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Response of Steelhead/Rainbow Trout (*Oncorhynchus mykiss*) Populations to Debris Flows

Abstract

To better understand the effects of debris flows on salmonid populations, we studied juvenile steelhead/rainbow trout (*Oncorhynchus mykiss*) populations in six streams in the Klamath Mountains of northern California: three affected by debris flows on 01 January 1997 and three that experienced elevated streamflows but no debris flows. We surveyed habitat and fish in study reaches on all six streams in September for three years following the disturbance. Pool depths, substrate size and substrate embededdness varied among streams but with no clear patterns to distinguish debris-flow from no-debris-flow streams. However, the debris-flow streams had significantly less canopy cover and significantly more woody debris. Debris-flow streams did not differ from no-debris-flow streams in biomass and numeric densities of both young-of-year and age 1 and older (age 1 +) *O. mykiss*. In debris-flow streams in the first year following the debris flows (1997), we observed low numbers of age 1 + *O. mykiss* and variable year-class strength of young-of-year fish. In 1997, the young-of-year cohort in one debris-flow stream exhibited exceptional growth. In all three debris-flow streams, age 1 + biomass increased each year through 1999 when total *O. mykiss* biomass in the debris-flow streams exceeded that in the no-debris-flow streams. Surprisingly, we collected larval coastal giant salamander (*Dicamptodon tenebrosus*) in all streams in all years. We suspect the recovery of juvenile *O. mykiss* following the debris flows may have been hastened by increased productivity stimulated by clearing of dense, alder-dominated riparian corridors while salamanders likely recolonized from nearby unaffected tributaries.

Keywords: disturbance, anadromous fish, juvenile salmonids, resilience, habitat quality

Introduction

Maintaining the resilience of anadromous salmonid populations to episodic environmental disturbance is integral to long-term conservation efforts (Bisson et al. 2009, Waldman et al. 2016). With that in mind, land managers now view the landscape as a dynamic mosaic of habitat with patches at varying levels of disturbance and recovery (Reeves et al. 1995). Effective management under this conceptual model, however, requires insight into the immediate impacts and time-frame for recovery from a variety of episodic disturbances.

In streams of the mountainous Pacific Northwest, flood-induced debris flows are a major episodic disturbance that affects the habitat of salmon and trout (family Salmonidae). The frequency and severity of debris flows associated with particular channel types is presumed to limit salmonid distributions in the region (May and Lisle 2012). However, although Sato (2006) recorded the near-extirpation of a small population of Kirikuchi charr (*Salvelinus leucomaenis japonicus*) after a debris flow and little evidence of recovery one year later, several longer term studies of resident salmonids have documented returns to pre-debris-flow densities after three to six years (Lamberti et al. 1991, Roghair et al. 2002, Danehy et al. 2012). In all four studies, the authors cite the proximity of source populations with access to the disturbed reaches (or the lack thereof) as one of the major factors influencing recovery. Thus, anadromous populations might be particularly resilient to debris flows as annual spawning runs provide the potential for rapid recolonization. However, studies of the effects of debris flows in systems accessible to anadromous salmonids remain rare.

After an exceptional series of rainstorms led to debris flows throughout the Klamath Mountains

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in northern California on 01 January 1997, we documented habitat conditions and the response of *O. mykiss* populations over the following three years in three streams that experienced debris flows and three neighboring streams that did not.

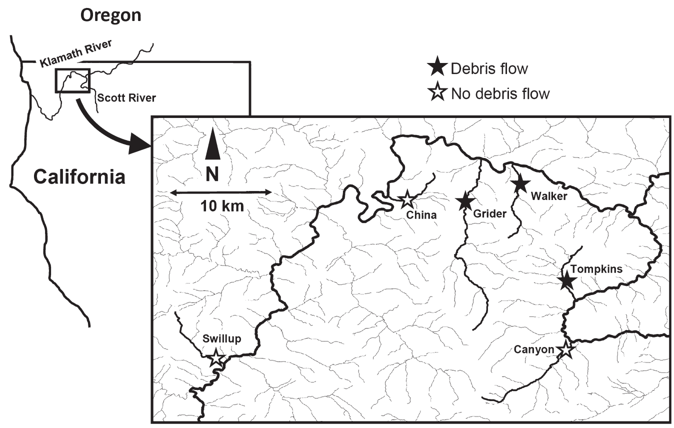

Figure 1. Map showing six sites used in a study of debris flow effects on *Oncorhynchus mykiss* in the Klamath Mountains, Siskiyou County, California.

Methods

Study Area

We studied six streams in the middle Klamath and Scott river basins of northwestern California (Figure 1). The heavily-forested, sparsely-populated region is marked by steep (mean slope in the six basins ≥ 50%), mountainous terrain prone to landslides. Little precipitation falls during the warm summers, but the cool, wet winters yield substantial rainfall, averaging 100–200 cm annually. The six study streams, 2nd- and 3rd-order tributaries to the Klamath and Scott rivers, drain watersheds (at the study sites) ranging 23–103 km^2. All six streams are accessible to anadromous salmonids (steelhead/rainbow trout, *O. mykiss*, Chinook salmon, *O. tshawytscha*, and Coho salmon, *O. kisutch*).

In late December 1996, a series of storms brought substantial rainfall to high elevations in the Klamath Basin. On 01 January 1997, continuing rainfall triggered numerous landslides which evolved into debris flows in many channels. Three of our study streams (Grider, Tompkins and Walker creeks) experienced large debris flows on 01 January 1997 while the other three (Canyon, China and Swillup creeks) experienced only elevated stream flows.

Field Methods

We collected physical and biological information from the six streams in September of 1997, 1998 and 1999. In 1997, we established study reaches with lengths of approximately 40 x the average wetted width. We collected physical habitat data at eleven evenly-spaced, cross-stream transects in each reach on each trip, following methods in Kaufmann et al. (1999). At each transect, we recorded stream width to the nearest 0.1 m. At five points evenly distributed along each transect we measured water depth and categorized the dominant substrate (bedrock, boulder [> 25 cm diameter], cobble [7–25 cm], coarse gravel [1.5–7 cm], fine gravel [0.2–1.5 cm], sand [< 0.2 cm], fines [no grit]) in a 1-m diameter circle centered on the point. We also estimated the average percent embededdness of any cobbles and boulders in the circles. At the midpoint of each transect, we used a hand-held spherical densiometer to estimate percent canopy coverage. We measured channel slope (gradient) between transects with a hand-held clinometer. After recording data for all transects, we strung a measuring tape down the center of the channel along the length of the reach and measured thalweg depths at slope breaks in the longitudinal profile, noting transitions between fast-water habitat and pools. We also measured downed wood (diameter > 10 cm, length > 2 m) and quantified the volume of downed wood within the bankfull channel of each reach.

We collected fish and amphibians throughout each reach in two passes with a backpack electrofisher. After each pass, we measured (standard length for fish, snout-vent length for salamanders and total length for frogs, to the nearest mm) and weighed (wet mass to the nearest 0.01 g) the captured animals. When passes yielded exceptionally high numbers of fish, we weighed and measured at least 44 individuals in each size class and counted the rest. We used length-frequency distributions to assign captured *O. mykiss* to one of two age classes: young-of-year or age 1 and older (age 1 +). The electrofishing catch data allowed us to generate maximum-likelihood depletion estimates of fish numbers by age-class (Van Deventer and Platts 1989). To estimate biomass, we summed the biomass of captured fish and added an estimate of the biomass of any uncaught fish (assigning the mean weight by size-class to uncaught individuals). We calculated numeric and biomass densities by dividing the estimates by the surface area of each reach in each year (mean width x reach length).

Analysis

We compared physical and biological attributes of the debris-flow and no-debris-flow streams using analyses of variance that recognized the repeated measurements in all six streams over three years. The error term for the evaluation of the debris flow effect was the variation among streams within the two debris-flow categories. Evaluation of annual variation and the interaction between year and the debris-flow effect used the overall error term. Proportional response variables (%Boulder/Cobble, %Embeddedness, and %Canopy Cover) were arcsin-square-root transformed to homogenize variances. Wood volume was expressed as cubic meters of wood per area of bankfull channel, and then log transformed to homogenize variances. We compared both the numeric and biomass densities of *O. mykiss* between the three debris-flow streams and the three no-debris-flow streams. We separately analyzed young-of-year and age 1 + fish. Analyses were conducted in SAS. We treated *P* values < 0.10 as worthy of consideration.

Results

While individual streams stood out in one or more of the habitat attributes we assessed, few consistent differences emerged between debris-flow and no-debris-flow streams (Table 1). At all sites, fast water habitat (riffles and runs) predominated and pools were rare (mean number of pools = 2, mean percentage pool habitat by length = 9). Mean pool depths varied among the streams, ranging 46–70 cm, but debris-flow and no-debris-flow streams did not detectably differ. Boulder and cobble substrate predominated in all the streams and proportions did not differ between debris-flow and no-debris-flow streams. Embededdness remained low in all the study reaches throughout the study and did not differ between the two groups of streams; the 3-y average embeddedness for the six streams ranged 10 to 20%. However, debris-flow streams differed significantly from no-debris-flow streams in both canopy cover and downed wood volume. Debris-flow streams averaged 23–51% canopy cover while no-debris-flow streams averaged 81–98%. Debris-flow streams held substantially more woody debris, particularly in the form of jams.

We collected individuals from seven aquatic vertebrate taxa over the three years of sampling (Table 2): juveniles of three salmonid species (*O. mykiss*, Chinook salmon, and Coho salmon), adult Klamath smallscale sucker (*Catostomus rimiculus*), larval and adult Pacific lamprey (*Entosphenus tridentatus*), larval and adult coastal giant salamander (*Dicamptodon tenebrosus*), and larval and adult coastal tailed frog (*Ascaphus truei*). Juvenile *O. mykiss* and larval coastal giant salamanders were the only ubiquitous taxa; *O. mykiss* composed 90% of the overall catch by numbers. Given that most juvenile Chinook and Coho salmon outmigrate from the study streams in late May through early June (Konnoff [1990] provides data for Grider Creek), well before our September samples, inferences about effects on these species lie beyond the scope of this study.

Total *O. mykiss* biomass ranged from 1.2–4.7 g m^{-2} and biomass of young-of-year fish was generally lower than the biomass of age 1 +. Numeric and biomass densities did not differ between debris-flow streams and no-debris-flow streams for either age group (Figure 2; Table 3), but the analysis of variance indicated year-to-year variation typical of wild populations. The analysis yielded marginal *P* values for the debris-flow x year interaction for both age groups of fish in terms of biomass (Table 3), reflecting a slightly stronger trend toward increasing biomass over

TABLE 1. Physical characteristics of study reaches in three streams that experienced debris flows in January 1997 and three streams with no debris flows in the Klamath River Basin. Means are for the three sampled years with standard deviation in parentheses for variables included in ANOVA comparisons. Annual data are provided for downed wood density to show a possible trend in the debris-flow streams.

Stream	Debris Flow	Strm. Order	Water-shed Area (km^2)	Reach Length (m)	Gradient (%)	Mean Width (m)	Mean Thalweg Depth (cm)	Mean Pool Depth (cm)	Mean % Bldr./Cob.	Mean % Embed.	Mean % Canopy Cover	Downed Wood Density (m^3 100 m^{-2})			
												’97	’98	’99	Mean
Canyon	No	3	64	240	5	9.4	46	70 (8.5)	75 (10.0)	10 (2.6)	91 (4.9)	0.3	1.3	0.1	0.6
China	No	3	24	200	3	4.2	26	53 (5.5)	55 (7.5)	15 (4.4)	81 (9.3)	0.6	1.7	2.5	1.6
Swillup	No	2	23	200	4	5.9	38	65 (2.5)	60 (16.1)	16 (2.1)	98 (2.4)	1.7	2.4	2.5	2.2
Mean	No		37	213	4	6.5	37	63	63	14	90	0.9	1.8	1.7	1.5
Grider	Yes	3	102	280	3	10.2	39	67 (4.7)	51 (4.5)	16 (1.7)	23 (3.9)	17.4	28.6	8.7	18.2
Tompkins	Yes	2	33	150	6	4.9	27	46 (8.6)	61 (9.3)	20 (2.6)	51 (14.7)	56.4	65.4	9.4	43.7
Walker	Yes	2	29	150	5	3.5	31	56 (11.3)	64 (20.0)	18 (9.3)	39 (5.4)	8.9	12.1	2.5	7.8
Mean	Yes		55	193	5	6.2	32	56	59	18	38	27.6	35.4	6.9	23.3
AANOVA results for the debris-flow effect ($F_{1,4}$ / P)								0.53/0.51	0.59/0.35	3.53/0.13	25.26/< 0.01		13.46/0.02		

TABLE 2. Densities of fishes and lamprey (numeric / biomass) and presence or absence of amphibians at sampling sites in three streams that experienced debris flows and three streams with no debris flows in the Klamath River basin. Numeric densities are expressed as individuals m^{-2}, biomass densities as g m^{-2}.

		No Debris Flow			Debris Flow		
Species	Year	Canyon	China	Swillup	Grider	Tompkins	Walker
Oncorhynchus mykiss YOY	1997	0.07 / 0.3	0.51 / 2.3	0.30 / 0.9	0.22 / 0.9	0.05 / 0.6	0.27 / 1.0
	1998	0.07 / 0.2	0.13 / 0.8	0.17 / 0.4	0.23 / 1.2	0.02 / 0.2	0.07 / 0.4
	1999	0.07 / 0.2	0.41 / 1.2	0.26 / 0.6	0.40 / 1.6	0.22 / 1.0	0.38 / 1.3
O. mykiss Age 1 +	1997	0.02 / 0.9	0.04 / 1.3	0.05 / 1.3	0.01 / 0.9	0.01 / 0.6	0.01 / 0.9
	1998	0.08 / 2.7	0.08 / 1.9	0.10 / 1.8	0.06 / 2.4	0.02 / 1.4	0.03 / 1.4
	1999	0.05 / 1.9	0.06 / 1.6	0.09 / 2.3	0.07 / 3.1	0.03 / 2.2	0.03 / 2.1
Chinook salmon (juveniles)	1997	•	•	•	•	•	•
	1998	•	•	•	< 0.01 / < 0.1	•	•
	1999	•	•	•	0.04 / 0.1	•	•
Coho salmon (juveniles)	1997	•	< 0.01 / < 0.1	•	•	•	•
	1998	< 0.01 / < 0.1	•	•	•	•	•
	1999	•	•	•	0.03 / 0.1	•	< 0.01 / < 0.1
Klamath smallscale sucker (adults)	1997	•	•	•	< 0.01 / 0.2	•	•
	1998	•	•	•	•	•	•
	1999	•	•	•	•	•	•
Pacific lamprey (larvae)	1997	•	< 0.01 / < 0.1	•	•	•	•
	1998	•	•	•	•	•	•
	1999	•	•	•	•	•	•
Pacific lamprey (adults)	1997	•	•	•	•	•	•
	1998	•	•	•	< 0.01 / 0.2	•	•
	1999	•	•	•	•	•	•
Coastal giant salamander (larvae)	1997	P	P	P$^{+adults}$	P	P	P
	1998	P	P$^{+adults}$	P$^{+adults}$	P$^{+adults}$	P	P
	1999	P	P	P$^{+adults}$	P	P	P
Coastal tailed frog (larvae)	1997	•	•	P$^{+adults}$	P	•	•
	1998	•	•	P	P	•	P
	1999	•	•	P$^{+adults}$	P	•	•

TABLE 3. Summary of repeated-measures ANOVA for juvenile *Oncorhynchus mykiss* numbers (fish m^{-2}) and biomass (g m^{-2}) by age-class for streams that experienced debris flows and streams with no debris flows. *F* values reflect more precise Mean Square (MS) values than those presented here.

Numbers (fish m^{-2})	Young-of-Year				Age 1 +			
Source	**df**	**MS**	***F***	***P***	**df**	**MS**	***F***	***P***
Between streams								
Debris flow	1	0.008	0.18	0.69	1	0.0006	0.31	0.61
Streams(Debris flow)	4	0.043			4	0.0018		
Within streams								
Year	2	0.048	4.8	0.04	2	0.0025	18.49	< 0.01
Year x Debris flow	2	0.001	0.13	0.88	2	0.0002	1.51	0.28
Error	8	0.01			8	0.0001		
Biomass (g m^{-2})								
Source	**df**	**MS**	***F***	***P***	**df**	**MS**	***F***	***P***
Between streams								
Debris flow	1	0.094	0.13	0.73	1	0.027	0.10	0.77
Streams(Debris flow)	4	0.711			4	0.271		
Within streams								
Year	2	0.421	4.29	0.05	2	2.454	17.99	< 0.01
Year x Debris flow	2	0.351	3.58	0.08	2	0.421	3.08	0.10
Error	8	0.098			8	0.136		

the three years in debris-flow streams (Figure 2). By 1999, the total biomass of *O. mykiss* in each of the debris-flow streams exceeded the biomass in any of the no-debris-flow streams (Figure 3).

Inspection of *O. mykiss* size distributions suggested differences between debris-flow and no-debris-flow streams (Figure 3). In the summer following the debris flows, age 1 + *O. mykiss* were rare in the three debris-flow streams, but some individuals exceeded 200 mm SL in each stream. Age 1 + *O. mykiss* were relatively abundant in no-debris-flow streams but individuals > 200 mm were absent. By 1999, however, there was little in the size distributions to distinguish debris-flow from no-debris-flow streams *except* that fish were notably larger in the debris-flow streams. Individual streams exhibited noteworthy variation in size distributions across the years. For example, the few young-of-year fish captured in Tompkins Creek (debris-flow) in 1997 were markedly larger than young-of-year in other creeks, with a median size of 90 mm SL (at least 25 mm longer than the median young-of-year size in any other creek in that year). The exceptional growth of the 1997 cohort in Tompkins Creek appeared to carry through to the larger size-classes in 1998 and 1999 (Figure 3).

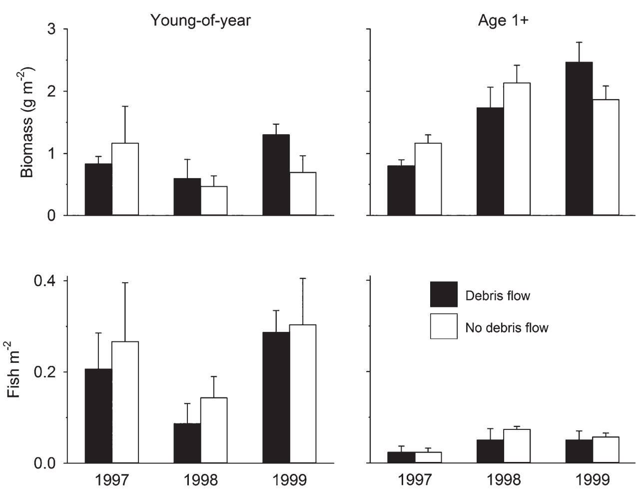

Figure 2. Mean biomass and numeric densities in September, 1997–1999 (with standard errors) for two age-classes of juvenile *Oncorhynchus mykiss*. Age 1 + includes all fish Age 1 and older.

We collected larval salamanders in all six streams in every year. Due to the variable and often low efficiency of electrofishing as a collec-

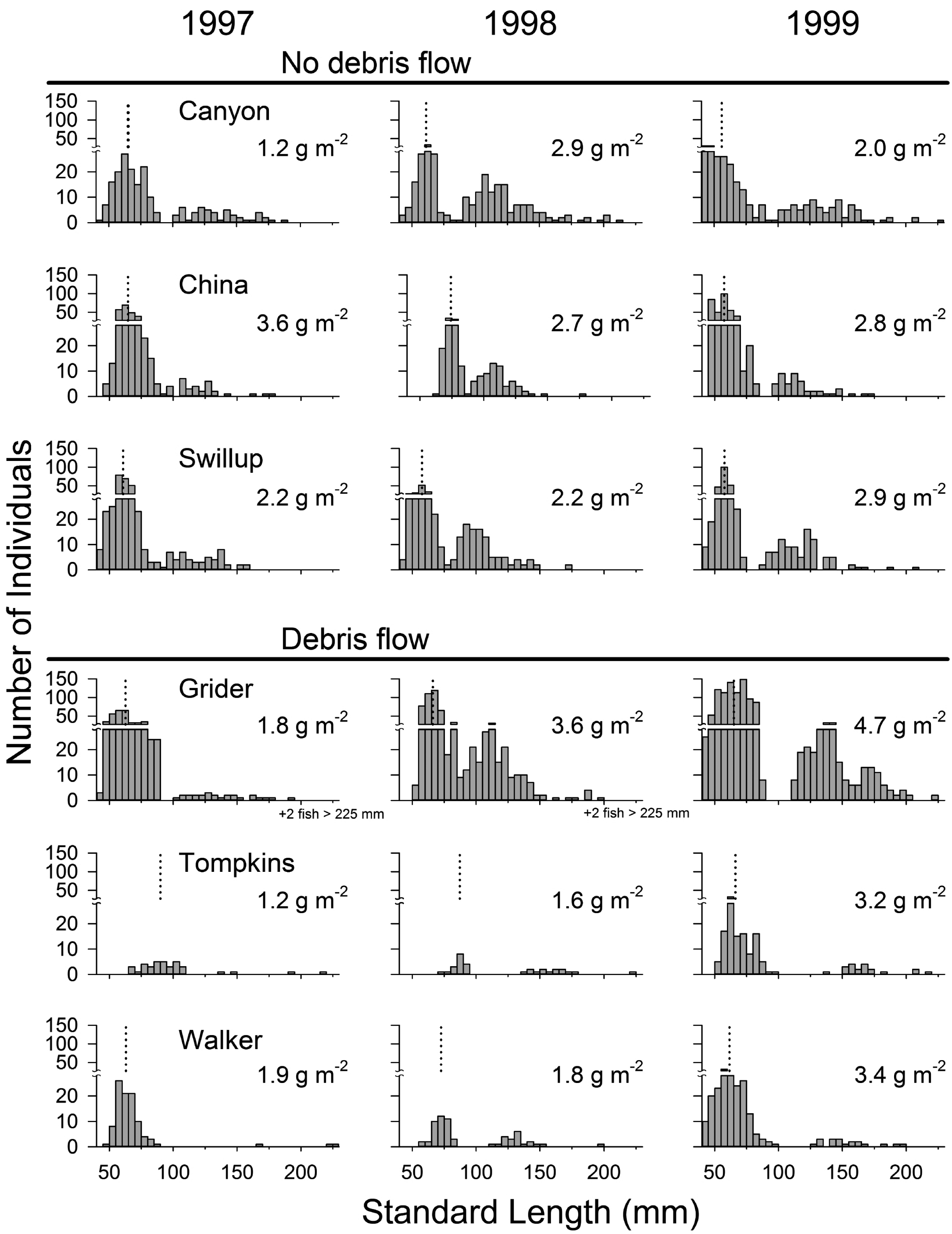

Figure 3. Length-frequency distributions and total biomass of juvenile *Oncorhynchus mykiss* in September, 1997–1999. Dotted lines indicate median length of young-of-year fish.

tion method for amphibians, we did not generate depletion estimates for salamanders or frogs. However, the measured biomass of larval salamanders rivaled and sometimes exceeded the biomass of individual age-classes of *O. mykiss*.

Discussion

Although channel changes in affected streams were visually striking, debris flows did not detectably degrade juvenile salmonid habitat in debris-flow streams. We found indications that the habitat changes wrought by the debris flows favored increased salmonid production, at least in the short term. We believe the lack of negative effects on salmonid habitat reflects two important conditions specific to our study sites. First, debris flows are the dominant process that structures most small to moderate-sized stream channels (1st–6th order) in the Klamath region, mobilizing large cobbles and boulders that then armor the streambed (May and Lisle 2012). Although the channel is thoroughly reworked, debris flows may not necessarily alter channel shape nor alter the size distributions and arrangements of bed material (Thomas E. Lisle, U.S. Forest Service, personal communication). This would explain the similarity in substrate characteristics in streams with and without recent debris flows (Cover et al. 2010, this study). Second, aerial photos (GoogleEarth) preceding the 1997 debris flows show that all six study streams had closed canopies dominated by white alder, suggesting the streams experienced relatively recent (< 50 y) debris flows (Cover et al. 2010). Large-diameter conifers, widely recognized as an important structural component of many salmonid streams (Bisson et al. 1987), were probably rare across all sites before the 1997 debris flows, creating limited potential for recruitment of large wood in any of the streams.

The reduced canopy cover and increased woody debris volume we observed could enhance salmonid production in alder-dominated channels (Fausch and Northcote 1992, Wilzbach et al. 2005, Harvey and Wilzbach 2010). However, in streams with alder-dominated riparian zones, the debris-flow-induced changes to riparian corridors and stream channels that might drive increased *O. mykiss* production are likely short-lived. Just eight years after debris flows in 12 Oregon streams, D'Souza et al. (2011) measured 70–95% shading, primarily from rapidly re-established red alder (*Alnus rubra*). Seven years after the 1997 debris flows, Cover et al. (2010) measured 75–80% canopy cover in two of the debris-flow streams included in our study (Tompkins and Walker creeks). The wood jams in the debris-flow streams in our study consisted mostly of small diameter stems, probably alder, which are prone to rapid decomposition. Thus, this study may document a brief window of increased productivity and habitat complexity in the first few years after disturbance.

Post-debris-flow physical habitat conditions appeared to combine with favorable ecological conditions resulting in exceptional survival and growth of the 1997 cohort of *O. mykiss*. We cannot exclude the possibility that some of the apparent differences in fish size between sites result from differences in growth between resident and anadromous *O. mykiss*. For example, Hodge et al. (2016) reported that the back-calculated mean lengths of 1 and 2 year old resident fish and steelhead that smolt at age 1 were significantly larger than the mean lengths of steelhead that smolt at age 2 and 3. However, because all six sites were accessible to anadromous fish and the anadromous life history is indicated for 90% of sampled adults in the Klamath Basin (Hodge et al., 2016), we assumed all sites would be similar in the mix of resident and anadromous individuals.

The reduced canopy cover associated with debris flows has been linked to increased aquatic primary productivity (Lamberti et al., 1991) which could ultimately increase food available to juvenile salmonids. Kiffney et al. (2004) reported dramatic increases in the abundances of Chironomidae and Baetidae (380% and 9300% compared to pre-debris-flow, respectively), two important taxa in the diets of juvenile steelhead, within the first year following a debris flow in a Washington stream. The riparian clearing associated with debris flows might also alter terrestrial food input. Studinski and Hartman (2015) recorded increased terrestrial invertebrate input biomass in streams subjected to extensive riparian logging (90% basal area harvest) compared to unlogged controls and linked the difference to a shift towards larger taxa.

Along with potential increases in available food, the 1997 young-of-year cohort likely benefited from reduced competition due to severe reductions in the density of older fish. Density-dependent growth is widely recognized in stream-dwelling salmonids (e.g. Grant and Imre 2005, Harvey et al. 2005, Lobón-Cerviá 2007), and in juvenile steelhead specifically (Myrvold and Kennedy 2015). Myrvold and Kennedy (2015) observed a negative relationship between young-of-year steelhead growth and age 1 + density but no evidence of density-dependence for older fish. The annual sequence of size distributions for Tompkins Creek seems to support their findings: exceptionally large young-of-year in 1997 (with almost no age 1 +) followed by exceptionally large age 1 + in subsequent years. Density-dependent growth, perhaps accompanied by higher survival, can contribute to the resilience of populations challenged by infrequent, catastrophic disturbance (Vincenzi et al. 2008).

Anadromous fish may be particularly well-suited to recover from debris flows, given the spatial segregation of juveniles and adults and high fecundity, however the timing of a debris flow undoubtedly influences the recovery. Although adult steelhead begin returning to the Klamath system in the fall, peak spawning typically occurs in March and April, so the direct effects (mortality or displacement) on steelhead of the 1997 events were likely limited to the 1996 young-of-year cohort and any 1 + juveniles. Had the debris flows occurred several months later, the 1997 year class—and the potential for rapid recovery—might have been lost as well.

In contrast to steelhead, all life stages of coastal giant salamanders spend multiple years in or near streams and are present year-round (Swanson et al. 1998), so the presence of larvae in all the study streams in all three years was unexpected. Because debris flows result in a violent and complete reworking of the stream substrate, it seems unlikely that refuges for larval amphibians existed within the debris-flow reaches. However, the locations of our study sites probably allowed recolonization from unaffected upstream reaches and tributaries.

This study adds to the growing literature documenting rapid recovery of salmonid populations following debris flows (e.g. Lamberti et al. 1991, Roghair et al. 2002) by contributing an example from streams accessible to anadromous populations. In the streams we studied, effects on *O. mykiss* were probably minimized by the timing of the debris flow, the persistence of habitat quality, increases in food for salmonids and density-dependent growth by young-of-year *O. mykiss* immediately following the disturbance. This study suggests that in streams with dense, alder riparian corridors the canopy opening and woody debris deposition resulting from debris flows yields temporary improvement in conditions for *O. mykiss* production. In this case, "recovery" to pre-disturbance conditions may well entail a return to a less productive state.

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Literature Cited

Bisson, P. A., J. B. Dunham, and G. H. Reeves. 2009. Freshwater ecosystems and resilience of Pacific salmon: habitat management based on natural variability. Ecology and Society 14:45.

Bisson, P. A., R. E. Bilby, M. D. Bryant, C. A. Dolloff, G. B. Grette, R. A. House, M. L. Murphy, K. V. Koski, and J. R. Sedell. 1987. Large woody debris in forested streams in the Pacific Northwest: past, present, and future. *In* E. O. Salo and T. W. Cundy (editors), Streamside Management: Forestry and Fishery Interactions. University of Washington Institute of Forest Resources Contribution 57. Pp 143-190.

Cover, M. R., J. A. de la Fuente, and V. H. Resh. 2010. Catastrophic disturbances in headwater streams: the long-term ecological effects of debris flows and debris floods in the Klamath Mountains, northern California. Canadian Journal of Fisheries and Aquatic Sciences 67:1596-1610.

Danehy, R. J., R. E. Bilby, R. B. Langshaw, D. M. Evans, T. R. Turner, W. C. Floyd, S. H. Schoenholtz, and S. D. Duke. 2012. Biological and water quality responses to hydrologic disturbances in third-order forested streams. Ecohydrology 5:90-98.

D'Souza, L. E., M. Reiter, L. J. Six, and R. E. Bilby. 2011. Response of vegetation, shade and stream temperature to debris torrents in two western Oregon watersheds. Forest Ecology and Management 261:2157–2167.

Fausch, K. D., and T. G. Northcote. 1992. Large woody debris and salmonid habitat in a small coastal British Columbia stream. Canadian Journal of Fisheries and Aquatic Sciences 49:682-693.

Grant, J. W. A., and I. Imre. 2005. Patterns of density-dependent growth in juvenile stream-dwelling salmonids. Journal of Fish Biology 67:100-110.

Harvey, B. C., J. L. White, and R. J. Nakamoto. 2005. Habitat-specific biomass, survival and growth of rainbow trout (*Oncorhynchus mykiss*) during summer in a small coastal stream. Canadian Journal of Fisheries and Aquatic Sciences 62:650-658.

Harvey B. C., and M. A. Wilzbach. 2010. Carcass addition does not enhance juvenile salmonid biomass, growth, or retention in six northwestern California Streams. North American Journal of Fisheries Management 30:1445-1451.

Hodge, B. W., M. A. Wilzbach, W. G. Duffy, R. M. Quinones, and J. A. Hobbs. 2016. Life history diversity in Klamath River steelhead. Transactions of the American Fisheries Society 145:227-238.

Kaufmann P. R., P. Levine, E. G. Robison, C. Seeliger, and D. V. Peck. 1999. Quantifying physical habitat in wadeable streams. EPA⁄620⁄R-99⁄003. National Health and Environmental Effects Research Laboratory, Western Ecology Division. US Environmental Protection Agency. Washington, DC.

Kiffney, P. M., C. J. Volk, T. J. Beechie, G. L. Murray, G. R. Pess, and R. E. Edmonds. 2004. A high-severity disturbance event alters community and ecosystem properties in West Twin Creek, Olympic National Park, Washington, USA. The American Midland Naturalist 152:286-303.

Konnoff, D. L. 1990. A prelogging study of fisheries and hydrology in Grider Creek. M.S. Thesis, Humboldt State University, Arcata, CA.

Lamberti, G. A., S. V. Gregory, L. R. Ashkenas, R. C. Wildman, and K. M. S. Moore. 1991. Stream ecosystem recovery following a catastrophic debris flow. Canadian Journal of Fisheries and Aquatic Sciences 48:196-208.

Lobón-Cerviá, J. 2007. Density-dependent growth in stream-living Brown Trout *Salmo trutta* L. Functional Ecology 21:117-124.

May, C. L., and T. E. Lisle. 2012. River profile controls on channel morphology, debris flow disturbance, and the spatial extent of salmonids in steep mountain streams. Journal of Geophysical Research 117.

Myrvold, K. M., and B. P. Kennedy. 2015. Density dependence and its impact on individual growth rates in an age-structured stream salmonid population. Ecosphere 6:1-16.

Reeves, G. H., L. E. Benda, K. M. Burnett, P. A. Bisson, and J. R. Sedell. 1995. A disturbance-based ecosystem approach to maintaining and restoring freshwater habitats of evolutionarily significant units of anadromous salmonids in the Pacific Northwest. American Fisheries Society Symposium 17:334-349.

Roghair, C. N., C. A. Dolloff, and M. K. Underwood. 2002. Response of a brook trout population and instream habitat to a catastrophic flood and debris flow. Transactions of the American Fisheries Society 131:718-730.

Sato, T. 2006. Dramatic decline in population abundance of *Salvelinus leucomaenis* after a severe flood and debris flow in a high gradient stream. Journal of Fish Biology 69:1849-1854.

Studinski, J. M., and K. J. Hartman. 2015. The effects of riparian logging on terrestrial invertebrate inputs into forested headwater streams. Hydrobiologia 743:189-198.

Swanson, F. J., S. L. Johnson, S. V. Gregory, and S. A. Acker. 1998. Flood disturbance in a forested mountain landscape interactions of land use and floods. Bioscience 48:681-689.

Van Deventer, J. S., and W. S. Platts. 1989. Microcomputer software system for generating population statistics from electrofishing data: user guide for MicroFish 3.0. General Technical Report INT-GTR-254. US Forest Service. Boise, ID.

Vincenzi S., A. J. Crivelli, D. Jesensekc, and G. A. DeLeo. 2008. The role of density-dependent individual growth in the persistence of freshwater salmonid populations. Oecologia 156:523-534.

Waldman, J., K. A. Wilson, M. Mather, and N. P. Snyder. 2016. A resilience approach can improve anadromous fish restoration. Fisheries 41:116-126.

Wilzbach, M. A., B. C. Harvey, J. L. White, and R. J. Nakamoto. 2005. Effects of riparian canopy opening and salmon carcass addition on the abundance and growth of resident salmonids. Canadian Journal of Fisheries and Aquatic Sciences 62:58-67.

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