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CHINOOK SALMON SPAWNING SITE SELECTION IS INFLUENCED BY SIZE OF MICROHABITAT PATCH

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Ecohydraulic approaches exist at reach, mesohabitat, and microhabitat scales, with little understanding of habitat patch size effects and scaling. This study tested different sizes of patch aggregation using microhabitat determined with 2D modeling against actual habitat utilization with 6,215 Pacific Chinook salmon redds. Spawners were found to select for meter-scale physical variables and microhabitat patch size, with size selection conditioned on habitat quality. When using the highest-quality habitat available, preferred patch sizes were 100-3000 m^2, whereas when any preferred quality of habitat was used, then preferred patch sizes were 100-9000 m^2. Fish densities were too low to exhibit much superimposition or other competitive degradation of performance. Based on this finding, statistical habitat-discharge relations overestimate habitat availability, because those relationships assume all microhabitat is useable regardless of contiguous area. Management would be improved if studies took into account the patch size needs and preferences of individual species lifestages.

1 INTRODUCTION

Modern efforts to manage and protect rivers necessitate a determination of the area of usable physical habitat at multiple flows for lifestages of aquatic species. Although diverse methods exist, microhabitat modeling is commonly used. It involves combining empirical habitat suitability curves (HSCs) with mechanistic simulations of hydraulics at river cross-sections to obtain a statistical estimate of habitat availability at a specified flow (i.e., weighted useable area). Recently, new technologies have enabled meter-scale topographic mapping and two-dimensional (2D) hydrodynamic modeling over hundreds of kilometers of river length. These data and model outputs can be used for spatially explicit ecohydraulic analyses within the context of a new paradigm known as near-census river science to produce not only standard microhabitat statistical metrics, such as the discharge-habitat availability plot, but also to explain spatial habitat patterns. The term ‘near-census’ is used herein to refer to comprehensive, spatially explicit, process-based approaches using the 1-m scale as the basic building block for investigating rivers. This concept implies that meter-scale data represents variables in great detail that approaches the population of conditions, but that there remains finer details at the continuum level.

An important open question regarding physical habitat is the extent to which organisms prefer a size of microhabitat patch. Trivially, there is a minimum patch size with insufficient space for an activity, but that is very small compared to the range of available patch sizes. For larger ones, evolutionary fitness may shape size preference. For example, an organism might seek a large patch that can hold a higher proportion of a population so that each individual may hide in plain sight amongst many for protection against predators and competitors. On the other hand, if the density of utilization is too great, then performance might suffer. Late spawners might even seek small, densely populated patches to superimpose their embryos over those of competitors. These factors suggest that preferred patch size might scale with population size to yield a moderately high utilization density. The goal of this study was to apply near-census data and ecohydraulic analyses to quantify and evaluate the sizes of microhabitat patches used by Pacific Chinook salmon on a regulated river.

The Yuba River drains 3480 km^2 in California, USA, with Englebright Dam blocking sediment flux 37.1 km from the end. After a short bedrock canyon, the 34-km alluvial lower Yuba River (LYR) segment has a single-thread channel (~ 20 emergent bars/islands) with low sinuosity, high width-to-depth ratio, mean width of 97 m, mean bed slope of 0.185%, mean bed surface sediment size of 97 mm, and slight to no entrenchment. The LYR receives little sediment influx due to upstream dams, but it stores vast mining sediment from historic hydraulic gold mining. Estimated bankfull discharge is 141.6 m^3/s. Among other fishes, Pacific anadromous salmonids use the LYR for several freshwater life stages, including Chinook salmon and steelhead trout.

2 METHODS

The experimental design for this study involved mapping 6,215 Chinook salmon redds over two spawning seasons and then using those observations to determine (1) avoided and preferred microhabitat patch sizes and (2) redd densities present in preferred patch sizes. Weekly Chinook redd surveys were conducted for the whole LYR by expert fish biologists in two spawning periods, fall 2009 to spring 2010 and fall 2010 to spring 2011, hereafter referred to as 2009-2010 and 2010-2011, respectively. Meanwhile, ecohydraulic experts developed a meter-scale 2D microhabitat model for LYR Chinook spawning in the entire 34-km segment. A 2D hydraulic model was first tested for an order magnitude range of in-channel flows and found within accepted norms for accuracy in predicting mass conservation, water surface elevations, depths, velocity magnitudes, and velocity directions. Then hydraulic model outputs for each spawning flow were combined with HSCs for depth, velocity, and substrate to yield meter-scale values of a combined habitat suitability index (CHSI) between zero and one. Ten random redd data sets were generated and put through the same computations as the real data to evaluate dataset size effects and likelihood that observed results were nonrandom. CHSIs were found to be higher at redds compared to non-utilized locations with a statistically significant difference at > 99% confidence compared to random data. CHSIs were then binned in 0.2 intervals (e.g., Fig 2) and tested to see if the forage ratio (i.e., FR is percent of redds found in a bin divided by percent of total wetted area composed of each bin) exceeded one, indicating a preference for that CHSI bin. CHSI values from 0.4-1.0 were found to be preferred, with the highest preference (i.e., highest FR) for CHSI values from 0.8-1.0 that represent highest-quality habitat (Figs. 1-2). For example, for the first year, the model identified 76.5% of redds as located in preferred habitat. Of the incorrect predictions, half of the redds were within 1.5 m of preferred habitat relative to a river with a mean width of ~ 100 m, so still quite good spatial success. Details about the methods are available in [1].

To evaluate whether spawners for each of two years preferred one or more microhabitat patch sizes of either preferred or highest-quality habitat, each contiguous area of habitat with CHSI values of 0.4-1.0 (or separately 0.8-1.0) was merged into a single polygon (i.e., a patch) and patch area was computed. Patches were then binned by size and the FR for each size class was computed, unless a size class had < 1% of wetted area, in which case it was excluded from analysis. That occurred in all cases only for the size class of 0-100 m^2. Patch sizes with the highest FRs were the ones most strongly preferred among the two sets tested for each year, and these are reported in the results below. Two measures of redd density were computed, (1) the number of redds per patch size class divided by the number of patches and (2) the area of patches per class, yielding the metrics redds per patch and redds per 100 m^2.

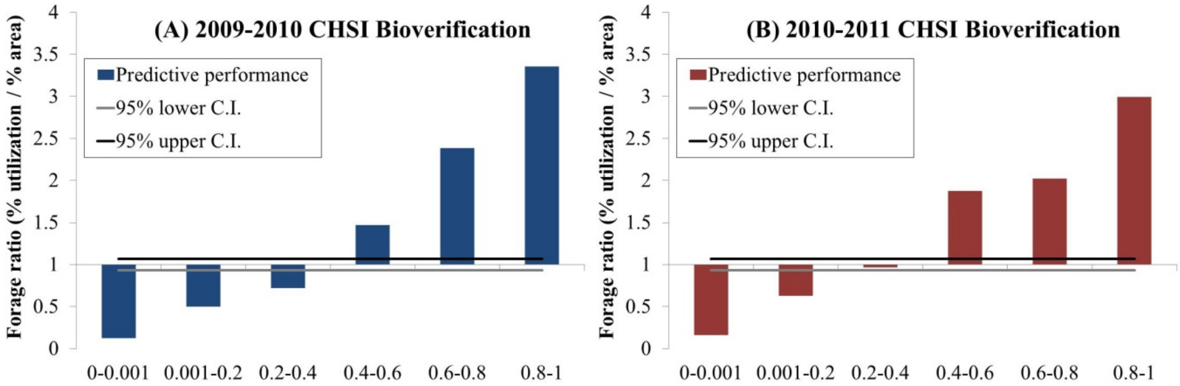

Figure 1. Forage ratio bioverification of CHSI bins. Values above and below bootstrapped statistical confidence limits represent preference and avoidance, respectively. Data within statistical limits exhibit random behavior.

3 RESULTS

Pacific Chinook salmon spawners had clear preferences for microhabitat patch size. Among patches that were identified as preferred habitat (i.e., FR > 1) but not highest-quality habitat, spawners used relatively small patch sizes compared to available sizes (Fig. 3a,c). For both years, patches of 100-1000 m^2 were the strongest preferred with sizes of 1000-9000 m^2 also preferred. Sizes of 9000 to 35,000 m^2 were largely avoided (i.e. FR < 1), but then the largest size class of 35,000 to 37,000 m^2 was preferred. A similar pattern of preference was observed both years, with 58% and 59% of all redds occurring in patch sizes of 100-9000 m^2 in 2009-2010 and 2010-2011, respectively.

Among patches identified as highest-quality habitat with the CHSI criteria, spawners used even smaller patches, with the highest preference being for 500-1000 m^2 both years (Fig. 2; Fig. 3b,d). Patches of 1,000-3,000 m^2 were also preferred. Roughly half of the highest-quality habitat patches whose area > 3,000 m^2 were avoided (i.e. FR<1), and the other half were selected equivalent to random behavior (i.e., FR~1). A similar pattern of preference was observed both years, with 72% and 69% of all redds occurring in patch sizes of 500-3,000 m^2 in 2009-2010 and 2010-2011, respectively. Comparing between the analyses of highest-quality habitat versus the broader domain of preferred habitat (i.e., CHSI of 0.4-1.0), the available area expands by a factor of ~ 2.5 for both years when the criteria is relaxed, and the median sizes of the utilized patches increase by a factor of ~ 4. In other words, Chinook spawners used smaller patches of highest-quality habitat in proportion to their availability whereas they used larger patches of preferred-quality habitat in proportion to their availability.

There were significant differences in redd density between patch sizes. Among all 4 tests (i.e. two years times two CHSI bin ranges), the smallest size class (0-100 m^2) consistently only had 1-2 redds per patch. Given how little of the river's wetted area these patches constituted, these few individual represent loners behaving differently from the rest of the population in terms of patch size, but not in terms of preference for highest quality hydraulic and substrate conditions. These individuals may be important in terms of population life history diversity, but not to understanding and supporting the bulk of the population. As expected, as preferred patch size increases, the number of redds per patch goes up as well, but not in sufficient proportion to the growth in area as shown by the forage ratio results (Fig. 3). Among all preferred patch sizes for all 4 tests, redd density by area instead of patch number ranged from 0.37 to 3.09 redds per 100 m^2, with an average of 1.20 redds per 100 m^2. These are relatively low densities and reflect the fact that the LYR has significantly more Chinook spawning habitat area than is needed for its current low population size. Neither microhabitat quality nor patch size availability are limiting in this river. Therefore, the preferences that Chinook spawners exhibited cannot be explained on the basis of needing to avoid harmful competitive effects, as all patch size classes had ample space to avoid significant superimposition given the spawner population size. Instead, the evidence supports the theory of hiding in plain sight in that many individuals do group together within a patch that is larger than strictly needed for their redds, but they do not seek exceedingly large patches to avoid contact. This is evident in Figure 2, where the redds are generally clustered in three zones- (1) three redds at the patch entrance on river left, (2) a primary group of redds clustered in the middle of the patch, and (3) a scattering of redds in the trailing tongue of the patch. None of these three areas exhibit significant density, yet large areas of highest-quality habitat in the same patch went unused, as did other highest quality patches nearby, so the spread was not optimized.

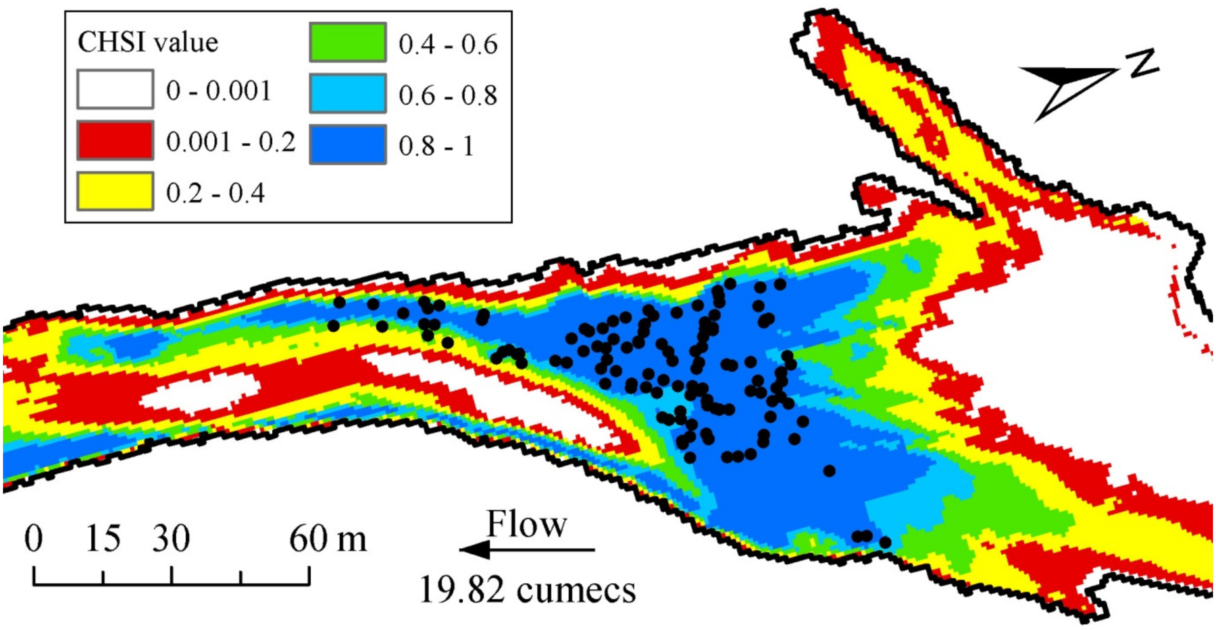

Figure 2. LYR site illustrating 2010-2011 highest quality spawning habitat patches (i.e., dark blue areas). Black dots are individual redds. The vast majority of redds are in a single 857-m^2 patch at this site.

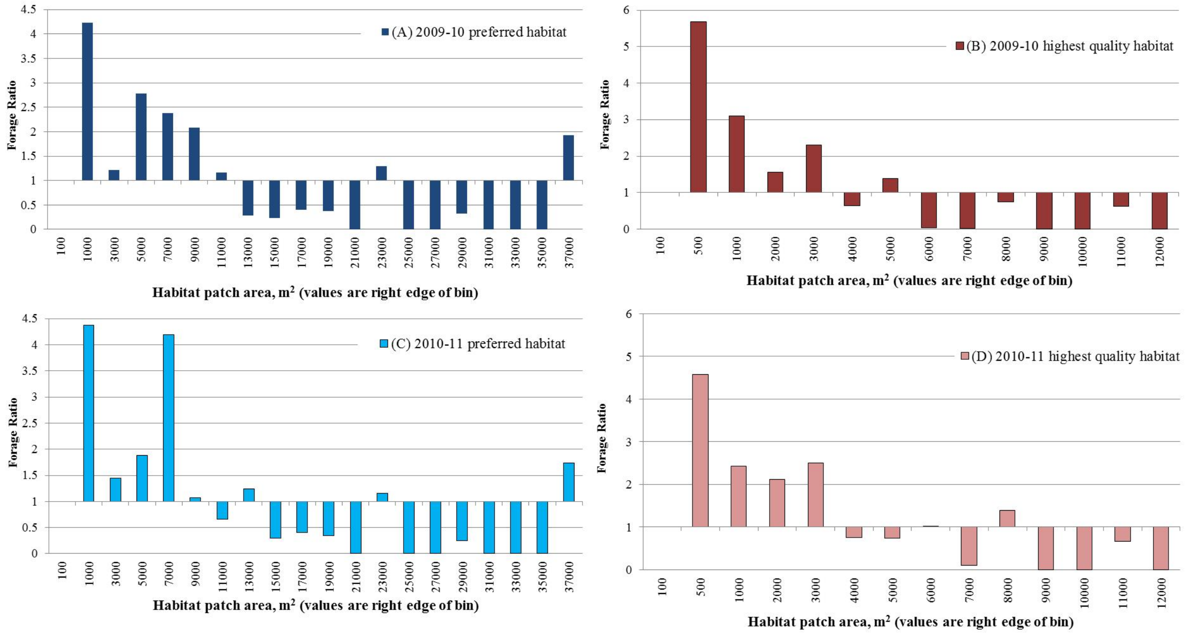

Figure 3. Forage ratio charts for preferred (a,c) and highest-quality habitat patches. The smallest size bin (0-100 m^2) always had an area of < 1% of total wetted area, so it was not appropriate to compute an FR for that size.

4 DISCUSSION

This study illustrated the ability of near-census 2D microhabitat modeling and geospatial analysis of microhabitat patches to reveal the behavior of Chinook salmon in preferring and avoiding certain sized habitat patches. A systematic pattern was found in which spawners selected for meter-scale physical variables and that was conditioned on having just the right size of microhabitat patch, which tended to be small compared to what is available on a river of this size. That allowed spawners to hide amongst many to avoid competitive harm. Although a few fish used patches < 100 m^2, most chose sizes of 100 to 3000 m^2 in the highest-quality habitat areas, as well illustrated in Figure 2. The only other patch size study we know of was by [2], who also reported a statistically significant relationship between habitat patch size and spawning preference for Chinook salmon in Idaho. However, that was a smaller stream and "patches" constituted long, narrow reaches evaluated from aircraft. At that coarse reconnaissance scale, utilized patches were 3000 to 200,000 m^2, with most < 30,000 m^2. These sizes are somewhat similar to reported in this study, but reflect a different spatial scale and thus are not really comparable. More studies are needed to confirm the findings reported herein.

Computation of a statistical habitat area versus discharge relationship is commonly used to ascertain the flow that provides the most habitat. It is possible that a flow that statistically has a lot of habitat may have too many small patches and with poor connectivity between them. This is especially likely for low flows. This study found that such relationships overestimate availability of preferred habitat and in the future should account for patch size preferences.

Finally, engineering design for projects such as spawning habitat rehabilitation should not aim to merely produce a large amount of habitat, but should make sure that landforms are designed to produce appropriately sized patches of microhabitat. Microhabitat patches were not perfectly aligned with morphological units, because flow is inertia and hydraulic variables change slower than the underlying landform. However, they were topographically steered by landforms at the scale of 0.1-1.0 channel widths.

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