

Evidence of continued effects from timber harvesting on lotic amphibians in redwood forests of northwestern California

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Abstract

We compared species richness and relative abundance of stream-associated amphibians in late-seral redwood forests with those in mid-seral, second-growth forests to examine the continued (as opposed to immediate) effects of timber harvest on amphibian populations. Lacking pre-harvest data on amphibian abundances for streams in the second-growth stands, we assumed that nearby tributaries transecting late-seral stands with similar topography and flora harbored similar numbers of animals as second-growth stands prior to harvest. The study was conducted in two blocks (ca. 160 km apart) with three matched-pairs of streams per block. The mid-seral forests (treatment, $n = 6$) ranged from 37 to 60 years post-harvest; the late-seral forests (control, $n = 6$) consisted of unharvested stands. We conducted nocturnal visual encounter surveys to sample for amphibians in spring, summer, and fall, for 2 years, with three repeated visits per season. Environmental factors, including water temperature, air temperature, and fine sediment loads were also recorded. Results indicated that amphibian species richness and relative abundances of lotic amphibians were significantly greater in the late-seral forest streams compared with streams transecting mid-seral forests. Water and air temperatures were similar in both forest types, but streams in mid-seral forests had greater amounts of fine sediments compared with the streams in the late-seral forests.

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1. Introduction

Recent efforts to understand the processes that create and maintain late-seral or old-growth forests (i.e., Foster et al., 1996; Franklin et al., 2002; Seymour et al., 2002) have increased our understanding of how different tree species and forest communities respond to various disturbance regimes. However, less is known about the responses of wildlife species to forest disturbance. In the Pacific Northwest, landscape changes from timber harvest threaten many forest-adapted species (Lomolino and Perault, 2000; Noss, 2000). Declines in amphibian species have been documented worldwide (Stuart et al., 2004), with habitat alteration as one of the leading causes of these declines (Collins and Storfer, 2003). However, we need to know more about how Pacific Northwest amphibians that are adapted to late-seral conditions (e.g., Welsh, 1990) respond to changes in forest and stream structure and re-setting of the seral

cycle. Forest stream-associated amphibians may be particularly sensitive to alterations in aquatic environments following disturbance (Walls et al., 1992; Welsh and Ollivier, 1998; for review see Bury and Corn, 1988). Three Pacific Northwest endemic species commonly co-occur in the forested stream habitats of northwestern California: the tailed frog (*Ascaphus truei*), southern torrent salamander (*Rhyacotriton variegatus*), and coastal (formerly Pacific) giant salamander (*Dicamptodon tenebrosus*) (Nussbaum et al., 1983; Petranka, 1998). These species all require year-round cold water for completion of egg and larval life stages (Brown, 1989; Petranka, 1998), and all have been shown to be sensitive, at least in some parts of the Pacific Northwest, to harvest-related alterations of aquatic habitats (Corn and Bury, 1989; Welsh and Ollivier, 1998; Welsh and Lind, 1996, 2002). Changes in temperature, humidity, and sediment load in the aquatic environment may each contribute to the decline of these amphibians following harvest, with increases in water temperature and sedimentation having the greatest impact on their fully aquatic larval stages (Dupuis and Friele, 1995; Welsh and Ollivier, 1998; Dupuis and Steventon, 1999). Fine sediments can fill interstitial spaces used as refugia,

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scour or shade periphyton (Alabaster and Lloyd, 1982; Newcombe and MacDonald, 1991), and lower production of stream macro-invertebrates (Murphy et al., 1981; Hawkins et al., 1983).

While harvest-related habitat alterations have been shown to negatively impact populations of *A. truei* in most regions of the Pacific Northwest (Bury, 1983; Corn and Bury, 1989; Kelsey, 1994; Bull and Carter, 1996; Dupuis and Steventon, 1999), abundant populations were reported in mid-seral redwood (*Sequoia sempervirens*) and Douglas fir (*Pseudotsuga menziesii*) forests of coastal northern California (Diller and Wallace, 1999). The foggy summers and mild winters of northwestern California's coastal forests may allow the species to persist in younger forests by maintaining favorable microclimate conditions, even in the absence of forest canopy cover. Other aquatic amphibians of the region may exhibit similar responses to those seen in *A. truei*, but current research is conflicting, showing a variety of responses to harvest-related habitat alterations. For example, *R. variegatus* is associated with conditions commonly found in late-seral forests, including cold water, low sediment load, and dense forest canopy (Welsh and Lind, 1996), but it is also found in coastal streams draining mid-seral forests (Diller and Wallace, 1996). *D. tenebrosus*, while found in most small streams in northwestern California, is less abundant in sediment-laden streams (Welsh and Ollivier, 1998). However, some workers have reported greater abundances of *D. tenebrosus* in streams draining harvested areas (Murphy et al., 1981).

Earlier studies have compared amphibian populations in late-seral and early (clear-cuts or young) to mid-seral forests (Hawkins et al., 1983; Bury, 1983; Corn and Bury, 1989; Welsh, 1993). We compared streams in late-seral and maturing mid-seral forests in two Parks in Humboldt County in order to further our understanding of the extent and duration of disturbance on lotic amphibian populations. Our first objective was to compare streams in late-seral and mid-seral forests to quantify differences in the amphibian assemblages and species' relative abundances. In the event that such differences were biologically meaningful, we wanted to be able to consider plausible explanations. Thus, the second objective of this study was to relate differences in environmental factors known to be important to lotic headwaters amphibians – air temperature, water temperature, and fine sediment load (Nussbaum et al., 1983; Corn and Bury, 1989; Welsh, 1990; Welsh and Ollivier, 1998) – to differences in amphibian species presence or abundance. Our final objective was to evaluate our results relative to both past and present forest management practices. Our goal here was to apply our findings to evaluate the potential of current riparian and stream protections in California forestry practices to sustain populations of stream amphibians on commercial timberlands in northwestern California.

Our approach was to compare overall amphibian species richness to examine differences in the number of species between streams draining late-seral and mid-seral forests. We also compared the relative abundances of the three most common lotic species (*A. truei*, *R. variegatus*, and *D. tenebrosus*) to determine whether numbers differed between seral stages.

2. Methods

2.1. Study area

This study was conducted in northwestern California in Humboldt County's coast redwood (*S. sempervirens*) forest. Redwood forests grow along the coastal belt from northern Monterey County to the southwest tip of Oregon (Sawyer et al., 2000), but as a result of timber harvest and other anthropogenic disturbance, late-seral redwood forest no longer forms a continuous belt. Late-seral redwood forests now occur at the north end of Humboldt County in Prairie Creek Redwoods State Park and Redwood National Park, and near the south end of the county in Humboldt Redwoods State Park (Fig. 1). The two regions are 160 km apart, and are hereafter referred to as the northern and southern study blocks, respectively. Coast redwood dominates the forest canopy of both replicate study blocks. The late-seral stands were not harvested because they were protected in State and National Parklands. Second-growth stands were harvested prior to the subsequent incorporation within Parklands.

Sawyer et al. (2000) identified 3 major sections and 25 sub-sections in the natural distribution of coast redwood. Both study blocks are on the Central Franciscan sub-section within the Northern Redwood Forest section, although there are noticeable differences in understory vegetation and substrate composition between the two study blocks. Distance to coast, elevation, and underlying geology may contribute to the

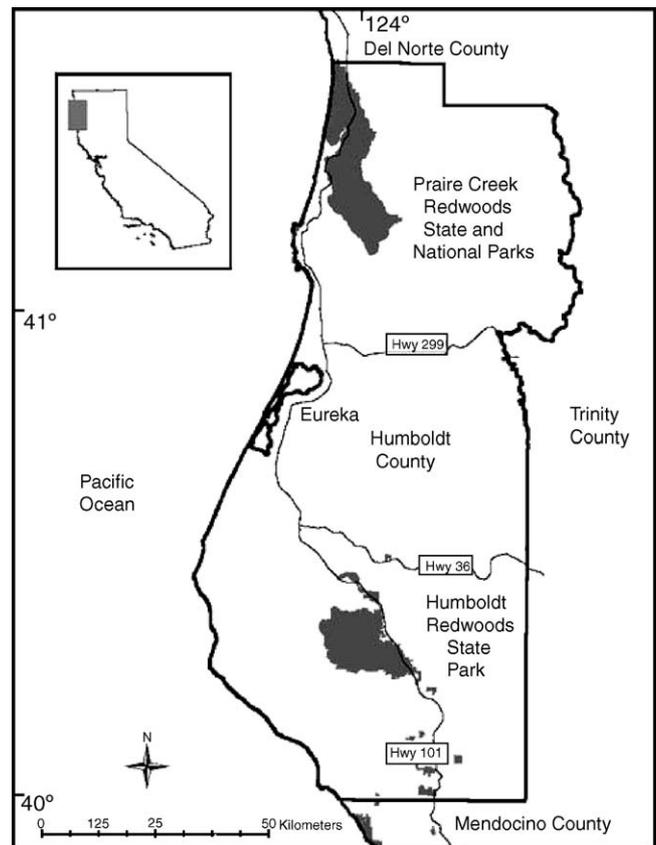


Fig. 1. Map of Humboldt County, California, with the study blocks shaded.

Table 1
Study stream pair locations

Block	Pair	Stream name	Harvest year	Basin area	Latitude	Distance to coast	Elevation (m)	Aspect	Mean gradient	Canopy closure	Sediment S^*
North	N1	“Hatchery”	None	484112	41°20'02"	4.6	67	SW	13.7	95.7	0.269
		“Fourteen”	1963	355674	41°20'15"	4.4	67	SW	10.7	100	0.614
	N2	Hayes	None	1365212	41°17'24"	5.3	12	W	9.3	93.2	0.285
		“Ladybird”	1945	563150	41°17'59"	4.6	12	SW	12.0	99.9	0.344
	N3	“Miners”	None	414953	41°22'02"	3.8	91	SE	8.0	98.4	0.370
		“Davison”	1962	474232	41°19'28"	3.6	79	SE	8.0	97.7	0.840
South	S1	Cabin	None	1860271	40°21'00"	37.0	61	SW	11.0	97.1	0.322
		Matthews	1946	537203	40°20'00"	37.2	152	SE	14.0	99.5	0.401
	S2	Decker	None	5695760	40°22'22"	36.0	61	E	3.6	95.7	0.246
		Drexler	1941	574737	40°22'39"	37.0	152	E	3.0	97.9	0.362
	S3	Cow	None	6003068	40°21'05"	34.0	61	SW	5.3	90.2	0.217
		Mill	1959	5397835	40°21'15"	29.2	122	SE	4.6	98.2	0.300

Stream pairs are grouped in two study blocks based on region. Quotation marks indicate stream names that we applied to streams that were unnamed on the maps consulted. Harvest year is indicated for mid-seral forest streams. Location, topographic map name, elevation (meters), and distance to coast (kilometers) were taken from maps. Aspect, gradient, and canopy closure for each stream were averaged from measurements taken at each reach. The mean (10 measures per stream) fine sediment load per stream based on S^* (ratio of maximum sediment depth to maximum residual pool depth) is listed in the last column.

vegetative differences noted between the study blocks (Table 1). The study streams in the northern block have thicker understory and range from 3.6 to 5.3 km to the coast and 12 to 91 m in elevation. The southern block is farther inland and slightly higher, with study streams ranging from 29.2 to 37.2 km to the coast and 61 to 152 m in elevation.

2.2. Study design

For the purposes of this study, we define the two seral stage categories of interest as follows: (1) “late-seral” forest has little evidence of human disturbance, with some trees >150 years old, and (2) “mid-seral” forest has been harvested for timber in the mid 1900s without riparian buffers (37–60 years since harvest). The mid-seral forests were densely forested, and if they were still managed as commercial timberlands, would be nearing the end of the 60–80 year harvest rotation cycle common for redwood in the region (Thornburgh et al., 2000).

We selected three matched-pairs of streams from each study block. Pairs of streams were selected in order to minimize within-pair differences in aspect, gradient, elevation, and distance to coast. Lacking pre-harvest data on amphibian abundances for streams in the second-growth stands, we assumed that nearby tributaries transecting late-seral stands with similar topography and flora harbored similar numbers of animals as second-growth stands prior to harvest. Pair-mates were located as close as possible to each other to help minimize localized differences in weather, geology, flora, and fauna (Table 1). Three pairs of streams were adjacent tributaries differing from each other only with respect to timber harvest history. The other three pairs of streams were tributaries in the same basin, but not adjacent. Pair-mates were within 6 km or less of each other. All study streams had greater than 90% canopy closure over the stream (Table 1). We addressed differences in the sub-basin area drained by each stream pair (Table 1) in our preliminary analysis (see below).

We mapped 200 m of each stream to serve as the sampling frame. Location of the mapped section of each stream was determined by comparability to its pair-mate, as well as access to the location at night. The mapped portion of each stream was divided into ten 20 m long reaches from which we randomly selected three non-consecutive reaches per stream for repeated amphibian sampling.

For each selected reach the search transect was defined as a 20 m length of stream, 5 m wide, centered on the stream (~100 m²). Generally, the transect included a 1–2 m wide strip of terrestrial habitat along each bank and a 1–2 m width of aquatic habitat, but this varied somewhat with stream topography and discharge. Each of the selected reaches was mapped as a grid, with start and end points marked with reflective tags. See Ashton (2002) for additional detail on study design and sampling method.

2.3. Amphibian sampling

We sampled for amphibians using visual encounter survey (VES) (Crump and Scott, 1994) in three seasons for 2 years: spring (28 April–1 June 2000, and 26 April–6 June 2001), summer (2 July–1 August 2000, and 17 July–17 August 2001), and fall (23 September–27 October 2000, and 16 October–1 December 2001). Each stream was sampled three times per season for a total of eighteen visits per stream. To help control for temporal fluctuations in amphibian surface activity levels within season, both streams of a pair were sampled on the same night (Heyer et al., 1994). Sampling order between pair-mates was determined by coin toss for each night. For each round of sampling, the sampling order was determined for the six pairs of streams by simple random sampling without replacement.

We sampled for amphibians by VES because of its low impact relative to other sampling techniques (Crump and Scott, 1994). It was important to use a low-impact method to avoid

habitat disturbance within the State and National Parks, and reduce the effect of the observer on the subjects and their habitats, which could influence the results of this repeated measures study (e.g., Cahill et al., 2001). The least intensive type of VES is simply looking for animals that are, more or less, in plain sight, rather than disturbing the habitat to seek animals in their hiding places. To be effective, this type of VES should be conducted when the target species are most likely to be encountered (Crump and Scott, 1994). The target species (*A. truei*, *R. variegatus*, *D. tenebrosus*) are all primarily nocturnal (Noble and Putnam, 1931; Slater, 1933; Nussbaum et al., 1983; Parker, 1994), so VES was conducted at night. Our previous observations of *A. truei* suggested activity all night with brief peaks in activity at dusk and dawn. Sampling was avoided during peak periods so that a single observer could sample both streams of a pair on a given night with equal opportunities to encounter amphibians.

For all amphibian sampling, the observer worked from downstream up. This makes it is easier to see into crevices, especially in higher gradient areas, whereas working in a downstream direction reduces the effectiveness of visual surveys of aquatic habitats because the observer's movement in the stream channel can mobilize sediment, reducing water clarity downstream, especially in lower gradient areas.

For each nocturnal VES, a single observer used a rechargeable handheld flashlight (Streamlight® Litebox® equipped with a 20-W flood lamp) and a headlamp (Petzel® Zoom™ equipped with a halogen bulb) to illuminate the search area. Care was taken to avoid directing flashlight beams beyond the area of the immediate search, as stray light beams to areas ahead might have sent amphibians into hiding before they could be observed and counted. Walking and crawling slowly upstream along the transect (wearing waders and kneepads), the observer visually searched terrestrial, emergent, and aquatic surfaces for exposed amphibians, inspecting crevices, occasionally brushing aside overhanging vegetation, but rocks, logs, or other cover objects were not turned or moved. The goal was to apply equal search effort to each reach without disturbing the habitat. Start time, end time, and total search time (about 20 min per transect) was recorded for each VES.

All amphibians observed within each transect were counted and recorded, with location and species noted on the grid map. A single, trained observer (D. Ashton) conducted all sampling to promote consistency. We were able to identify all amphibians encountered to species and age class (and gender for most adult *A. truei* and *R. variegatus*) without handling. In an attempt to reduce observer effects, prolonged illumination of amphibians was avoided. In most cases, amphibians encountered did not attempt to flee. Although amphibian sampling was focused on lotic headwater stream species, some lentic and terrestrial species were also encountered.

Because this study used a repeated measures design, intended only to detect differences – should they exist – in animal and species numbers between treatments, no attempt was made to differentiate individual animals (no marking). The parameter of interest was the number of amphibian encounters

per sample night. Although some individuals were probably detected multiple times during the study, this is not a concern because we were not attempting to estimate population sizes.

2.4. Environmental measurements

To compare key environmental factors between late-seral and mid-seral redwood forest streams, we measured several factors thought to be important to lotic headwaters amphibians based on previous research: water temperature, air temperature, and fine sediments (see citations in Section 1). We manually measured water temperature and air temperature using a digital thermometer at the upper end of each sampling reach on each sampling night. Fine sediment loads were measured in each stream using S^* . S^* is a simplified estimator for V^* (Lisle and Hilton, 1992), a method for evaluating mobile stream sediments in northwestern California streams that examines the ratio of maximum sediment depth to maximum residual pool depth (S. Hilton, personal communication). We randomly selected 10 pools per stream and measured pool sediments at the end of the fall sampling period (during low flow) by probing the pools with a calibrated metal rod to measure sediment depth, maximum pool depth, and pool tail depth. We used this relative measure of pool sediment depth to compare sediment deposition within stream sets.

2.5. Statistical methods

We used Microsoft® Excel® for data entry and management, and performed analyses using Number Crunching Statistical Software (NCSS® 2000 release) (Hines, 2000) and SAS v 9.1 (SAS® 2003). We checked for normality using a bootstrap selection of the individual counts and examined the distributions of the various parameter estimates. While the individual count data were certainly not normally distributed, the bootstrap distributions indicated that the distributions of the parameter estimates of interest were indeed approximately normal. Therefore, we proceeded with an analysis of variance (ANOVA) in SAS using the PROC MIXED (SAS, 2003) procedure on the untransformed data, which takes into account both the spatial and temporal aspects of the repeated measures design. With stream as the unit of analysis, we tested the following statistical null hypotheses: (1) there is no difference in amphibian abundance and assemblage between forest seral stage and (2) there is no difference in key environmental factors (air temperature, water temperature, and sediment load) between seral stages. For most variables we had two among streams factors (block, stage) and two factors within streams (year and season). There was some natural variability in basin area (Table 1), so we initially added it as a covariate. However, adding basin area did not change the residual mean square, so it was not included in the final model. Sediment load (S^*) was only measured in fall of 2000, so year and season were not factors in sediment analysis. An α of 0.10, deemed more appropriate for ecological studies (Toft, 1991; Underwood, 1997), was used for all tests.

We tested for differences in species richness between blocks and seral stage categories by first including all 11 amphibian

Table 2
Amphibian encounters in 2000 and 2001

Species	2000				Total	2001				Total
	Northern		Southern			Northern		Southern		
	Late	Mid	Late	Mid		Late	Mid	Late	Mid	
<i>Ascaphus truei</i> , all ages	154	1	54	4	213	75	0	32	2	109
<i>A. truei</i> , adult and sub-adult	39	1	14	1	55	33	0	15	0	48
<i>A. truei</i> , metamorph	58	0	22	0	80	27	0	6	2	35
<i>A. truei</i> , larvae	57	0	18	3	78	15	0	11	0	26
<i>Rhyacotriton variegatus</i>	25	1	0	1	27	21	1	0	5	27
<i>Dicamptodon tenebrosus</i> ^a	263	92	286	151	792	321	101	476	178	1076
<i>Aneides vagrans</i>	0	0	14	1	15	0	0	6	3	9
<i>Aneides flavipunctatus</i>	0	0	6	7	13	0	0	1	5	6
<i>Batrachoseps attenuatu</i> ^b	0	0	2	0	2	0	0	3	0	3
<i>Ensatina eschscholtzii</i>	2	3	0	0	5	5	4	1	1	11
<i>Taricha granulosa</i> ^b	0	0	0	1	1	0	0	4	2	6
<i>Rana boylei</i>	0	0	25	194	219	0	0	39	103	142
<i>Rana aurora</i> ^b	0	1	0	0	1	0	5	0	0	5
<i>Pseudacris regilla</i> ^b	0	0	1	0	1	0	0	2	0	2
Total encounters	444	98	388	359	1289	422	111	564	299	1396
Total species richness	4	5	7	7		4	4	9	8	

Numbers of amphibian encounters by study block (northern and southern) and forest seral stage (late and mid), with *A. truei* listed by life stage.

^a Spring 2000 excluded for this species because abundance was not quantified.

^b Rarely encountered species.

species and life stages encountered during amphibian sampling. We then performed a second richness analysis excluding four species that were not adequately sampled with our method and were rarely detected (<10 detections); the Pacific treefrog (*Pseudacris regilla*), California slender salamander (*Batrachoseps attenuatus*), northern red-legged frog (*Rana aurora*), and the rough-skinned newt (*Taricha granulosa*) (Table 2).

For post-metamorphic *A. truei* (adult, sub-adult, and recent metamorph) and all stages of *R. variegatus* we used count data from all three seasons (spring, summer, and fall) and both years. Larval *A. truei* were excluded from the relative abundance analysis because the sampling method is inappropriate for quantifying tadpoles of this species. For the first spring sampling season we had only recorded “presence” data for *D. tenebrosus*, so the first spring season was not included in the relative abundance analysis for this species.

We compared reach level air and water temperatures between study blocks, seral stage category, and season in a three-factor ANOVA. To test for differences in sediment load among streams we used a two-factor ANOVA with stream as the unit of analysis, and study block and seral stage as factors.

3. Results

3.1. Amphibian richness

In 108 nights of sampling spanning two years, 11 species of amphibians were detected, representing 2685 encounters (Table 2). For both years, species richness was greater in the southern block with 9 species detected in 2000 and 10 in 2001 (Table 2; $\bar{X} = 6.33$ species per stream). In the northern block, five species were detected each year (Table 2; $\bar{X} = 3.67$ species per stream). Total species richness was similar between the two

seral stages at the block level (Table 2), however, at the stream level, richness was significantly greater (d.f. = 1, $F = 9.09$, $P = 0.0167$) in streams draining late-seral forests (Fig. 2A). The difference in richness between study blocks was greater than

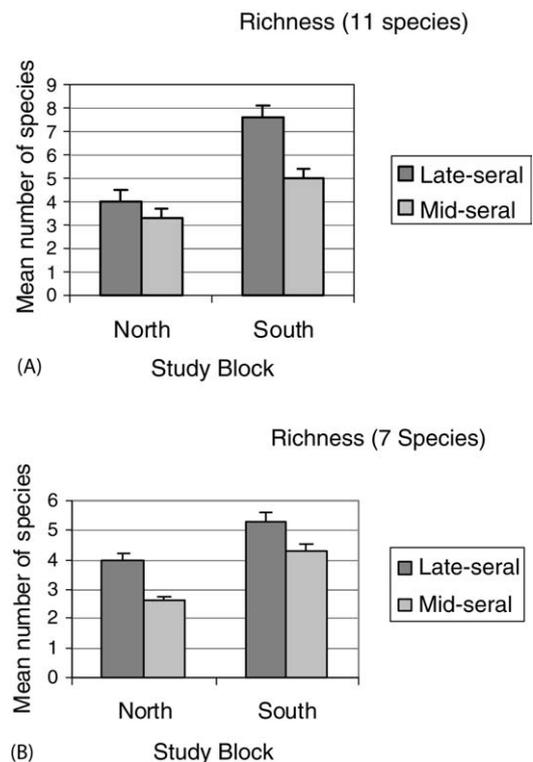


Fig. 2. Histograms showing species richness by seral stage and block. (A) Species richness including all 11 species encountered. (B) Species richness excluding four rarely encountered species; seven species included. Error bars represent one standard error around the mean.

the difference between seral stages (d.f. = 1, $F = 23.27$, $P = 0.0013$), with more species detected in the southern block (Fig. 2A). The four rarely encountered species (<10 detections; *P. regilla*, *R. aurora*, *B. attenuatus*, *T. granulosa*), were deemed to be uninformative and therefore removed from the analysis. Removing the four rarely detected species, while changing the effect size, did not change the direction of the results (more species in both the southern block and late-seral forests; block d.f. = 1, $F = 9.00$, $P = 0.017$; seral stage d.f. = 1, $F = 5.44$, $P = 0.048$; Fig. 2B).

3.2. Amphibian relative abundance

The three headwater-associated species, *A. truei*, *D. tenebrosus*, and *R. variegatus*, were the only species detected in numbers suitable for an analysis of relative abundance (Table 2). While the foothill yellow-legged frog (*Rana boylei*), a diurnal frog that inhabits more open, higher-order stream environments, was abundant in a single pair of streams in the southern block, it was scarce in all other streams and was therefore excluded from our comparisons of abundance.

3.3. *A. truei*

We encountered 322 *A. truei* (Table 2). Including all post-metamorphic stages ($n = 218$) in the analysis revealed no

significant difference between study blocks, but the difference between seral stages was highly significant, with more post-metamorphic *A. truei* at the late-seral sites (Table 3). Season was also significant, with the recent metamorphs contributing to greater numbers in the fall (Table 3). However, we found high variability in the number of recent metamorphs both between reaches within streams, and between streams within seral stage. This patchy distribution of recent metamorphs reflected an asynchronous development and transformation from tadpoles, and suggested that we had an insufficient number of sample reaches to accurately portray the relative quantities of this life stage at the stream level. Consequently, we re-analyzed the *A. truei* data excluding the recent metamorphs, using only the sub-adult and adult life stages ($n = 103$). The difference between seral stages here was highly significant, with 98.6% of the tailed frog detections in the late-seral reaches (Table 3). Here, study block also was significant, with 98.1% of detections occurring in the northern block (Table 3; Fig. 3A).

3.4. *D. tenebrosus*

Of the 1868 detections of *D. tenebrosus* (Table 2), most (99%) were larval salamanders; however, data from all life stages (larvae, neotenic adults, and terrestrial adults) were grouped together. *D. tenebrosus* accounted for 61% of all amphibian encounters in both blocks. There were more than

Table 3
Repeated measures, partial hierarchical analysis of variance (ANOVA) of three amphibian species (tailed frog with two life stages) by seral stage, study block, season; with relevant interactions and Bonferroni multiple comparisons

Factor	d.f.	<i>F</i>	<i>P</i>	Multiple comparisons ^a
Tailed frog, post-metamorphic				
Seral stage	1, 8	17.61	0.0030	LS > MS
Block	1, 8	3.97	0.0815	
Season	2, 14.1	8.60	0.0036	fa > sp, fa > su
Seral stage × block	1, 8	4.35	0.0706	
Seral stage × season	2, 585	16.35	<0.0001	LS fa > LS sp, LS su LS fa > MS sp, MS su, MS fa
Block × season	2, 586	8.78	0.0002	N fa > N sp, N su N fa > S sp, S su, S fa
Tailed frog, adults and sub-adults				
Seral stage	1, 31.9	63.63	<0.0001	LS > MS
Block	1, 31.9	12.66	0.0012	N > S
Season	2, 15.1	4.46	0.0299	fa > sp
Seral stage × block	1, 31.9	12.61	0.0012	LS N > MS N, LS S, MS S LS S > MSN, MS S
Seral stage × season	2, 585	8.94	0.0001	LS sp > LS su, LS fa, MS sp, MS su, MS fa LS Su > MS sp, MS su, MS fa
Block × season	2, 1.31	1.31	0.2706	
Coastal giant salamander				
Seral stage	1, 4.11	10.53	0.0303	LS > MS
Block	1, 4.05	0.82	0.4158	
Season	2, 12.3	16.47	0.0003	sp > fa, su > fa
Seral stage × block	1, 4.01	0.02	0.8838	
Seral stage × season	2, 480	1.50	0.2246	
Block × season	2, 482	4.38	0.0130	S sp > S fa, S su > S fa
Southern torrent salamander				
Seral stage	1, 3.97	2.68	0.1775	
Block	1, 3.98	2.38	0.1981	
Season	2, 600	7.30	0.0007	sp > su
Seral stage × block	1, 3.97	4.53	0.1008	
Seral stage × season	2, 600	3.36	0.0353	LS sp > LS su, MS su
Block × season	2, 600	4.38	0.0130	N sp > N su

^a Multiple comparison codes: LS, late-seral; MS, mid-seral; N, north block; S, south block; sp, spring; su, summer; fa, fall.

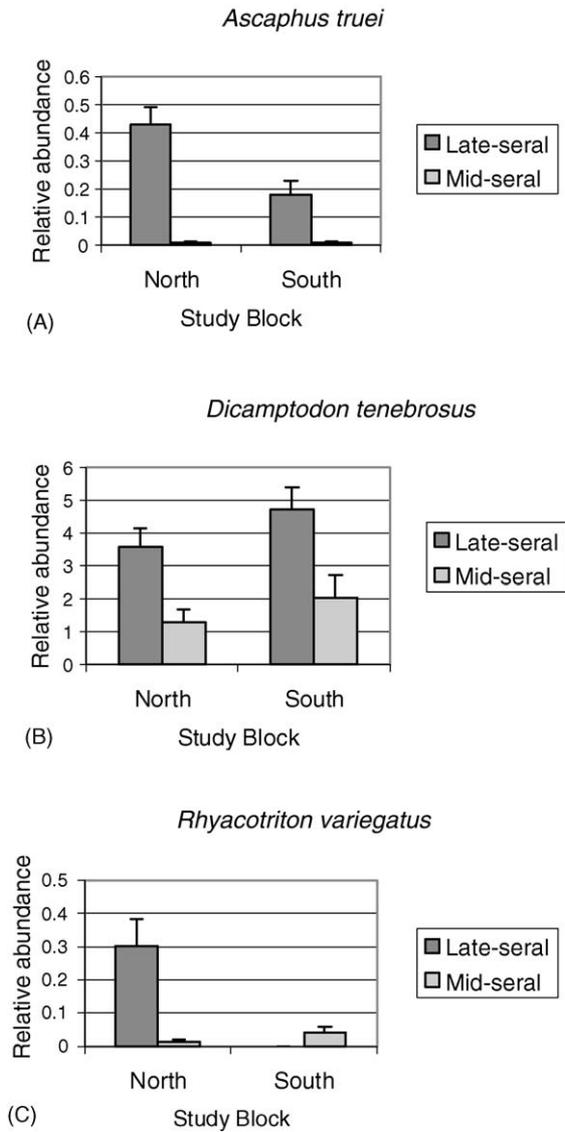


Fig. 3. Histograms showing mean relative abundance per stream per season for three lotic species: (A) *Ascaphus truei* adults and sub-adults only; (B) *Dicamptodon tenebrosus* all life stages; (C) *Rhyacotriton variegatus* all life stages. Error bars represent one standard error around the mean.

twice as many detections occurring in streams draining late-seral forests (72%) compared with streams draining mid-seral forests (Table 2), with the difference being highly significant (Table 3; Fig. 3B). Within streams, the difference between seasons also was significant, with the fewest encounters in the fall. No difference was detected between blocks (Table 3).

3.5. *R. variegatus*

We detected *R. variegatus* 54 times during the 2 years of sampling (Table 2). Most (89%) *R. variegatus* were found in the northern block, with all but two of the northern block detections occurring in late-seral forests (96%). In the southern block, only six *R. variegatus* were found, three in each of two mid-seral forest streams (Fig. 3C). Neither seral stage nor study block alone showed significant differences in detections of *R.*

variegatus (Table 3). However, the season effect was highly significant, as were interactions between season and seral stage and season and study block, with significantly more encounters in the spring in both the late-seral and in the northern block (Table 3).

3.6. Environmental factors

Overall the southern block was significantly warmer by several degrees celsius (water d.f. = 1, $F = 36.95$, $P = 0.0003$; air d.f. = 1, $F = 16.18$, $P = 0.0038$) (Fig. 4A and B). However, within blocks there was little difference between seral stages for

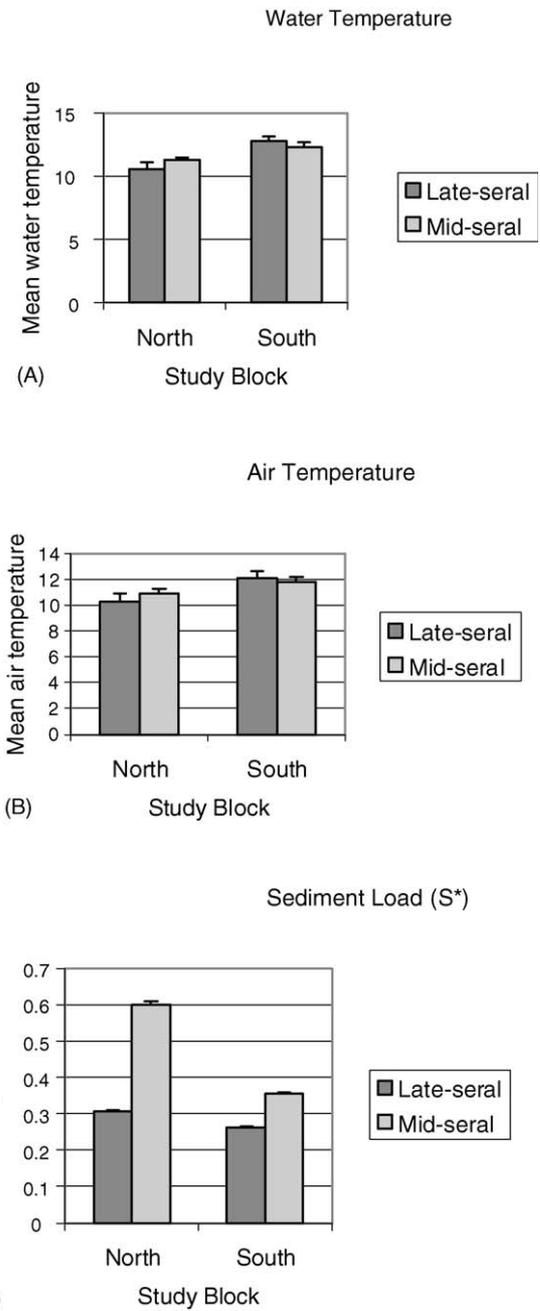


Fig. 4. Histograms comparing: (A) mean water temperature (°C), (B) Mean air temperature (°C), and (C) sediment load (S^*), by seral stage and block. Error bars represent one standard error around the mean.

both water temperature (d.f. = 1, $F = 0.45$, $P = 0.5219$) and air temperature (d.f. = 1, $F = 0.16$, $P = 0.6999$), with differences between forest types very slight (<0.5 °C), and probably not biologically significant.

Northern block streams had higher fine sediment loads compared to streams in the southern block (d.f. = 1, $F = 3.68$, $P = 0.091$), probably due to differences between blocks in underlying geology, erosion rates, rainfall or other regional factors. However, more importantly, in both study blocks the mid-seral forest streams had significantly more fine sediment than late-seral forest streams (d.f. = 1, $F = 6.29$, $P = 0.036$) (Fig. 4C). Fine sediment loads were higher in the mid-seral member of every pair (Table 1).

4. Discussion

Previous studies have found differences in amphibian species composition (e.g., Bury, 1983; Welsh, 1990), and higher relative numbers of some species, in late-seral compared to younger forest seral stages (e.g., Welsh and Lind, 1991; Welsh et al., 2005). While our understanding of the ecological roles of amphibians in forest ecosystem processes is incomplete, their importance is sufficiently well documented (e.g., Davic and Welsh, 2004) to merit concern when species are missing, or their numbers depressed, relative to what would be found in a forest ecosystem with a complete complement of native species present in ecologically functional numbers (see Franklin et al., 2002).

This study compared amphibian numbers in low-order (headwater) streams draining late-seral and mid-seral redwood forests. We found that total amphibian species richness, and the relative abundances of three lotic amphibians, were lower, and fine sediment loads were greater, in streams draining mid-seral forests (Table 3). We also considered differences in water temperatures as a possible explanatory factor for differences observed in amphibian numbers (e.g., Welsh et al., 2005). However, there were no significant differences in water temperatures between the seral stages, and all water temperatures recorded were well within the reported thermal tolerances for *A. truei*, *R. variegatus*, and *D. tenebrosus* (Brattstrom, 1963; Claussen, 1973; Brown, 1975; Welsh and Lind, 1996). Therefore, our results suggest that fine sediments alone were enough to alter population levels.

Previous research has demonstrated that elevated levels of fine sediments negatively impact lotic amphibians (reviewed in Corn et al., 2003). For example, Welsh and Ollivier (1998), studying the effects of a storm-induced slope failure associated with a road construction project, compared sediment impacted streams to nearby control streams. They demonstrated that fine sediment impacts alone were enough to depress stream amphibian populations. While our findings here were similar to those of Welsh and Ollivier (1998), with both studies recording depressed populations of amphibians in streams with elevated fine sediment loads, these studies differ by timescale in two ways: the duration of sediment input, and the recovery time since initial input. Welsh and Ollivier (1998) made field observations at less than 1 year after a single large-scale input

of sediment; our field observations occurred 37–60 years after initial impact. Here, we found that older, chronic sediment inputs from long past timber harvest operations can have a similar impact on amphibian populations as the acute sediment inputs studied by Welsh and Ollivier (1998).

A study in western Oregon comparing lotic amphibian populations in mid-seral Douglas-fir forest streams (14–40 years since harvest) to streams in un-logged Douglas-fir forests, also suggested that detrimental sediment impacts may be long-lasting (Corn and Bury, 1989). In the Oregon Coast Range, stream amphibian populations had not recovered 35–50 years after clearcut timber harvesting (Bury and Pearl, 1999). In addition, genetic evidence suggests that it may take hundreds of years after population recovery for the restoration of genetic heterozygosity (Curtis and Taylor, 2003).

Some of our results indicated that unique aspects of the life histories of some the species we detected, especially some non-target species (see Section 2), influenced their distributions in and along the stream reaches independent of the response variables incorporated into our study design. For example, the greater number of species detected in the southern block (Table 2) may be the result of eco-physiological restrictions of some of these less frequently encountered species (i.e., terrestrial salamanders of the genera *Aneides* and *Batrachoseps*). The understory vegetation was thicker in the northern compared to the southern block, resulting in more exposed rocky substrates along the stream channels of the southern block. The southern block also was significantly warmer (i.e., higher air temperatures). Terrestrial plethodontid salamanders are highly susceptible to desiccation (Feder, 1983), and may have been drawn closer to the streams in the southern block due to the warmer, and probably drier, upslope conditions there compared with the northern block. It is also possible that these habitat differences affected our ability to detect some species (Crump and Scott, 1994), with the increased openness of streamside habitats making it easier to detect terrestrial salamanders along the banks of the southern compared with the northern block.

The more open understory and greater exposed rocky substrates in the southern compared with the northern block may also explain the high detections of *R. boylei* in the southern block compared with its absence in the northern block (Table 2). This frog, which favors larger streams with more open canopy (Hayes and Jennings, 1988), was also more common along the mid-seral streams ($>85\%$ of detections; Table 2). *R. boylei* was especially abundant in one pair of 2nd order streams, both located further down the stream continuum (Vannote et al., 1980) compared with the other stream pairs, and closer to confluences with 3rd order streams, where breeding occurs.

In the northern block, *R. variegatus* was much more common than in the southern block with 46 out of 48 (96%) of northern block captures occurring in late-seral streams (Table 2). Interestingly, in the southern block we found a contrary relationship, with all six *R. variegatus* detected there occurring in two mid-seral forest streams, with three detections per stream (Fig. 3C). Although the sample size is small, these

data appear to contradict our overall findings of higher numbers in the late-seral forest streams in the spring (Table 3). However, one of these southern block streams (Matthews) had the highest gradient in the study (Table 1), suggesting that gradient may be an important factor influencing the distribution of *R. variegatus*. The other southern block stream with *R. variegatus* (Mill) was low gradient but had the lowest level of fine sediment of all the second-growth streams in the study, a level comparable to the late-seral forest streams (Table 1). *Rhyacotriton variegatus* is a headwater specialist, with morphological adaptations for cold, highly oxygenated seeps, springs, and 1st order streams (Welsh and Karraker, 2005), habitats typically having higher gradients and lower fine sediment loads (Montgomery, 1999; Gomi et al., 2002). Recent research has indicated that stream gradient can influence amphibian distributions in aquatic systems (e.g., Murphy et al., 1981; Diller and Wallace, 1996, 1999; Wilkins and Peterson, 2000). However, this association with gradient is most likely a proximal effect of stream network processes (see Montgomery, 1999; Gomi et al., 2002) where fine sediments that will fill in the coarse streambed interstices frequented by amphibians, accumulate in low gradient sections, and are flushed through high gradient sections (Welsh and Ollivier, 1998). This relationship is more likely to be detected in streams that have experienced disturbances, both natural and anthropogenic. The fact that most streams in this study were low gradient (Table 1) and supported high numbers of amphibians, yet most *A. truei* and *R. variegatus* found in mid-seral forest (=previously harvested) streams occurred in the higher gradient reaches, appears to support this interpretation.

The perception that stream gradient has a major influence on numbers of stream amphibians appears to derive primarily from studies conducted on commercial timberlands where the seral continuum has been truncated (e.g., Diller and Wallace, 1996, 1999; Wilkins and Peterson, 2000). Welsh et al. (2000) examined this proposition and found it lacked support when late-seral sites were included in the analysis. Welsh et al. (2000) concluded that it was a real effect on commercial timberlands primarily because of insufficient stream protections during and after forest harvest, an effect that can be particularly detrimental where the underlying geology is of a softer material (see also Welsh and Lind, 2002; Welsh and Karraker, 2005).

It might be argued that because of relatively recent changes in stream protections under California's forest practice rules (FPA, 1973) our results, which derive from stands harvested prior to 1973, have no management implications today. However, even after implementation of the 1973 Forest Practice Act, which added riparian buffers primarily to the fish-bearing reaches of mid-order streams, transport of fine sediments from harvested areas is still problematic. Most of these fine sediments now come from the still inadequately buffered low-order or headwater streams (e.g., Lewis, 1998), with poorly designed road crossings also making a contribution (Furniss et al., 1991). Riparian management under the current rules still offers insufficient protection to low-order headwater and intermittent stream channels (Welsh, 2000; Sheridan and Olsen, 2003). Furthermore, harvest-related negative impacts to

the upper reaches may be long-lived, with recovery times longer than the timber harvest rotation cycle typical of the redwood region (this study). Under these conditions, headwater amphibians, both then (pre-1973), and now, do not have time for population recovery between harvest events. Under current regulations we expect that headwater amphibian populations will continue to decline in northwestern California until forest management in the riparian zone focuses on maintaining both healthy, self-sustaining ecosystem processes and resident species throughout the stream network from the headwaters down stream to the estuaries (see Gomi et al., 2002; Lowe and Likens, 2005).

5. Conclusions

Since European settlement, more than 95% of the late-seral redwood forests have been harvested for timber (Noss, 2000), resulting in rapid, large-scale alteration of habitats important to many amphibian species. Our research indicates that recovery of headwaters amphibian assemblages may be suppressed for many decades after timber harvest in northwestern California, long after recovery of the forest canopy. While this study does not demonstrate a direct cause and effect from fine sediments, it is consistent with the results of numerous other studies implicating fine sediments in the decline of stream amphibians (see Corn et al., 2003). Together these studies constitute a preponderance of evidence demonstrating that fine sediments are a leading factor in suppressing amphibian populations in headwater streams of the Pacific Northwest.

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