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Large Wood Aids Spawning Chinook Salmon (*Oncorhynchus tshawytscha*) in Marginal Habitat on a Regulated River in California

Running Head:

Large Wood Aids Spawning Salmon

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ABSTRACT

To determine whether large wood (LW, ≥1-m length, ≥10-cm diameter) plays a role in Chinook salmon (*Oncorhynchus tshawytscha)* redd (i.e. egg nest) placements in a regulated, Mediterranean-climate, medium-sized river (where channel width is less than the upper quartile of length of potential instream wood pieces), characteristics of 527 large wood pieces, locations of 650 redds, and mesohabitat 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, CA. LW was regularly distributed across the study reach an average 70 LW pieces km^{-1}. Some LW clustering was evident at islands and meander bends. Spawners built 85% of redds within one average channel width (31 m) of LW. Spawners utilized LW within a 10 m radius 36% of the time in the upper 3 km rehabilitated reach, and 44% of the time in the lower 4.7 km marginal habitat reach. A greater percentage of LW was utilized in riffles in the upper 3 km reach where 90% of redds were built, while a larger percentage of spawners used LW in riffles in the lower 4.7 km reach. LW-redd interactions occurred at greater rates than by random chance alone in the lower 4.7 km reach, which implies that LW aids spawning in marginal habitats. River managers and salmonid spawning habitat rehabilitation (SHR) projects should take LW additions into consideration as an important component of river rehabilitation.

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 spawning habitat for adult Pacific salmon (*Oncorhynchus spp*.) (Merz *et al.,* 2004; Wheaton *et al*., 2004a,b). Increasingly, large wood (LW, ≥1 m length, ≥10 cm diameter) placements are used to improve juvenile Pacific salmonid habitat (Roni and Quinn, 2001). However, physical and ecological processes associated with LW may be important for adult salmonid spawning too, because wood removal from streams homogenizes habitats and reduces refugia, which contributes to fisheries population declines (Sedell *et al.*, 1990). Thus, it is timely to assess whether LW should be incorporated into adult salmonid spawning habitat rehabilitation (SHR) projects.

LW can create complex in-channel hydraulics that promote zones of scour and deposition (Abbe and Montgomery, 1996), help accumulate spawning gravels for Pacific salmon (House and Boehne, 1985), support substrate rejuvenation and hyporheic flows (Bryant *et al*., 2005), provide hydraulic refugia (Bisson *et al*., 1987), and enhance pool formation (Buffington *et al*., 2002). Such processes also create cover and refugia zones for juvenile fish rearing and adult fish holding (Roni and Quinn, 2001). Micro- and mesohabitat variability associated with individual LW pieces and LW aggregations offers all salmonid life stages thermal refugia, structural partitioning that provides protection from predation, and visual isolation that lowers inter-species competition (Dolloff, 1983). Nutrients and substrate for aquatic organisms are supplied via biological processing and degradation of the wood itself (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 salmonid juveniles, macroinvertebrates, terrestrial animals, and birds (Naiman *et al.*, 2002; Merz and Moyle, 2006).

Whether termed geomorphic variation, habitat heterogeneity, or channel complexity, instream physical characteristics and processes directly influence biological characteristics and processes in freshwater environments, including salmonid spawning behavior and redd (i.e. egg nest) site selection (Bjornn and Reiser, 1991; Baxter and Hauer, 2000; Buffington *et al*., 2004; Wheaton *et al*., 2004c). Variations in velocity, depth, and channel substrate have traditionally been used to predict where salmonid spawning may occur (e.g. PHABSIM; Raleigh *et al*., 1986; Milhous *et al*., 1989), but limitations exist with this methodology. PHABSIM does not take into account structural complexity provided by LW, boulders, undercut banks, overhanging vegetation, pools, turbidity, or turbulence, all of which create micro- and macrohabitat refugia for aquatic organisms (Sedell *et al.,* 1990). A geomorphological approach to salmonid spawning rehabilitation may additionally use slope, channel morphology, bedforms, vertical hydraulic gradient, hydraulic conductivity, or hyporheic flows to more accurately predict the extent of spawning habitat within a river (Geist and Dauble, 1998; Escobar and Pasternack, 2009).

Juvenile salmonids have been shown to utilize LW structures as overhead cover, while visual isolation and velocity refugia use occurred only in concert with use as cover (Fausch, 1993; Crook and Robertson, 1999). When artificial structures were used to mimic LW, juvenile coho (*O. kisutch*) sought out the greatest amount of structural complexity during the winter, particularly when flooding was simulated (McMahon and Hartman, 1989). Edge habitats in larger rivers with wood structure contained higher densities of juvenile salmonids, predominately in winter (Beechie *et al*., 2005). Increases in rearing habitat in two Oregon streams achieved in large part by LW additions resulted in increased over-winter survival rates of juvenile coho (Solazzi *et al*., 2000).

Instream structural complexity, including LW, provides refugia for salmonids before and during spawning activities, as well as after the culmination of reproductive events when energy conservation is critical for protecting redds. Spawning salmoids 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). Smaller males hover in safe zones such as cover provided by LW, and dart out when spawning opportunities arise because they are typically not able to establish their own territory (Esteve, 2005; Allen *et al*., 2007). Females establish channel bed territory in competition with other females, and expend tremendous amounts of energy preparing the channel bed for spawning activities (Fleming and Gross, 1994). 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 and Warren, 2003), thus helping to organize population-scale spawning behavior. Once spawning is complete, reproductive success is enhanced by the defense of redds until female death (Quinn, 2005).

House and Boehne (1985) reported on the deposition of suitable gravels and subsequent use by salmonid spawners in coastal Oregon when gabions (wire enclosed cobble walls), LW, and boulders were installed after stream cleaning. Stream reaches with pools formed by LW provided cover and increased habitat volume, supporting increases in coho and cutthroat trout (*O. clarki*) biomass (Fausch and Northcote, 1992). A study on resident brown trout (*Salmo trutta*) spawning preferences in Ontario, Canada found that as habitat quality decreased, there was a 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 (*Oncorhynchus tshawytscha)* redds were 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 microhabitat refugia by spawning Chinook from placed boulders, lodged LW, and existing pools when coupled with salmonid spawning habitat rehabilitation (SHR) tools such as gravel augmentation and riffle enhancement.

On regulated rivers, dams capture sediment and LW inputs and attenuate peak flows downstream, causing profound changes to riparian vegetation and the river channel. Regulated rivers are also commonly subjected to numerous engineered alterations (Brown and Pasternack, 2008). These direct and indirect impacts drive the direction and rate of change in downstream channel adjustment (Petts and Gurnell, 2005). Sustained periods of regulated low flows starved of sediment supply promote channel incision, loss of riffle-pool relief, and coarsening of channel substrate in gravel-bedded rivers (Kondolf, 1997; Brown and Pasternack, 2008). These channel adjustments negatively affect instream ecological responses that promote successful spawning in salmonid-bearing rivers. SHR projects, in conjunction with flow re-regulation, have become increasingly important to regulated river managers as a means to mitigate dam impacts (Brown and Pasternack, 2008). With stakeholders intent on increasing successful salmonid spawning conditions, it is appropriate to consider the relationship between LW and salmonid spawning success in the context of regulated rivers and SHR techniques. This study is significant because it illustrates important physical and ecological relationships between LW and spawning Chinook salmon behavior.

2.0 CONCEPTUAL MODEL

A systematic approach to the role of LW in relationship to salmon spawning behavior was developed using a conceptual model analogous to habitat suitability curves, which 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 (Raleigh *et al.*, 1986). A simple, process-based model (Fig. 1) examining spatial relationships between LW locations, redd locations and meso-habitat units was developed by hypothesizing that the association between Chinook salmon redd densities and LW densities might be shown as a modified Guassian curve. Degraded channel conditions with inadequate LW densities, and thus lower habitat heterogeneity, would yield low redd densities. As ecosystem function, channel complexity, and LW densities increase to robust natural conditions, redd densities might respond by increasing to optimum levels. Excessive levels of LW could block access to the river bed, promote fine-sediment deposition, and reduce velocities to stagnation; a hypothetical estimate of ~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 sought 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, distribution, and morphology, (2) Chinook salmon redd distribution, and (3) mesohabitat unit distribution, with an evaluation of (4) LW-redd-mesohabitat interactions across hydraulic (~10^{-1}-10^{0} channel widths in downstream length), geomorphic (~10^{0}-10^{1} widths), and reach scales (~10^{1}-10^{2} widths). Depending on flow conditions, hydraulic and geomorphic units can both function as ecological mesohabitats, defined by Moir and Pasternack (2008) as "the interdependent set of the same physical variables over a discernible landform known as a morphological unit (e.g., scour pool, riffle, and lateral bar)". Hydraulic unit analysis was also used to ascertain LW-redd-habitat interactions at the microhabitat scale, defined by Moir and Pasternack (2008) as "the localized depth, velocity, temperature, and substrate at a point in a river without regard to the surrounding conditions". The initial conceptual model was tested and modified based on study results.

3.0 STUDY AREA

The study encompassed a 7.7 km reach on the highly altered lower Mokelumne River (LMR) (Edwards, 2004; Pasternack *et al.,* 2004; Elkins *et al.,* 2007), from Camanche Dam 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 Mokelumne River watershed originates in the central Sierra Nevada at 3048 m above mean sea level (amsl), draining 1624 km^2 of central California. 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 and Mediterranean-montane climate zones, respectively. The watershed experiences hot dry summers and cool wet winters. Virtually all precipitation occurs October through April, mostly as snow above ~1200 m amsl. Peak snowmelt runoff takes place April-June. Mean annual precipitation (rain or snow water equivalent) in the Mokelumne River watershed 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).

The LMR is a medium-sized river as defined by the relationship between channel width and riparian tree height, where channel width is less than the upper quartile of potential instream wood pieces (Gurnell *et al*., 2002). Dam outflows averaged 10 m^3/s during the study period. Channel width averaged 31 m and varied from 15-83 m, while riparian trees could surpass 25 m in height. Mean riparian corridor width was 20±14 m, with ~30% fragmentation by pasture and agricultural fields (Edwards, 2004). Over one-half of the study reach was leveed, while numerous abandoned streamside gravel-mining pits were connected to the channel (Edwards, 2004). Agricultural fields were often terminated <10 m from the channel, and pasture could run to river's edge. Alder (*Alnus rhombifolia*) and willow (*Salix sp.*) were dominant riparian tree species, 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.

The California Department of Fish and Game has operated the Mokelumne River Fish Hatchery, owned by the East Bay Municipal Utility District (EBMUD), at the base of Camanche Dam since dam completion in 1964 as a means to mitigate the loss of salmon spawning habitat above the dam. Yearly EBMUD reports (e.g. Workman and Rible, 2007) estimate that an average 4436 adult Chinook salmon per year (minimum

250, maximum 16128) have returned to the river since 1964. An average of 70% of returning adults were harvested by the hatchery between 2002-2007. In the 2005-2006 spawning season 2157 redds were built, compared to 755 redds in 2006-2007, and 306 in 2007-2008. The area encompassed by Chinook redds ranged from 5.9 m^2 to 9.7 m^2 between 1992-1995, averaging 8 m^2 (Hartwell, 1996).

Extensive gravel augmentation and spawning bed enhancement has occurred on the LMR within the study site (Wheaton *et al*., 2004b; Pasternack *et al.,* 2004; Merz *et al*., 2006; Elkins *et al*., 2007). From 1999-2007, annual spawning habitat rehabilitation projects placed a total of 29 873 tonnes of gravel and cobble to fill abandoned instream gravel mining pits and create spawning habitat according to detailed designs (Wheaton 2004*b*). 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). Placed gravel was contoured to provide heterogeneous micro- and mesohabitat features for spawning, rearing, and adult holding habitat (Wheaton *et al*., 2004a,c). Boulder clusters were used to provide structural variation within the channel. Individual LW pieces were introduced sparingly, mostly buried in gravel so that stability was assured.

4.0 METHODS

A 7.7 km reach was identified where approximately 90% of redds on the LMR are built yearly. This study collected data on existing LW structures in relationship to the development of Chinook salmon redds during the 2006-2007 spawning season.

4.1 LW data collection

Criteria for inclusion of wood pieces in the survey were length ≥1 m and diameter

≥10 cm. In all habitat zones where physical characteristics suggested that spawning activity might occur, geographic location, mesohabitat type, and attributes (qualitative and quantitative measures described below) were recorded for each LW piece. Surveyed LW included living trees with some portion of the trunk submerged and canopy overhanging the channel, LW living or dead fully within the wetted channel in various stages of decay, LW deposited within the bankfull channel, and LW accumulated on or along mesohabitat channel features such as bars, meander bends, and islands. 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 m^3/s, only location and mesohabitat type were recorded. A Trimble Pathfinder PRO XRS GPS unit with real-time, sub-meter horizontal accuracy was used to record the geographic location of each LW piece.

Quantitative 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, and percent of immersion was estimated.

Leaves were used to identify live LW to genus, while dead LW was occasionally identified by bark characteristics. Origin was defined as bank erosion when roots were present, as cut or placed when evident by visual inspection, as limb breakage when the 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 algae covered <50% of the LW piece or >50% bark was present, heavily decayed when algae covered >50% of the LW piece or <50% of the bark was present, and waterlogged when the LW piece was fully immersed and resting on the channel bed with no other feature holding the piece in place.

LW morphology in terms of presence of leaves, 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. LW accumulations were noted only when deemed significant and could consist of any number of LW pieces greater than one individual piece. Significance was noted, but not quantitatively measured, when an accumulation was observed to play a role in flow direction, velocity, channel scour, or sediment deposition at typical flows during the study period.

The DBH equation with the highest product per input values was selected to calculate LW volume in an effort to consider all wood including trunks, limbs, and branches entering the channel.

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

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 per water surface hectare (t/ha) using a wood density of 500 kg/m^3.

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. Snorkeling surveys in the mid-1990's showed that spawning salmon did not build redds in LMR pools, thus EBMUD fisheries biologists did not survey pools for redds. Redd locations were recorded using a Trimble Pro XR GPS unit with sub-meter accuracy achieved by post-survey differential correction, then monitored for superimposition and scour in subsequent weeks using a GPS real-time mapping function.

4.3 Mesohabitat unit data collection

Mesohabitat units were designated as riffle, run, glide, and pool according to depth and surface velocity combinations based on known elements of the hydrologic signature of the LMR (Hartwell, 1996; Merz and Setka, 2004). 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, and transcribed onto an EBMUD river map. 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 commonly included within the dominant mid-channel mesohabitat type.

4.4 GIS database

In compliance with existing regional data standards, the study used the projected coordinate system NAD 1983 State Plane California III FIPS. LW and redd GPS coordinates were imported and projected in ArcMap 9.2 (ESRI, 2006) as shapefiles, with lines depicting LW length and orientation to flow, infinitesimal points representing redds, and polygons delineating mesohabitat units. If a mesohabitat type held the majority of a LW piece, the entire area of that mesohabitat was counted as area occupied by LW; likewise for redds. As an additional analysis tool, polygons were created every 25-m in the downstream direction and encompassed the bankfull channel.

4.5 Data analysis

To elucidate relationships within micro- and mesohabitats, buffers were created for LW and redd shapefiles. After discussions with EBMUD fisheries biologists who had observed Chinook salmon using approximately half the channel width while spawning, a conservative 10-m radii buffer zone was selected as the limit within which a salmon might swim in-between spawning activity. A 5-m radii was selected because it encompassed the average size of redds on the LMR of ~8 m^2 (~2 m by 4 m in elliptical shape) (Hartwell, 1996), in which case LW might provide partitioning from inter-species competition. A 2.5-m radii was selected as an indicator of LW playing a microhabitat role in redd location selection, because of LW influences on localized depth, velocity, temperature, substrate, and downwelling and upwelling created by channel roughness and consequent pressure differentiation (Brunke and Gonser, 1997; Moir and Pasternack 2008). Redds were counted as associated with a LW piece only when an individual redd point fell within an elongated LW buffer zone. Percent of channel covered by buffers was calculated to assess whether tested relationships were ecologically meaningful.

If a redd was located upstream of a LW piece and within a buffer zone, it was construed that the LW piece was influencing downwelling, and thus the association indicated optimal redd habitat. Conversely, if the location of a redd was downstream of a LW piece, it was interpreted as the LW piece providing cover or other refugia during spawning activity. LW-redd channel margin and mid-channel associations were analyzed to determine lateral distribution of LW and redds within the channel.

At the mesohabitat scale, percent of LW utilized by spawners in riffles was calculated to better understand how LW might influence salmon spawning in optimal mesohabitat units. Because of the non-parametric occurrences of no redds and no LW in some mesohabitat units, a matrix was constructed so that instances of LW-redds, LW-no redds, no LW-redds, and no LW-no redds could be analyzed individually. Additionally, LW and redds were depicted as totals per 100-m increment, with islands, gravel bars, meander bends, and LW accumulations notated and assessed visually to clarify spatial patterns.

Calculation of LW and redd densities per mesohabitat unit-type per 25-m polygon resulted in values <1. These values were normalized to 929 m^2 (30.5 m x 30.5 m) so the data could be presented at a scale of ~one channel width on the LMR. Normalized values were averaged for each mesohabitat type for statistical analysis. Non-parametric Kolmogorov-Smirnov measures were used to test for significant differences in average densities of LW and redds within mesohabitat types. The non-parametric Wilcoxon/Kruskal-Wallis rank sum test was used to check for significant differences in average densities of LW and redds between mesohabitat types.

At the reach scale, the 7.7-km study reach was divided based on mesohabitat characteristics: an upper 3-km reach designated as Reach 1, and a lower 4.7-km reach designated as Reach 2. Reach 2 was defined as marginal habitat for spawners because it supported a very low proportion of redds when compared to Reach 1, and, there was a significant increase in area of glide-pool mesohabitat in Reach 2. Cumulative downstream frequency was used to illustrate longitudinal distribution of LW in terms of accumulation or dispersal patterns as well as to depict redds in terms of cluster or dispersal patterns.

Observed two-unit mesohabitat sequences (e.g. riffle-pool or run-glide) were reported as ratios in a transition probability matrix, such that all possible transitions of a specific habitat type equaled one (Grant *et al.,* 1990). 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 to explore whether river regulation had affected mesohabitat unit distribution in the study reach.

To evaluate whether statistically significant LW-redd associations had occurred on the LMR, five 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 Reaches 1 and 2. All pools were excluded from these analyses since no redds were reported in pools. All analyses performed between LW pieces and existing redds were duplicated for each of five LW-random point data sets. The random data sets, which were uniformly distributed within the areal domain of the mapped river reaches (Pitman, 1993), were created in ArcMap using Hawth's Tools v.3.26. The five random data set results were averaged to provide one number to test against empirical LW-redd data using the independent one-sample student's t-test (Zar, 1999).

5.0 RESULTS

5.1 Large wood abundance, distribution, and morphology

Of the LW found within the study reach, 340 pieces were located in mesohabitat units where there was a reasonable probability of spawning activity. These LW pieces were measured and mapped, and hereafter will be 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 187 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 to discuss large wood in general.

Total LW was distributed downstream at a rate of 70 pieces km^{-1} with an $R^2=0.99$ (Fig. 3). The majority of active LW pieces were angled approximately parallel to flow, with 57% oriented 135°-225° to flow. Less than 20% of active LW pieces spanned the channel laterally by more than 6 meters. Forty percent of active LW pieces resided partially on a bank, and 59% rested within 2.5 m of a channel margin. Gravel bars and islands made up 5% of the bankfull channel area yet held 12% of active LW pieces. Of active LW pieces, 84% were protruding out of the water to some degree, including those pieces that were residing on the bank but within the bankfull channel.

Tree species identification was limited because of variability in decay condition. Only 22% of active LW pieces were identifiable: alder (50 pieces), valley oak (8), cottonwood (3), ash (1), and willow (12). Thirty-six percent of active LW originated from bank erosion. An additional 5% of active LW originated from anthropogenic activities, as evidenced by cuts at one or both ends. Decay classifications showed that 11% of active LW pieces were fresh, 24% lightly decayed, 49% heavily decayed, and 16% waterlogged.

Eighty-five percent of active LW pieces had no green leaves and were considered dead, the remaining 15% were recorded as live LW. 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 active LW with limbs <2 cm in diameter, 66% had no small branches, while 19% had ≥20 small limbs.

Active LW accumulations of 2 or more pieces (hereafter called logjams) played a significant role in micro- or mesohabitat dynamics in 11 instances. Logjams were located at meander bends (Figs. 4a, c), where a live tree overhanging or entirely in the channel provided a stable structure for active LW to lodge against (Figs. 4a, b, c, d), in backwater areas where active LW deposited during the falling limb of high flows (Figs. 4a, e), at islands (Figs. 4a, c, e), and in riffles and runs (Figs. 4a, b, c, e). No logjam contained more than 10 active LW pieces, although smaller wood pieces were present in most accumulations.

Active LW piece volume ranged from 0.02 m^3 to 27 m^3, averaging 1.0 m^3. Field observations suggested that inactive LW pieces were of average active LW volume, for an estimated volume of 517 m^3 for 527 total LW pieces in the study reach. Total wood load for the study reach was 9.2 t/ha.

5.2 Redd distribution

Longitudinal redd distribution indicated high correlation between redd distribution and the full study reach, $R^2 = 0.76$ (Fig. 3), although 36% of redds were built in the first 500-m below Camanche Dam where intensive SHR projects had occurred. Seventy-five percent of redds were sited on SHR gravels distributed throughout the study reach (Fig. 4). Across the full 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. Eighty-eight percent of redds in Reach 2 were located in riffles, while the remaining 12% were distributed evenly between runs and glides. In Reach 2, 56% (38 of 68) of redds were located in one SHR project just below Hwy 88, another 32% were built near islands.

5.3 Mesohabitat unit distribution

Using transition probability analysis, glides were most often followed by riffles, pools were most often followed by glides, and riffles were most often followed by glides (Table 1). Riffles encompassed 20% of Reach 1 river habitat, runs 16%, glides 41%, and pools 23% (Fig. 4). In Reach 2, riffles encompassed 11% of river habitat, runs 5%, glides 34%, and pools 50%. Reach 2 was dominated by 3.5 km of glide-pool zones from 3200-4800 m, 5600-6400 m, and 6600-7700 m (Figs. 4c, d, e) downstream of Camanche Dam. Riffles covered 42 662 m^2 in total area, runs 26 700 m^2, glides 107 130 m^2, and pools 112 000 m^2. Islands covered 10 073 m^2 and gravel bars 3 936 m^2.

5.4 LW-redd-mesohabitat interactions

In Reach 1, active LW located in riffles was utilized by spawners 68% of the time (32 of 47 LW pieces) within a 10 m radius, and in Reach 2, 44% of the time (24 of 55), for an average 55% utilization of active LW located in riffles across the 7.7 km study reach. Redds were present with and without active LW in riffles, glides, and runs, whereas LW was present in all mesohabitat types regardless of whether redds were present (Fig. 5). When redds were present in a specific 25-m polygon, active LW was present in the same polygon 50% of the time across the full study reach, 48% of the time in Reach 1, and 56% of the time in Reach 2. Redd densities were highest in Reach 1, where greater than 10-redds/929 m^2 were present in 22 riffles and 12 glides. Conversely, Reach 2 had four riffles and one glide with densities greater than 10-redds/929 m^2.

Greater than 90% of active LW pieces were within 10 m of the channel margin, as were the majority of redds (Table 2h). Channel margin versus mid-channel results overlapped because channel width averaged just 31 m, such that 71% of LW-redd intersections occurred within 10 m of mid-channel (Table 2e) at the same time 56% were within 10 m of the channel margin (Table 2h). Redd placements upstream versus downstream of active LW pieces showed that redds tended to be placed downstream of LW pieces (Table 2i, j).

Active LW buffer coverage in Reach 1 was approximately equal across mesohabitat types, with 27% of riffle, 33% of run, and 33% of glide area encompassed within 10 m buffers, and in Reach 2, 43% in riffles, 48% in runs, and 33% in glides. The highest degree of coverage by redd buffers occurred in Reach 1, with 71% of available riffle area covered within 10 m buffers, while 27% of available area was covered in both runs and glides. Percentages of redd buffer coverage declined considerably in Reach 2, with 32% of available riffle area covered within 10 m buffers. Intersections between active LW and redds encompassed even smaller areas. In Reach 1 within 10 m buffers, 17% of riffles areas were covered by LW-redd intersections, as were 6% of runs and 12% of glides, and in Reach 2, 13% in riffles, 8% in runs, and 2% in glides. The microhabitat scales used for analyses were deemed ecologically appropriate considering LW-redd intersections encompassed minimal amounts of available channel.

Redds were heavily clustered in the SHR project sites (Fig. 6). Outside of SHR sites, active LW and redds peaked together in low densities in riffle zones at islands and gravel bars. Islands and gravel bars captured active LW at a rate of ~20 LW pieces per

100 m section, whereas rates ranged from 0-10 active LW pieces per 100 m elsewhere.

At the reach scale, total LW pieces were within one average channel width of redds 85% of the time, with an $R^2 = 0.73$. Results of non-parametric Kolmogorov-Smirnov tests indicated no significant differences in average total LW density between mesohabitat types. There were significant differences in average redd densities between riffles and all other mesohabitat types ($p < 0.001$), but no significant differences between glides and runs ($p > 0.10$). When testing differences in densities of active LW and redds within mesohabitat 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 ($p = 0.4158$).

Empirical LW-redd intersections were significantly greater than the randomly generated LW-point intersections across the full study reach. In Reach 2 empirical associations were significantly greater at every scale, but in Reach 1 were only significant at the 10 m scale (Table 3). Mid-channel intersections were significantly greater than random intersections at every scale in both reaches. Channel margin intersections were significantly less than random intersections at every scale in Reach 1, but were significantly greater at every scale in Reach 2. Upstream/downstream intersections were generally not significantly greater than random intersections except downstream of a LW piece in Reach 2.

6.0 DISCUSSION

Spawners placed redds closer to LW than by random chance alone across the full study reach and particularly in Reach 2 (Table 3), which constituted a zone of marginal micro- and mesohabitats. The initial conceptual model (Fig. 1) was not validated in this study; utilization of LW for spawning does not follow a simple statistical distribution, such as those commonly observed for substrate, depth, and velocity utilization. Mesohabitat type was observed to be the first-order control on redd location, regardless of active LW density. Next, the occurrence of SHR in Reach 1 overwhelmingly attracted spawners to the artificially created, highly preferred microhabitat conditions. However, this study found that LW is positively associated with Chinook salmon redd locations across microhabitat, mesohabitat, and reach scales. LW additions are beneficial to spawning salmon on regulated rivers where channel degradation, LW deficits, and marginal habitat exist, as well as in rehabilitated reaches.

6.1 LW in a regulated river

LMR wood load measures of 9.2 t/ha were compared to other reported values of wood loading worldwide (Keller and Swanson, 1979; Bilby and Bisson, 1998; Gurnell *et al.,* 2002). Most wood load measures come from smaller mountainous streams or from larger rivers than the LMR, which illustrates how little is known about current wood abundance on rivers, or what ecologically appropriate wood loads might be for a given river. Wood loads for Sierra Nevada 2^{nd} to 5^{th} order streams, located between ~1000-2000 m amsl in the Stanislaus and Tuolumne River watersheds, were observed as 25-100 t/ha (Ruediger and Ward, 1996). Another Sierra Nevada study reported values from eastern slope, high elevation, headwater streams, where loads ranged from 2-19 t/ha (Berg *et al.,* 1998). Although the Mokelumne River emanates from the Sierra Nevada, these values are marginally comparable to the LMR study reach, where elevation is <100 m and the historic forest type was oak woodlands locally and coniferous forest upstream.

A more equivalent reach size of 40-m width on the MacKenzie River in the Pacific Northwest, OR reported 5 t/ha (Keller and Swanson, 1979), though forest types differ considerably between temperate rain-forest and Mediterranean-montane climates. Most analogous may be reaches from the Mediterranean-montane climate Drome and Ain Rivers of France with values ranging from 1-30 and 21-164 t/ha, respectively (Piegay *et al*., 1999; Lassettre *et al*., 2008).

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. A wood load of 55 t/ha was predicted for rivers in unmanaged or lightly managed river systems with mixed conifer and hardwood forests. The LMR, a highly managed river, had a wood load of 9.2 t/ha, ~20% of that predicted for a lightly managed river. This low level of wood is an indicator of cumulative negative effects imposed by river regulation and management on geomorphic and ecological processes provided by LW.

Logjams and individual LW pieces, whether channel spanning, along a channel margin, or lodged in-channel, can form dynamic micro- and mesohabitat structures along the river continuum that influence flows and provide habitat heterogeneity for aquatic species (Maser and Sedell, 1994). This study identified 11 logjams as small as 2 LW pieces that had observable effects on channel condition as evidenced by gravel and sand deposition, forced riffles and runs, and bank protection. This evidence suggests that LW on the LMR does influence micro- and mesohabitat processes, and that LW placements could be targeted toward influencing specific channel processes.

LW on the LMR has been reduced from historic levels, like so many other rivers in the United States (e.g. Hall and Baker, 1982; Triska, 1984; Wooster and Hilton, 2004) and Europe (Gurnell and Petts, 2002). LW deficits in regulated channels are due to LW removal, longitudinal disconnection from the upper watershed, and riparian corridor fragmentation. On the LMR, LW transport from above Camanche Dam is lost. Although LW is regularly distributed, the riparian corridor is fragmented, coupled with a wood load of ~20% of modeled projections. Furthermore, as a biological-structural component, LW may not remain in-place or whole at temporal scales of years to decades. These observations suggest that LW additions may be periodically needed for decades while riparian corridor fragmentation is rehabilitated (Brooks *et al*., 2006). The addition of multiple LW pieces intended to improve wood budget deficits and provide micro- and mesohabitat spawning structure might be thought of similarly to periodic gravel additions in SHR projects below dams that amend sediment budget deficits. The volume of recurring LW additions in salmonid-bearing river reaches below dams should be based on knowledge of wood fluxes into reservoirs (Moulin and Piegay, 2004) and regulated outflows below-dam.

A pilot project placed 35 LW pieces (~35 m^3) into a logjam along the channel margin of the LMR in summer 2007, using existing riparian structure as natural linchpins and boulders as instream ballast. In summer 2008, another 20 LW pieces (~20 m^3) were added to increase the complexity of the initial logjam, and additional individual LW pieces were placed mid-stream using boulders to secure them. Preliminary biological monitoring has documented that both adult spawning salmon and juveniles have utilized the placed structures.

6.2 Redd occurrence on a regulated river

Substrate size, channel depth, and flow velocity are strong microhabitat variables affecting redd locations (Elkins *et al.,* 2007), particularly in gravel-augmented sections as indicated by the clustering of redds in SHR zones of the study site. The co-occurrence of these rehabilitated ecosystem variables may help explain why LW-redd relationships were significantly different from random point tests just 30% of the time in Reach 1 (Table 2). Though Reach 2 contained ~10% of redds, 86% of the tested relationships were statistically significant. In marginal habitat zones, spawners seeking areas where the presence of LW mitigated marginal microhabitat variables such as velocity, substrate, or depth might help explain the differences between Reach 1 and 2 random tests.

6.3 Mesohabitat units in regulated rivers

Channel units may repeat themselves in sequences that provide information about important properties of a river reach. Transition probability analysis (Grant *et al.,* 1990) has been underutilized and may become more valuable now that detailed spatial datasets of fluvial landforms are becoming more available. An important first step is to determine common transition patterns for diverse natural and regulated streams. Pristine gravel-bedded rivers, as the LMR was historically, exhibit riffle-pool sequences (Richards, 1976). Mesohabitat unit distributions revealed by the Markov chain analysis on the LMR reflect long-term degradation that occurs on regulated rivers (Table 1, Fig. 4). Specifically, the abundance of transitions from riffles and pools to glides rather than to each other may be indicative of a loss of riffle-pool relief. 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). These factors help explain why heavily regulated flow regimes lead to riffle degradation, and consequently the difficulty of riffle rejuvenation without coincident SHR practices, including gravel augmentation and re-regulated flows.

6.4 LW-redd-mesohabitat interactions

Merz' (2001) study of LW-redd interactions on the LMR reported that 29% of redds were built within 3-m of LW in three 100-m study sections, and that LW-redd associations increased in the downstream direction as slope decreased. Subsequently, in the 2002-2003 spawning season, gravel augmentation as well as LW and boulder additions increased habitat heterogeneity, and in two SHR riffles, 70 redds were placed within 10 m of 93% of available structural elements (Wheaton *et al*. 2004c). By comparison, in Reach 1, 68% of active LW in riffles (32 of 47 pieces) were within 10 m of 132 redds (23% of spawners) during the 2006-2007 spawning season. In Reach 2, 44% of active LW in riffles (24 of 55) were within 10 m of 28 redds (41% of spawners). A greater percentage of LW was utilized in Reach 1 riffles where 90% of redds were built, indicating that LW was not avoided when microhabitat conditions were optimal. A larger percentage of spawners used LW in riffles in the Reach 2 marginal habitat zone, indicating that LW attracted spawners by providing additional micro- and mesohabitat complexity.

Bilski (2008) studied hyporheic flows, water quality, and Chinook salmon embryo survival on the LMR during spawning season 2006-07. Measurements were taken at paired sites, one with and one without structure; LW was the structural element at four of eight sites. Vertical hydraulic gradient means and surface water velocities were found to be significantly greater where structure was present. Incubation tubes located above LW and boulder structures experienced higher degrees of dissolved oxygen concentrations, pH values, and downwelling than the paired non-structural sites. These conditions improved embryo development, growth, and survival in marginal habitat, though not at statistically significant rates. Zimmer and Power (2006) found that brown trout redds in Ontario, Canada were significantly associated with LW in non-preferred habitats with low slopes and impacted riparian corridors. In conjunction with the results of this study, evidence of targeted use of LW by salmonid spawners when marginal habitat is encountered is beginning to accumulate.

There are few discussions in the literature about the distance that a spawner might travel in-between a redd location and cover, or direction of movement to and from a redd. Crisp and Carling (1989) studied Atlantic salmonids in England, noting ‘exceptional’ behavior of one female spawner moving to and from a pool ~10 m away in the midst of redd construction. This single observation, LMR biologists’ anecdotal evidence of Chinook adults using approximately half of the channel width while spawning, and other salmonid behavioral studies indicate that salmonid spawners use LW for cover and refugia. Future studies may discover that there are average or optimal distances from redd locations to cover locations for spawners waiting for or actively engaged in the reproduction process, which could help guide LW placements.

One important question that arises is whether other environmental factors might create co-occurrence effects that helped produce positive mesohabitat LW-redd associations but were not captured in this study. For instance, islands and gravel bars in Reach 2 were associated with greater densities of LW pieces and redds (Figure 6). These mesohabitat features may help explain the mechanistic development of channel conditions favorable to spawners by promoting flow convergence, increasing local slope, and creating optimal hyporheic flow conditions for spawning (Geist and Dauble, 1998). Wheaton *et al*. (2004c) reported that on the LMR overhanging trees, bank undercuts, gravel berms, boulder clusters, and pools were used in similar capacities to LW. Channel margin conditions such as riparian vegetation influences and bank undercutting might co-correlate with LW. On the other hand, Smokorowski and Pratt's review (2007) showed that across multiple studies, habitat heterogeneity, including experimental manipulation of LW, was positively correlated to fish community health and diversity, suggesting that LW itself plays an important role in ecosystem health. Which environmental variables contribute the most to redd placements, particularly in marginal habitat, remains to be answered. This study contributes empirical evidence that illuminates significant spatial relationships between LW and redds.

6.5 Conceptual model revisited

It was initially conceptualized that LW-redd associations might follow a pattern similar to habitat suitability curves. The high incidence of redds that were not associated with LW (Fig. 5) indicated that a positive linear relationship between LW and redds at low levels was not valid. Redds were found to occur preferentially in riffles with high quality microhabitat characteristics. Absence of LW or low LW densities did not preclude presence of redds, especially where the stream was enhanced by SHR. Even so, spawners in SHR riffles often situated redds close to LW, and in marginal habitats an even higher percentage of spawners positioned redds close to LW. High numbers of redds were associated with the full range of wood densities, in riffles up to 15 pieces per 929 m^2; in glides up to ~7 pieces; in runs up to ~4 pieces. The results stratified by mesohabitat type do show an envelope line of decreasing redds as LW density increases, but an inadequate range of LW densities exists, due to projected LW deficits, for this result to be certain. Furthermore, it was conjectured that a median amount of LW 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, 5, 6). Geomorphic mesohabitat associations were not statistically analyzed, but visual inspection showed that LW-redd associations in Reach 2 marginal habitat occurred at islands, bars, and bends in association with LW (Fig. 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. The highest measured rate of ~20 LW pieces per 929 m^2, clustered at an island margin, did not cover the channel bed, rather, it contributed to some of the highest mesohabitat variation in Reach 2. There were no areas in the study reach where LW precluded redd building, suggesting that a substantial increase of LW would positively affect salmon spawning in river systems where significantly less LW is present than predicted wood loadings (Gurnell *et al.*, 2002).

The results of this study lead to a greater understanding of LW-redd relationships on a regulated, medium-sized, Mediterranean-montane climate river. LW influences, though supply limited, were active on the LMR across four magnitudes (10^{-1}-10^{2}) of spatial scale. Results of this study were used as the basis for a revised conceptual model of LW benefits to spawning salmonids at varying spatial scales (Table 4). Strategic incorporation of LW into SHR projects will provide habitat heterogeneity and create channel complexity at multiple scales by helping to restart micro- and mesohabitat processes that are currently lacking in marginal habitat zones in regulated rivers (Table 4). A greater understanding of LW processes will help guide river management decision-making when considering LW placements in association with SHR project objectives.

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Table 1. Mesohabitat transition probability analysis
(A) Observed transitions versus (B) random sequence probabilities.
Positive values in (C) indicate which transitions predominate.

A. Observed Transition Probabilities				
Downstream unit	Upstream unit			
	Riffle	Run	Glide	Pool
Riffle	0	0.27	0.61	0.25
Run	0.32	0	0.12	0.08
Glide	0.55	0.55	0	0.67
Pool	0.13	0.18	0.27	0
Total	1	1	1	1
B. Transition Probabilities, random sequencing				
Downstream unit	Upstream unit			
	Riffle	Run	Glide	Pool
Riffle	0	0.38	0.42	0.37
Run	0.44	0	0.27	0.22
Glide	0.37	0.41	0	0.41
Pool	0.19	0.21	0.31	0
Total	1	1	1	1
C. Observed minus random transition probabilities				
Downstream unit	Upstream unit			
	Riffle	Run	Glide	Pool
Riffle	0	-0.11	0.19	-0.12
Run	-0.12	0	-0.15	-0.14
Glide	0.18	0.14	0	0.26
Pool	-0.06	-0.03	-0.04	0
Total	0	0	0	0

Table 2. Microhabitat analyses of empirical LW-redd data						
	Reach 1, upper 3 km	%	Reach 2, lower 4.7 km	%	Full study reach, 7.7 km	%
(a) # LW in potential redd habitats	192		148		340	
# Redds	582		68		650	
TOTAL INTERACTIONS						
(b) Total LW-redds intersecting within a 2.5 m radius [2]	23	4.0	7	10.3	30	4.6
Total LW-redds intersecting within a 5 m radius [2]	94	16.2	14	20.6	108	16.6
Total LW-redds intersecting within a 10 m radius [2]	204	35.1	30	44.1	234	36.0
MID-CHANNEL INTERACTIONS						
(c) LW within 2.5 m of mid-channel [1]	22	11.5	2	1.4	24	7.1
Redds within 2.5 m of mid-channel [2]	96	16.5	12	17.6	108	16.6
LW-redds intersecting within 2.5 m of mid-channel [2]	10	1.7	3	4.4	13	2.0
(d) LW within 5 m of mid-channel [1]	40	20.8	19	12.8	59	17.4
Redds within 5 m of mid-channel [2]	188	32.3	28	41.2	216	33.2
LW-redds intersecting within 5 m of mid-channel [2]	29	5.0	6	8.8	35	5.4
(e) LW within 10 m of mid-channel [1]	112	58.3	65	43.9	177	52.1
Redds within 10 m of mid-channel [2]	402	69.1	62	91.2	464	71.4
LW-redds intersecting within 10 m of mid-channel [2]	142	24.4	25	36.8	167	25.7
CHANNEL MARGIN INTERACTIONS						
(f) LW within 2.5 m of channel margin [1]	129	67.2	71	48.0	200	58.8
Redds within 2.5 m of channel margin [2]	49	8.4	5	7.4	54	8.3
LW-redds intersecting within 2.5 m of channel margin [2]	3	0.5	3	4.4	6	0.9
(g) LW within 5 m of channel margin [1]	156	81.3	103	69.6	259	76.2
Redds within 5 m of channel margin [2]	107	18.4	17	25.0	124	19.1
LW-redds intersecting within 5 m of channel margin [2]	17	2.9	10	14.7	27	4.2
(h) LW within 10 m of channel margin [1]	173	90.1	145	98.0	318	93.5
Redds within 10 m of channel margin [2]	315	54.1	51	75.0	366	56.3
LW-redds intersecting within 10 m of channel margin [2]	103	17.7	27	39.7	130	20.0
UPSTREAM-DOWNSTREAM INTERACTIONS						
(i) Redds upstream of LW						
Within 2.5 m [2]	20	3.4	1	1.5	21	3.2
Within 5 m [2]	37	6.4	6	8.8	43	6.6
Within 10 m [2]	91	15.6	11	16.2	102	15.7
(j) Redds downstream of LW						
Within 2.5 m [2]	13	2.2	6	8.8	19	2.9
Within 5 m [2]	48	8.2	9	13.2	57	8.8
Within 10 m [2]	132	22.7	21	30.9	153	23.5
[1] percentages equal the number in column to left divided by # LW * 100						
[2] percentages equal the number in column to left divided by # Redds * 100						

Table 3. t-scores and corresponding significance of random tests (excluding all pool areas). Actual relationships between LW and redds occurred at rates greater than by random chance alone where t-score results were data>random.
(a) data>random, (b) no difference, (c) random>data
For all tests, t-statistic = 2.776, P = 0.05, df = 4

All LW-redd intersections	10 m	5 m	2.5 m
Reach 1	7.68, (a)	2.43, (b)	15.65, (c)
Reach 2	32.75, (a)	22.24, (a)	14.57, (a)
7.7 km study reach	3.44, (a)	24.6, (a)	2.98, (a)
Mid-channel intersections			
Reach 1	33.15, (a)	12.39, (a)	12.69, (a)
Reach 2	28.35, (a)	19.3, (a)	31.3, (a)
Channel margin intersections			
Reach 1	5.29, (c)	11.83, (c)	7.95, (c)
Reach 2	43.62, (a)	22.14, (a)	23.74, (a)
Upstream-downstream intersections			
Reach 1			
Upstream	1.3, (b)	5.7, (c)	1.3, (b)
Downstream	25.8, (a)	2.4, (b)	13.3, (c)
Reach 2			
Upstream	2.5, (b)	3.2, (a)	1.0, (b)
Downstream	16.6, (a)	11.8, (a)	25.2, (a)

Table 4. Conceptual model of LW benefits to spawning salmonids

Reach scale, 10^1-10^2		
	LW structural elements	
		lodge at channel margins > mid-channel
		lodge at islands, gravel bars, meander bends
		lodge individually or in jams of 2 or more pieces
		influence channel morphology
Mesohabitat scale, 10^0-10^1		
	LW influences	
		flow velocity
		flow convergence/divergence
		channel roughness
		gravel deposition
		sediment storage
		bed and bank scour
		structural complexity
Microhabitat scale, 10^{-1}-10^0		
	LW influences	
		local slope
		hyporheic flow
		convective acceleration
		shear turbulence
	LW serves as refugia	
		cover
		flow variation
		safe resting zones
		intra-species competition
		temperature
		predation

List of Figures

Fig. 1. Initial conceptual model of LW-redd-habitat unit relationships on a regulated river in a Mediterranean climate zone. Table 4 depicts a new conceptual model based on study results.

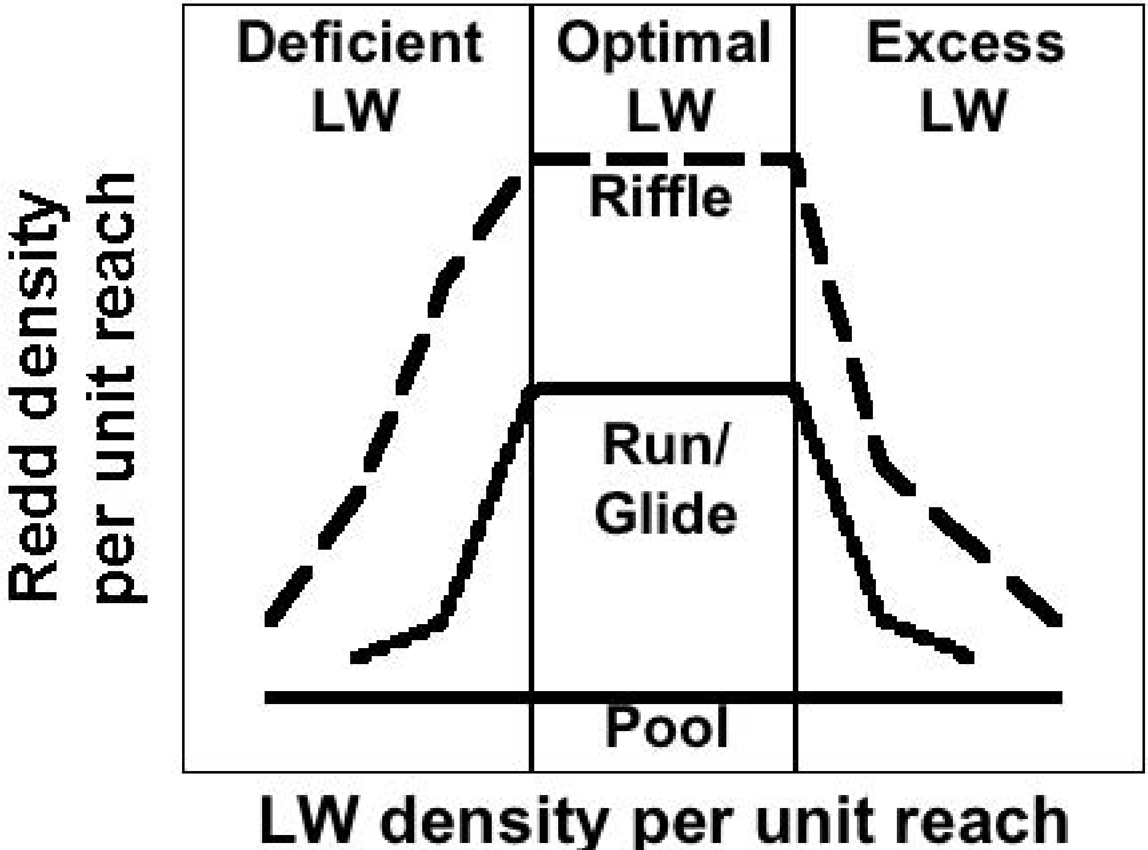
Fig. 2. Mokelumne River watershed. Study reach started at the hatchery fish fence directly below Camanche Dam and extended 7.7 km downstream to Mackville Bridge Road.

Fig. 3. Cumulative downstream frequency curves for LW and redds. LW $R^2 = 0.99$, redds $R^2 = 0.76$. Reach 1 contained 39% of study reach length, 36% of total LW pieces, and 90% of redds. Reach 2 contained 61% of study length, 64% of total LW pieces, and 10% of redds.

Figs. 4a to 4e. LW, redds, and geomorphic features below Camanche Dam, a) 0-1500 m, b) 1500-2700 m, c) 2700-3850 m, d) 3850-5700 m, and e) 5700-7050 m. Reach 1 encompassed the first 3 km. Reach 2 encompassed 3-7.7 km.

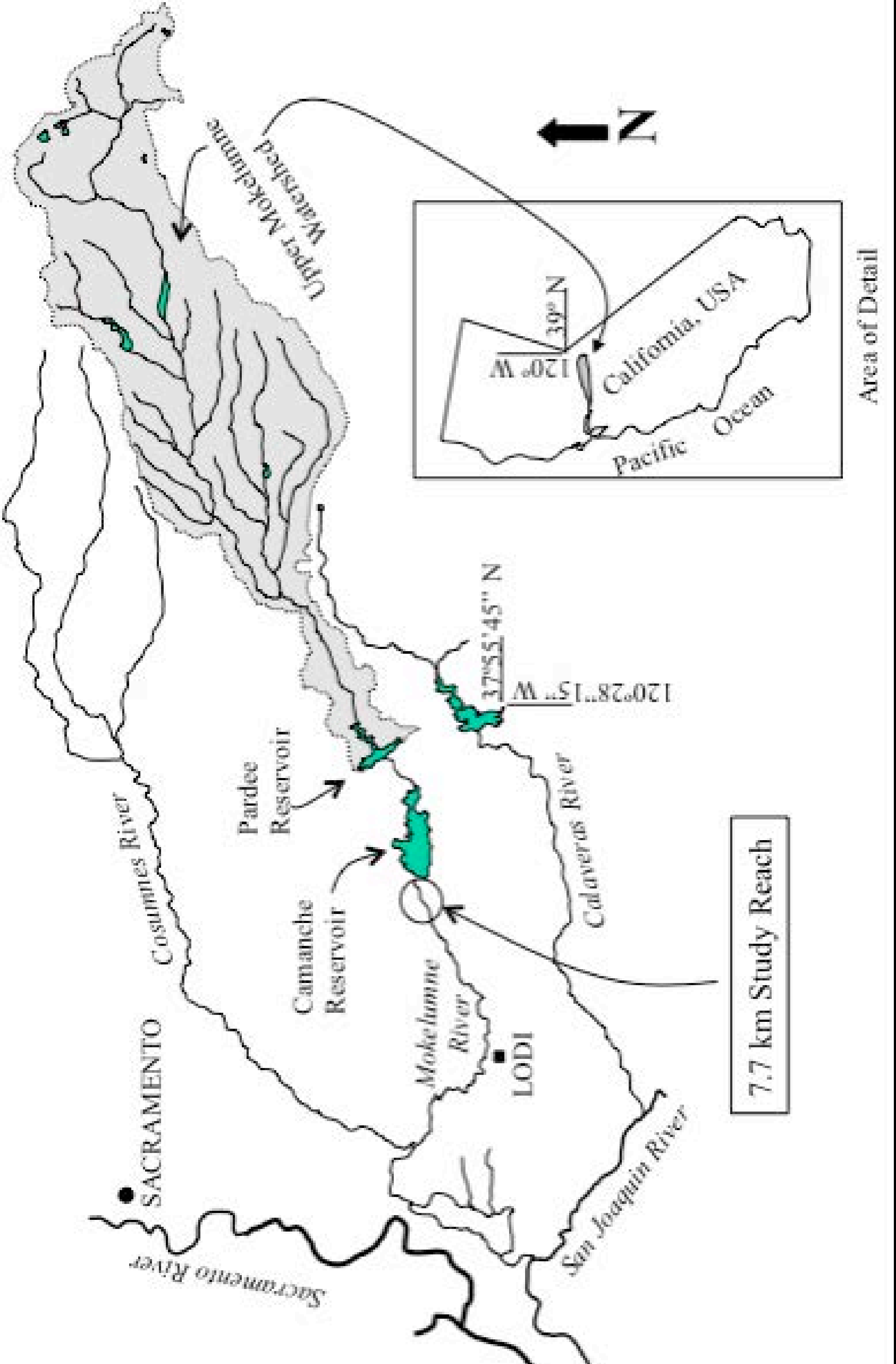
Fig. 5. Density plots of LW versus redds per habitat type. Note differing scales on each axis. Low correlations (e.g. riffles R^2=0.11) were attributed to the high number of data points where x or y=0.

Fig. 6. LW-redd geomorphic interactions per 100 m. Spawners heavily utilized SHR mesohabitat units in Reach 1. Three prominent islands had highest LW densities of ~20 LW pieces per100 m, while redds in Reach 2 marginal habitat peaked at two islands located.



Deficient LW
Optimal LW
Excess LW
Riffle
Run/ Glide
Pool
Redd density per unit reach
LW density per unit reach

Fig 1



Upper Mokelumne Watershed
N
120° W
38° N
California, USA
Pacific Ocean
Area of Detail
37°55'45'' N
120°28'15'' W
Pardee Reservoir
Camanche Reservoir
Cosumnes River
Calaveras River
7.7 km Study Reach
Mokelumne River
LODI
SACRAMENTO
Sacramento River
San Joaquin River

Fig 2

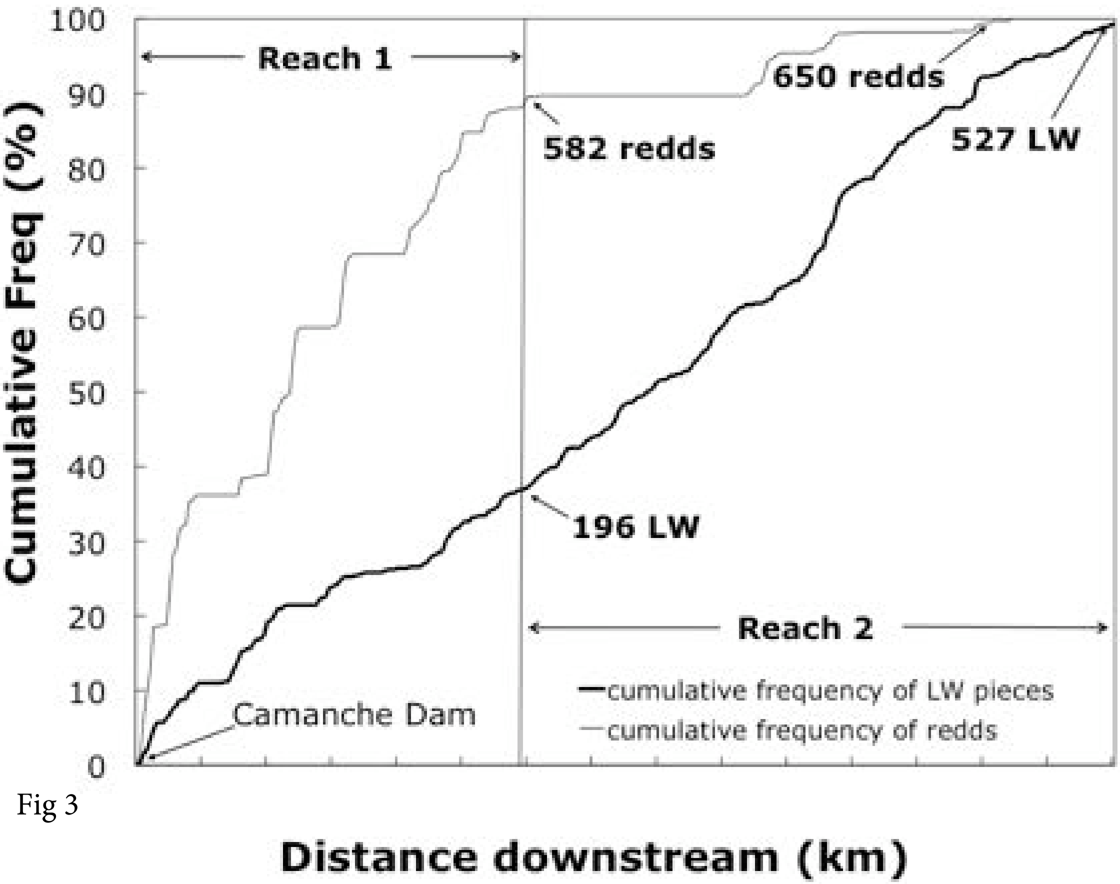
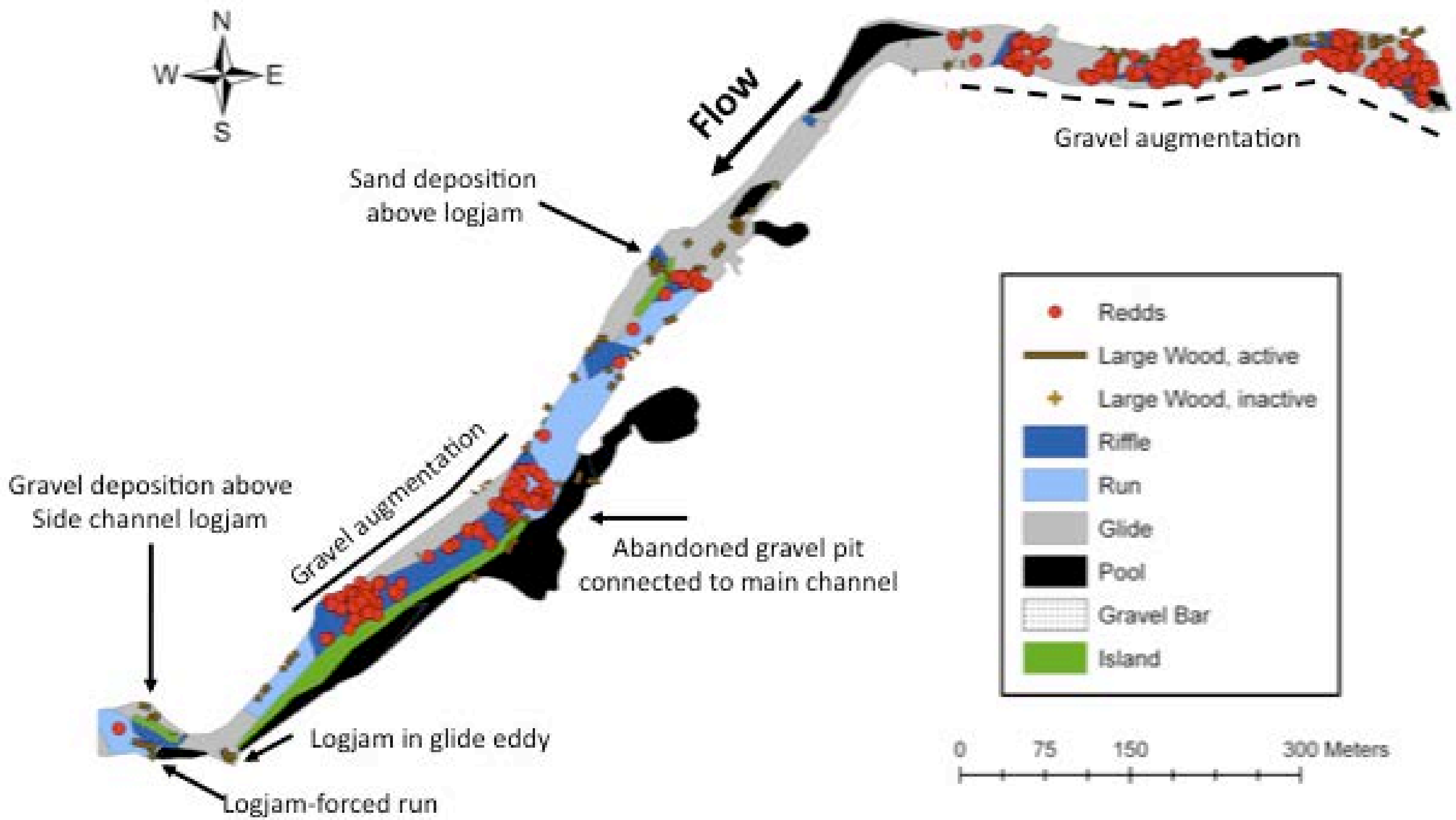

Cumulative Freq (%)
100
90
80
70
60
50
40
30
20
10
0
Reach 1
650 redds
582 redds
527 LW
196 LW
Reach 2
cumulative frequency of LW pieces
cumulative frequency of redds
Camanche Dam
Distance downstream (km)

Fig 3



N
W
E
S
Flow
Gravel augmentation
Sand deposition
above logjam
Gravel augmentation
Gravel deposition above
Side channel logjam
Abandoned gravel pit
connected to main channel
Logjam in glide eddy
Logjam-forced run
Redds
Large Wood, active
Large Wood, inactive
Riffle
Run
Glide
Pool
Gravel Bar
Island
0
75
150
300 Meters

Fig 4a

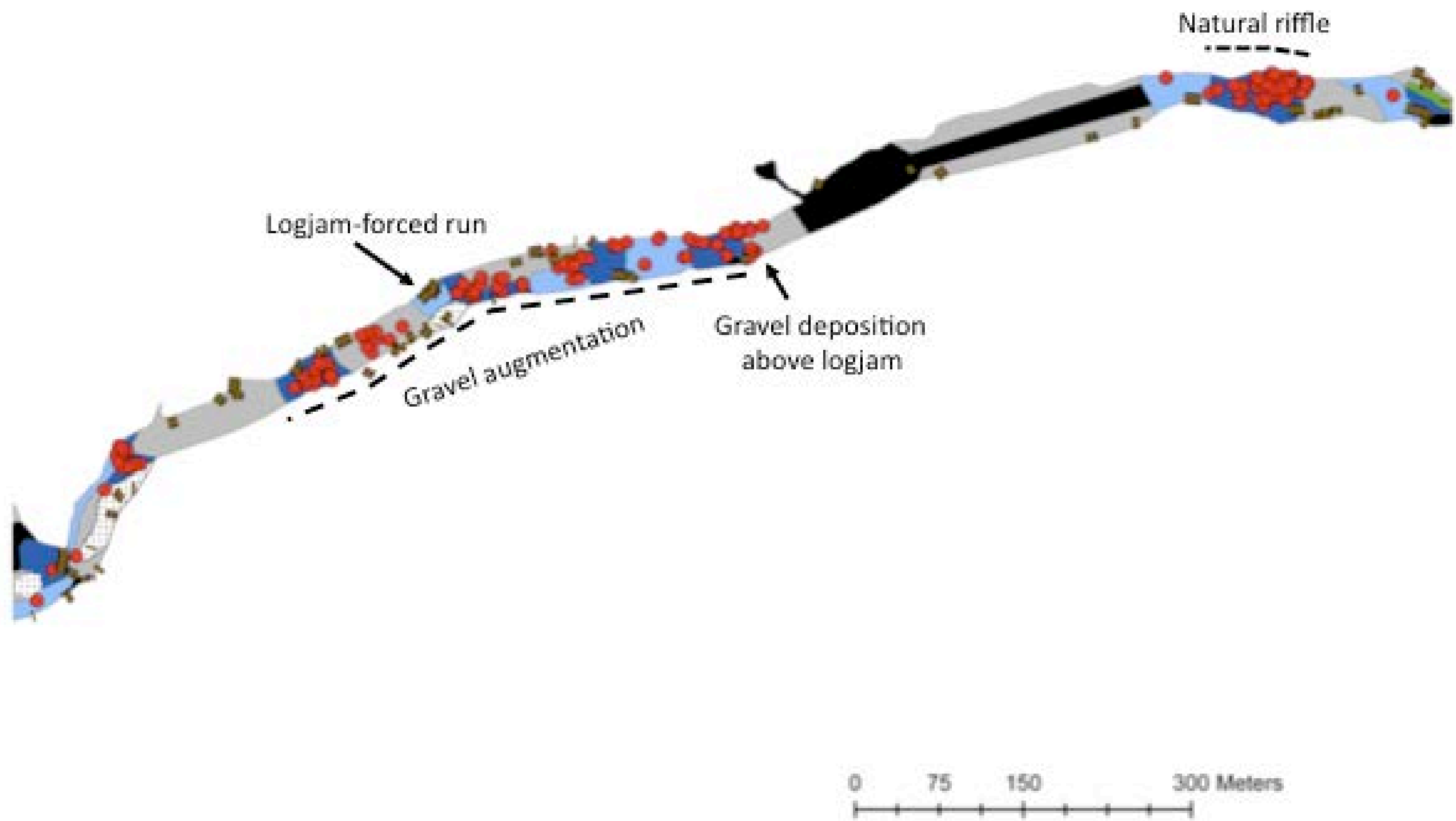

Natural riffle
Logjam-forced run
Gravel deposition
above logjam
Gravel augmentation
0
75
150
300 Meters

Fig 4b

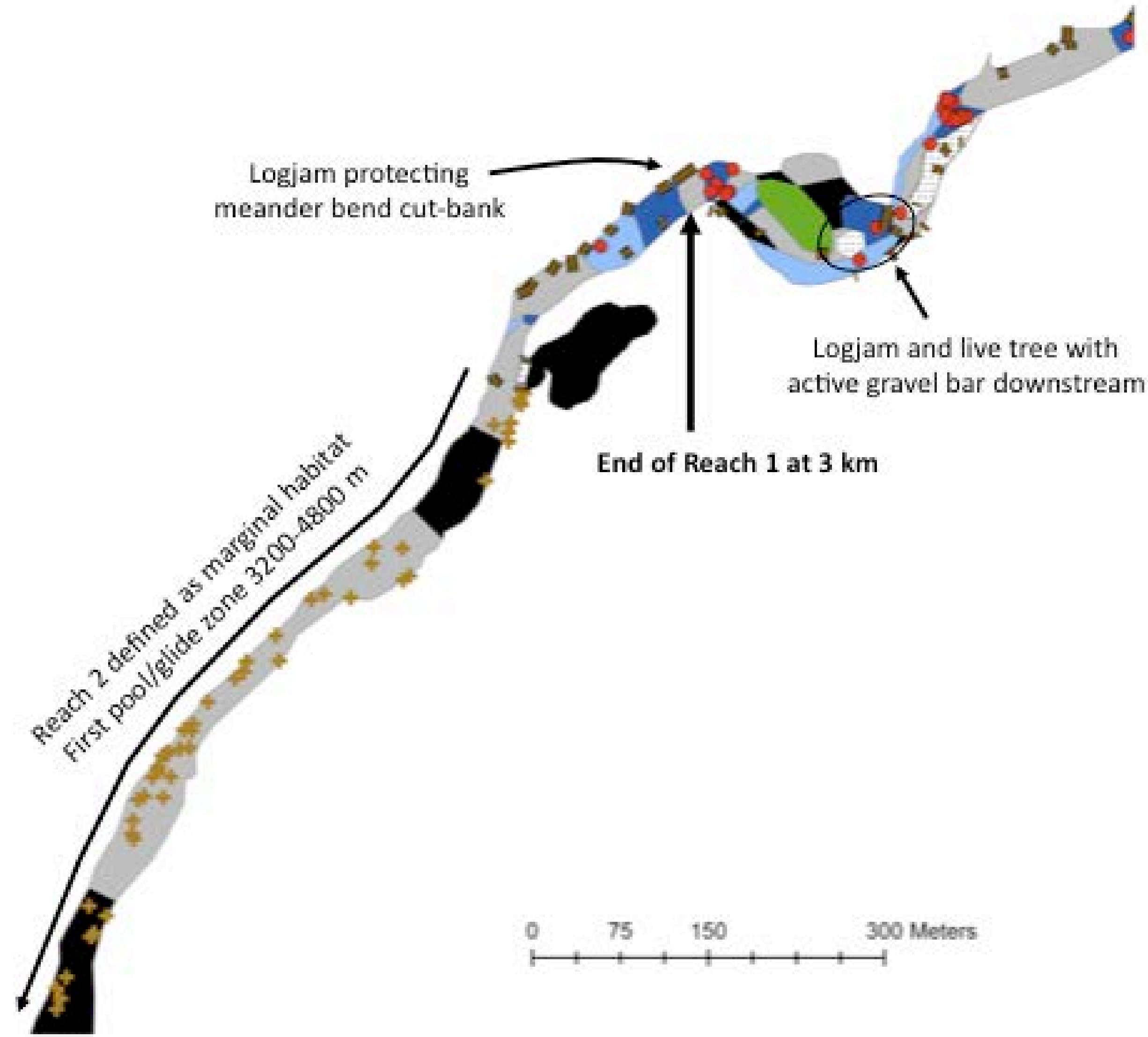

Logjam protecting
meander bend cut-bank
Logjam and live tree with
active gravel bar downstream
End of Reach 1 at 3 km
Reach 2 defined as marginal habitat
First pool/glide zone 3200-4800 m
0
75
150
300 Meters

Fig 4c

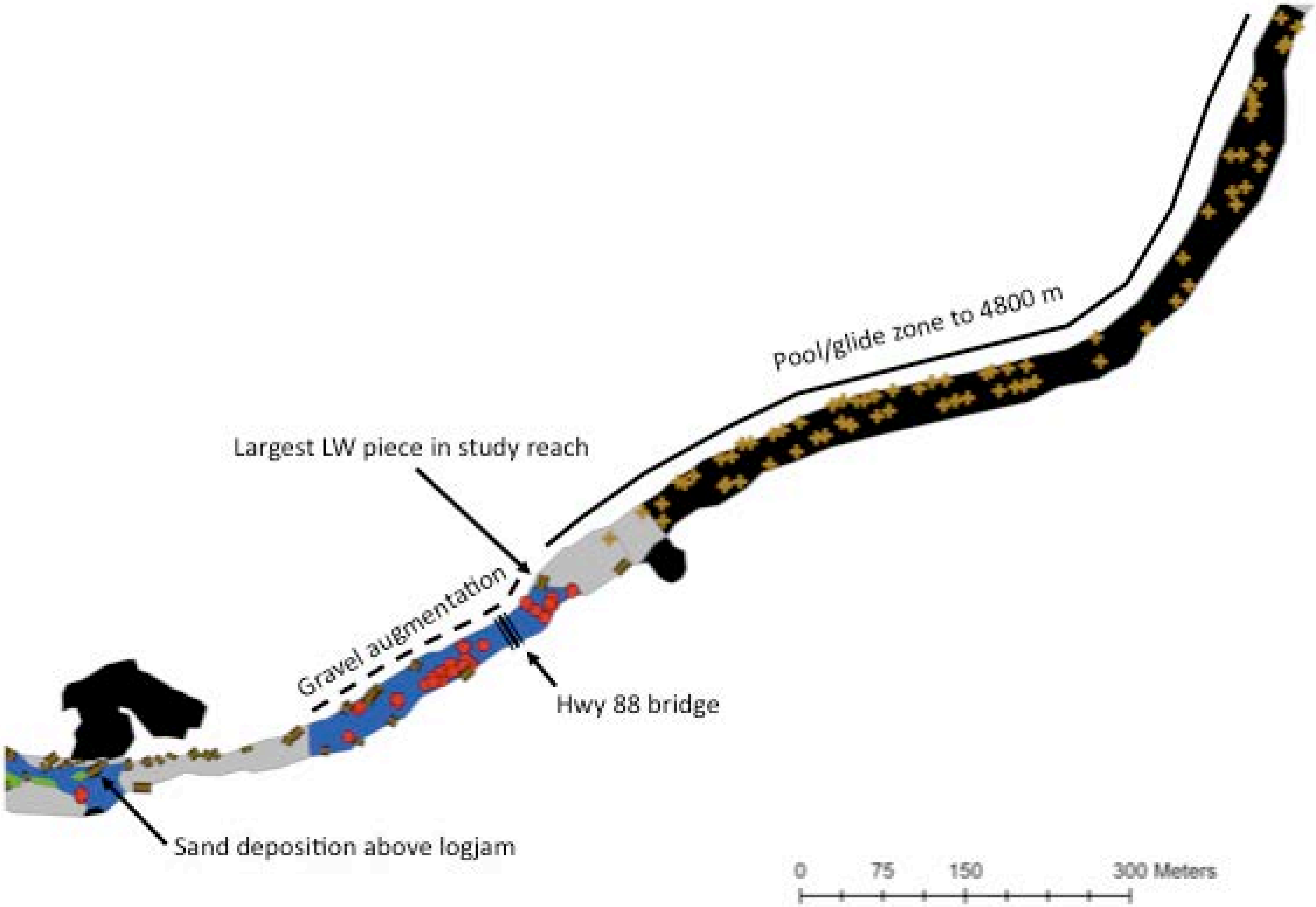

Pool/glide zone to 4800 m
Largest LW piece in study reach
Gravel augmentation
Hwy 88 bridge
Sand deposition above logjam
0
75
150
300 Meters

Fig 4d

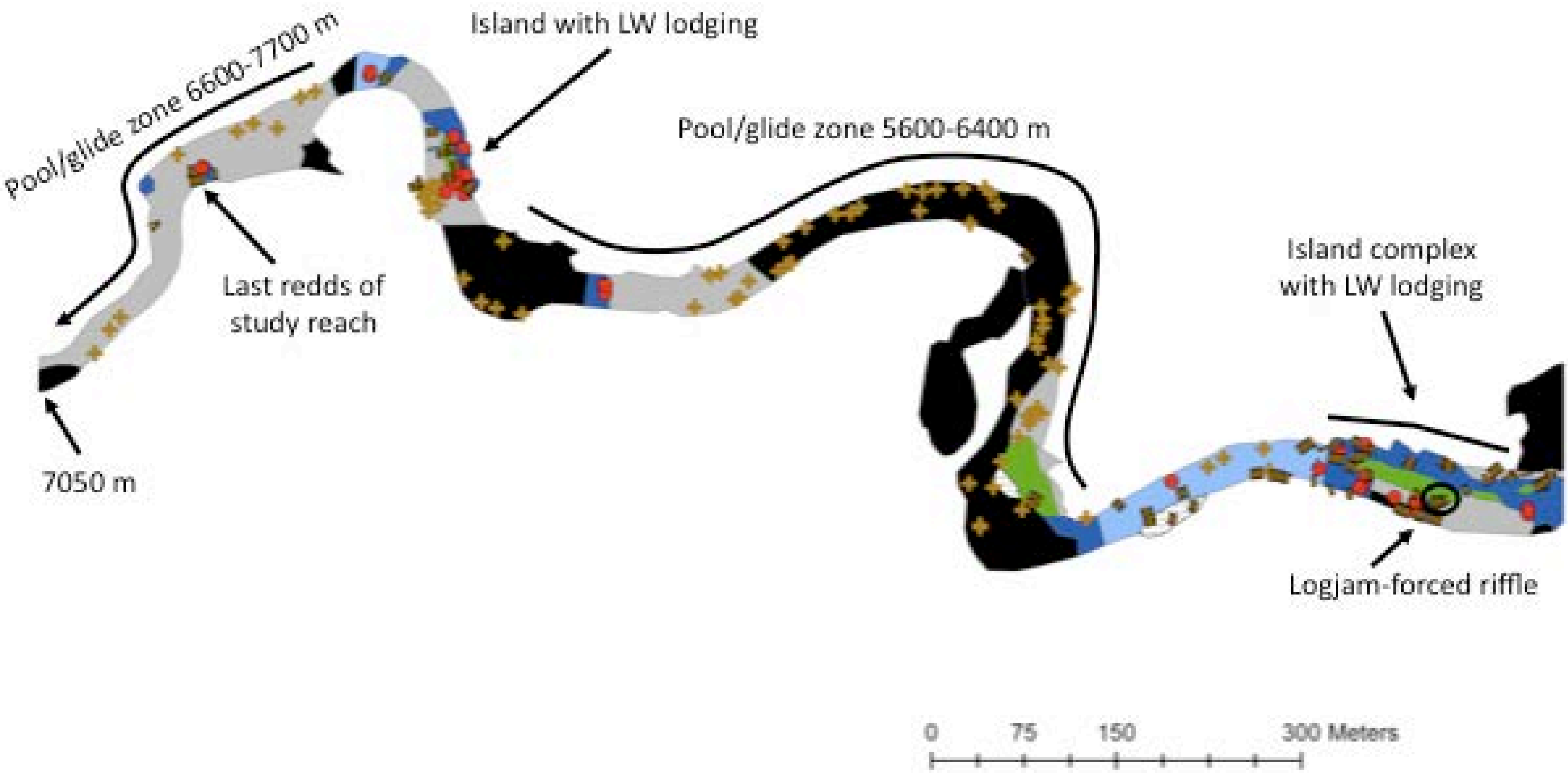

Pool/glide zone 6600-7700 m
Island with LW lodging
Pool/glide zone 5600-6400 m
Last redds of
study reach
7050 m
Island complex
with LW lodging
Logjam-forced riffle
0
75
150
300 Meters

Fig 4e

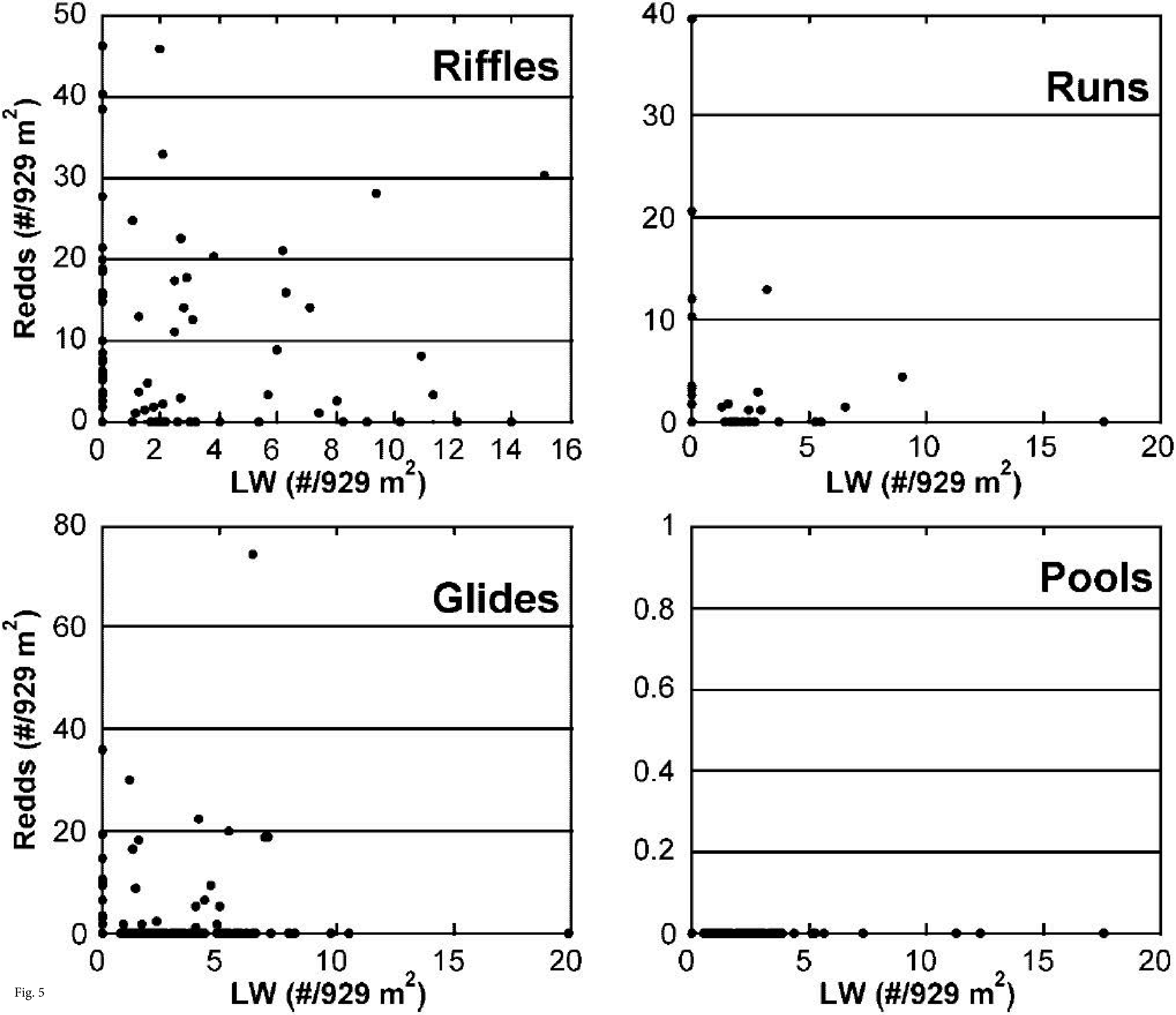


Fig. 5

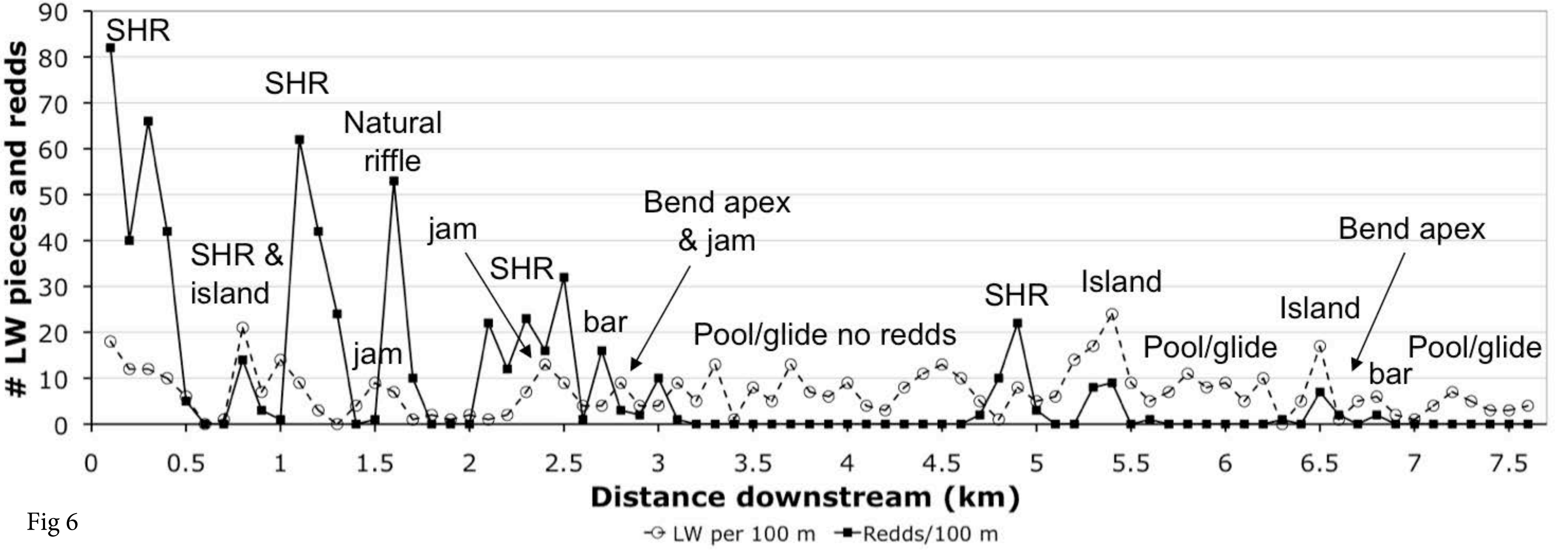

SHR
SHR
Natural riffle
SHR & island
jam
jam
SHR
bar
Bend apex & jam
Pool/glide no redds
SHR
Island
Pool/glide
Island
Bend apex
bar
Pool/glide
LW pieces and redds
Distance downstream (km)
LW per 100 m
Redds/100 m

Fig 6