

Role of Hardwood in Forming Habitat for Southern California Steelhead¹

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Abstract

Large wood (LW) is known to be very important to fish habitat in conifer-dominated streams of the Pacific Northwest, but has not been well studied in hardwood-dominated streams of the central California coast. In July and August 2006, we studied the occurrence and function of hardwood LW in relation to stream habitat and threatened steelhead (*Oncorhynchus mykiss*) distribution in the hardwood-dominated Upper Salinas River watershed in central-coastal California. We sampled 15 sites located on four tributaries and on the main stem of the Salinas River. At each site, we measured the volume of fallen dead LW (logs, root wads), standing trees, and not-standing live wood (exposed roots, living fallen trees) within the bankfull width. Fish density and length were estimated by a snorkel survey. Willow (*Salix* spp.), oak (*Quercus* spp.), California sycamore (*Platanus racemosa*), and Fremont cottonwood (*Populus fremontii*) dominated the sites. Fallen dead LW volume within the bankfull width averaged 47.6 m³/ha (SD = 58.2) across all sites. Total LW volume, including fallen dead, not-standing live wood, and standing live and dead trees averaged 222.0 m³/ha (SD = 173.7). Fallen dead LW volumes on the central coast were almost 16 times less than conifer-dominated sites in the Pacific Northwest, but similar to volumes on private hardwood-dominated north coast sites. At 13 sites at least half the pools were formed due to LW, or experienced some influence of LW. An average of 4.01 fish/m (SD = 3.08) were observed at 14 sites. Steelhead were observed at 9 sites, averaging 0.23 fish/m across 14 sites (SD = 0.35). Hardwood LW appears to be an important component of steelhead habitat in central-coastal California streams, due to its influence on pool formation.

Keywords: fish habitat, hardwood, large woody debris, Oncorhynchus mykiss, pools, rainbow trout, steelhead, Salinas River

Introduction

Large wood (LW) plays a key role in the creation and maintenance of fish habitat in small coastal streams in the Pacific Northwest (McMahon and others 1996, Naiman and others 1998). LW, defined as pieces of wood with length ≥ 1 m, and diameter ≥ 10 cm, influences channel geomorphology by stabilizing channels and trapping gravel that fish use for spawning. LW is also used as habitat by macroinvertebrates, important food for fish. Pools often form under logs that have fallen into a stream, or immediately upstream of wood jams.

¹ An abbreviated version of the paper was presented at the Sixth California Oak Symposium: Today's Challenges, Tomorrow's Opportunities, October 9-12, 2006, Rohnert Park, California.

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Most studies of LW have been conducted in areas dominated by coniferous forest, such as the Pacific Northwest and the northern California coast. A notable exception is the work by Opperman (2005) in which LW was surveyed in hardwood-dominated watersheds in Northern California (Mendocino, Sonoma, Marin, Contra Costa and Alameda counties). He found that LW loading (volume per unit area of stream) was consistently lower than that observed in conifer-dominated systems. Nevertheless, hardwood LW still formed channel-spanning wood jams that contributed to the formation of pools. Streams he sampled on public lands had consistently higher LW loading than streams on private land, suggesting that land management practices may affect the volume of LW and, in turn, the quality and quantity of habitat available for anadromous salmonids. Hardwood LW tends to have a shorter residence time in streams than coniferous LW, potentially because it decays and disintegrates at a faster rate than coniferous LW (Hyatt and Naiman 2001). Consequently, in hardwood-dominated systems there is a need to achieve higher rates of recruitment from the riparian zone to ensure adequate instream loading. Because recruitment is determined by both riparian stand conditions and land management practices, it is especially important that landowners be informed about LW's crucial role in conserving fish habitat.

Pools are the primary refuge for steelhead (*Oncorhynchus mykiss*)⁵ and other anadromous salmonids during hot weather in northern California (Nielsen and others 1994). Pool spacing is a decreasing function of LW abundance in small, coastal streams in British Columbia (Rosenfeld and Huato 2003). The role of LW in streams is known to vary with stream size, with LW having a stronger influence in small streams (Gurnell and others 2002). The LW pieces in a small stream are relatively large in comparison with the bankfull width and are therefore more likely to form wood jams and pools. Beechie and Sibley (1997) showed that the size of LW pieces that formed pools in northwestern Washington streams increased with increasing channel width, and that pool spacing was a function of the interaction of LW abundance and channel slope. LW played a large role in the formation of 63 to 74 percent of pools in streams of the conifer-dominated Pacific Northwest (Andrus and others 1988, Carlson and others 1990, Fausch and Northcote 1992, Montgomery and others 1995). Similarly, LW formed 76 percent of pools in Colorado streams in conifer-dominated old-growth subalpine forest (Richmond and Fausch 1995). In contrast, less than 15 percent of pools in streams in the mixed-wood forest of the Boreal Shield in Ontario, Canada, were formed or influenced by LW, likely due to the small size of boreal trees, and the resulting small average size of the LW pieces (mean diameter = 16.7 cm, SD = 1.6) (Kreutzweiser and others 2005). In northern hardwood forest streams in the Adirondack Mountains, wood influenced only about 5 percent of pools (Kraft and others 2002).

The Salinas River and its tributaries have been designated by the National Marine Fisheries Service as critical habitat for steelhead, listed as "threatened" under the Federal Endangered Species Act. The watershed is part of the south-central California Coast Evolutionarily Significant Unit (ESU) for steelhead. The upper watershed is in San Luis Obispo County, where 70 percent of the land is privately owned. Agriculture, including vineyards, dryland farming, row crops and cattle production, is the dominant land use. The river experiences elevated rates of bank

⁵ Steelhead and rainbow trout are the same species, *Oncorhynchus mykiss*. Steelhead are the anadromous, that is, ocean-going, form of the species. For the remainder of this paper we will refer to all *O. mykiss* as steelhead.

erosion and significant loads of sediment, nutrients, pesticides and other pollutants, possibly as a result of land use. The steelhead in the Nacimiento River, San Antonio River, and upper Salinas River (south of San Miguel) are believed to form one of three discrete populations in the Salinas Basin, the other two being in Gabilan Creek and Arroyo Seco (Boughton and others 2006). The populations are expected to have relatively low stray rates of spawners from one to another, and as such, to have relatively small rates of genetic exchange between populations. We chose to focus on the upper Salinas River watershed because spawning steelhead can still migrate to this area, while the Nacimiento and San Antonio rivers have impassable dams.

Information on fish habitat and steelhead abundance is scarce for the California central coast and, prior to this study, virtually non-existent for the upper Salinas River. We conducted this study to provide an estimate of LW loading in the watershed for comparison with other published accounts of LW loading for streams dominated by coniferous or hardwood riparian forests. We surveyed the fish community to determine the distribution and density of steelhead and other native fish species as well as to determine the occurrence of non-native fish species. Finally, we examined the role of hardwood LW in forming pools.

Methods

Study Sites

We studied 15 sites within the upper Salinas River watershed mainstem and 4 tributaries (4 sites on the mainstem Salinas River, two on Atascadero Creek, one on Rinconada Creek, five on Trout Creek, one on Tassajera Creek, and two on Santa Margarita Creek) (*fig. 1*). Because Tassajera Creek is a tributary to Santa Margarita Creek, we considered them to be one tributary to the mainstem Salinas River. Twelve sites were on private land and three were on public land. Land cover at the sites included hardwood forest, hardwood rangeland, and urban. Sites ranged in elevation from 213 to 448 m.

Surveys of each site were conducted between July 5 and August 10, 2006, when temperatures normally are at the annual maximum, and therefore most limiting to the distribution of cold-water fish such as steelhead. Flows in the upper Salinas River tend to be low at this time of year, and averaged $0.097 \text{ m}^3/\text{s}$ ($SD = 0.077$) for the 14 sites that had water. The 15th site was dry throughout the study period.

Large Wood and Riparian Habitat Sampling

At each site one reach approximately 300 m long, the experimental unit, was marked using a hip chain. Reach length delineation was conducted prior to wood surveys and in conjunction with fish snorkel surveys. Six measurements of bankfull width were made at approximately 50-m intervals, following the protocol of Harrelson and others (1994). Site elevations and locations were determined with a handheld Global Positioning System (Garmin 72TM).⁶

⁶ The use of trademarked equipment in this study does not imply endorsement by the University of California.

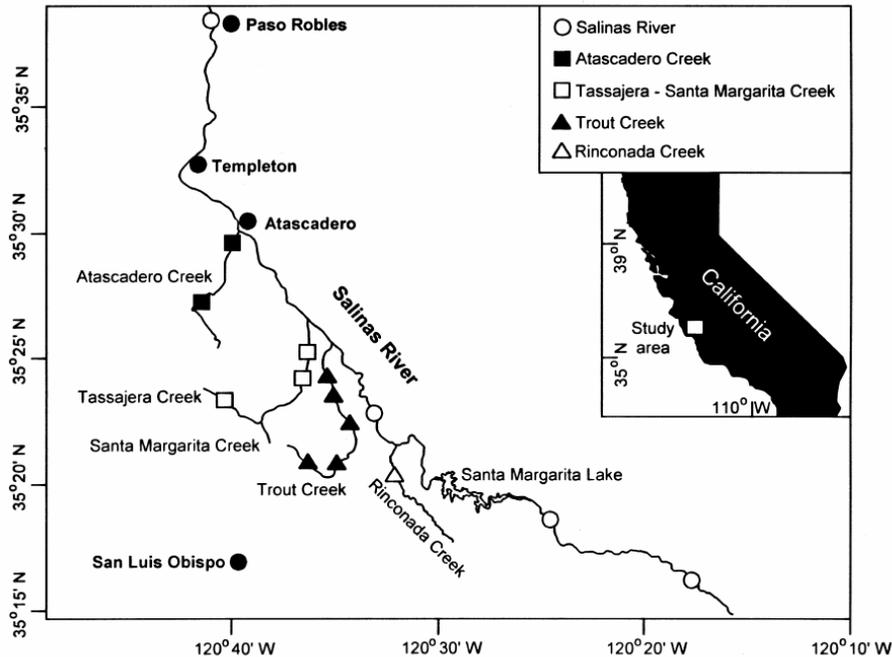


Figure 1—Map of the Upper Salinas River watershed showing sample sites on the mainstem Salinas River and four tributaries.

Studies of large wood and stream habitat in more northern regions have focused upon fallen dead wood, often termed large woody debris (LWD). However, we frequently observed standing trees within the bankfull width, and also observed live trees growing or fallen horizontally, and exposed live roots that functioned similarly to fallen dead wood pieces. We enumerated all trees and pieces in the bankfull width that met the large wood criteria, in order to determine the prevalence of standing trees, horizontal live trees, and roots relative to LWD in these south-central California sites. Large wood was categorized as fallen dead LW, not-standing live LW (live trees growing or fallen horizontally, exposed live roots), standing LW (both live trees and snags), and other LW (pieces of wood that did not fit the other categories; for example, a piece for which we could not determine whether it was alive or dead). For three pieces of wood in the fallen live and standing categories (out of a total of 953) it was not possible to determine status as standing or fallen. These pieces were included in the calculation of total LW but excluded from calculations in which wood was separated into fallen live and standing categories.

At each site, within the bankfull width, we measured the volume of wood in each category that met the LW criteria. LW was defined as a piece of wood with length ≥ 1 m, and diameter ≥ 10 cm. We measured diameter at the midpoint if the piece was fallen, and diameter at breast height (DBH) if it was standing. We also measured length, species (if identifiable), distance along the reach, channel position (bank, partially spanning, spanning), angle to stream flow, input source, input mechanism, input distance, state of decay, relationship to wood jams, relationship to pool formation, and function (formed pool, caused wood jam, stabilized bank, provided cover, aided riparian regeneration, stored sediment, or scoured the bank). The height of standing trees from the base to the point at which all branches were less than 10-cm diameter was measured with a clinometer (Haglof Electronic Clinometer

- Metric Degrees™). To obtain a more accurate estimate of wood volume for trees with major branches that grew horizontally or bent back toward the ground (for example, some *Quercus* sp. and *Salix* sp.) we measured the length of branches using a 5-m stadia rod. We calculated the volume for each piece of LW using the formula, $v = l\pi r^2$, where v = volume, l = length, and r = radius = diameter/2.

Instream Habitat Sampling

For each pool at each site, we measured length, maximum width, maximum depth, noted pool type (plunge pool over boulder, mid-channel, lateral scour, dammed, meander) and recorded the degree of LW influence on pool formation. Pools were considered (1) caused by LW, (2) enhanced by LW – LW caused an existing pool to be deeper, or to have overhanging banks, (3) influenced by LW – wood provided shade and cover, or (4) no influence of LW – the pool was formed by bedrock or lateral scour of sediment on a meander bend.

Fish Snorkel Sampling

A single pass snorkel survey of each site was conducted by one person, beginning at the downstream end of the site and moving upstream. For some run sections in which depths were less than 10 cm and algae reduced visibility, schools of small minnows and suckers were sampled by visual observation from the stream bank to avoid repeatedly counting the same individuals. Fish were identified to species whenever possible. To ensure consistency of counts and species identification, the same person conducted the snorkel survey at all sites.

Data Analysis

Raw data were entered into Excel™ and tables transferred to an ACCESS™ database. Descriptive statistics were calculated in S-Plus™ (Insightful Corporation 2001), and graphics were developed in Excel and SigmaPlot™.

Results

Fourteen tree species were identified at one or more of the fifteen study sites. Willow (*Salix* spp.), oak (*Quercus* spp.), California sycamore (*Platanus racemosa*), and Fremont cottonwood (*Populus fremontii*) were dominant (table 1).

Fallen dead LW volume within the bankfull width averaged 47.6 m³/ha across the 15 sites (SD = 58.2). The volume of not-standing live wood averaged 15.0 m³/ha (SD = 11.2). Standing live and dead trees contributed a high volume within the bankfull width (fig. 2). The volume of standing LW averaged 159.4 m³/ha (SD = 172.4). We counted an average of 31 standing trees within the bankfull width at each site (SD = 21). When averaged within site, and then across sites, the average volume of each standing tree was 2.69 m³ (SD across sites = 3.36). At several sites, such as Salinas_1, Tassajera-Santa Margarita_2, Tassajera-Santa Margarita_3, and Trout_3, specimens of *P. racemosa* and *Q. lobata* with very large DBH contributed to the volume of standing LW. Total LW volume averaged 222.0 m³/ha (SD = 173.7).

Table 1—Tree species observed at 15 sites in the upper Salinas River watershed.

Genus	Species	Common name
<i>Acer</i>	<i>macrophyllum</i>	Bigleaf maple
<i>Acer</i>	<i>negundo</i>	Boxelder
<i>Alnus</i> *		Alder (White or Red)
<i>Fraxinus</i>	<i>velutina</i>	Velvet (or Arizona) ash
<i>Juglans</i>	<i>californica</i>	California black walnut
<i>Pinus</i> *		Pine
<i>Pinus</i>	<i>sabiniana</i>	Grey pine
<i>Platanus</i>	<i>racemosa</i>	California sycamore
<i>Populus</i>	<i>fremontii</i>	Fremont cottonwood
<i>Quercus</i> *		Oak
<i>Quercus</i>	<i>agrifolia</i>	Coast live oak
<i>Quercus</i>	<i>douglasii</i>	Blue oak
<i>Quercus</i>	<i>lobata</i>	Valley oak
<i>Salix</i>	<i>laevigata</i>	Red willow
<i>Salix</i>	<i>lasiolepis</i>	Arroyo willow
<i>Sequoia</i>	<i>sempervirens</i>	Redwood
<i>Umbellularia</i>	<i>californica</i>	California laurel

*Indicates LW identifiable to genus only.

Trout Creek provided the most complete set of sites along an altitude gradient. Fallen dead wood volume was highest at the more upstream sites, and declined as the creek descended to the lower gradient valley floor at Trout_3 (*fig. 2*). The large volume of standing wood at Trout_3 was composed mainly of mature California sycamore. Live trees at Trout_4 were mainly willows with DBH less than the LW criterion, resulting in low values in both the standing LW and not-standing live LW categories. Standing trees at Trout_5 were mainly red willow.

We assessed the proportion of pools at each site for which (1) LW was the primary cause of the pool, (2) LW contributed to pool formation, or enhanced the habitat value of an existing pool, or (3) LW had no influence on the pool (*table 2*). Because site Trout_3 was dry throughout the study it was excluded from this assessment. At five of fourteen sites the majority of the pools were formed primarily by LW. At an additional four sites LW enhanced pool formation or influenced pool habitat value for a majority of pools. At least half the pools experienced some influence of LW at thirteen of fifteen sites. Salinas_3 was the only site at which the majority of pools were not influenced by LW.

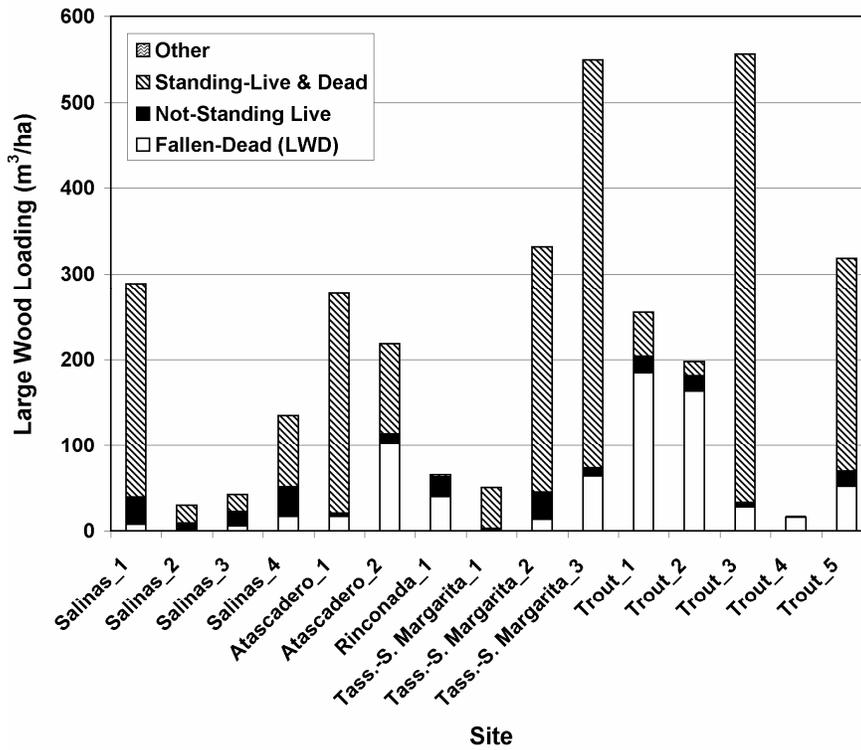


Figure 2—Loading of large wood at 15 sites in the upper Salinas River watershed. Within each tributary and the mainstem Salinas River, the sites are numbered from upstream to downstream with 1 being the most upstream site. The fallen dead category corresponds to the large woody debris category commonly used in more northern regions.

Table 2—Role of LW in the formation of pools in the upper Salinas River watershed.

Site	Number of Pools (pools/100 m)	Pools Formed Primarily by LW (%)	Pools	
			Enhanced or Contributed to by LW (%)	Pools Uninfluenced by LW (%)
Salinas_1	0.30	0	100	0
Salinas_2	0.91	33.3	33.3	33.3
Salinas_3	1.60	40	0	60
Salinas_4	0.33	100	0	0
Atascadero_1	1.33	25	75	0
Atascadero_2	1.29	75	0	25
Rinconada_1	0.56	50	0	50
Tass.-S. Margarita_1	0.96	0	66.67	33.3
Tass.-S. Margarita_2	1.37	60	40	0
Tass.-S. Margarita_3	1.26	25	75	0
Trout_1	2.00	0	50	50
Trout_2	0.95	66.67	33.3	0
Trout_4	1.28	50	25	25
Trout_5	2.56	66.67	22.2	11.1

Fish were observed at all fourteen sites with water. We observed seven native and six non-native fish species (*table 3*). Between one to seven native species were seen at a given site, and between zero to five non-native species (*fig. 3*). Salinas_1 had only one identified native species, Sacramento sucker, while Tassajera-Santa Margarita_1, Trout_1 and Trout_2 had only steelhead.

Table 3—Native and non-native fish species observed in the upper Salinas River watershed.

Native		Non-native	
<i>Catostomus occidentalis</i>	Sacramento sucker	<i>Ameiurus</i> sp.	Bullhead
<i>Gasterosteus aculeatus</i>	Threespine stickleback	<i>Cyprinus carpio</i>	Carp
<i>Lavinia exilicauda</i>	Hitch	<i>Lepomis cyanellus</i>	Green sunfish
<i>Lavinia symmetricus subditus</i>	Monterey roach	<i>Lepomis macrochirus</i>	Bluegill
<i>Oncorhynchus mykiss</i>	Rainbow trout / steelhead	<i>Micropterus dolomieu</i>	Smallmouth bass
<i>Ptychocheilus grandis</i>	Sacramento pikeminnow	<i>Micropterus salmoides</i>	Largemouth bass
<i>Rhinichthys osculus</i>	Speckled dace		

Total fish density averaged 4.01 fish/m (SD = 3.08) (*fig. 4*). Native fish density, except steelhead, averaged 3.02 fish/m (SD = 2.94), while non-native fish density averaged 0.04 fish/m (SD = 0.14). The highest proportion of non-native fish occurred at Salinas_3. Unidentified fish were usually minnows smaller than 6 cm and were difficult to identify to species.

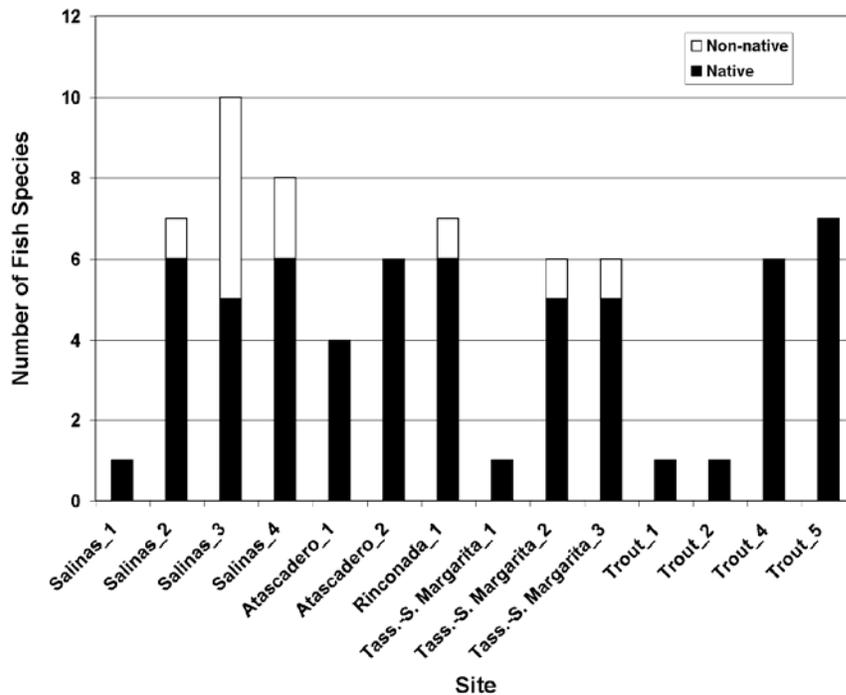


Figure 3—Number of native and non-native fish species observed at 14 sites in the upper Salinas River watershed.

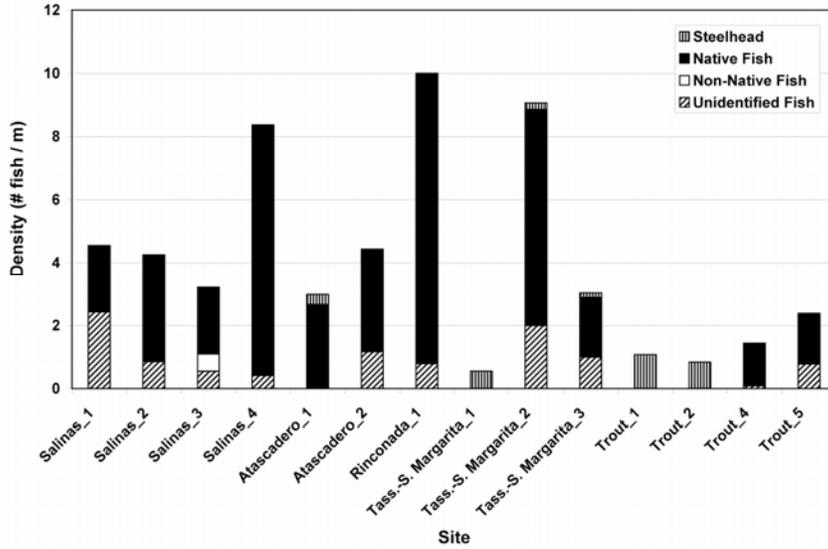


Figure 4—Density of steelhead, other native, non-native, and unidentified fish at 14 sites in the upper Salinas River watershed.

Steelhead were observed at nine out of fourteen sites (*fig. 4*), averaging 0.23 fish/m (SD = 0.35). Steelhead densities at Atascadero_2, Trout_4, and Trout_5 were 0.327 fish/m, 0.016 fish/m, and 0.003 fish/m, respectively, and are thus difficult to discern in the figure. Steelhead were not observed at any mainstem sites during the regular snorkel surveys. One steelhead juvenile was observed during a preliminary survey of Salinas_3 on July 13, 2006. However, when the full snorkel survey was conducted on August 10, 2006, no steelhead were observed.

Discussion

Hardwood LW appears to have an important impact on fish habitat in our study sites. LW was responsible for the formation of a majority of pools at about one-third of our sites, and was influential in forming pool shape or providing overhead cover at another third of the sites. The presence of hardwood LW is improving fish habitat in this watershed through its influence on pool formation and function.

A large component of LW within the bankfull width was composed of standing trees at our study sites. This contrasts with the conceptual model of conifer-dominated streams in the Pacific Northwest, in which the channel contains mainly fallen dead LW as opposed to standing trees (Naiman and others 1998). In these northern streams, the channel bed comprises a large proportion of the bankfull width and is wet for most of the year (Pollock 1998). Standing trees may be more likely to be present within the bankfull width in streams on the southern-central California coast due to the Mediterranean climate. For example, the Salinas River experiences a large difference between summer base flows and annual maximum flows, with nearly 90 percent of the annual precipitation falling between November and April (Farnsworth and Milliman 2003). Winter storms often cause large flows for short periods of time and result in bankfull widths that are large in comparison with summer wetted widths. Saplings can become established within the bankfull width channel during the extensive low-flow periods. In our study sites, the roots of trees within the channel were often exposed and were frequently associated with pools. It

appears that scouring around the roots during high flows may hollow out pools. At some sites, these pools were the last refuges for fish as the water dried up (e.g., Salinas_1).

Standing trees within the bankfull width only interact with the stream up to the bankfull depth, so the full volume of a standing tree may overestimate its role relative to fallen dead LW volume. However, standing trees may be particularly important in forming fish habitat in south-central coastal streams due to their ability to anchor wood jams. While fallen dead LW pieces may form the key piece in a jam, the rapid decay rate of hardwood may make these jams short lived. A jam anchored by a standing tree is likely to be more persistent in a hardwood-dominated system. Standing trees within the bankfull width are also very likely to fall within the bankfull width once they die, contributing to fallen dead LW.

Native fish species were present at all 14 sites with water. Non-native fish species were in lower abundance than natives at all sites. The number of native species tended to increase downstream along the mainstem and along each tributary, potentially due to changes in gradient, velocity, and temperature. Native species less adapted to cooler temperatures and higher velocities may have been excluded from the cooler, higher gradient sites. Non-native species tended to be observed at the more downstream sites on the mainstem and tributaries. Sites with non-native species were generally warmer and had lower flow velocities⁷, which may have allowed non-native species to compete more readily with native species. Sites with steelhead tended to have cooler water temperatures and be located at the upstream, higher elevation end of each tributary. Young-of-the-year steelhead were usually observed in shallow riffles over a gravel bottom, while juvenile steelhead were observed in deeper water such as runs or pools. Adult steelhead were usually observed in pools, and under large wood. Steelhead were present at nine sites (64 percent). This may represent the minimum distribution of steelhead across these sites in 2006, because our sampling was done at the hottest time of the year when we would expect steelhead to be restricted to the coolest locations, and to be using refugial habitat such as deep, cool pools.

Sites in the upper Salinas River watershed had loadings of fallen dead LW comparable to privately owned sites studied by Opperman (2005) in Northern California (*table 4*). Mean loading was one third that of conifer-dominated Sierra Nevada sites, and only one-sixteenth that of conifer-dominated sites in the Pacific Northwest. While it may be unreasonable to expect hardwood-dominated areas to contribute the volume of LW possible in conifer forests, average volumes at our predominantly private sites were less than half that of hardwood-dominated public sites (e.g., protected watersheds within parks) studied by Opperman (2005) in Northern California.

⁷ Unpublished data, Lisa C. Thompson, Wildlife, Fish, and Conservation Biology Department, University of California, Davis, California.

Table 4—Comparison of instream LW loading (m^3/ha) across regions of western North America.

Region	n	Mean (SD)	Median (interquartile)	Maximum
Pacific Northwest (BC, WA, OR) ^a	62	752 (810)	535 (315, 858)	4500
Sierra Nevada conifer ^b	12	160 (99)	159 (108, 209)	=382
No. CA hardwood, protected watersheds ^c	9	115 (33)	107 (93, 137)	=173
No. CA hardwood, private land ^c	23	42 (43)	20 (14, 59)	=146
So. CA hardwood (this study)	15	47 (58)	17 (11, 58)	=164

^a Data from Andrus and others (1988), Harmon and others (1986), and Keller and Tally (1979).

^b Data from Berg and others (1998)

^c Data from Opperman (2005)

It may be possible for private landowners in the upper Salinas River watershed to increase the volume of dead fallen hardwood LW in streams on their properties through the use of best management practices (BMPs) as suggested in Opperman and others (2006). Such practices have not yet been determined or tested for this region, but would likely include activities to: (1) promote the regeneration of hardwood riparian trees such as oaks, California sycamore, Fremont cottonwood, and willows; (2) promote the survival of hardwood seedlings; (3) allow trees to reach a size at which their DBH would be sufficient to allow them to function as LW; and (4) leave fallen dead LW in the channel to contribute to fish habitat such as pools. The development of BMPs for LW would thus be a valuable step in riparian management and steelhead recovery, given the broad distribution of fish in the watershed, the concerns of landowners over fish-related regulations, and the role of hardwood LW in contributing to pool habitat. The adoption of voluntary BMPs should increase the capacity of private landowners, resource agency staff, and public interest groups to cooperate in the management of fish-bearing streams on hardwood-dominated lands.

Acknowledgments

We gratefully acknowledge the landowners who allowed us access to their properties for this project. We thank Jeff Opperman for generously assisting us with the development of our field protocol, and for joining us in the field to ensure that our methods were comparable to those he used in Northern California. We thank the Upper Salinas-Las Tablas Resource Conservation District for assistance with locating sites for this study. The comments of Richard R. Harris and an anonymous reviewer greatly improved the manuscript. Funding for this study was provided by the University of California Division of Natural Resources CORE Grant Program.

References

- Andrus, C.W.; Long, B.A.; Froelich, H.A. 1988. **Woody debris and its contribution to pool formation in a coastal stream 50 years after logging.** Canadian Journal of Fisheries and Aquatic Sciences 45: 2080-2086.
- Beechie, T.J.; Sibley, T.H. 1997. **Relationships between channel characteristics, woody debris, and fish habitat in northwestern Washington streams.** Transactions of the American Fisheries Society 126: 217-229.
- Berg, N.; Carlson, A.; Azuma, D. 1998. **Function and dynamics of woody debris in stream reaches in the central Sierra Nevada, California.** Canadian Journal of Fisheries and Aquatic Sciences 55: 1807-1820.

- Boughton, D.A.; Adams, P.B.; Anderson, E.; Fusaro, C.; Keller, E.A.; Kelley, E.; Lentsch, L.; Nielsen, J.; Perry, K.; Regan, H.; Smith, J.J.; Swift, C.; Thompson, L.; Watson, F. 2006. **Steelhead of the south-central/southern California coast: Population characterization for recovery planning.** U.S. Dep. Commer., NOAA Tech. Memo. NMFS-SWFSC-394, 123 p.
- Carlson, J.Y.; Andrus, C.W.; Froehlich, H.A. 1990. **Woody debris, channel features, and macroinvertebrates of streams with logged and undisturbed riparian timber in northeastern Oregon, U.S.A.** Canadian Journal of Fisheries and Aquatic Sciences 47: 1103-1111.
- Elliott, J.M. 2000. **Pools as refugia for brown trout during two summer droughts: trout responses to thermal and oxygen stress.** Journal of Fish Biology 56: 938-948.
- Farnsworth, K.L.; Milliman, J.D. 2003. **Effects of climatic and anthropogenic change on small mountainous rivers: the Salinas River example.** Global and Planetary Change 39: 53-64.
- Fausch, K.D.; Northcote, T.G. 1992. **Large woody debris and salmonid habitat in a small coastal British Columbia stream.** Canadian Journal of Fisheries and Aquatic Sciences 49: 682-693.
- Gurnell, A.M.; Piegay, H.; Swanson, F.J.; Gregory, S.V. 2002. **Large wood and fluvial processes.** Freshwater Biology 47: 601-619.
- Harmon, M.E.; Franklin, J.F.; Swanson, F.J.; Sollins, P.; Gregory, S.V.; Lattin, J.D.; Anderson, N.H.; Cline, S.P.; Aumen, N.G.; Sedell, J.R.; Lienkaemper, G.W.; Cromack, Jr., K.; Cummins, K.W. 1986. **Ecology of coarse woody debris in temperate ecosystems.** Advances in Ecological Research 15: 133-302.
- Harrelson, C.C.; Rawlins, C.L.; Potyondy, J.P. 1994. **Stream channel reference sites: an illustrated guide to field technique.** General Technical Report RM-245. Fort Collins, CO: Rocky Mountain Research Station, USDA Forest Service.; 66 p.
- Hyatt, T.L.; Naiman, R.J. 2001. **The residence time of large woody debris in the Queets River, Washington, USA.** Ecological Applications 11:191-202.
- Insightful Corporation. 2001. **S-Plus 6 for Windows guide to statistics, volume 1.** Insightful Corporation, Seattle, WA; 712 p.
- Keller, E.A.; Tally, T. 1979. **Effects of large organic debris on channel form and fluvial processes in the coastal redwood environment.** In: Adjustments of the fluvial system: Tenth annual geomorphology symposia series. Kendall/Hunt Publishing; Binghampton, NY; 169-197.
- Kraft, C.E.; Schneider, R.L.; Warren, D.R. 2002. **Ice storm impacts on woody debris and debris dam formation in northeastern U.S. streams.** Canadian Journal of Fisheries and Aquatic Sciences 59: 1677-1684.
- Kreutzweiser, D.P.; Good, K.P.; Sutton, T.M. 2005. **Large woody debris characteristics and contributions to pool formation in forest streams of the Boreal Shield.** Canadian Journal of Forestry Research 35:1213-1223.
- McMahon, T.E.; Zale, A.V.; Orth, D.J. 1996. **Aquatic habitat measurements.** In: Murphy, Brian R.; Willis, David W., editors. Fisheries techniques, 2nd edition. Bethesda, Maryland: American Fisheries Society; 83-120.
- Montgomery, D.R.; Buffington, J.M.; Smith, R.D.; Schmidt, K.M.; Pess, G. 1995. **Pool spacing in forest channels.** Water Resources Research 31: 1097-1105.
- Naiman, R.J.; Fetherston, K.L.; McKay, S.J.; Chen, J. 1998. **Riparian forests.** In: Naiman, Robert J.; Bilby, Robert E., editors. River ecology and management. New York: Springer; 289-323.

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- Nielsen, J.L.; Lisle, T.E.; Ozaki, V. 1994. **Thermally stratified pools and their use by steelhead in Northern California streams.** Transactions of the American Fisheries Society 123: 613-26.
- Opperman, J.J. 2005. **Large woody debris and land management in California's hardwood-dominated watersheds.** Environmental Management 35(1): 1-12.
- Opperman, J.J.; Merenlender, A.M.; Lewis, D.J. 2006. **Maintaining wood in streams: A vital action for fish conservation.** University of California Division of Agriculture and Natural Resources 8000 Series, Publication 8157; 11 p.
<http://anrcatalog.ucdavis.edu/pdf/8157.pdf>
- Pollock, M.M. 1998. Biodiversity. In: Naiman, R.J.; Bilby, R.E., editors. River ecology and management. New York: Springer; 430-452.
- Richmond, A.D.; Fausch, K.D. 1995. **Characteristics and function of large woody debris in subalpine Rocky Mountain streams in northern Colorado.** Canadian Journal of Fisheries and Aquatic Sciences 52: 1789-1802.
- Rosenfeld, J.S.; Huato, L. 2003. **Relationship between large woody debris characteristics and pool formation in small coastal British Columbia streams.** North American Journal of Fisheries Management 23: 928-938.