

Table 3—Mean captures (number per 100 trap-nights) of amphibians across the moisture gradient in old-growth stands (standard deviations are in parentheses)

Species	Oregon Coast Range			Oregon Cascade Range			Southern Washington Cascade Range		
	Dry <i>n</i> = 8	Moderate <i>n</i> = 14	Wet <i>n</i> = 5	Dry <i>n</i> = 7	Moderate <i>n</i> = 9	Wet <i>n</i> = 12	Dry <i>n</i> = 7	Moderate <i>n</i> = 11	Wet <i>n</i> = 9
Northwestern salamander	0.009 (.016)	0.015 (.033)	0.021 (.047)	0.013 (.023)	0.045 (.112)	0.097 (.202)	0.280 (.549)	0.209 (.268)	0.134 (.210)
Pacific giant salamander	.031 (.039)	.062 (.061)	.049 (.031)	0	.028 (.062)	.100 (.119)	0	.004 (.013)	.034 (.061)
Olympic salamander ^a	.030 (.051)	.030 (.051)	.049 (.047)	0	.027 (.061)	.006 (.019)	0	.015 (.024)	0
Ensatina	.500 (.209)	.419 (.258)	.451 (.107)	.587 (.381)	.370 (.224)	.211 (.287)	1.001 (1.132)	.746 (.909)	.199 (.174)
Western redback salamander	.452 (.383)	.556 (.342)	.563 (.352)	.008 (.021)	.029 (.058)	.019 (.067)	.092 (.225)	.021 (.056)	.077 (.185)
Roughskin newt	.192 (.235)	.079 (.127)	.215 (.406)	.008 (.022)	.161 (.171)	.166 (.238)	.197 (.188)	.158 (.325)	.020 (.046)
Tailed frog	0	.032 (.046)	.153 (.122)	.008 (.022)	.316 (.924)	.119 (.247)	.143 (.101)	.095 (.071)	.214 (.332)
Red-legged frog	.004 (.012)	.002 (.009)	0	.025 (.067)	.040 (.121)	.002 (.008)	.033 (.051)	.088 (.111)	.061 (.099)

^a Olympic salamanders do not occur at the north end of the Cascade Range in Washington or the south end of the Cascade Range in Oregon. Correct sample sizes are: Oregon dry (3), moderate (5), wet (10); Washington dry (6), moderate (6), wet (3).

Table 4—Significant associations between amphibian abundances and major physiographic and vegetative gradients (negative associations in parentheses)

Variable	Northwestern salamander	Pacific giant salamander	Olympic salamander	Ensatina	Western redback salamander	Roughskin newt	Tailed frog	Red-legged frog
Stand age				(XXXX) ^a				
Elevation				(XXXX)		(XXXX)	XXXX	(XXXX)
Aspect		XXXX					XXXX	
Slope				XXXX	XXXX			(XXXX)
Water				(XXXX)				
Talus					XXXX			
DF1A ^b	XXXX							
DF2A ^c								
DF1M ^d	(XXXX)	XXXX						
DF2M ^e		XXXX		(XXXX)				

^a *P* < 0.05.

^b Correlated with stand development (Spies and Franklin, this volume).

^c Correlated with amount of coarse woody debris (Spies and Franklin, this volume).

^d Correlated with increasing temperature (Spies and Franklin, this volume).

^e Correlated with increasing moisture (Spies and Franklin, this volume).

Habitat Associations

More significant associations of amphibian abundance with physiographic variables were found than with vegetation variables (table 4). Analysis of covariance controls for differences among provinces (for example, elevations were generally lower in the Coast Range), but gradients within provinces may complicate interpretation of these results. For example, elevation was highest in Washington in the north, but in the Cascade Range in Oregon the southern stands were highest.

Responses of individual species varied widely with habitat variables. Northwestern salamanders were more abundant in cool old-growth forest than in other combinations. Pacific giant salamanders were more abundant in warmer, wetter stands than in other conditions. The abundance of Olympic salamanders was low in all provinces, and this species was not related to any of the gradients examined.

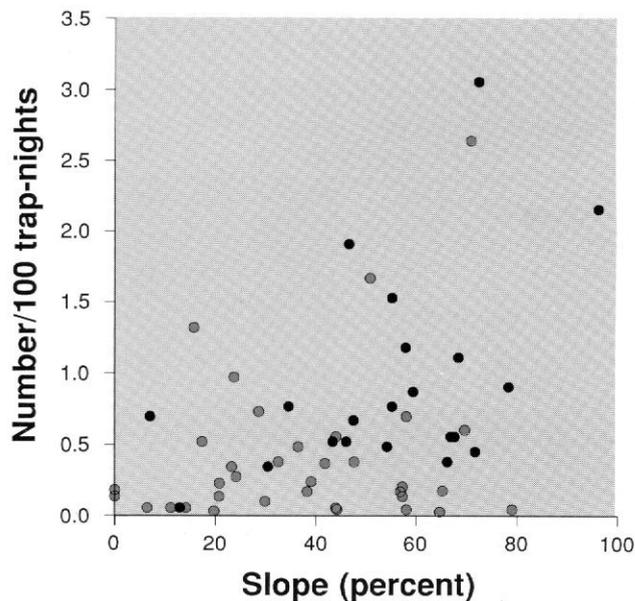


Figure 2—Abundance of western redback salamanders related to slope. Shown here are stands in Washington and the Oregon Coast Range where this species was present. Filled circles are stands with talus, open circles are stands without talus present on the pitfall grid.

Ensatina was more abundant in younger, drier stands, and steeper stands at lower elevations, than in other combinations of conditions. Western redback salamanders were more abundant on steep slopes (fig. 2). Roughskin newts were most abundant at lower elevations, and tailed frogs were more abundant at higher elevations with southern exposures than in other situations. Red-legged frogs were most abundant at lower elevations with flatter slopes.

Regional Patterns

Based on the multidimensional scaling of species richness, the Oregon Coast Range appears to be distinct from the Cascade Range, whereas the Cascade Range in Oregon and Washington shows a degree of overlap (fig. 3a). This observation is supported by a separate analysis: the nonhierarchical clustering of three pools of stands (table 5). Two of these pools identify stands in the Oregon Coast Range and Washington Cascade Range; the largest pool (pool 1) contains most of the stands in the Oregon Cascade Range and half of the Washington stands. The Coast Range pool had the highest species richness, with six species present in more than 50 percent of the stands, and the Washington pool had the lowest richness, with only three species present in more than 50 percent of the stands.

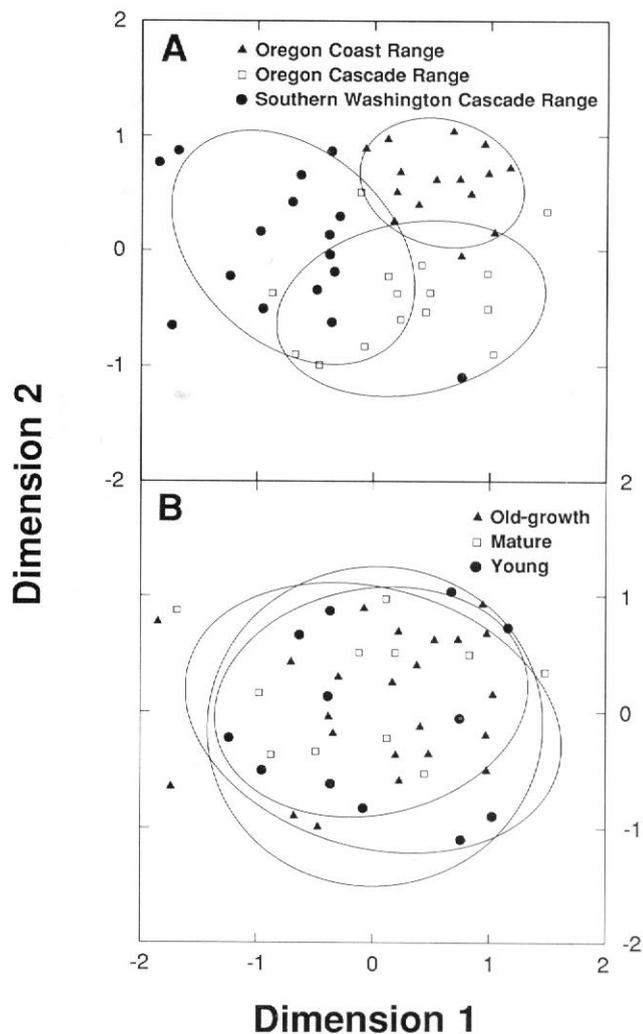


Figure 3—Multidimensional scaling of the presence or absence of 12 amphibians in 55 forest stands in Oregon and Washington: (a) stands identified by province (ellipses enclosing about 75 percent of the stands are drawn about the centroids of each province) and (b) stands identified by habitat type.

Plotting the MDS by age-class shows no discernible differences among old-growth, mature, and young stands (fig. 3b). Ellipses that enclose about 75 percent of the stands in each age-class essentially overlap completely.

Table 5—Nonhierarchical clustering of 12 amphibian species (presence-absence) in 55 forest stands in Oregon and Washington

Pool ^a	Province	Number of stands	Species present in at least 50 percent of stands in each pool (percentage)	Species absent from all stands in pool
1	Oregon Cascade Range	15	Ensatina (100)	Cascades frog
	Washington Cascade Range		Roughskin newt (75)	
	Oregon Coast Range	11	Tailed frog (71)	
2	Oregon Coast Range	3	Western redback salamander (50)	
	Washington Cascade Range	10	Tailed frog (100)	Clouded salamander Pacific giant salamander Olympic salamander
	Oregon Cascade Range		Ensatina (77)	
Oregon Cascade Range	3	Red-legged frog (69)		
3	Oregon Coast Range	12	Ensatina (100)	Cascades frog Oregon slender salamander
	Oregon Cascade Range		Clouded salamander (93)	
	Washington Cascade Range	1	Pacific giant salamander (93)	
	Oregon Cascade Range	1	Western redback salamander (93)	
			Roughskin newt (57)	
			Northwestern salamander (57)	

^a Three nonoverlapping pools of stands were generated using K-means clustering.

Biogeography

The occurrence of amphibians among and within provinces varied greatly. Six species of terrestrial salamanders were widely distributed in the Pacific Northwest (fig. 4), and species richness was concentrated in western Oregon and north coastal California. Among these six species of widespread occurrence, the number present in any locality varied from zero to four and changed over relatively short distances.

Five salamanders were endemic in Oregon and Washington (fig. 5), and most had non-overlapping ranges. Three other endemic species in Idaho and northern California are not examined here.

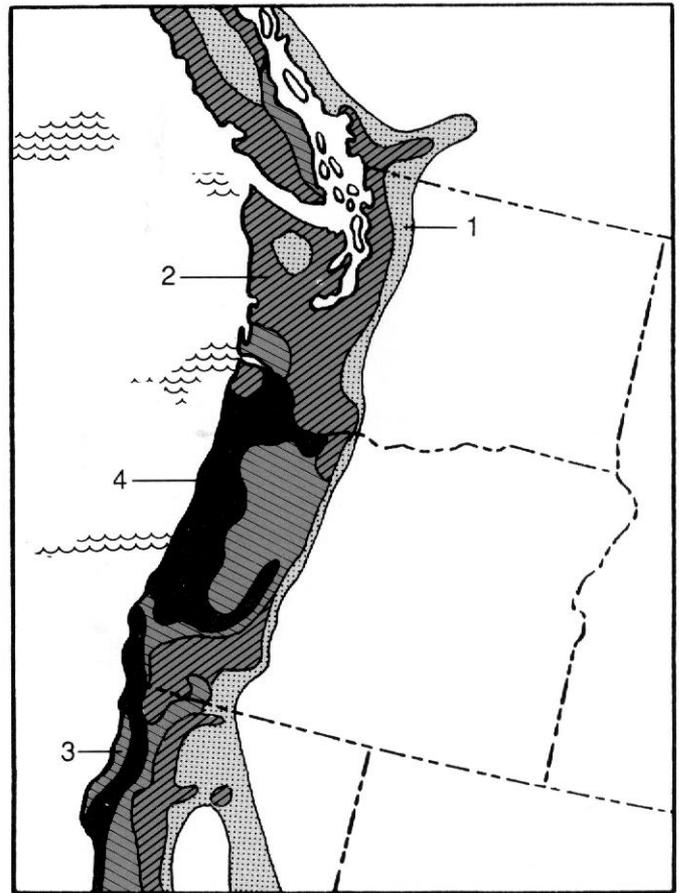


Figure 4—Overlap in the ranges of six widespread terrestrial salamanders (black, California slender, clouded, Dunn's, ensatina, and western redback) in the Pacific Northwest. Numbers (1-4) indicate number of co-occurring species.

Discussion

Variation Across Provinces, Chronosequences, and Moisture Gradients

The lack of response by terrestrial amphibians to the moisture gradient in the Coast Range might be due to several factors. The moisture gradient was not strong, and most stands tended to be relatively dry. Old-growth stands in the Coast Range tended to be similar to the drier old-growth forest in the Cascade Range (Spies and Franklin, this volume).

Mean abundance of species differed more among provinces than across either the chronosequence or moisture gradients (table 2). Most species were more common in one province than in the other two. Large numbers of both the roughskin newt and northwestern salamander were captured in only a few stands, resulting in high variance that clouds interpretation of trends. The observed geographic variation in

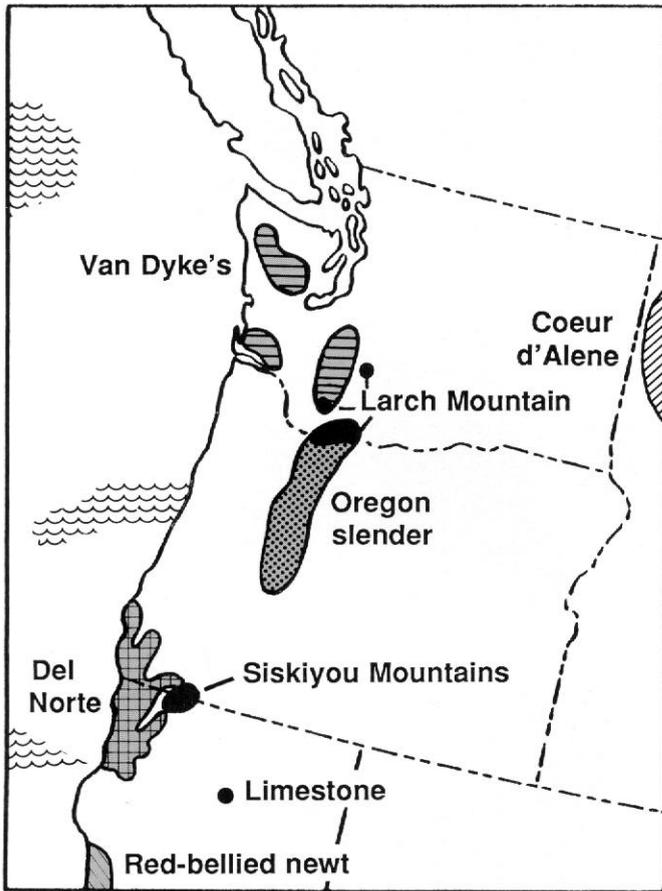


Figure 5—Distributions of eight salamanders endemic to the Pacific Northwest.

captures may reflect the location of special habitat features in certain stands more than any environmental differences among provinces.

The resident amphibians apparently are somewhat similar in naturally regenerated Douglas-fir forests. All stands sampled had established canopies and generally contained large amounts of coarse woody debris, which are characteristics that may reduce differences among stand types (young to old growth, wet to dry).

Habitat Associations

Some of the observed patterns of abundance may be due to special habitat features required by certain species. These may include aquatic habitats, down wood, and rocky slopes.

Proximity to water for aquatic breeders—The strong interaction between province and stand age for roughskin newts might be better explained by the proximity of breeding habitats than by dependence on unknown forest characteristics.

Newts migrate to ponds, slow-moving streams, or other standing bodies of water to breed. Migration may extend over considerable distances. Twitty (1966), for example, reported that newts may move hundreds of meters to and from breeding sites, and that individuals displaced several kilometers away (some over 10 km) returned to home waters. Thus, a favorable site for breeding is a focal point for migration. Capture of newts in pitfall traps may represent no more than movement by the animal through the forest. The newt may only temporarily depend on that place of capture. Capture of migratory species in one type of habitat, however, may also suggest that they prefer or require these upland conditions after the breeding season.

Similarly, adult northwestern salamanders migrate to ponds for breeding, and then both adults and juveniles return to land. The proximity of ponds or slow-moving creeks may also determine the occurrence and abundance of this species in forested stands. Frogs and toads also breed and live most of their lives in or near water. In particular, ranid frogs are aquatic or mostly aquatic throughout their lives, and the tailed frog breeds in small streams. The location of these ponds or flowing waters will strongly influence the occurrence of these species in surrounding forest stands. During rains, however, frogs may move out onto the forest floor to forage, and they may occasionally disperse overland. Additional studies are needed to better address the importance of dual habitats (aquatic breeding and upland nonbreeding sites) in the life histories of forest amphibians.

Searches were conducted in vernal ponds in the Oregon Cascades (Gilbert and Allwine, this volume c). Most of the ponds were in mature and old-growth stands. These habitats proved to be important breeding areas for northwestern salamanders and ranid frogs. The relation between the stability (predictable occurrence) of vernal ponds and forest developmental stage needs further investigation.

Coarse woody debris—Time-constrained collecting and surveys of down wood suggest that coarse woody debris is important habitat for several species of plethodontid salamanders, including ensatina, clouded salamanders and Oregon slender salamanders (Aubry and others 1988; Aubry and Hall, this volume; Bury and Corn 1988a; Corn and Bury, this volume b; Gilbert and Allwine, this volume c). Natural disturbances (for example, fire) add appreciable debris to young stands, but these features do not persist as the stand matures. Forest stands do not accumulate new, large pieces of down wood until the forest reaches old-growth conditions and debris inputs increase as a result of natural tree mortality (Franklin and others 1981, Harmon and others 1986, Spies and others 1988).

Although ensatina was the only one of eight species suspected of having a strong association with down wood, none of the amphibians collected in pitfall traps were related to the habitat variable (DF2A) for coarse woody debris (table 4). Clouded salamanders and Oregon slender salamanders were not well-sampled by pitfall trapping, but time-constrained collection indicate that they are most abundant in stands with high amounts of coarse woody debris.

Ensatina is a generalist and may be competitively displaced by the clouded salamander where they are sympatric (Corn and Bury, this volume b). In Oregon, clouded salamanders were most abundant in less-decayed classes of down wood, mostly in decay-classes 1 and 2 (Bury and Corn 1988a; Corn and Bury, this volume b). Clouded salamanders and Oregon slender salamanders, however, do not occur in the Cascade Range in Washington, and in that region ensatina uses a broader range of microhabitats (Aubry and others 1988) than ensatina in the Cascade Range in Oregon, where all three species occur (Bury and Corn 1988a), or in the Oregon Coast Range where ensatina and clouded salamanders are sympatric (Corn and Bury, this volume b). The density of ensatina also may not be strongly related to the amounts of coarse woody debris in stands because that species is a generalist. Ensatina may, however, require coarse woody debris as breeding habitat (Aubry and others 1988).

Raphael and Barrett (1984) found that the abundance of ensatina in northern California was correlated to the density of large Douglas-fir trees. They found few ensatina in the youngest stands (less than 150 years old) they studied, however, and they included ensatina with species associated with old-growth stands. We cannot explain why ensatinas were ubiquitous in Oregon and Washington and had no apparent correlation with old growth.

Rocky habitats-We think the most underestimated environmental factor affecting salamanders is underlying soils, and particularly the occurrence of talus (rock rubble) in the Pacific Northwest. Western redback salamanders are associated with steep slopes and talus (fig. 2). Steepness of slope and the presence of talus are related factors because talus is more often exposed on hillsides than on valley floors where rocky soils are often covered with alluvium or deeper soils. Most western plethodontid salamanders frequent talus slopes (Dumas 1956, Herrington 1988, Nussbaum and others 1983, Ramotnik and Scott 1988), including the Larch Mountain, Siskiyou Mountain, and Del Norte salamanders. Also, Dunn's and Van Dyke's salamanders occur in talus habitat or along rocky streambanks (Dumas 1956, Corn and Bury 1989).

The strong association of the woodland salamanders with talus or rocky soils may override other habitat relations. For example, both Raphael (1988c) and Welsh and Lind (this volume) indicate that the Del Norte salamander is most

numerous in the oldest seral stages of Douglas-fir/hardwood forest in northern California. Soil types were not indicated, however, so these relations may be incidental to an uneven distribution of rocky habitats. We suggest that the occurrence and abundance of most species of woodland salamanders are more likely to be related to the presence of rocky outcrops or underlying talus than to forest development (stand age) or amounts of coarse woody debris. Determining this relation is essential to future studies of western salamanders and their habitats.

Herrington and Larsen (1985) and Herrington (1988) suggest that forested talus slopes were required by the Larch Mountain salamander and some other salamanders. The response of salamanders to the removal of forested stands on talus slopes, however, has not been examined critically. Individuals may simply move underground (Ovaska and Gregory 1989; N. Scott, unpubl. manuscript). Insufficient evidence is available to resolve this question, but it is a major issue because many forested areas of the Cascade and Coast Ranges in the Pacific Northwest have soils dominated by talus or rock rubble. These areas may be open slopes, partly forested, or totally overgrown with trees. Thus, considering both the substrate (for example, soil versus talus) and forest conditions (for example, clearcut versus closed canopy) is increasingly important in evaluating the occurrence and abundance of terrestrial salamanders.

Managed Stands

Bury and Corn (1988a) used pitfall traps in five clearcut sites (all less than 10 years old) in the Cascade Range in Oregon and Washington to describe the occurrence and abundance of the herpetofauna in managed stands. The relative abundance of the herpetofauna in these clearcuts differed markedly from six comparable young stands that were naturally regenerated. Reptiles predominated in clearcuts, which most likely was a response to increased solar radiation and higher ambient temperatures. The Pacific treefrog also was most abundant in clearcuts, which reflects its propensity for invading openings (Bury 1983). Interestingly, clearcut stands that we sampled in the Oregon Coast Range in 1984-85 did not show such marked differences in terrestrial species (Corn and Bury, this volume b).

Although tailed frogs were captured in pitfall traps in closed-canopy forests, they were absent or rare in clearcuts (only 1 percent of the total catch). Both the Olympic salamander and the tailed frog seem to be sensitive to timber harvest, and the survival of these species may depend on the availability of cool streams for breeding and larval development as well as the presence of adjacent forested habitats for shade and retention of stream substrate quality (Bury and Corn 1988a; Bury and others, this volume b, Corn and Bury 1989). Assessing the effects of logging in streamside and upland forests is urgently needed.

Biogeography

Regional patterns-Both multidimensional scaling and non-hierarchical clustering generated clear patterns separating the three provinces (fig. 3a, table 5) but not the forest age-classes (fig. 3b). This result is underscored by the strong differences among provinces in the abundance of species that occurred in all provinces, and by the general lack of abundance differences among habitat types.

Analyses of the amphibian communities were somewhat surprising because distribution differences among the provinces for several species had little apparent influence on the results. Considerably more overlap was found between the Cascade Range in Oregon and Washington than between either Cascade Range group and the Oregon Coast Range despite the absence of clouded salamanders and Oregon slender salamanders in Washington. Biogeography, however, appears to play a much more important role in the organization of amphibian communities than do forest habitat gradients. Thus, a mandate exists to better document species' occurrence, and their centers of diversity, biogeographic relations, and distributional limits.

Importance of endemic amphibians-Eight species of terrestrial salamanders in the Pacific Northwest have restricted distributions (fig. 5), five in Oregon and Washington. Even widespread species, however, are not distributed over the entire region (fig. 4). The superimposing of the ranges of endemic and widespread species of salamanders would further complicate which species might be expected to occur in a given province or area. The specialized habitats and disjunct distributions of many species also confounds generalizations about herpetofaunas. Marked differences in the herpetofauna depend on the geographic location sampled.

We suspect that the distribution patterns of individual species may influence the organization of herpetological communities more than factors such as forest age, once canopy is re-established. In most areas of the Pacific Northwest, however, herpetological studies have been insufficient to compile reliable community profiles (accurate lists of resident species and relative numbers of species).

Still, herpetological communities can be understood; relatively few species of amphibians and even fewer reptiles live in the Pacific Northwest. An intensive study in a project area

usually can reveal almost all of the common species and many of the rarer ones, if the searcher knows what to look for and if sites are sampled during appropriate weather (Corn and Bury 1990).

Management Suggestions

Localized distributions and special habitat requirements of amphibians may make managing of selected species easier than might be anticipated. The presence of small permanent streams or headwaters is an indicator that Olympic salamanders or tailed frogs may occur in the area. Another key factor is to recognize the importance of distinct microhabitats. Presence of talus or rocky substrate, for example, is a clue that one or more species of plethodontid salamanders likely inhabit the site.

Management strategies need to be individually tailored. Most of the "common" amphibians, such as ensatina and clouded salamanders, are apparently not irreversibly affected by current timber harvest activities. Thus, we would recommend that most attention be directed at endemic species with small geographic ranges (fig. 5). All five of the endemic species in Oregon and Washington are already proposed for Federal listing as threatened or are protected by individual States.

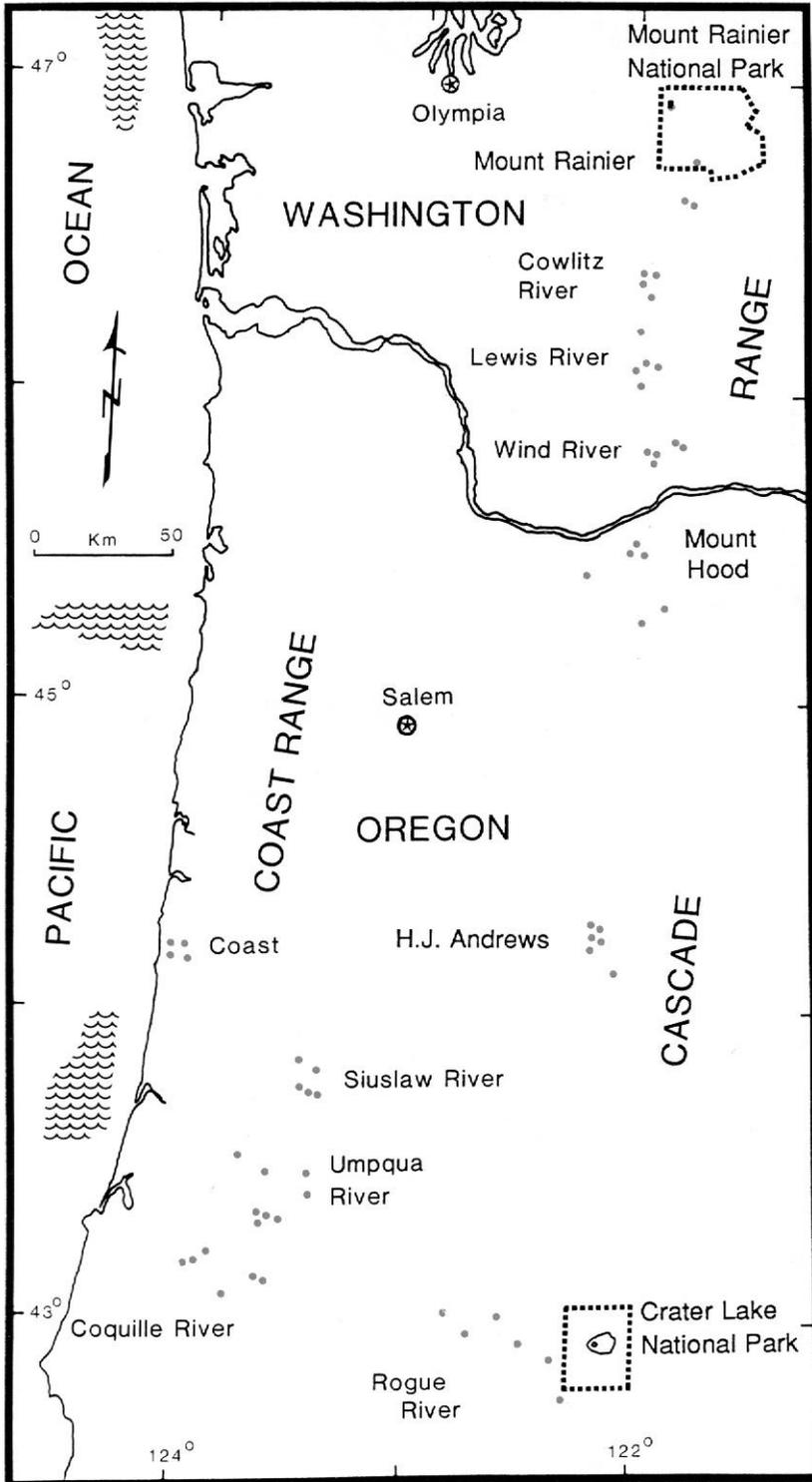
A long-term perspective needs to be developed. Species that require large, well-decayed down wood may be continually reduced in numbers in managed forests because tree removal reduces or eliminates the input of fallen woody debris. Coarse woody debris, therefore, is not carried over from sequential harvests, and terrestrial amphibian populations may suffer as a result.

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Locations of streams sampled.

Aquatic Amphibian Communities in Oregon and Washington

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Abstract

We sampled first- and second-order streams in naturally regenerated forests (young, mature, and old-growth stands) in three provinces: the Southern Cascade Range of Washington, the Oregon Cascade Range, and the Oregon Coast Range. We found no significant differences in physical habitat variables (except stream gradient in one of the three provinces) nor in densities of amphibians among the provinces. Giant salamanders were the most abundant amphibians, followed by tailed frogs. Dunn's salamander and Olympic salamander were less common, partly because they did not occur in all the watersheds we examined. These four species differed markedly in their microhabitat use: tailed frogs were most often found in riffles; Olympic salamanders frequented riffles and banks or

shallow seeps; giant salamanders were about equally abundant in pools and riffles; and Dunn's salamanders mostly occurred on stream banks. Three species have aquatic larvae, and they appeared to occupy different ecological niches. Amphibian densities and biomass were 10 and 4 times greater, respectively, than those reported for salmonid fishes in small streams. Thus, amphibians can be the predominant vertebrates in headwaters in Pacific Northwest forests. In the Oregon Coast Range, we found that the number of species, the densities, and the biomass of resident amphibians were 2 to 7 times greater in streams flowing through uncut forests than in logged areas. Responses of amphibian populations to timber harvest may differ regionally, and more comparative studies are needed on amphibian communities in managed stands.

Introduction

Concerns have been expressed about how timber harvest affects salmonid fishes in Pacific Northwest streams (see Brown 1985, Meehan and others 1984, Salo and Cundy 1987). Recent studies in western Oregon indicate that both salmonids and the Pacific giant salamander are common in streams in uncut and logged habitats (Hawkins and others 1983, Murphy and Hall 1981, Murphy and others 1981). Other studies suggest, however, that logging has negative impacts on aquatic amphibians, particularly those with narrow environmental tolerances (Bury 1968, Bury and Corn

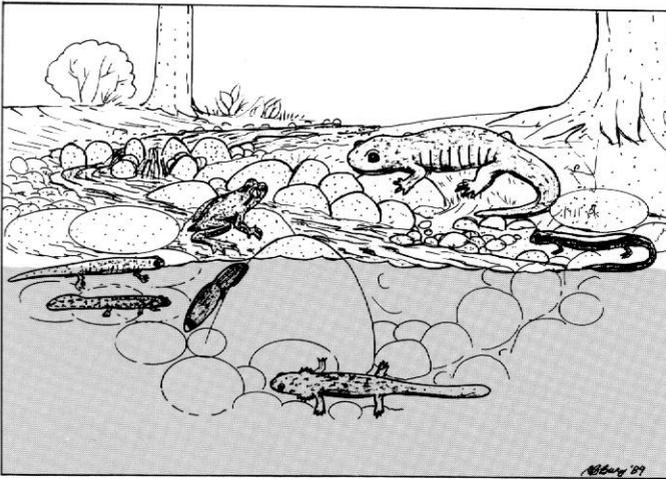


Figure 1—Aquatic and semi-aquatic amphibians of headwaters and small streams in Oregon and Washington (from left to right): Olympic salamander, tailed frog (adult above, tadpole below), Pacific giant salamander (adult above, larva below), Dunn's salamander (no aquatic larvae).

1988b, Metter 1964, Nussbaum and others 1983). Negative effects from logging also may be intensified in headwater streams (Corn and Bury 1989).

Integrated management of forests requires an understanding of the complex ecosystems of headwater streams, and how they function. Headwaters and other small channels provide nursery habitat for salmonids (Hartman and others 1987, Sedell and Swanson 1984) and are important in maintaining downstream fish habitat and water quality (Rice and others 1979). Everest and others (1985), furthermore, reported that upslope activities (for example, road development or timber harvest) and manipulation of canopy or streambank vegetation create immediate changes in the equilibrium of small streams.

Hairston (1987) estimated that the biomass of both terrestrial and aquatic salamanders was greater than that of any other vertebrate predators in the southern Appalachian mountains. To date, we lack comparable estimates of the biomass of different vertebrate groups in Pacific Northwest forests. Although amphibians are the dominant vertebrates in some Northwestern headwater streams (Bury 1988, Murphy and Hall 1981, Nussbaum and others 1983), large gaps exist in our understanding of how these species function in aquatic or riparian communities. We know little about the effects of habitat alteration on their survival.

The structure of Douglas-fir forests varies considerably (Spies and Franklin, this volume) and, for that reason, we need to investigate how amphibian populations vary across

successional gradients. In this paper, our objectives are to determine the occurrence and abundance of amphibians in streams flowing through three successional stages (young, mature, and old-growth) of naturally regenerated Douglas-fir forests in western Washington and western Oregon, compare amphibian communities in streams in uncut forests to streams in logged areas, discuss the major physical characteristics of streams and the microhabitat associations of aquatic amphibians, and identify regional patterns in the density and biomass of amphibians in headwater streams.

Geographic Distributions and Life Histories

Four species (or groups of sibling species) of aquatic amphibians (fig. 1) occur in the temperate forests of the Pacific Northwest: Olympic salamanders, giant salamanders (genus *Dicamptodon*), Dunn's salamanders, and tailed frogs. Distribution maps are based mostly on locality records in Nussbaum and others (1983), with additional information from Bury (1968), Good and others (1987), Green and Campbell (1984), and our recent field work. Range maps presented here are new interpretations; they were designed to denote areas lacking records as well as areas with known faunas.

Good and others (1987) indicate that the Olympic salamander comprises at least three genetically distinct groups in the following areas: the Olympic Peninsula to northwestern Oregon, the Coast Range from central Oregon to northern California, and the Cascade Range of Oregon and Washington (fig. 2). This species requires cool waters, and individuals are usually found only in the splash zone or shallows of seeps and streams (Nussbaum and Tait 1977, Nussbaum and others 1983).

Giant salamanders are widespread in the Pacific Northwest (fig. 2). Pacific giant salamanders are large (up to 350 mm long) and inhabit streams and standing water over a relatively wide range of temperatures. Their eggs and larvae occur in water, but transformed juveniles and adults may live on land. Cope's giant salamander is a smaller species that is mostly aquatic and neotenic (Nussbaum 1970). The Rocky Mountain giant salamander, which occurs in interior areas (Daugherty and others 1983), is not discussed here.

The tailed frog is distributed similarly to the giant salamander (fig. 3). Eggs and tadpoles of this frog require cool, flowing waters (Bury 1968, 1988; de Vlaming and Bury 1970; Metter 1964; Nussbaum and others 1983). Their larval stage reportedly lasts for 2 to 3 years (Metter 1967) and, in the Rocky Mountains, adults may not breed until 7 to 8 years of age (Daugherty and Sheldon 1982). Tailed frogs occur in disjunct populations, especially in interior or drier areas (Daugherty and Sheldon 1982, Metter 1967).