sites with uniform conditions. In this sense, our study was unable to answer the general question: *"Does the structure of managed riparian zones in small streams influence the presence and or abundance of aquatic- and riparian-associated vertebrates?"* because we could not examine biophysical responses at a scale appropriate to the question.

Finding the right approach to this question remains problematic. The prospect of locating study sites large enough to experimentally implement different buffer treatments at a scale permitting evaluation of variable buffer widths or tree spacing on vertebrate populations is daunting. The alternative approach, relying on simulation modeling or landscape analysis to predict those same effects, often involves many untested (and often incorrect) assumptions. We believe knowledge of life cycles and species' habitat requirements is a necessary precursor to large-scale modeling; therefore, we advocate continued investigations at the species level while exploring alternate methods of scaling up hypothesis testing to the assemblage and landscape level using a combination of controlled small watershed studies, as in the Hubbard Brook or Alsea Watershed investigations, and new methods of landscape analysis. Information derived from such studies will more effectively inform decision-makers charged with balancing the tradeoff between wood production and environmental protection of headwater aquatic and riparian ecosystems.

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