Technique for Adjusting Spawning Depth Habitat Utilization Curves for Availability

Mark Gard
U.S. Fish and Wildlife Service
Sacramento, California 95821 USA

ABSTRACT: A technique to adjust depth habitat utilization curves for spawning to account for low availability of deep waters with suitable velocity and substrate was evaluated in the Merced and American rivers, California. Habitat use data were used to derive initial habitat utilization curves for depth and were modified by a series of linear regressions to define the relative rate of decline, with increasing depth, of habitat use versus the availability of waters with suitable velocities and substrates. This technique allows the effects of availability on use to be estimated but does not overcorrect for effects of availability. Results suggest that there may be a limitation of depth on spawning separate from availability. Such a limitation would need to be considered in developing spawning habitat suitability curves using a mechanistic model.

KEY WORDS: Chinook salmon, habitat availability, habitat suitability curves, habitat utilization, Instream Flow Incremental Methodology, IFIM, Physical Habitat Simulation system, PHABSIM, spawning.

INTRODUCTION

Habitat suitability criteria (HSC curves) are used within the Physical Habitat Simulation system (PHABSIM), a part of the Instream Flow Incremental Methodology, to translate hydraulic and structural elements of rivers into indexes of habitat quality (Bovee and Bartholow 1996). Historically, most HSC curves have been developed from observations of microhabitat use (Bovee and Bartholow 1996). Recently, investigators have taken a new approach to developing HSC criteria for juvenile salmonids by using mechanistic models, based on bioenergetics theory (Fausch 1984, Addley 1993, Barry and Coon 1997, Braaten et al. 1997). These models assume that juvenile salmonids choose microhabitats that maximize their net energy intake. However, similar models have not been developed for salmonid spawning.

Two techniques have been used historically to develop HSC curves from observations of microhabitat use: (1) utilization curves, derived directly from frequencies of observations of microhabitat use; and (2) preference curves, derived by dividing frequencies of microhabitat use by frequencies of microhabitat availability (Moyle and Baltz 1985; Parsons and Hubert 1988; Bartholow et al. 1990; Beecher 1995; Bovee and Bartholow 1996). Computer simulations (Morhardt and Hanson 1988) and empirical data sets (Bovee and Bartholow 1996) have indicated that preference, calculated as the ratio of use to availability, overcorrects for effects of microhabitat availability on microhabitat use, principally due to effects of the tails of the frequency distributions where there are a limited number of data points. As a result, values of microhabitat variables that had low use can have high suitability because of very low availability. Additionally, in testing whether HSC curves developed on one stream are transferable to another stream, Bovee and Bartholow (1996) found that preference curves, calculated from the ratio of use to availability, were not transferable but that utilization curves were. Thus, Bovee and Bartholow (1996) recommended using utilization curves for habitat suitability criteria and treating the effects of microhabitat availability on microhabitat use by sampling equal areas of different mesohabitat types.

Another area of disagreement that has arisen in developing HSC curves from observations of microhabitat use is whether habitat suitability curves describing the depth of chinook salmon (*Oncorhynchus tshawytscha*) spawning should be modified to have a suitability of 1.0 (depth not limiting) for all depths greater than the peak of the HSC curve derived directly from microhabitat use data (Raleigh et al. 1986; California Department of Water Resources 1993, 1994). This modification assumes that microhabitat use in deeper waters is solely a function of availability. Such a modification (suitability of 1.0 for deep waters) can have a substantial effect on the relation between spawning habitat area and streamflow (Shirvell 1989; California Department of Water Resources 1994), increasing the flow at which WUA reaches its maximum value. The modification has been used for both utilization and preference curves.

To date, Rubin et al. (1991) has presented the only intermediate approach between utilization and preference curves by calculating HSC curves from densities of fish (including zero densities) in cells with measured microhabitat parameters. The Rubin et al. (1991) method is similar to the utilization approach in that HSC curves are calculated from habitat use; however, it differs from the utilization approach in that cells with no fish are also used to calculate the HSC curves. This approach avoids the problems noted above for the preference curve approach by not using the ratio of use to availability. It may also address the issue of depth limitation for spawning, since all available habitat is taken into account in calculating the HSC curves. The main drawback of this method is that considerable sampling effort is required for occupied and unoccupied locations. In contrast, the traditional utilization curve approach only involves sampling occupied locations.

In this paper, I offer another intermediate method between preference and use, which may be easier to apply than the Rubin et al. (1991) method. My method may also be the first reported method that addresses the issue of depth limitation for spawning, which takes into account the relative rate of decline with increasing depth of habitat use versus availability of habitat with suitable velocity and substrate. My approach avoids the problems noted by Morhadt and Hanson (1988) and Bovee and Bartholow (1996) in using the preference approach by only modifying the upper end of the depth utilization curve. I was able to successfully apply my approach to develop chinook salmon spawning depth HSC for two California Central Valley streams. Results of this study suggest that there may be a limitation of depth on spawning separate from availability. Such a limitation would need to be considered in developing spawning HSC using a mechanistic model.

STUDY SITES

The study was part of investigations conducted by the U.S. Fish and Wildlife Service and the California Department of Fish and Game to identify instream flow requirements for anadromous fish in streams within the Central Valley of California, pursuant to the Central Valley Project Improvement Act (Title XXXIV of P.L. 102-575). The rivers selected for study in these investigations (Merced, American, and Sacramento) were chosen because they were the only major regulated Central Valley streams for which additional investigations were needed to identify instream flow requirements. Investigations on the Sacramento River are not included in this paper because they are ongoing.

The Merced River, located in the San Joaquin River basin, drains 2,693 km^2 and the American River, located in the Sacramento River basin, drains 5,376 km^2. Both rivers arise along the western flank of the Sierra Nevada in California (Figure 1). The study was conducted in a 16-km reach of the Merced River directly below Crocker-Huffman Dam and in a 9-km reach of the American River 2.1 km below Nimbus Dam (Figure 1). These two study reaches were chosen because they represent the portions of the two rivers with the highest use by spawning fall-run chinook salmon during the past decade (California Department of Fish and Game 1994, 1995). The two study reaches have gravel beds and no tidal influence. Seven sites in the Merced River and five sites in the American River

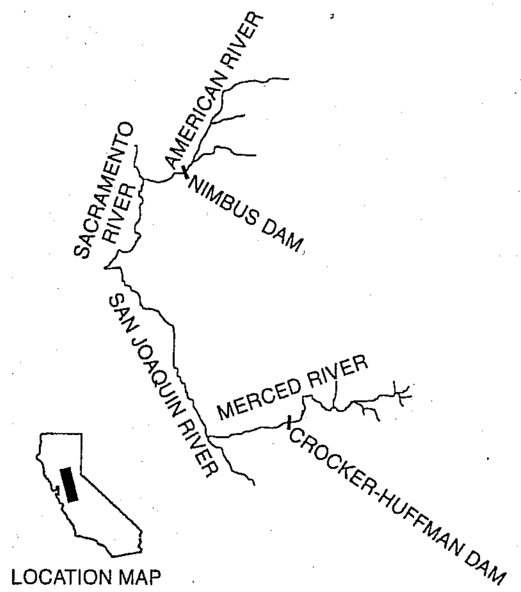

FIGURE 1. Location of the American and Merced rivers, California, and study reaches used to evaluate a technique for adjusting spawning depth habitat utilization curves for availability.

were selected to measure chinook salmon redd microhabitat characteristics and model available habitat as a function of flow. These twelve sites are areas in the two study reaches that have experienced some of the most extensive spawning by fall-run chinook salmon during the past decade (U.S. Fish and Wildlife Service 1996, 1997).

METHODS

Field Measurements

Transects were placed in the seven study sites on the Merced River and the five study sites on the American River across the most frequently used spawning areas, as identified by substrate size and aerial photography of redd distribution. I collected data (depth, velocity, and substrate) along transects for input into the hydraulic and habitat simulation models within the PHABSIM using the procedures outlined in Trihey and Wegner (1981). Lateral cell boundaries (verticals) were established across each transect at set intervals or where I observed differences in bed elevations, water velocity, or substrate composition. I established at least 20 verticals across the wetted width of each transect and defined cells as the area halfway between measurement points. Data collected at each vertical included bed elevation, mean water column velocity (at 0.6 of the total depth), and substrate classification. I measured water surface elevations to the nearest 0.3 cm, depths to the nearest 3.0 cm, and water column velocities to the nearest 0.3 cm/s. Dominant substrate was visually assessed using a modified Brusven index (Platts et al. 1983). I collected cell depths, velocities, and substrate data at a midrange flow, and measured water surface elevations and discharges at three-to-four flows (20-250% of the midrange flow) for each site (U.S. Fish and Wildlife Service 1996, 1997). The flows used for calibration in the American River were the releases reported by the U.S. Bureau of Reclamation (unpublished data) from Nimbus Dam. For the Merced River, the flows used for calibration were calculated from depth and velocity measurements at all transects (not separated by a diversion or return flow), for which measurements were taken during a given period of steady flow.

To create stream-specific HSC curves, depth, velocity, and substrate data were collected on 186 fall-run chinook salmon redds in the Merced River between 12 and 14 October 1996 at 12 sites (seven of which were the study sites) at a flow of 7.79 m^3/sec, and on 218 fall-run chinook salmon redds on the American River between 6 and 7 November 1996 at the five study sites at a flow of 78.64 m^3/sec. Flows were stable from the beginning of the spawning period through the dates of data collection. I measured all recently constructed redds (redds without periphyton) at each site that could be conclusively identified. Depth and velocity data were collected at 0.5 m upstream of the redd pit, where hydraulic conditions were assumed to be similar to the redd location before construction. I measured depth to the nearest 3.0 cm and water column velocity to the nearest 0.3 cm/s at 0.6 of the total depth. Dominant substrate was visually assessed in the tailspill by using a modified Brusven index (Platts et al. 1983).

Hydraulic Modeling

Hydraulic data were calibrated using procedures outlined in Milhous et al. (1989). I used the IFG4 component of PHABSIM for most transects, and the MANSQ or Water Surface Profile (WSP) components of PHABSIM for a few transects that could not be calibrated with IFG4 (U.S. Fish and Wildlife Service 1996, 1997) to simulate water surface elevations. Depths were calculated from bed elevations and water surface elevations, and velocities were computed in IFG4 using the velocity data collected at the midrange flow and by using Manning's equation (Milhous et al. 1989).

Habitat Suitability Criteria Development

Frequency distributions of HSC data were calculated for depth and velocity. I entered these data into the PHABSIM suitability index curve development program (CURVE), and used the exponential smoothing option to compute the HSC curves (U.S. Fish and Wildlife Service 1996, 1997). Substrate criteria were developed by: (1) determining the number of redds with each substrate-size class, (2) calculating the proportion of redds with each substrate-size class (number of redds with each substrate-size class divided by total number of redds), and (3) calculating the HSC value for each substrate-size class by dividing the proportion of redds in that substrate size class by the proportion of redds with the most frequent substrate-size class.

Depth Habitat Suitability Criteria Correction

I constructed multiple sets of HSC, differing only in the suitabilities assigned for optimum depth increments, to determine how the available river area with suitable velocities and substrates varied with depth. Ranges of suitable velocities and substrates were determined from the HSC curves derived above, with suitable velocities and substrates defined as those with HSC values greater than 0.5. I selected a range of depths for each river, starting at the depth at which the initial depth of HSC reached 1.0, through or just beyond the greatest depth at which there were redds or available habitat. A series of HSC sets were constructed where: (1) all of the sets had the same velocity and substrate HSC curves, with values at 1.0 for the suitable velocity and substrate range with all other velocities and substrates assigned a value of 0.0; and (2) each set had a different depth HSC curve. To develop the depth HSC curves, I assigned each HSC set a different 15-cm depth increment within the selected depth range to have an HSC value of 1.0, and I gave the other 15-cm increments and depths outside of the depth range a value of 0.0 (e.g., 60-75 cm depth HSC value equal 1.0, <60 cm and >75 cm depths HSC value equals 0.0 for a depth increment of 60-75 cm). Each HSC set was run in HABTAE (the portion of PHABSIM that translates hydraulic and structural data into habitat quality) using the calibrated hydraulic decks for all study sites at the flow at which HSC data were collected. I used the resulting habitat output to determine the available river area with suitable velocities and substrates for all 15-cm depth increments.

To modify the HSC depth curves to account for the low availability of deep water having suitable velocities and substrates, I used a sequence of linear regressions to determine the relative rate of decline of use versus availability with increasing depth. I defined habitat use by spawning chinook salmon as the number of redds observed in each depth increment for each river. I standardized availability and use by computing relative availability and use, so that both measures would have a maximum value of 1.0. Relative availability and use were calculated by dividing the availability and use for each depth increment by the largest value of availability or use. To produce linearized values of relative availability and use at the midpoints of the depth increments (i.e., 67.5 cm for the 60-75 cm depth increment), I used linear regressions of regressed relative availability and use versus the midpoint of the depth increments. Linearized use was divided by linearized availability for the range of depths where the regression equations predicted positive relative use and availability. I standardized the resulting use-availability ratios so that the maximum ratio was 1.0. To determine the depth at which the depth HSC would reach zero (the depth at which the scaled ratios reached zero), I used linear regression with the scaled ratios versus the midpoint of the depth increments. Linear regressions were conducted using the statistical functions of the QuattroPro™ spreadsheet software. The biological rationale of these procedures is that the relative rate of decline of use versus availability is related to the quality of depths for spawning habitat.

RESULTS

For the American River, suitable velocities were 40-90 cm/s and substrates were 2.5-7.5 to 7.5-10 cm diameter whereas suitable velocities for the Merced River were 30-75 cm/s and 5-10 cm for suitable substrates. The initial Merced depth HSC showed that suitability rapidly decreased for depths greater than 30 cm. For the American River, suitability decreased for depth greater than 60 cm (Figure 2). Subsequently, the depth ranges selected for the depth HSC correction were 30- 120 cm for the Merced River and 60-180 cm for the American River. The results of the initial regressions showed that chinook spawning habitat availability dropped with increasing depth, but not quite as quickly as use based on the ratio of use to availability (Figure 3). The result of the final regression (r^2 = 0.85, P = 0.077) for correction of the Merced River depth criteria was that the scaled ratio reached zero at 7.3 m; thus, the Merced depth criteria were modified to have a linear decrease in suitability from 1.0 for the highest depth in the original criteria which had a suitability of 1.0, to a suitability of 0.0 at 7.3 m. The result of the final regression (r^2 = 0.85, P = 0.009) for correction of the American River depth criteria was that the scaled ratio reached zero at 3.3 m; thus, the American River depth criteria were modified to have a

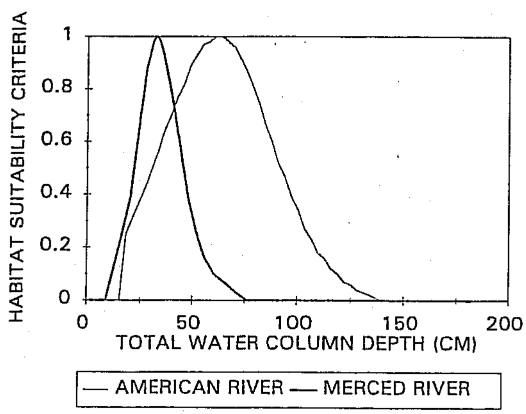

FIGURE 2. Initial Habitat Suitability Criteria (HSC) depth curves for chinook salmon spawning in the American and Merced rivers. These curves were derived directly from microhabitat use data prior to the application of the technique to adjust the spawning depth habitat utilization curves for availability.

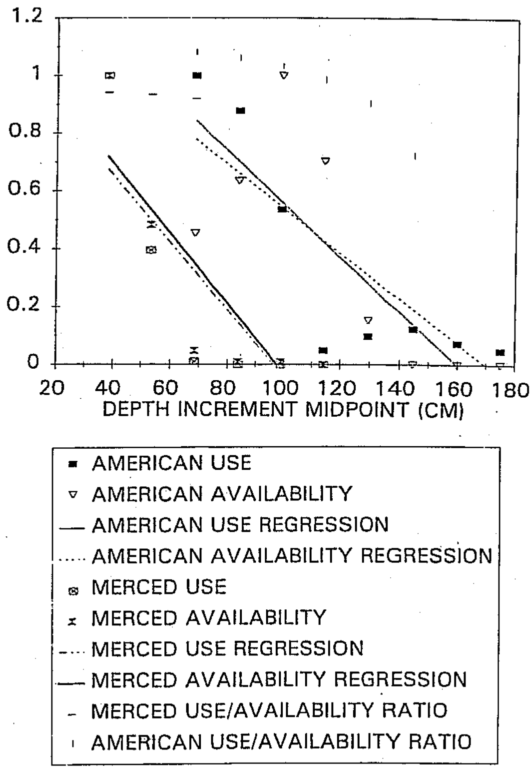

FIGURE 3. Relations between relative availability and use and depth for the Merced and American rivers. Points are relative use, relative availability, or the ratio of the linearized use to linearized availability for the Merced or American rivers. Lines are the results of the linear regressions of the depth increment midpoint versus relative availability (r^2 = 0.71, P = 0.03) and use (r^2 = 0.66, P = 0.048) for the Merced River, and relative availability (r^2 = 0.56, P = 0.03) and use (r^2 = 0.76, P = 0.005) for the American River.

linear decrease in suitability from 1.0 for the highest depth in the original criteria, which had a suitability of 1.0, to a suitability of 0.0 at 3.3 m. The resulting criteria, along with the velocity and substrate criteria, are shown in Figure 4.

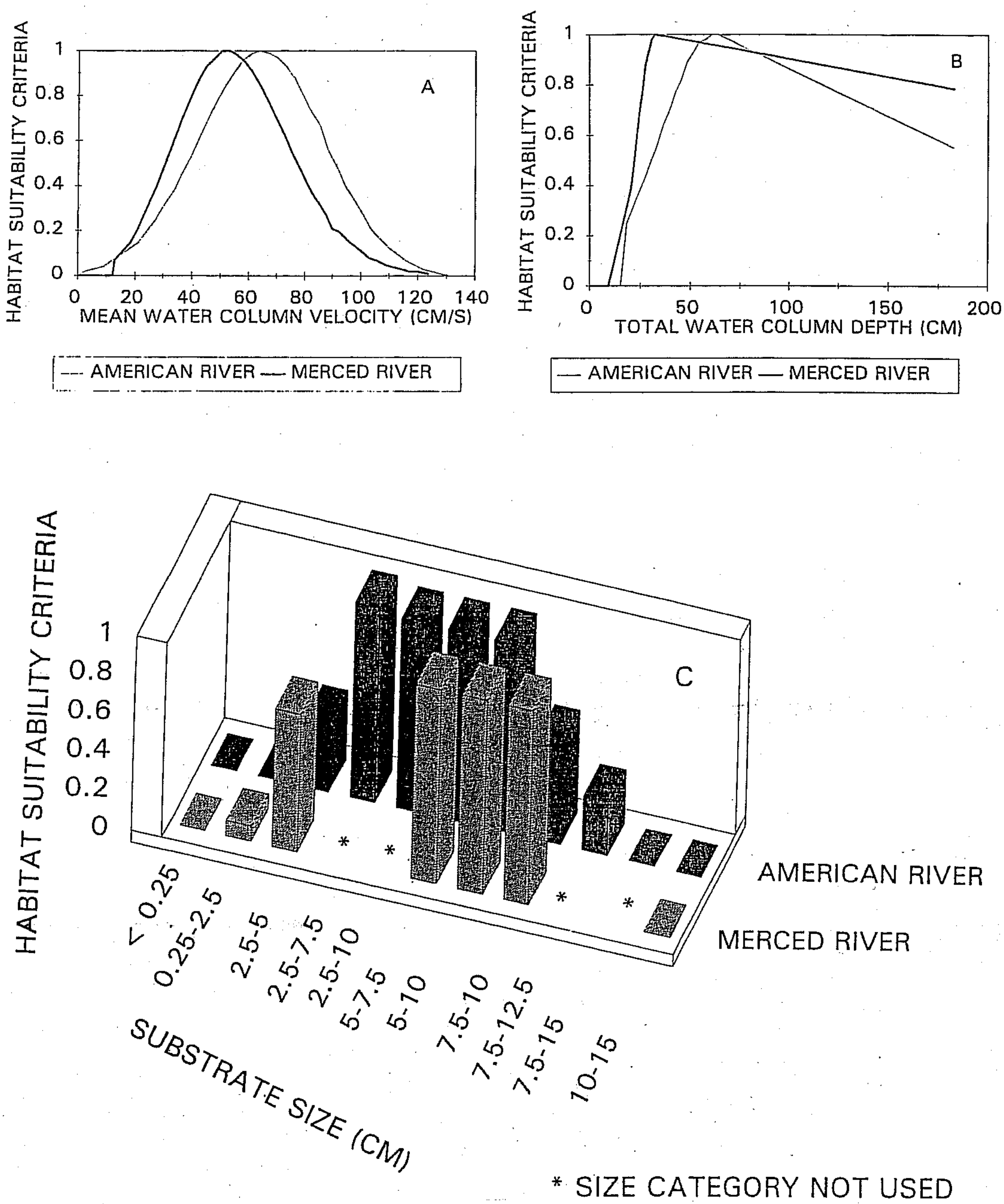

FIGURE 4. American and Merced river chinook salmon spawning Habitat Suitability Criteria (HSC) curves: (A) velocity suitability curves, (B) depth suitability curves, and (C) substrate suitability curves. Depth curves were the result of the adjustment technique presented in this paper.

DISCUSSION

The rapid decrease in suitability for the initial Merced River and American River depth HSC was most likely due primarily to the low availability of deeper water with suitable velocities and substrates, rather than a selection by the salmon of only shallow depths for spawning. As a result, the initial depth HSC curves probably substantially underestimated the suitability of deeper waters for spawning. In contrast, the modified depth HSC curves take into account the effects of availability of deeper water with suitable velocities and substrates. In addition, the modified depth HSC avoid the problem of overcorrecting for availability inherent in the preference curve approach, since suitability up through the peak of the depth HSC curve is still determined solely by habitat use.

This study presents an intermediate approach for determining the suitability of deep waters for chinook salmon spawning. In contrast to the approach reported in Rubin et al. (1991), my approach eliminates the need to collect additional data for unoccupied locations if microhabitat use data are collected from the sites used to model habitat versus flow. This intermediate approach may be more appropriate than either using HSC based entirely on frequency of use of depths, or by modifying HSC to have a suitability of 1.0 for all depths greater than the peak of the HSC curve. In fact, these two approaches are limiting cases of the technique described above. Specifically, the original HSC depth curve should be used if use is not being affected by availability. If use is not affected by availability, the result of the initial regression of relative available versus depth will be that availability increases with depth. In contrast, the original HSC depth curve should be modified to have a suitability of 1.0 for all depths greater than the peak of the HSC curve if use is entirely controlled by availability. If use is entirely controlled by availability, the final linear regression would show that the scaled use-availability ratio increases with depth, indicating that availability decreases faster than use with increasing depth.

Results of this study suggest that there may be an effect of depth on spawning microhabitat use independent of availability, beyond the minimum depth required for spawning. Specifically, suitability of deep waters is not solely a function of availability, since for both rivers, use decreased faster than availability with increasing depth, based on the decrease in the use-availability ratio with increasing depths. A mechanistic model for salmonid spawning would have to address the adult and egg or larval life stages. Specifically, bioenergetic considerations and physical abilities of adult salmonids will limit the maximum velocity and substrate size used for spawning, and some minimum depth is necessary to physically allow salmonids to spawn. In contrast, requirements of the developing eggs and larvae for sufficient intragravel velocities will set a lower limit on the velocity and substrate size used for spawning. Specifically, if it is assumed that flow in the river channel and in the gravel are, respectively, turbulent and laminar, and that the head loss over a given distance is the same for the river channel and in the gravel, equations in Albertson and Simons (1964) can be combined to produce the following equation:

$$V_g = 3\frac{d^2}{\kappa}\frac{(\mu+\eta)}{\mu}\frac{V_w}{D^2}$$

where V_g is intragravel velocity, d and κ are substrate grain size and permeability coefficent, μ is dynamic viscosity of water, η is dynamic eddy viscosity in the channel, V_w is mean water column velocity, and D is total water column depth. The above equation is consistent with the results of this study because, for a fixed water column velocity, intragravel velocity decreases with increasing water column depth. Thus, requirements for sufficient intragravel velocities should result in use decreasing faster than availability with increasing depth. Mechanistic models of spawning may prove to be the best means to develop HSC criteria, which are not affected by availability, and, thus, show promise for future research.

The depth at which the modified HSC curve reaches zero has no biological significance; rather, it is a convenient way to describe in the criteria the rate of decline of suitability with depth. For example, the greater depth at which the Merced River HSC reaches zero, compared to that of the American River HSC, does not indicate that salmon in the Merced River use deeper water than in the American River. Instead, the greater depth for the Merced River shows that the relative rates of decline of use and availability are closer for the Merced River than for the American River, as shown by the relative slopes of the lines in Figure 3. In fact, the salmon in the American River use deeper waters than in the Merced River, but that reflects primarily the difference in availability of deeper waters with suitable velocity and substrates between the two rivers.

Although the statistical significance of the regression equations has been given in this paper, a lack of statistical significance (for example, relative to $P = 0.05$) should not be viewed as a reason to reject the results of an analysis using this technique. The regressions are used to linearize the data, rather than test the hypothesis of the statistical significance of the relation between two variables. Thus, even though the final regression for correcting the Merced River depth criteria was not significant at $P = 0.05$, the resulting depth at which the scaled ratio equaled zero is still valid. The lack of statistical significance in this case was primarily due to the low number of degrees of freedom, versus a lack of linearity of the scaled ratio-depth pairs used in the regression.

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