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**Investigating the Role of Large Woody Materials to
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Large Wood Aids Spawning Chinook Salmon (*Oncorhynchus tshawytscha*) in Marginal Habitat on a Regulated River in California

ABSTRACT

To determine whether large wood (LW, ≥ 1 -m length, ≥ 10 -cm diameter) plays a role in Chinook salmon redd (i.e. egg nests) placements in a regulated, medium-sized, Mediterranean-climate river, characteristics of 542 large wood pieces, locations of 650 redds, and habitat unit delineations (riffle, run, glide, pool) were collected during a spawning season along a 7.7 km reach directly below Camanche Dam on the Mokelumne River (average width 31 m). Large wood was regularly distributed across the study reach with an average of 70 LW pieces km^{-1} . Some LW clustering was evident at islands. Chinook spawners built 75% of observed redds at spawning habitat rehabilitation sites, and 85% of redds were within one average channel width of large wood. At the hydraulic scale of $\sim 10^{-1}$ channel widths, redds were within a 10 m radius of large wood 36% of the time. These results suggest that spawners had the opportunity to utilize large wood as cover and refugia. In the lower 4.7 km where marginal habitat was prevalent, redds were within a 5 m radius of large wood 21% of the time and within a 2.5 m radius 10% of the time, indicating use of the hydraulic properties of instream large wood structures. Results from randomized tests indicate that large wood-redd interactions systematically occurred at a greater rate than by random chance alone in the lower 4.7 km, but not in the upper 3 km, which implies that large wood aids spawning in marginal habitats.

Key Words: large wood, gravel rivers, Chinook salmon, ecohydraulics, fluvial geomorphology, river rehabilitation

1.0 INTRODUCTION

River rehabilitation projects often use gravel augmentation to improve Pacific salmon (*Oncorhynchus spp.*) spawning habitat (Merz et al. 2004; Wheaton et al. 2004a,b) and large wood placements to improve juvenile Pacific salmon habitat (Roni and Quinn 2001). However, physical and ecological processes associated with large wood (LW, ≥ 1 m length, ≥ 10 cm diameter) may be important for spawning too, because wood removal from streams homogenizes habitats and reduces refugia, which contributes to fisheries population declines (Sedell et al. 1990). In addition, stream flow in the vicinity of LW develops complex structures that promote gravel deposition, substrate rejuvenation, and hyporheic flows (Abbe et al. 2003; Bryant et al. 2005). Thus, it is timely to assess whether LW should be incorporated into fish spawning habitat rehabilitation (SHR) projects.

1.1 Instream wood

The importance of naturally occurring input, transport, and *in situ* decomposition of large wood to stream ecology and function is undisputed. LW enters a stream in multiple forms: as live trees with canopies fallen into the channel and rootwads attached to the bank, as broken branches, or as dead trees whole or in pieces and with or without limbs and rootwad. LW can range in size from individual pieces along channel margins to aggregations that span the channel regardless of width. Flow regime, channel configuration, and wood recruitment processes arrange and rearrange LW spatially and

temporally (Gurnell et al. 2002). Distribution of LW frequently occurs discontinuously throughout a river, often correlating to key geomorphic structures in lowland reaches (Piegay 2003).

Once in a channel, LW may remain anchored locally or become lodged en route along its downstream journey until it fragments via decomposition and physical processes. Downstream transport in response to the local hydrograph smoothes LW into cylindrical shapes, and may break it into particles too small to consider as LW. Ultimately, LW can reach the ocean where it provides refugia and nutrients for marine organisms (Maser and Sedell 1994).

Anchored or lodged LW can create complex in-channel hydraulics that promote zones of scour and deposition, creating accumulations of spawning gravels for Pacific salmon, providing hydraulic refugia (Bisson et al. 1987), and creating pools by forcing flows to scour channel beds and banks. Such processes also create cover and refugia zones for juvenile fish rearing and adult fish holding (Roni and Quinn 2001). Channel complexity and habitat heterogeneity associated with individual LW pieces and aggregations offers all salmon life stages hydraulic and thermal refugia, structural partitioning that provides protection from predation, and visual isolation that lowers inter-species competition (Dolloff 1983). The wood itself supplies nutrients and substrate for aquatic organisms (Anderson et al. 1978). Moreover, structural properties of LW are a factor in the retention of salmon carcasses, which provide important marine-derived nitrogen (N) to N-limited terrestrial ecosystems and organic nutrients to salmon juveniles, macroinvertebrates, terrestrial animals, and birds (Naiman et al. 2002; Merz and Moyle 2006).

1.2 Channel modifications involving LW

LW in channels may be scrutinized and removed for a variety of socio-economic reasons—a cumulative action that, coupled with other anthropocentric alterations to river ecosystem health, has led to the continued loss of in-channel habitat complexity. Wood removal from streams to facilitate navigation has been a common practice throughout the world. By the late 1700's instream wood removal became a serious endeavor as the introduction of steamboats made commerce and transportation along rivers highly feasible. In the United States (U.S.), citizen-led companies were formed to make inland waterways navigable, and engaged in channel widening, dredging, and obstacle removal (e.g., Colles 1785). Triska (1984) documented decades of governmental efforts in the 1800's to maintain an open channel on the Red River in Louisiana, U.S., by repeated clearing of extensive instream wood rafts. Modern justifications for wood removal include concern over structural and personal property safety, recreational safety, safe navigation for boating and shipping, and to enhance perceived aesthetic values. River managers and water resource engineers remove wood from stream channels to decrease hydraulic roughness and increase conveyance capacity (Shields and Nunnally 1984).

Logging practices have had acute effects on the amount of LW in mountainous stream channels. Intensive logging in the U.S. Pacific Northwest (PNW) in the early 1900's delivered large amounts of silt and wood into streams from increased erosion on steep, clearcut hillsides. On the other end of the spectrum, splash-dam logging required removal of all instream obstacles so that logs could be floated down low-order channels (Nilsson et al. 2005). Logging practices today are more closely regulated, but the legacy of 100+ years of indiscriminate logging continues to be felt across multiple spatial scales in forests and rivers.

By the mid-1900's state regulatory agencies along the U.S. Pacific coast designed wood removal projects, meant to create fish passage and promote sediment flushing, in response to declines in salmon fish populations brought on by logging (Wooster and Hilton 2004). Hall and Baker (1982) reported that as many as 1000 logjam removal projects were performed over a 45-year period in the Suislaw River basin of western Oregon, and suggested similar numbers for other PNW watersheds. After decades of concerted efforts to clean streams via wood removal, a study by Bilby (1984) concluded that indiscriminant wood removal could lead to channel instability and create adverse effects on fish populations, and suggested modifications to stream management guidelines so that LW pieces influencing channel morphology were left instream.

Dams capture sediment and LW inputs above-dam and attenuate flows below-dam. Channel morphology impacts below-dam are complex and vary over time and space. The loss of longitudinal connection with upstream sediment and LW supplies, along with profound changes to riparian vegetation, play primary roles in the direction and rate of change in channel adjustment (Petts and Gurnell 2005). Regulated flows can lead to channel incision and coarsening of channel substrate because dam outflows are concentrated in a stable location with no sediment inputs (Kondolf 1997). Such channel adjustments—including alteration of gravel substrate size range, channel depth, and flow velocity—can negatively affect instream ecological responses that promote successful spawning in salmon-bearing rivers. SHR projects, in conjunction with flow re-regulation, have become increasingly important to regulated river managers to mitigate dam impacts (Brown and Pasternack, 2008). While SHR projects have considered the effects of diminished sediment supply and muted hydrographs on salmon spawning success, few have considered the role of LW losses on below-dam salmon spawning success.

1.3 Salmon declines and management response

A stark example of the dichotomy between healthy riverine ecosystem function and anthropocentric needs can be seen in the ongoing decline of anadromous Pacific salmon populations in western North America. Salmon population declines have been precipitated by overfishing, variations in ocean productivity, channel alterations, and significant habitat loss due to societal needs to manipulate water and waterways for water supplies, flood control, and river navigation. Similar pressures on salmon populations have been felt worldwide (Lackey 2008).

Anadromous Atlantic salmon (*Salmo salar*) populations in Northeastern U.S. historically ranged as far south as Connecticut (Montgomery 2003), but today, only one small population is found in Maine and is listed as endangered under the Endangered Species Act (NMFS 2000). All other Northeastern U.S. populations have been extirpated. Salmon populations in Northeastern Canada are less threatened. Although the Inner Bay of Fundy salmon is listed as endangered and the Lake Ontario salmon as extirpated under the Canadian Species At Risk Act (COSEWIC 2005), many populations remain robust. In Europe, Atlantic salmon populations range from a designation of healthy in the more northerly and less-developed countries of Iceland, Scotland, Norway, and Ireland; to vulnerable in Russia; to critical in Portugal, France, Denmark, and Sweden; to extinct in the more densely developed countries of Germany, Switzerland, and the Netherlands (Hindar 2004).

A comparable pattern of Pacific salmon population health exists in western U.S. and Canada. Alaska and Canada have many robust salmon populations. For instance, no Alaskan salmon populations are listed under the Endangered Species Act. In western

Canada, four salmon populations are listed as endangered and one as threatened under the Species At Risk Act (COSEWIC 2005). Along the U.S. Pacific coast, where commercial and development pressures have negatively affected salmon populations (Lackey 2008), numerous salmon populations are classified as extirpated, endangered, threatened, or are candidates for listing under the Endangered Species Act (NOAA 2005).

In the eastern Pacific Ocean, Japan's salmon populations crashed in the late 1800's because of overfishing; today remnant wild populations are overshadowed by hatchery stocks bred for commercial purposes (Nagata and Kaeriyama 2004). In the far east of Russia, most salmon populations are healthy, with just 1% of species considered extinct, 7% at high risk, and 92% having moderate or low risk of extinction (Augerot 2004). Overfishing by commercial fisheries and poaching by organized operations—and some local residents—for the production of caviar are the largest pressures on salmon populations in Russia.

Wild salmon populations were already in decline due to habitat losses and overfishing by the late 1800's along the U.S. Pacific coast; as a result, salmon hatcheries were developed to provide stock for ocean fisheries (Montgomery 2003). Hatcheries today are often operated as mitigation for the loss of historic salmon spawning grounds due to damming (e.g., Federal Energy Relicensing Commission (FERC) 1998) – and successfully provide large percentages of ocean fisheries stock. For example, ~70% of salmon harvested in Puget Sound in the 1990's were of hatchery origin (Mobrand et al. 2005).

It is unknown whether wild salmon populations that exist in close proximity to hatcheries can remain viable under the continuing influx of hatchery releases. Recent U.S. government-sponsored hatchery reform initiatives aim to develop scientifically defensible operating strategies that manage individual broodstocks as either genetically-segregated “hatchery populations” or as a genetically-integrated component of existing “natural populations” - with both alternatives designed to assist in the conservation and recovery of wild populations (Mobrand et al. 2005).

Hatchery mitigation, regardless of operating strategy, is no substitute for natural habitat. After decades of unsuccessful policy decisions surrounding the conservation of salmon and their habitat, U.S. federal and state government agencies have responded to continuing salmon declines and habitat losses by implementing rehabilitation and monitoring programs aimed at improving riverine and riparian ecosystem processes that support salmon freshwater life stages (e.g. CDFG 1998; FERC 1998; NMFS 2007). Instream habitat rehabilitation and other river rehabilitation projects (e.g., water quality, riparian management, bank stabilization) have increased in number, but projects often lack specific measurable goals used to evaluate success, and long-term monitoring of completed projects is rarely funded (Kondolf and Micheli 1995; Downs and Kondolf 2002). These shortcomings lead to confusion about how rehabilitation project outcomes are objectively determined.

To encourage objective project evaluations, the National River Restoration Science Synthesis (NRRSS) was established to develop a U.S. river restoration project database and deliver specific recommendations to improve the scientific basis of river restoration. NRRSS reported over 1000 recent projects in the PNW aimed at restoring channel complexity (Katz et al. 2007) and ~750 instream habitat enhancement projects in California (Kondolf et al. 2007). In a final report, NRRSS recommends conducting strategic pre- and post-project monitoring with standardized methods so that scientific principles can begin to emerge from an aggregation of individual projects (Bernhardt et

al. 2007).

California has instream rehabilitation and monitoring guidelines in place (CDFG 1998; Gerstein 2005). In California's Central Valley, implementation of SHR projects (a subset of instream rehabilitation projects) has been driven by concern over the loss of historically robust Chinook salmon (*O. tshawytscha*) and steelhead (*O. mykiss*) runs as a consequence of hydraulic mining, instream gravel mining, damming, water diversions, channelization, and land use (Yoshiyama et al. 1998). SHR projects in the Central Valley have generally not included LW placements because of liability concerns and a lack of science-based approaches (Wheaton et al. 2004a).

1.4 Large wood research

Most research on LW dynamics has originated in the PNW (e.g. Keller and Swanson 1979; Harmon et al. 1986; Bisson et al. 1987; Abbe and Montgomery 1996). Consequently, the PNW has been more aggressive in implementing LW enhancement projects intended to recreate complex aquatic habitat for salmon, by providing missing hydraulic structural components that restart geomorphic processes (e.g. House and Boehne 1985; Cederholm et al. 1997; Solazzi et al. 2000; Abbe et al. 2003).

Relationships between LW and juvenile salmon have been widely explored in the context of pool formation (Fausch and Northcote 1992), hydraulic refugia (Shirvell 1990), safety versus food availability (Grand and Dill 1997), and habitat use (Inoue and Nakano 1998; Beechie et al. 2005). Roni and Quinn (2001) evaluated the biological response of juvenile salmon to wood placements in 30 PNW reaches. They found significantly higher juvenile salmon densities in areas treated with artificial wood structures compared to densities in reference reaches.

In a review of instream restoration techniques, Roni et al. (2002) report that in the PNW, LW placements were considered successful in terms of rejuvenating physical processes such as increasing pool frequency and depth and promoting LW and sediment retention. On the other hand, variable biological responses were attributed to differences in study timing and the species studied. Inconsistent project outcomes highlight the need for concerted post-project monitoring efforts and rigorous syntheses of the knowledge gained from individual rehabilitation projects.

Although salmon populations range along much of the North American Pacific coast, climate gradients between the PNW and California's much drier Mediterranean climate zones suggest that there may be fundamental differences in LW dynamics between the two bioregions. The temperate-maritime climate of the PNW provides abundant rain, fog, and mild temperatures that generate forests with very high biomass productivity (Naiman et al. 2000). Hardwood species dynamics in PNW riparian corridors were initially overlooked because adjacent conifers were bigger, more prevalent, and decomposed more slowly than hardwoods (Harmon et al. 1986). In addition, many PNW studies were conducted in steep, narrow, headwater channels where conifers dominate (Keller and Swanson 1979; Bisson et al. 1987; Montgomery et al. 1995). PNW studies that have considered riparian hardwood dynamics found that hardwood species deplete more quickly from instream than coniferous species (Naiman et al. 2000), but are nonetheless effective in providing complex channel structure (Keim et al. 2002).

In contrast to the PNW, California's Mediterranean climate zones impose moisture limitations through a summer drought and winter precipitation weather pattern (Opperman 2005) that restrict yearly growth cycles of mixed conifer-hardwood forests

and riparian corridors on the coast, in the oak woodlands that dominate Central Valley foothills, and throughout riparian corridors of Central Valley rivers. Coniferous forests of the Sierra Nevada are likewise subjected to a modified Mediterranean-montane climate where moisture and temperature limitations apply; in addition, yearly snows and snowmelts are climatic influences (Kondolf and Batalla 2005).

Recent research in California's coastal Russian River tributaries drew attention to climate differences between California and the PNW (Opperman 2005). This study indicated that hardwood tree species represent a larger portion of inputs to channels in California when compared to PNW watersheds, but do not have the same channel spanning capabilities as coniferous LW because of smaller size and lower longevity. A key finding showed that when hardwood trees were key members of logjams, they were more likely to be fallen, alive, and rooted into the channel banks—rather than detached and dead. These key members were instrumental in the stability of logjams because living trees rooted into a stream bank have greater longevity than dead, detached LW.

Although Mediterranean-climate LW size and species composition may differ from the PNW, Ferguson (2005) found that LW additions significantly increased juvenile coho salmon (*O. kisutch*) densities at the pool scale in coastal California's Lagunitas Creek. Few studies have explored instream LW processes in California's Central Valley (Merz 2001) or Sierra Nevada (Berg et al. 1998). Additional LW studies in California's Mediterranean climate zones may help validate important geomorphic and ecological concepts associated with LW for this region (Merz et al. 2006).

1.5 LW-redd interactions

Spawning salmon create redds (i.e. egg nests) in streams under suitable physical conditions. Variations in velocity, depth, and channel substrate (i.e. "physical habitat") have traditionally been used to predict where salmon spawning may occur (e.g. PHABSIM; Milhous et al. 1989), but limitations exist with this methodology. PHABSIM does not take into account the structural complexity provided by LW, boulders, undercut banks, overhanging vegetation, pools, turbidity, and turbulence in streams, all of which create macro- and microhabitat refugia for aquatic organisms (i.e. "habitat heterogeneity", Sedell et al. 1990). Habitat heterogeneity and channel complexity directly influence instream physical and biological characteristics and processes, which in turn affect spawning behavior and subsequent redd site selection (Wheaton et al. 2004c). Using a geomorphological approach, Geist and Dauble (1998) suggested that spawning habitat predictions could be improved by measuring heterogeneous geomorphic features such as slope, channel morphology, and bedforms, as well as channel subsurface features such as vertical hydraulic gradient, hydraulic conductivity, and associated hyporheic flows, in order to more accurately predict the extent of spawning habitat within a river.

The importance of LW to salmon population health can be seen in Smokorowski and Pratt's (2007) meta-analysis of the effect of experimental habitat manipulations to physical structure and cover for fish, including LW removal and additions. Their review reported relatively strong and consistent correlations between habitat heterogeneity and fish communities, and found that the loss of habitat heterogeneity had negative effects on fish diversity. Crook and Robertson (1999) reviewed studies where experiments tested LW in providing overhead cover, visual isolation, and velocity refugia to juvenile salmon. They found, as did Fausch (1993), that LW functioned as overhead cover for juvenile salmon in every instance, while response to LW as visual isolation and velocity refugia occurred only in concert with using LW structures as cover. Fausch and

Northcote (1992) found that reaches with pools formed by LW provided cover and increased habitat volume thereby supporting a greater biomass of coho salmon and cutthroat trout (*O. clarki*) than in simplified stream reaches in the same creek. In a study using artificial structures to mimic LW, juvenile coho sought out the greatest amount of structural complexity during the winter, particularly when flooding was simulated (McMahon and Hartman 1989).

These studies and reviews show that LW performs important geomorphic and hydraulic functions for fish populations, yet few studies have specifically examined interactions between LW and salmon redd locations. House and Boehne (1985) reported on the deposition of suitable spawning gravels and subsequent use by spawners in coastal Oregon when gabions (wire enclosed cobble walls), LW, and boulders were installed after stream cleaning. A study on resident brown trout (*Salmo trutta*) spawning preferences in Ontario, Canada found that as habitat quality decreased, there was a statistically significant increase in the association of redds with LW (Zimmer and Power 2006).

On the Mokelumne River in California's Central Valley, Merz (2001) found that Chinook salmon redds were significantly associated with available wood greater than 5 cm in diameter and 30 cm in length, while Wheaton et al. (2004c) reported increases in use of structural cover and hydraulic refugia by spawning Chinook from placed boulders, lodged LW, and existing pools when coupled with gravel augmentation and riffle enhancement. With stakeholders intent on increasing successful spawning conditions, it is appropriate to consider the relationship between LW and spawning salmon success in the context of spawning habitat rehabilitation (SHR) techniques.

1.6 Salmon spawning behavior

Quinn (2005) provides detailed discussions of Pacific salmon behavior and ecology, noting that male Chinook salmon tend to arrive at spawning grounds before females to increase their probability of spawning success. Spawning males are vulnerable to multiple stressors including inter- and intraspecies competition, interspecies predation, and hydraulic and thermal variations in channel conditions. Males can spawn multiple times over a period of weeks before death (Quinn 2005), but must have nearby refugia for resting and cover (Bjornn and Reiser 1991). Each male spawner competes with other males to establish territory, which then provides access to females. Smaller males typically do not establish their own territory, so these individuals must have nearby safe zones from which to hover and dart out of when spawning opportunities arise (Esteve 2005; Allen et al. 2007). Refugia for spawning males in-between spawning and territory-guarding activities may be provided by LW pieces or aggregations along channel margins, in pools, or lodged mid-channel, as well as by other structural complexes such as streambed variations, riparian vegetation overhanging the channel, and under-cut banks.

Female Chinook salmon benefit from complex channel structure upon arrival at the spawning grounds, particularly if they are not yet ready to lay their eggs and so need a holding location until fully ripe (Quinn 2005). Physical habitat partitioning provided by LW allows females to be within close proximity of one another, avoid confrontation, and simultaneously construct redds (Dolloff 1983; Merz 2001; Dolloff et al. 2003), thus helping to organize population-scale spawning behavior. When ready to spawn, females establish channel bed territory in competition with other females, then expend tremendous amounts of energy preparing the channel bed and defending their redd

(Fleming and Gross 1994). Females turn on their side and whip their tails back and forth against the channel substrate until a sizeable pit is opened, ready for egg deposition and male fertilization. Site preparation stirs up fine sediments that drift downstream out of the redd zone, leaving behind sediments that provide larger interstitial spaces needed for optimal hyporheic flows for incubating eggs. Males swim alongside females as eggs are laid, releasing sperm to fertilize the eggs. The female covers the eggs—and proceeds to defend the redd from superimposition by other spawning females until she dies. The amount of channel bed area utilized for one redd by a spawning female Chinook salmon has been reported as ranging from 1-10 m² in an elliptical shape, and is often dependent upon female size (Bjornn and Reiser 1991).

Many studies have concentrated on salmon behaviors during spawning events, but few have looked at what salmon are doing when not in the act of spawning. Fleming et al. (1996) recorded a behavior termed ‘cruising’ in Atlantic salmon, where salmon swam over a large area without chasing or being pursued. Healey et al. (2003) calculated energy consumption of sockeye salmon (*O. nerka*) during pre-spawning holding in pools, during reproductive activities, and during defense of redds or territory. They reported data for a “holding position”, but none for swimming, darting to refugia, or redd defense. It would be beneficial to know what ancillary behaviors occur when spawning salmon are in their natal environment.

Quinn (2005) suggested that redd building, spawning, and defense take place over a period of days. Neilson and Banford (1983) reported redd defense by Chinook females for up to 25 days, where early-arriving females defended redds for longer periods of time. Once spawning is complete, reproductive success is enhanced by the defense of redds—considered to be an evolutionary behavioral trait—until female death (Quinn 2005). Regardless of length of survival after spawning, it would seem that females must have safe resting zones amidst spawning activity and redd defense. Instream structural complexity, including LW, may provide refugia for female salmon before and during spawning activities, as well as after the culmination of reproductive events when energy conservation is critical for protecting redds.

2.0 CONCEPTUAL MODEL

Although studies have validated the importance of LW to juvenile salmon life stages, a systematic approach to the role of LW in relationship to salmon spawning behavior has not yet been developed. In this study, a conceptual model for the use of LW in spawning behavior is proposed and evaluated by examining spatial relationships between LW locations, redd locations, and habitat units. Previous LW studies have suggested that LW accumulations may exhibit longitudinal and latitudinal variations depending upon size and geomorphic pattern within a river (Piegay and Gurnell 1997). Redd locations are often associated with physical habitat variables such as depth, velocity, and channel substrate (Milhous et al. 1989). Other studies have shown positive associations between LW and redd locations (Merz 2001), particularly with respect to habitat quality (Zimmer and Power 2006).

Habitat suitability curves are widely used in ecology to achieve an understanding of limits and ranges of environmental variables associated with specific organisms, by providing a quantitative framework within which to make predictions. These frameworks are often convex-upward parabolic in shape. Appropriate examples are the habitat suitability curves developed for Chinook salmon spawning that predict optimal conditions and the limiting range of velocity, depth, pH, temperature, and channel

substrate (Raleigh et al. 1986). In this study, predictions of the relationship between large wood and spawning site selection were made within a similar framework utilizing variations in LW and redd abundance structured along habitat units.

A simple, process-based model was developed hypothesizing that the relationship between Chinook salmon redd densities and LW densities might show a convex-upward parabolic trend, with peak redd density associated with intermediate LW density in habitat units where physical conditions were conducive to spawning activities (Fig. 1). It was conjectured that degraded channel conditions with depressed LW densities, and thus lower habitat heterogeneity and hydraulic complexity, would yield low redd densities. A straightened, overdeepened channel designed for flood conveyance and devoid of any structure could be a worst-case scenario of channel degradation. In degraded channels where spawning activities are likely to occur, LW additions may be periodically needed for decades while riparian corridor health is rehabilitated (Brooks, 2006). Rehabilitation projects involving periodic LW additions might be thought of similarly to periodic gravel additions, in SHR projects below dams, which are intended to make up the sediment budget deficit as well as provide suitable spawning substrate.

As ecosystem function and channel complexity increase to robust natural conditions, LW densities and redd densities might increase together to optimum levels. Median levels of LW would be best in providing structural complexity and cover, such that redd densities could peak to highest levels. In this scenario, LW would be abundant enough to provide cover and refugia but not to the extent where it might obstruct large portions of the channel bed.

High levels of LW, for example as a result of a completely clogged channel due to logging or storm damage, might not produce suitable hydraulics, substrate, or channel space for spawning activity. For a channel 30 m wide, using a hypothetical hardwood length of 10 m, a diameter of 30 cm, and assuming each piece had settled to the bed parallel to flow, it would take 100 pieces of LW ($\sim 75 \text{ m}^3$) to cover the channel bed from bank to bank. At 1 m uniform depth, 300 LW pieces would be needed to fill the wetted channel at one cross-section. A hypothetical estimate of $\sim 50\%$ channel bed coverage might be enough to preclude any spawning activity due to blockage of the bed by LW.

Using this conceptual model as the initial framework within which to consider LW-redd associations, this study seeks to expand scientific understanding of the spatial relationships between LW and Chinook salmon redds, with the possibility of application to SHR projects in Mediterranean-climate regions. The specific objectives of this study were to characterize (1) LW abundance and distribution, (2) Chinook salmon redd distribution, and (3) habitat units across reach ($\sim 10^2$ channel widths), geomorphic ($\sim 10^0$ - 10^1 channel widths), and hydraulic scales ($\sim 10^{-1}$ - 10^0 channel widths). Once described individually, these components were integrated in order to more closely study their interactions. This was achieved by evaluating (4) relationships between LW, redds, and habitat units across multiple spatial scales. Additionally, the conceptual model was tested and modified based on study results. This study is significant because it illustrates important physical and ecological relationships between LW and spawning salmon behavior.

3.0 STUDY AREA

The study was conducted on the lower Mokelumne River (LMR) of central California, U.S., a highly regulated river that has experienced extensive channel alterations including hydraulic and instream gold mining, instream gravel mining, levee

building, damming, channelization, diversions, and repeated wood removal. The Mokelumne River watershed originates in the central Sierra Nevada at 3048 m above mean sea level (amsl), draining 1624 km² of central California (Fig. 2). The upper watershed is mountainous and forested, flowing west into oak woodland foothills and terminating in the lowland Central Valley at its confluence with the San Joaquin River. California's Central Valley and Sierra Nevada are characterized as Mediterranean climate zones with dry, hot summers and cool, wet winters; virtually all precipitation occurs October through April. Mean annual precipitation in the Mokelumne River watershed during 1928-2007 averaged 114 cm/yr at Salt Springs Reservoir (elev. 1128 m amsl) and 115 cm/yr at Pardee Reservoir (elev. 173 m amsl) (CDEC 2008). Most precipitation falls as snow at Salt Springs and as rain at Pardee.

In the 2006 water year (October-September), central California and the Sierra Nevada experienced above average precipitation. Camanche Dam (elev. 28 amsl) storm releases exceeded 100 m³/s for 25 days in January 2006. Outflows during spring snowmelt reached maximum capacity of 145 m³/s for 18 days in April 2006. In water year 2007 precipitation was 70% of average at 79 cm. During the study period, September 2006-March 2007, reservoir outflows averaged 10 m³/s (CDEC 2008). Elevated outflows with a peak of 45.5 m³/s occurred September 21, 2006 to October 2, 2006 and were intended to mimic flow variations that signal Chinook salmon to begin their upstream journey to spawn. No LW data were gathered during elevated outflows.

To meet water supply, hydropower, and flood control needs of a growing regional population, 14 significant water impoundments and 6 powerhouses regulate flows of the Mokelumne River (East Bay Municipal Utility District (EBMUD) 1999). Two dams regulate flows as the river descends into the Central Valley. Pardee Dam became operational in 1929 and Camanche Dam in 1964. Both dams are operated by EBMUD and supply municipal and agricultural water to a variety of customers locally and in the eastern portion of the San Francisco Bay Area. Camanche Dam is the lowest non-passable barrier in the watershed and is considered the head of the lower Mokelumne River (LMR). Flood frequency analysis revealed a dramatic reduction in flow magnitude for all recurrence intervals once regulation began (Pasternack et al. 2004). Prior to the completion of Pardee Dam, annual peak flows 1904-1929 exceeded 200 m³/s in 16 of 26 years. Before Camanche Dam was completed but after Pardee Dam was operational, annual peak flows 1930-1964 exceeded 200 m³/s in 5 of 35 years. Since 1965, annual peak flows have never exceeded 200 m³/s. Releases at Camanche Dam peaked above 145 m³/s twice, in 1987 and 1997, both times requiring use of the emergency spillway. The 1998 FERC agreement requires minimum Camanche Dam outflows of 4.25 m³/s.

The study reach encompassed a portion of the lower Mokelumne River, a 7.7 km section starting from the base of Camanche Dam and proceeding downstream to Mackville Bridge Road near Clements, CA (upstream 38°13'35" N, 121°01'32" W, downstream 38°12'19" N, 121°05'35" W) (Fig. 2). The study site encompasses the majority of spawning habitat on the LMR; 90% of total observed redds during the 2006-2007 spawning season were located in the study reach. Channel width averaged 31 m and varied from 15-83 m, while numerous riparian trees surpassed 25 m in height. Based on the relationship between channel width and riparian tree height, Gurnell et al. (2002) would categorize a system such as the LMR as a medium-sized river, where channel width is less than the upper quartile of potential instream wood pieces.

Channel adjustments associated with Camanche Dam include decreases in slope, width, and channel elevation amsl due to channel incision from pre-Camanche Dam

values (Edwards 2004) as a result of levees, decreased stream power, and vegetative channel encroachment (Pasternack et al. 2004; Elkins et al. 2007). Meander ratio of the study reach was 1.20, indicating a sinuous channel that prior to regulation had medium flow strength, low to medium bank erodibility, and low to medium sediment supply (Knighton 1998). Channel migration is highly restricted by levees, but also by bedrock outcrops of the Mehrten Formation that are occasionally revealed through eroded Arroyo Seco alluvial terraces (Edwards 2004, Pasternack et al. 2004).

Land use in the study area includes a fish hatchery at the dam face, pasture, vineyards, orchards, cropland, and homes. Over one-half of the study reach was leveed, while numerous abandoned streamside gravel-mining pits are connected to the channel (Edwards 2004). Some agricultural fields were <10 m from the channel, and pasture could run to river's edge. Edwards (2004) reported mean riparian width of 20 ± 14 m within the study reach, with about 30% of the riparian zone fragmented by pasture and agricultural fields. Alder (*Alnus rhombifolia*) and willow (*Salix sp.*) dominated the riparian zone, with valley oak (*Quercus lobata*), cottonwood (*Populus fremontii*), black walnut (*Juglans hindsii*), box elder (*Acer negundo* var. *Californicum*), and Oregon ash (*Fraxinus latifolia*) present in smaller numbers (Edwards 2004).

The California Department of Fish and Game has operated the Mokelumne River Fish Hatchery (owned by EBMUD) at the base of Camanche Dam since 1964 as a means to mitigate the loss of salmon spawning habitat above the dam. A fish fence at the base of the dam directs returning spawners into the hatchery via a fish ladder. Spawners' eggs and sperm are processed and used by the hatchery to produce juvenile salmon stock for ocean fisheries. An average 70% of returning adult salmon swam up the fish ladder and into the hatchery between 2002-2007.

The LMR supports about 35 native and non-native fish species, including five anadromous species: fall-run Chinook salmon, winter-run steelhead trout, American shad (*Alosa sapidissima*), striped bass (*Morone saxatilis*) and Pacific lamprey (*Lampetra tridentata*) (Merz and Workman 1998). Based on data from yearly EBMUD reports (e.g. Workman and Rible 2007), estimated adult Chinook salmon escapement has averaged 4436 fish per year (minimum 250, maximum 16128) since Camanche Dam completion in 1964. Variation between years in the number of returning salmon affects the number of instream spawners and thus redds. For example in the 2005-2006 spawning season 2 157 redds were built, compared to 755 redds in 2006-2007, and 306 in 2007-2008. In a 4-year study on the LMR, 1992-1995, the amount of area encompassed by Chinook redds ranged from 5.9 m^2 to 9.7 m^2 , averaging 8 m^2 (Hartwell 1996).

In 1991, the FERC dam relicensing process prompted adoption of a SHR program that to-date has produced an extensive, multi-agency, multi-year rehabilitation program that has addressed (1) the natural flow regime by varying flow releases on a few occasions, (2) the natural sediment and channel-adjustment regimes through annual gravel augmentation and spawning bed enhancement, and (3) channel-floodplain interactions by creating side-channel refugia and reducing the stage required for flow to spill out of the banks (e.g. Pasternack et al. 2004; Merz and Setka 2004a; Elkins et al. 2007; Henson et al. 2007). This research paper adds to the ecological and geomorphic knowledge base of the LMR.

Extensive gravel augmentation and spawning bed enhancement has occurred in multiple channel locations up to 10 km downstream of the dam, specifically to enhance spawning habitat for fall-run Chinook salmon (Wheaton et al. 2004b; Pasternack et al. 2004; Merz et al. 2006; Elkins et al. 2007). During 1999-2007, annual SHR projects

placed a total of 29 873 tonnes of gravel and cobble in the LMR to fill abandoned instream gravel mining pits and create spawning habitat according to detailed designs (Wheaton 2004b). Most of this material was used in the 500 m reach directly downstream of Camanche Dam to re-create a riffle-pool longitudinal profile with an average bed slope of 0.004, while downstream slopes average 0.001 (Elkins et al. 2007). To enhance Pacific salmon spawning, rearing, and adult holding habitat, placed gravel was contoured to provide heterogeneous micro- and meso-habitat features within the channel (Wheaton et al. 2004a,c). Boulder clusters were used to provide structural variation within the channel. Individual LW pieces were used sparingly, mainly buried in gravel with about one meter of the buried LW protruding from the channel bed so that stability was assured.

4.0 METHODS

EBMUD provided an ArcMap shapefile of the LMR during Camanche Dam baseflow conditions, circa 2004, that was used as a template to map, visualize, and analyze LW, redd, and habitat unit relationships at multiple spatial scales. The resulting ArcMap and ArcGIS 9.2 database (ESRI 2006) were used to analyze each key variable independently and to evaluate their integrated relationships. In compliance with existing regional data standards, the project used the projected coordinate system NAD 1983 State Plane California III FIPS.

Upon cursory inspection of the data, marked differences between segments of the study reach were evident, thus multiple analyses were performed not only across the full 7.7 km study reach, but also divided into upper 3 km and lower 4.7 km reaches (hereafter Reach 1 and Reach 2, respectively) so that the best possible conclusions could be drawn from the data set. All analyses were performed between active LW (located in habitat units where there was a probability of spawning activity) and redds.

4.1 LW data collection

Criteria for inclusion of wood pieces in the survey were length ≥ 1 m and diameter ≥ 10 cm. Every LW piece used in analyses rested within the bankfull channel. In all habitat zones where physical characteristics suggested that spawning activity might occur, location, habitat unit, and attributes (qualitative and quantitative measures described below) were recorded for each LW piece. When LW was located in pools or glides with no local spawning activity, and had little chance of transport to spawning habitat at flows of $10 \text{ m}^3/\text{s}$, only location and habitat unit were recorded.

Surveyed LW included living trees with some portion of the trunk submerged and canopy overhanging the channel, LW living or dead fully within the channel boundaries in various stages of decay, LW deposited on channel banks and edges, and LW accumulated on geomorphic channel features such as bars, meander bends, and islands. A Trimble Pathfinder PRO XRS GPS unit with real-time, sub-meter horizontal accuracy was used to record the geographic location of each surveyed LW piece.

Quantitatively and qualitative attributes adapted from Gurnell et al. (2002) and Moulin and Piegay (2004) were recorded to characterize each LW piece. Length and diameter at both ends were obtained using tape measure and tree caliper, with recorded accuracies of ± 10 cm and ± 2 cm, respectively. When inaccessible, visual estimates were made for length and second diameter. Orientation to flow was estimated to the nearest 45° by clockwise position of the smallest diameter end in relation to upstream flow. Leaf characteristics were used to identify live LW species, while dead LW species were

occasionally identified by bark characteristics. Origins of LW pieces were identified as bank erosion when roots were present, as cut or placed when evident by visual inspection, as limb breakage when LW piece could be matched up with a nearby scar on a riparian tree, and as unknown in all other cases. Decay classifications included fresh when the LW piece was alive, lightly decayed when a LW piece had <50% algal growth on the visible portion of LW or >50% bark, heavy abrasion when algae covered >50% of the piece or >50% of the bark was missing, and waterlogged when the LW piece was fully immersed and resting on the channel bed with no other feature assisting in lodging the piece into place. An additional metric reported percentage of LW that was submerged to some degree. Analyses were performed to determine degree of lateral distribution as well as whether larger scale geomorphic structures might capture LW at a higher rate than an average channel margin where riparian trees may or may not be present.

LW morphology in terms of presence of limbs, bark, and root structure was recorded for each piece. Large limbs were delineated as ≥ 2 cm and small limbs as ≤ 2 cm in diameter. Number of large limbs, small limbs, and root ball condition were indicators of relative length of time that LW pieces had been instream. LW accumulations were noted only when deemed significant and could consist of any number of LW pieces greater than one individual piece. Significance was subjective, but was generally determined when an accumulation appeared to play a geomorphic role in flow direction and velocity, channel scour, or sediment deposition at typical flows during the study period.

LW volume was calculated using the diameter at breast height (DBH) equation. The DBH equation is typically used to estimate standing tree volume based on trunk diameter measured at a height of 1.35 m above ground. The DBH equation was selected for this study because it yielded the highest volume when compared to other volume equations and thus was used in an effort to consider all wood volume entering the channel:

$$Volume = \pi * (DBH^2 * .00007854) * (height / 3) \quad (1)$$

where DBH was the largest measured diameter of each LW piece.

To quantify reach scale abundance, wood loading within the study reach was calculated as tonnes/hectare of water surface area using an average wood density of 500 kg/m³. Wood load measures were compared to other reported values (e.g. Keller and Swanson 1979, Bilby and Bisson 1998, Gurnell et al. 2002, Piegay 2003) to determine how LW volume of the LMR study reach compared to wood loading worldwide.

4.2 Redd data collection

EBMUD fisheries biologists performed weekly Chinook salmon redd surveys from late September 2006 through January 2007, wading and canoeing the 16 km spawning habitat reach from Camanche Dam fish fence to Elliot Road. Redd locations were recorded using a Trimble Pro XR GPS unit with sub-meter accuracy achieved by post-survey differential correction. Existing redds were monitored for superimposition and scour in subsequent weeks using a GPS real-time mapping function.

Cumulative number of redds in the downstream direction was used to determine reach scale patterns of redd distribution. Analysis of redd numbers per habitat type was used to focus on the interaction of redds and geomorphic components of the study reach. Specific redd placements were analyzed in relationship to LW pieces and habitat units to help illuminate important physical and biological linkages between spawning salmon behavior and instream LW pieces.

4.3 Habitat unit data collection

An EBMUD habitat shapefile of the study reach was printed and used in the field to help guide delineation of habitat units. Habitat units ($\sim 10^0$ - 10^1 channel widths in length) were designated as riffle, run, glide, and pool according to depth and surface velocity combinations that were based on known elements of the hydrologic signature of the LMR (Hartwell 1996, Merz and Setka 2004b). Riffles were delineated where velocity was >0.75 m/s and depth <0.9 m (fast and shallow); runs where velocity was >0.75 m/s and depth >0.9 m (fast and deep); glides where velocity was <0.75 m/s and depth <1.5 m (slow and shallow); and pools where velocity was <0.75 m/s and depth >1.5 m (slow and deep). Velocity and depth were periodically measured and visually extrapolated to an encompassing area. Surface velocity was estimated using the float method by timing the travel of a leaf over a specified distance three times, with the results averaged to a mean velocity. Depth was measured using a stadia rod to within ± 10 cm accuracy. Although channel margin depths were generally shallower than mid-channel depths, channel margins were often included within the dominant mid-channel habitat type.

4.4 GIS database

LW and redd GPS coordinates were imported and projected into ArcGIS 9.2 as shapefiles. In the LW shapefile, lines accurately depicted LW length and orientation to flow. In the redd shapefile, redds were depicted as infinitesimal points. Habitat units were drawn as polygons into a third shapefile using the editor tool in ArcGIS 9.2.

A mid-channel line shapefile was built with a point placed every 25 m in the downstream direction. Semi-rectangular polygons were built in-between each mid-channel point, resulting in 304 consecutive polygons 25 m in length in the downstream direction and encompassing at minimum the bankfull channel width. Within each polygon the area of each habitat type was extracted using the ArcGIS 9.2 clip function, and LW and redd counts per polygon per habitat type were extracted using the intersect function. If a habitat within a polygon held the majority of a LW line location, the entire area of that habitat was counted as area occupied by LW. Redds were depicted as points, so the polygon within which the redd fell was counted as area occupied by redds. Densities of LW and redds were calculated as number of LW or redds per area of habitat type per polygon. Thus, as many as 8 densities could be calculated for one 25-m polygon based on the area of up to 4 habitat types (riffle, run, glide, pool) and the count of 2 independent variables (LW and redds). Since division by area resulted in most densities with values <1 , LW and redds per polygon per habitat type were normalized to a 929 m^2 ($30.5 \text{ m} \times 30.5 \text{ m}$) area so that the graphical depiction of this data was presented at a scale of approximately one channel width.

4.5 Data analysis

Channel units may repeat themselves in sequences that provide information about important properties of a river reach. Grant et al. (1990) applied Markov chain analysis to two mountain streams to study the tendency for repeating series of habitat units to develop. To build a transition probability sequence for this study, observed two-unit habitat sequences (e.g. riffle-pool or run-glide) were reported as ratios in individual cells of the matrix, such that all possible transitions of a specific habitat type equaled 1. Empirical observations were compared against a series of random sequence probabilities

obtained from a random number generator. The comparison yielded a preferred sequence probability value, where positive values indicated that one habitat unit preferentially followed another. This method was used on habitat unit data on the LMR to detect whether river regulation had affected habitat unit distribution in the study reach.

Normalized LW and redd densities were averaged for each habitat type for statistical analysis. For example, riffles were present in 108 of 340 polygons, and 58 of those riffles also contained redds, so the normalized densities for redds in 58 riffles were summed, then divided by 108 (i.e. the number of polygons that contained riffles). With this data, non-parametric Kolmogorov-Smirnov measures were used to test for significant differences in average densities of LW and redds within habitat types. The Wilcoxon/Kruskal-Wallis rank sum test was used to test for significant differences in average polygon densities of LW and redds between habitat types.

Relationships between LW distributions, redd locations, and habitat types were evaluated across reach, geomorphic, and hydraulic spatial scales. At the reach scale, cumulative downstream frequency was used to depict longitudinal distribution of LW in terms of accumulation or dispersal patterns; likewise, redds in terms of cluster or dispersal patterns. Second, an electivity index, similar to that used by Elkins et al. (2007) to determine whether Chinook salmon on the LMR preferentially used predicted high-quality habitat, was calculated as percent of LW pieces and redds per habitat type divided by percent of habitat type.

$$LW \text{ electivity index} = 100 \times \frac{\% LW}{\% \text{ habitat type}} \quad (2)$$

$$Redd \text{ electivity index} = 100 \times \frac{\% \text{ redds}}{\% \text{ habitat type}} \quad (3)$$

For both indices, a value of 1 signified that LW pieces or redds were present in equal abundance to habitat availability, a value <1 that there were fewer LW or redds than available habitat, and a value >1 an indicator of habitat where LW or redds were present in greater abundance than available habitat. Pool habitat types were not included in the electivity index analysis because LW was most often mapped but not measured in pools, thus yielding an uneven data set, and redds were never observed in pools. This measure was intended to indicate if there were habitats in which LW pieces had a higher incidence of lodging as well as to elicit the preference of spawners in their selection of habitats.

Three tests were used to evaluate interactions at geomorphic scales. First, LW and redd densities derived from the 304 polygons were graphed against each other to test for correlations. Secondarily, because of so many occurrences of ‘no redds’ and ‘no wood’ among the 304 polygons and across habitats, an occurrence matrix was constructed so that instances of LW-redds, LW-no redds, no LW-redds, and no LW-no redds could be analyzed individually. Third, a graph was built of LW and redd counts per 100 m increment, where the first data point included all LW and redds in the first 100 m downstream of Camanche Dam, the second point all LW and redds from 101-200 m, and so on. Habitat units, islands, gravel bars, meander bends, and LW accumulations were notated on the graph and assessed visually against LW and redd distributions in order to clarify reach scale (~10² channel widths), geomorphic scale (~10⁰-10¹ channel widths), and hydraulic scale (~10⁻¹-10⁰ channel widths) patterns.

In order to elucidate relationships at hydraulic spatial scales, the ArcMap 9.2 buffer tool was used to build shapefiles consisting of 10 m, 5 m, and 2.5 m radii circles around each wood line, which created elongated circles based on length, and around each

redd point. After discussions with EBMUD fisheries biologists who had observed salmon using approximately half the channel width while spawning, a conservative 10 m radii buffer was selected as the limit within which a salmon might swim in-between spawning activity. A 5 m radii buffer was selected because this radii encompassed the estimated size of redds on the LMR of $\sim 8\text{m}^2$ (~ 2 m by 4 m in elliptical shape) (Hartwell 1996). Thus, a LW piece within a 5 m radii may allow a spawner to take advantage of local influences on flows that create optimal conditions for a redd location. Furthermore, a spawner need only move a short distance to take advantage of LW as cover and refugia. The 2.5 m radii buffer was selected as an indicator of LW playing a direct role in redd location selection because of LW influence on localized upwelling and downwelling created by channel roughness and consequent pressure differentiation (Brunke and Gonser 1997). LW and redd buffer shapefiles of the same scale were then intersected using an ArcGIS 9.2 intersection function. Redds were considered to be influenced by a LW piece at each scale only when an individual redd data point fell within a LW buffer zone. In addition, a simple tally was made, using field observations coupled with the constructed ArcMap, of the number of redds within a 10 m radius of LW pieces that were determined to be present because of hydraulic variations caused by the LW piece.

To determine how much channel area was covered by buffers versus how much channel area was available for use by spawners, percent of channel covered by 10 m, 5 m, and 2.5 m buffers of LW, redds, and LW-redd intersections was calculated. This analysis was used to assess whether selected buffer sizes were ecologically meaningful. For instance, if 100% of available channel were included in the same-size buffer layers of LW and redds, it might not be ecologically meaningful to suggest that LW influenced redd placement in that area.

To clarify the degree of latitudinal use of the channel by spawners and their relationship with LW, 10 m, 5 m, and 2.5 m intersections that occurred in mid-channel versus along channel margins were analyzed. Buffer shapefiles of 10 m, 5 m, and 2.5 m were created around the mid-channel line shapefile so that same-scale analyses could be performed. In this analysis, both the LW and mid-channel buffers had to contain the redd point in order for that combination to be counted as associated together.

To determine if redds were located more often upstream or downstream of LW, the occurrence of redds within 10 m, 5 m, and 2.5 m of LW pieces in the upstream and downstream directions was tallied using the same buffer intersections. Some redds were counted more than once depending upon the number and position of LW pieces that were close to a specific redd. In this analysis, if a redd was located upstream of a LW piece, it was construed that the LW piece was influencing hyporheic flow. On the other hand, if a redd was located downstream of a LW piece, it was interpreted as the LW piece providing cover or other refugia for the spawner.

To evaluate the statistical significance of results from the empirical LW-redd analyses, 5 random spatial data sets with the same number of points as observed redds were generated for the entire study reach, as well as separately for Reach 1 and Reach 2. This test was done to examine whether the empirical LW-redd spatial relationships could also be explained by randomly located redds. All pools were excluded from random analyses since spawners did not utilize pools. Intersections between the randomly generated data sets and the field-acquired LW data set were analyzed using 10 m, 5 m, and 2.5 m radii buffers. All analyses performed between LW pieces and redds were duplicated for LW pieces and the randomly generated point sets. After tallying each LW-random point intersection analysis, each set of 5 analyses were averaged to provide one

number that could be compared against the actual LW-redd intersection analyses. Finally, two-tailed t-tests (Zar, 1999) were performed to test for significant differences between the number of LW-redd intersections and the average of 5 LW-random point intersection analyses. In each t-test, the hypothesized mean equaled the number of actual LW-redd intersections and the population mean equaled the corresponding mean of each LW-random point analysis.

5.0 RESULTS

Geostatistical analyses indicated that, at multiple spatial scales, LW plays an important role on the LMR when spawning female Chinook salmon select redd locations. Statistical tests validated that spawners placed redds closer to LW than by random chance alone at reach, geomorphic, and hydraulic scales. LW-redd associations increased in the downstream direction, as did the proportion of marginal spawning habitat. LW morphology, distribution, and abundance; redd distribution and abundance; habitat unit distribution; and a detailed description of the study reach with respect to notable geomorphic characteristics and ecological interactions involving LW, redds, and habitat units, are reported below.

5.1 Large wood morphology, distribution, and abundance

Of the LW found within the study reach, 340 pieces were located in habitat units where there was a probability of spawning activity. These LW pieces were measured and mapped (hereafter referred to as active LW). Average active LW length and diameter was 6.9 ± 4.0 m and 23 ± 12 cm, respectively, with maximum length 27 m and diameter 155 cm. An additional 202 LW pieces were mapped but not individually measured because they resided in pool and glide zones where no spawning activity occurred (hereafter referred to as inactive LW). When discussed collectively, active and inactive LW will be referred to as total LW, while LW will be used from this point forward to discuss large wood in general. Total LW was regularly distributed in the downstream direction (Fig. 3).

LW pieces in stream channels tend to orient parallel to flow so that the least amount of surface area is subject to gravity and drag forces and thus is most stable (Braudrick and Grant 2000). On the LMR, the majority of active LW pieces were angled approximately parallel to flow, with 57% angled between 135° and 225° to flow. Field observations suggested that roots were often oriented upstream and boles downstream, although this parameter was not recorded. Less than 20% of active LW pieces spanned the channel laterally by more than 6 m.

Tree species identification was limited because of variability in decay condition. Decay classifications revealed that 11% of active LW pieces were fresh, 24% were lightly decayed, 49% were heavily decayed, and 16% were waterlogged. Only 22% of active LW pieces were identifiable: alder (50 pieces), valley oak (8), cottonwood (3), ash (1), and willow (12). Five active LW oak pieces along a 150 m reach on river right at the channel margin were the only clearly evident broken branches, and were clustered below oak trees that dominated the upper bank (Fig. 4d). One dead oak tree with multiple branches and a root system still intact was the largest recorded active LW piece, located just upstream of Hwy 88 bridge at channel edge on river right (Fig. 4c). The one identified ash tree was slumped into the channel but alive in a pool zone (Fig. 4c). All identified willows and cottonwoods were attached to the bank, alive, and overhanging the channel.

Origin was difficult to determine, as 67% of active LW pieces were not attached to a root system. Since total LW recruitment could only occur downstream from Camanche Dam, it is probable that most total LW originated from bank erosion, but only 36% of active LW could be easily identified as such. An additional 5% of active LW originated from anthropogenic activities, as evidenced by cuts at one or both ends of a LW piece.

Lateral distribution analyses indicated preferential active LW deposition against geomorphic structures such as channel banks, gravel bars, meander bends, and islands (Fig. 4). Forty percent of active LW pieces resided partially on a bank, and 59% rested within 2.5 m of the bank. Few active LW pieces were fully submerged; 84% were protruding out of the water to some degree, including those pieces that were completely out of the water and residing on the bank but within the bankfull flow channel. Gravel bars and islands made up 5% of the bankfull channel area yet held 12% of the LW pieces.

It is unknown how long individual *in-situ* LW pieces might stay lodged in a regulated channel before transport or disintegration. Larger limbs do not decay or break as quickly as smaller branches, consequently some highly decayed active LW had more than one large limb attached to the main trunk. About 80% of active LW pieces had no leaves and were considered dead; 15% were recorded as alive. Fifty-two percent of active LW pieces had at least one large limb ≥ 2 cm in diameter attached to the main trunk, while 10% had more than 10 large limbs. Of limbs < 2 cm in diameter, 66% had no small branches and 19% had ≥ 20 small limbs. No small branches indicated a relatively long amount of time in the channel, while many small limbs suggested recent deposition into the channel.

Active LW accumulations of 2 or more pieces (hereafter called logjams) played a significant role in hydraulic or geomorphic channel units in 11 instances. Logjams were located at meander bends (Figs. 4a, 4b), where a live tree overhanging or entirely in the channel provided a stable structure for active LW to lodge against (Figs. 4a, 4b, 4e), in backwater areas where active LW deposited during the falling limb of high flows (Figs. 4a, 4e), at islands (Figs. 4a, 4d), and in pools and runs (Figs. 4b, 4c). Active LW appeared to play a role in the creation of 2 pools and 1 run (Figs. 4a, 4b). No logjam contained more than 10 active LW pieces, although wood pieces smaller than those defined as LW were present in some accumulations.

Active LW piece volume ranged from 0.02 m³ to 27 m³, averaging 1.0 m³. Field observations suggested inactive LW pieces were of average active LW volume, for an estimated volume of 532 m³ for 542 total LW pieces in the study reach. Total wood load for the study reach was 9.2-tonnes/hectare; similar to other highly managed rivers.

5.2 Redd distribution and abundance

Fully 582 (90%) of redds were located in Reach 1, and another 68 redds were located in Reach 2 (Fig. 3). Across the study reach as well as in Reach 1, 56% of redds were located in riffles, 36% in glides, 8% in runs, and 0% in pools. Thirty-six percent of total redds were built in the first 500 m below Camanche Dam where SHR projects took place 2001-2007. In Reach 2, 56% of redds (38 of 68) were located in a SHR project just below Hwy 88 (Fig. 4d), while 88% of redds were located in riffles. Runs and glides each supported 6% of redds in Reach 2. Seventy-five percent of redds in the 7.7 km study reach were sited on SHR gravels.

5.3 Habitat unit distribution

The Markov chain analysis revealed that the LMR exhibits the type of habitat degradation that can occur in regulated rivers, with riffle-pool sequences smoothed into riffle-glide-pool sequences (Table 1, Fig. 4). Glide-pool sequences encompassed a third of the study reach in three distinct segments: 3200-4800 m, 5600-6500 m, and 7200-7700 m downstream from Camanche Dam, whereas discrete units of riffles and glides were most prevalent across the study reach (Fig. 4). Islands covered 10 073 m² in total area and gravel bars 3 936 m², while habitat unit area ranged from runs at 26 700 m², riffles at 42 662 m², glides at 107 130 m², to pools at 112 000 m². Habitat variability existed due to meander bends, islands, gravel bars, and local slope differentials.

Reach 2 was defined as marginal habitat for spawners because of 1) the low proportion of redds when compared to Reach 1, and 2) the increase in area of glide-pool habitat units in Reach 2. In Reach 1 glides were associated with riffles, while in Reach 2 glides were associated with pools. In Reach 1, SHR projects improved spawning habitat and rejuvenated riffles and glides, such that riffles encompassed 20% of available habitat, runs 16%, glides 41%, and pools 23% (Figs. 4a, 4b). Reach 2 was dominated by a cumulative 3 km of glide-pool zones (Figs. 4c, 4d, 4e, 4f). Two islands and one meander bend provided most of the habitat variability in Reach 2. In contrast to Reach 1, Reach 2 riffles encompassed 11% of available habitat, runs 5%, glides 34%, and pools 50%.

5.3.1 Geomorphic narrative of study reach

In the first 400 m below Camanche Dam, 230 redds (35% of total redds in study reach) were built in SHR project areas. Six active LW pieces on river right in the first 100 m (Fig. 4a) were living, overhanging trees slumping perpendicular to the channel, with lower trunks in water and canopies above water surface. An additional 6 active LW pieces in this area overhung the channel and were dead. Slumping occurred in this area because of the re-activation of the floodplain-channel connection during less than bankfull flows, which was created by raising channel bed elevation with augmented gravel (Elkins et al. 2007).

Bedrock outcropping created the first channel bend at 500 m. The first active logjam was located on river right near the upstream end of an island at 800 m, with a live, overhanging tree as the key piece. Although velocity and depth classified this area as a riffle, this logjam was partially buried in sand and silt rather than in gravel. Downstream of the island, active LW strand lines existed along both channel margins, particularly river right to 1050 m. At 1000 m, an abandoned gravel pit connected to the main channel created a large backwater pool.

In the riffle extending from 1000-1250 m, 130 redds (20% of total) were located on gravel placed and contoured during a 2002 SHR project. Two logjams were located at 1350 m and 1450 m on the outside of a channel bend, where bedrock constricted the channel on river left. The first logjam was at the apex of the bend in a backwater glide on river left. The key active LW piece was dead with roots attached to the bank and leafless canopy angled into the water. The second logjam on river left created an active LW-forced run along its mid-channel edge, with a pool upstream of the jam. The key piece was a live alder with a full root system that had fallen into the channel due to bank slumping. About 50% of the canopy was above water surface and fully leafed. Two other active LW pieces in this logjam were located upstream of the live tree, closer to the bank, and were dead with higher levels of decay. Directly across the channel on river

right, two active LW pieces spanned a 6-m wide side channel formed between a gravel bar and the channel bank. This logjam created a zone of sediment deposition with small gravels upstream and a shallow scour pool downstream.

From 1540-1630 m, a natural riffle still intact after regulation supported 62 redds (10% of total) (Fig. 4b). The glide-pool that followed was formerly a longer degraded reach, but a SHR project recreated a riffle-glide zone from 2100-2600 m that supported 73 redds (11% of total). At 2350 m a strand line of active LW pieces started along the back of a gravel bar on river left and extended downstream, indicating deposition during the falling limb of a hydrograph. Directly across from the gravel bar on river right was a logjam that, in combination with the bar, forced the formation of a run. All active LW in the logjam was dead; the key piece had remnant roots still attached to the bank and was protruding into the channel roughly perpendicular to flow.

On river right from 2450-2575 m, five oak limbs that originated from a group of oak trees on the upper bank lined the channel margin. A gravel bar at 2600 m captured active LW pieces along its apex. The channel constricted into a natural riffle above the bar, supporting 20 redds (3% of total), and became a run alongside the bar. No SHR projects occurred in this area, though downstream transport of previously placed gravels may have been the source of gravel for this riffle. The bar and channel constriction marked the beginning of a meander bend.

At 2800 m, a logjam on river right was anchored between the channel bank and a small island (or channel margin fragment) of about 36 m² and populated with one tree. The key piece in the jam was oriented parallel to flow with roots upstream (Fig. 4c). The jam and island promoted sediment deposition by introducing a large-scale flow barrier directly upstream of a backwater zone on river right, an island in mid-channel, and the main channel on river left. The most active gravel bar of the study reach was located just downstream of this barrier at 2825 m. At this bar, sediment deposition had occurred during the most recent high flow releases due to the proceeding roughness elements. Varying proportions of other identified gravel bars were covered by growing grass, thus exhibiting hardening of the bar surface. At 3000 m on river right, a 2-piece jam that may have provided some bank protection shielded a heavily eroded outer bank of a meander bend. An active LW strand line, along river right from 3000-3150 m, suggested that LW transported through the meander at high flows and deposited along the channel margin.

The longest glide-pool zone in the study reach began at 3200 m and continued to 4800 m (Figs. 4c, 4d). Inactive LW pieces lined the channel, ranging from alive and slumped into the channel to dead with no small limbs. Some LW transport was evident in the placement of pieces that were entwined with more stable LW lodged into the bank or into the channel bed. The largest recorded LW piece in the study reach—an oak with multiple large limbs, no small limbs, and a remnant root structure (no soil)—was located at 4750 m on river right just upstream of the Hwy 88 Bridge (Fig. 4d). It had entered the LMR about 100 m upstream of its current location, and was transported a short distance downstream during high flows of the 2006 water year.

A gravel-augmented riffle from 4800-5400 m supported 38 of 68 total redds (56% of redds in Reach 2) (Figs. 4d, 4e). The longest active LW strand line of the study reach was located from 4900-5450 m on river right, suggesting that at high flows, LW transported through the glide-pool zone, and that LW in the zone became mobile and transported downstream as well. At 5200-5400 m, a three-island complex split the channel (Fig. 4e). The dominant habitat units alongside the islands were riffles, and 17 redds were located in this section (25% of redds in Reach 2). Redds are mostly located

along river left, with a few on river right at the end of the downstream island. A logjam was located at the head of the first island – a willow complex growing mid-channel at 5200 m. Key pieces were partially buried in a sand and silt accumulation zone that had formed at the head of the island. Another logjam was present at 5300 m at the top of the third and biggest island. Two key pieces were lodged onto the bank, with one key piece against the upstream side of an alder. This jam forced the formation of a small riffle. Three large active LW pieces formed the beginnings of a strand line on river left from 5300-5570 m. An active beaver lodge was located along river right at 5300 m.

The second of three extensive glide-pool zones followed from 5600-6500 m, interrupted only by a small riffle zone supporting two redds at 6200 m (Figs. 4e, 4f). At 5800 m and following a meander bend, one inactive LW piece with a remnant root structure was stretched 14 m across the 20 m wide channel, the greatest amount of blockage perpendicular to flow in the study reach. A companion piece of inactive LW >10 m in length, with its remnant root hooked over the perpendicular inactive LW piece, was oriented parallel to flow. A number of other inactive LW pieces were located in this area indicating a deposition zone during high flows, where flows encountered a sharp bend that depleted stream power enough to deposit these large yet buoyant objects.

At 6500 m an island split the channel, with a backwater glide on river left and the main channel on river right (Fig. 4f). The backwater glide was a deposition zone, where inactive LW pieces formed a loose logjam. Active LW pieces that were present alongside the island were lodged above the water surface, partially instream, and completely submerged. The riffle in the dominant channel on river right of the island supported eight redds (12% of those in Reach 2). The last meander bend of the study reach, at 6600 m, supported two redds and featured a run at its apex. A small riffle at 6800 m held the final two redds of the study reach; they were located close to the channel margin on river left where 3 active LW pieces were lodged. A final glide-pool zone dominated the rest of the study reach from 7200-7700 m.

5.4 LW-redd-habitat unit interactions

Results of non-parametric Kolmogorov-Smirnov tests indicated no significant differences when testing average total LW density between habitat types, thus active LW density distributions were statistically indistinguishable throughout the study reach. There were significant differences in average redd densities between riffles and all other habitat types ($p < 0.001$), but no significant differences in average redd densities between glides and runs ($p > 0.10$). No redds were present in pools.

When testing differences in densities of active LW and redds within habitat types, non-parametric Wilcoxon/Kruskal-Wallis test results revealed that average redd densities were significantly higher than average active LW densities in riffles ($p < 0.0032$) and glides ($p < 0.0001$), but not significantly different in runs ($p = 0.4158$).

At the reach scale, 85% of the time at least one active LW piece was within one average channel width (31 m) of every identified redd. Total LW occurred regularly downstream (Fig. 3) at a rate of 70 pieces km^{-1} ($R^2 = 0.99$). Reach 1 held 36% of total LW pieces in 39% of the total study reach length; Reach 2 held 64% of total LW pieces in 61% of the total study reach length. Longitudinal redd distribution, on the other hand, showed that 90% of redds were located in Reach 1, yet an $R^2 = 0.76$ indicated a high degree of correlation between redd distribution and the full study reach.

The active LW electivity index analysis revealed that active LW was regularly distributed in approximately equal abundance to availability in Reach 1 across riffles at a

value of 1.1, runs at 1.0, and glides at 0.9. Active LW distribution was more variable in Reach 2, where a riffle value of 1.3 suggested that there were more active LW pieces than expected for the % of available area; active LW in runs was present equal to availability with a value of 1.0; and in glides active LW was less abundant than habitat availability would suggest with a value of 0.8.

The redd electivity index results indicated that riffles were strongly preferred for redd placements in Reaches 1 and 2 with values of 2.1 and 2.4, respectively. Runs were not preferred in either Reach 1 or 2, with values of 0.4 and 0.5, respectively. Glides were not preferred either, with values of 0.7 in Reach 1 and 0.3 in Reach 2.

Polygon density plots showed that total LW was present in all habitat types; with and without redds in riffles, runs, and glides; and strictly without redds in pools (Fig. 5). Redds were present with and without active LW in riffles, glides, and runs. A glide at 5200 m held the highest density of active LW at 20 LW pieces/929 m². The highest densities of redds were located in riffles. In Reach 1 riffles, 12 polygons had a value greater than 20-redds/929 m², in contrast to Reach 2 where just 1 polygon had a similar value. In addition, five glides in the upper 300 m of Reach 1 had densities greater than 20-redds/929 m².

Occurrence matrix analyses of the polygon density plots revealed that when redds were present in a specific polygon, active LW was present in the same polygon 50% of the time across the study reach, 48% of the time in Reach 1, and 56% of the time in Reach 2. The higher rate of association between LW and redds in Reach 2 may be an indicator of the importance of larger geomorphic units and the role they play in creating complex habitat in suboptimal conditions.

When LW, redds, and habitat units were considered at a scale of 100 m increments in the downstream direction, there was a striking pattern of redds heavily clustered in the SHR project sites in Reach 1. Outside of SHR sites, active LW and redds peaked together in low densities at islands (Fig. 6). Redds were also clustered in non-SHR riffle zones, particularly around islands and at gravel bars. In Reach 2, twenty-two of 68 redds (32%) were built near islands, suggesting that larger scale geomorphic features may influence spawners in their selection of redd locations in marginal habitat. Islands and gravel bars captured active LW at a rate of ~20 LW pieces per 100 m section, whereas counts ranged from 0-10 LW pieces per 100 m in other reach sections.

At hydraulic scales of 10 m, 5 m, and 2.5 m radii, spatial analyses revealed that the number and percentages of LW-redd relationships increased as radii increased (Table 2). Because Reach 1 held 90% of the study redds, Reach 1 results were often similar to full study reach results. Reach 2 had higher percentages of LW-redd intersections at each scale than Reach 1, suggesting differences in habitat suitability and consequently in the use of LW by salmon between Reach 1 and 2. A separate tally based on field observations and the constructed ArcMap showed that 4 active LW pieces lodged within hydraulically active zones appeared to play a significant role in 33 redd placements (5% of redds) at the 10 m radii scale.

Mid-channel, as a proxy for the channel thalweg, held few redds and even fewer LW pieces (Table 2). As buffer sizes centered on mid-channel radiated further from the origin, LW-redd intersections increased. The majority of LW pieces were within 2.5 m of the channel margin, and greater than 90% were within 10 m of the channel margin. Additionally, the majority of redds were within 10 m of the channel margin. Mid-channel versus channel margin results overlapped to some extent because channel width averaged just 31 m, thus 71% of LW-redd intersections occurred within 10 m of mid-

channel at the same time 56% occurred within 10 m of the channel margin. Redd placements upstream versus downstream of active LW pieces showed that redds tended to be placed downstream of LW pieces more than upstream, except at the 2.5 m radii scale in Reach 1.

Buffers used in the hydraulic analysis covered a range of areas when compared against total habitat areas. Active LW buffer coverage in Reach 1 was approximately equal across habitat types, with 27% of riffle, 33% of run, and 33% of glide area encompassed at the 10 m buffer scale. Active LW buffers in Reach 2 encompassed more area, with an average of 39% across riffles, runs, and glides at the 10 m scale. The highest degree of coverage by redd buffers occurred in riffles in Reach 1, with 71% of available area covered by 10 m redd buffers. Red buffers in Reach 1 covered 27% of runs and glides at the 10 m buffer scale. Percentage of redd buffer coverage declined considerably in Reach 2, with 32% of available riffle area covered by 10 m redd buffers.

Although large percentages of habitat were covered in the buffer analyses, intersections between active LW and redds encompassed much smaller areas. In Reach 1 at the 10 m buffer scale, 17% of riffles areas were covered by LW-redd intersections, 6% in runs, and 12% in glides. Reach 2 percentages were lower, with 13% in riffles, 8% in runs, and 2% in glides at the 10 m buffer scale. Intersections encompassing minimal amounts of available channel habitat suggest that the buffer sizes used in these analyses were ecologically appropriate.

T-tests between empirical LW-redd results and LW-randomly generated spatial data results showed that across the study reach, actual LW-redd intersections were significantly greater than random intersections at the 10 m and 5 m scale, while at the 2.5 m scale random intersections were significantly greater than actual LW-redd intersections (Table 4). In Reach 1, LW-redd intersections were significantly greater than random intersections at the 10 m scale, exhibited no difference at the 5 m scale, and random intersections were significantly greater than actual LW-redd intersections at the 2.5 m scale. Conversely, in Reach 2 LW-redd intersections at all scales were significantly greater than random intersections, which strengthens the implication that LW plays a more important role for spawners in marginal habitat. Mid-channel intersections were significantly greater than random intersections at every scale and across the entire study reach. Channel margin intersections were significantly less than random intersections at every scale in Reach 1, whereas in Reach 2 LW-redd intersections were significantly greater than random intersections at every scale. Upstream/downstream intersections were variable across both reaches. In Reach 2, LW-redd intersections at every scale were significantly greater downstream of a LW piece than random intersections.

6.0 DISCUSSION

The initial conceptual model was not validated in this study. A revised conceptual model predicts that LW is positively associated with salmon redd locations across reach, geomorphic, and hydraulic scales. In regulated rivers where LW deficits, habitat unit degradation, and marginal habitat exists, LW additions could be beneficial to spawning salmon. What follows below is a discussion of the effects of river regulation, management, and habitat rehabilitation on ecosystem ecology and geomorphology, with respect to LW, redd placements, habitat units, and interactions between these variables.

6.1 LW in a regulated river

LW pieces were regularly distributed across the study reach (Figs. 3 and 4),

suggesting that riparian recruitment was active and wood transport limited. How might LW recruitment be active with the riparian corridor leveed, fragmented, and LW supply limited from the upper watershed? Regulated flows help to create hardened banks (Petts and Gurnell 2005) where riparian trees then have the opportunity to establish at channel margins. On the LMR, even with 30% riparian corridor fragmentation (Edwards 2004), riparian trees lined both sides of the channel along much of the study reach, thus providing ample opportunities for LW to enter the channel. Once LW pieces entered the channel, potential transport events might occur once a year if at all, and even then only for a limited number of days. For instance, any LW piece that slumped into the channel in water year 2006 during high flow releases did not experience similar high flows for at least two years and as a result may settle firmly into the channel bed or along the channel margin before the next high flow release. The proliferation of slumped-in inactive LW pieces along three long glide-pool zones in Reach 2 were indicative of this process.

Logjams and individual LW pieces, whether channel spanning, lodged mid-channel, or along a channel margin, can form dynamic hydraulic and geomorphic structures along the river continuum that influence flows and provide habitat heterogeneity for aquatic species (Maser and Sedell 1994). These dynamic processes exist on medium-sized and larger rivers (Crook and Robertson 1998, Geist and Dauble 1998, Piegay 2003, Latterell and Naiman 2007), including on the LMR (Merz 2001, Wheaton et al. 2004c), where 11 logjams as small as 2 LW pieces had a measurable effect on channel condition as evidenced by gravel deposition, LW-forced pools and runs, and bank protection.

Gurnell et al. (2002) compared wood loading in 152 rivers worldwide, using regression analysis to develop relationships between relative wood availability and riparian forest types in rivers with little to no management. They predicted a wood load of 55 tonnes/hectare in hardwood riparian corridors in natural or lightly managed river systems. In contrast, wood load on the LMR of 9 tonnes/hectare was six times lower than their prediction, an indicator of cumulative negative effects imposed upon geomorphic and ecological processes by river regulation.

Interestingly, the amount of LW in the study reach was perceived by the field crew to be quite abundant. This anecdotal response may well reflect general public perception across the U.S. (Chin et al. 2008). In the Chin et al. (2008) study, wood in river channels was perceived negatively, when compared to channels with no wood, by a sampling of college students in geography/environmental science classes in 7 of 8 states (Texas, Missouri, Illinois, Iowa, Georgia, Connecticut, and Colorado). Only Oregon students considered wood as significantly positive in river channels, which may be because pioneering work in recognizing LW as ecologically and geomorphically valuable has occurred in the PNW.

6.1.1 LW additions to regulated rivers

Latterell and Naiman (2007) found that abundant LW and intact transport mechanisms on the salmon-bearing Queets River in Washington State, U.S., created what they termed as a spiraling cascade effect, with LW pieces and accumulations in dynamic equilibrium with the channel and its hydrograph. Their conclusion suggests that there are vast potentials for increases in biocomplexity and system integrity if more LW was available to spawners on the LMR and other salmon-bearing regulated rivers, coupled with gravel augmentation and flow releases more in tune with a watersheds' natural hydrograph.

Brooks et al. (2006) recommended that if an increase in LW abundance was desired in a regulated river, periodic LW additions may be needed for up to decades until a successful riparian corridor rehabilitation project could supply the river with its LW needs. This study suggested that LW additions below dams are needed intermittently regardless of riparian corridor condition. LW deficits in regulated channels are due to 1) LW removal from the channel, 2) dams, which prevent LW transport from the upper watershed, and 3) riparian corridor fragmentation. It is not feasible to think that riparian corridor rehabilitation would replace all of the variables affecting LW loading in regulated rivers. The volume of periodic LW additions below dams should be based on knowledge of upper watershed wood fluxes into upstream reservoirs (Moulin and Piegay 2004) and regulated outflows below-dam.

LW placements have the capability to promote scour and deposition of river gravels (Montgomery et al. 1995) and to create habitat for juveniles (Roni and Quinn 2001). Geomorphic effects that redirect flows and improve habitat heterogeneity could be achieved by placing multiple LW pieces along channel bends, islands, and gravel bars. Riparian trees at water's edge combined with boulders positioned instream could serve as natural linchpins for channel margin logjams. A pilot project using existing riparian structure as natural linchpins and boulders as instream ballast placed 20 LW pieces into a logjam along on the LMR in summer 2007. In summer 2008, 20 additional LW pieces were added to increase the complexity of the initial logjam. Biological monitoring will reveal what, if any, life stages of salmon utilize the structure.

LW placements intended to influence local flow conditions and redd placements have been implemented on the LMR, by positioning individual LW pieces in mid-channel locations using boulders as ballast, during SHR gravel placement projects (Wheaton et al. 2004c). Merz (2001) and Wheaton et al. (2004c) showed that individual LW pieces were effectively utilized on the LMR by spawners. Consequently, results from this study, combined with previous observations from the LMR, show that optimally placed LW additions to regulated river channels create large- and small-scale geomorphic and ecological effects beneficial to spawning Chinook salmon.

6.2 Redd occurrence on a regulated river

Habitat type and accompanying substrate size, channel depth, and flow velocity were strong variables affecting redd locations (Elkins et al. 2007), with 90% of total redds located in Reach 1, 75% built in SHR zones across the study reach, 59% situated in riffles, and 33% in glides. In addition, LW was a strong variable affecting redd locations, as evidenced by 85% of redds within one average channel width (31 m) of at least one LW piece. Redds were highly stratified longitudinally, with 36% of total redds in the first 500 m of Reach 1 and just 10% (68) located in Reach 2.

Reach 2 had marginal spawning habitat compared to Reach 1, as evidenced from the highly stratified differences in redd and habitat unit distribution between the reaches. Reach 2 had less riffle and glide habitat than in Reach 1, with much of the glide habitat in Reach 2 associated with extensive pools rather than with riffles. LW-redd relationships were stronger in Reach 2 compared to Reach 1, which indicates that LW is an important component of habitat heterogeneity, and that LW provides channel complexity where ecological functions are dampened. At islands and point bars in Reach 2, macro-scale geomorphic structures and greater densities of LW pieces—in conjunction with habitat units and their associated characteristics—appeared to be the primary drivers in creating channel conditions favorable to spawners.

6.3 Habitat unit degradation in regulated rivers

Habitat unit distributions on the LMR reflect long-term habitat degradation that occurs on regulated rivers (Table 1). Loss of sediment supply from upstream of dams limits the potential for riffle-pool self-sustainability. Regulated flows dampen natural hydrographs (for the LMR see Pasternack et al. 2004), resulting in long periods during which low-flow channel non-uniformity concentrates peak local shear and lift stresses on riffle crests (MacWilliams et al. 2006). This persistence drives riffles to scour slowly but surely (Paintal, 1971), diminishing riffle-pool relief over decades. The problem is often exacerbated by anthropogenic modifications to the channel boundary (Petts and Gurnell 2005), which also limits the effectiveness of flow re-regulation as a rehabilitation tool (Jacobson and Galat 2006; Brown and Pasternack 2008). All of these factors help explain why heavily regulated flow regimes lead to riffle degradation, and consequently the difficulty of riffle rejuvenation without concomitant gravel augmentation, SHR, and re-regulated flows.

6.4 LW-redd-habitat unit interactions on the lower Mokelumne River

LW pieces and accumulations are primary components of habitat heterogeneity (Bilby 1984; Bisson et al. 1987; Abbe and Montgomery 1996; Piegay 2003; Latterell and Naiman 2007) that can create favorable habitat conditions for spawning salmonids (House and Boehne 1985; Bjorn and Reiser 1991, Merz 2001; Zimmer and Power 2006). Associations between LW and redds on the LMR were closely examined by Merz' (2001) study in two 100 m reaches approximately 2 km apart and downstream of this studies' extent. Results from Merz' (2001) study included: 1) the proportion of redds associated with LW increased as slope decreased, and 2) redds in both study reaches were significantly associated with LW. Zimmer and Power's (2006) study of spawning trout found that redds were significantly associated with LW in non-preferred habitats. This study concurs with Merz' (2001) and Zimmer and Power's (2006) conclusions that redds were associated with LW at higher rates in marginal habitat.

There are very few discussions in the literature about the distance that a spawner might travel in-between a redd location and cover. Crisp and Carling (1989) studied Atlantic salmon in England, noting as an exception in behavior one female spawner moving to and from a pool ~10 m away in the midst of redd construction. This lone observation coupled with LMR biologists' anecdotal evidence of spawners using approximately half of the channel width while spawning, hints that LW located in riffles and glides could be potentially advantageous to spawners for cover, refugia, and direct hydraulic effects. Further studies are needed to determine where and how often spawners move while waiting or actively engaged in the reproduction process. Such studies may discover that there are average or optimal distances from redd locations to cover locations for spawners, which would help guide LW placements intended as structural components compared to those intended as hydraulic components.

It is important to keep in mind that LW was not the only physical structure that spawners may have used for cover, for instance Wheaton et al. (2004c) reported that on the LMR overhanging trees, bank undercuts, gravel berms, boulder clusters, and pools were used in similar capacities. In addition, the relationships discussed herein between LW and spawning salmon were inferred rather than directly observed. The researchers collected field data on LW only, never attempting to observe actual interactions between LW and spawners. Nevertheless, this study contributes empirical evidence that

illuminates important spatial relationships between LW and redds.

6.4.1 Reach and geomorphic scale interactions

The degree of correspondence between LW and redds at reach ($\sim 10^2$ channel widths) and geomorphic scales ($\sim 10^1$ - 10^0 channel widths) suggests that LW is an integral component of habitat heterogeneity on the LMR. One important question that arises is whether other environmental factors might create co-occurrence effects that helped produce positive LW-redd associations but were not captured in this study. For instance, LW on the LMR lodged at higher rates at islands in Reach 2, thus contributing to habitat heterogeneity and positively affecting channel conditions for spawners (Figs. 5 and 6). Did the islands, LW at the islands, or a combination of variables including the islands and LW, create conditions conducive to salmon spawning in the marginal habitat of Reach 2? Islands and associated LW in Reach 2 were clearly related to redd placements (Fig. 6). It is probable that the islands were the mechanistic drivers of habitat heterogeneity, with LW along island margins a contributing factor. Geist and Dauble (1998) might suggest, for instance, that the geomorphic structure of the island promoted flow convergence, which increased local slope, which in turn created optimal hyporheic flow conditions for spawning. On the other hand, Smokorowski and Pratt's review (2007) showed that across multiple studies habitat heterogeneity—including experimental manipulation of LW as an important structural component—was correlated to fish community health and diversity. Thus, the question of which environmental variables contribute the most to redd placement near an island in marginal habitat remains to be answered with further study.

Although this research was not designed to explore variables outside of those fully discussed herein, it is likely that channel margin condition (riparian vegetation influences and bank undercutting) would be co-correlated with LW, since LW was highly associated with channel margins. In mid-channel areas where LW was not as prevalent yet was more likely to be hydraulically active, co-occurrence variables could include depth, velocity, and channel substrate.

6.4.2 Hydraulic scale interactions

At hydraulic scales ($\sim 10^1$ channel widths), most notably 36% of redds across the study reach were located within 10 m of LW, and 44% in Reach 2 (Table 2). The association of LW with redds decreased as progressively smaller radii were tested. This result infers that on the LMR, LW was primarily used as cover and refugia at larger hydraulic scales (10 m) rather than as hydraulic structures directly related to redd placement at smaller scales (5 and 2.5 m). In Reach 1, LW-redd associations were significantly greater than by random chance alone only at the 10 m scale, again indicating the use of LW as a structural cover component. Conversely, LW-redd associations were significantly greater than by random chance alone at all hydraulic scales in Reach 2. The differences between Reach 1 and 2 LW-redd intersections signify that where physical habitat conditions were marginal, LW pieces played a more active role in redd placements at all hydraulic scales.

The weakest relationship between LW and redds existed at the 2.5 m scale, where just 5% of redds are associated with LW. Yet even at this scale, random test results showed that these empirical associations were greater than by random chance alone. Thus, LW is a fundamental channel element utilized across multiple spatial scales.

6.4.3 Mid-channel interactions

Mid-channel analyses showed that at all scales and across both study reach segments, all LW-redd associations with respect to mid-channel were significant greater than by random chance alone. This was the only test where Reach 1 results were equally significant across scales and at the same rate as in Reach 2. It is likely that spawners were attracted to mid-channel where velocities provided optimal hyporheic flows into redds (Geist and Dauble 1998). This result suggests that placement of individual LW pieces near mid-channel during SHR projects would be beneficial to spawners.

6.4.4 Upstream/Downstream interactions

When considering upstream and downstream position of redds from a LW piece, redds built downstream of LW pieces occurred at greater rates than those placed upstream. One might expect to find more associations from the upstream direction, under the assumption that LW pieces were enhancing hyporheic flows. The greater incidence of redd placement downstream of a LW piece could indicate that female spawners swim upstream to use LW as cover and velocity refugia, using river currents to drift downstream and back to the redd when needed. The literature rarely discusses spawner movement away from a redd, let alone direction, so the interpretation of this result remains problematic at this time.

6.5 Revised conceptual model

It was initially conceptualized that LW-redd associations might follow a pattern similar to habitat suitability curves, so that at relatively low levels LW and redds would be positively associated; when an increase was seen in LW, a corresponding increase would be seen in redds. Results showed that at the reach scale LW was evenly distributed longitudinally (Fig. 3), while at the geomorphic scale LW was clustered at islands (Fig. 6). Redds, on the other hand, were preferentially clustered in riffle units regardless of the amount of LW in those areas. The high incidence of redds that were not associated with LW (Fig. 5) indicated that the portion of the conceptual model that postulated a positive linear relationship between LW and redds at low levels was not valid. Instead, there were negative linear relationships in riffles, runs, and glides, as redd densities generally decreased while LW densities increased. Furthermore, it was conjectured that a median amount of LW contributing to habitat heterogeneity would support the highest number of redds. In contrast, results showed that LW densities were significantly lower than redd densities in numerous locations where redd densities were high (Figs. 4 and 6). Finally, the initial conceptual model was constructed to suggest that too much LW could clog the channel, resulting in a decrease in the number of redds. There were no areas in the study reach where LW precluded redd building, thus no conclusions could be drawn from this portion of the conceptual model.

These results lead to an alternate conceptual model of LW-redd relationships on a regulated medium-sized river that incorporates the three spatial scales used to analyze the project data: reach, geomorphic, and hydraulic (Fig. 7). At the reach scale, LW was positively associated with redd locations. On the LMR, LW was most highly associated with redds at the geomorphic scale, where 85% of the time redds were constructed within one channel width of a LW piece. In addition, strong associations between LW and redds occurred at macro-scale geomorphic units, such as in natural and gravel-augmented riffles and glides, as well as near islands and gravel bars. At hydraulic habitat scales up

to 10 m in radius, LW was an important secondary component of the physical habitat micro-scape, serving spawners primarily as cover and refugia but up to 10% of the time providing direct hydraulic variation that created desirable channel conditions.

Strategic incorporation of LW into SHR projects could provide habitat heterogeneity and create channel complexity at multiple scales by restarting geomorphic and hydraulic processes that are currently lacking in regulated rivers. This conceptual model could be used as a guide when considering SHR project objectives associated with LW placements.

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List of Publications

None