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TRANSFERABILITY OF HABITAT SUITABILITY CRITERIA FOR A STREAM BREEDING FROG (*RANA BOYLII*) IN THE SIERRA NEVADA, CALIFORNIA

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***Abstract.*—Instream flow modeling is one tool historically used by resource managers to assess habitat suitability for aquatic species, including fish and benthic macroinvertebrates. Until recently, these methods had not been used for amphibians. Instream flow modeling requires quantitative habitat suitability criteria across a range of hydraulic conditions. We developed regional habitat suitability criteria (HSC) from data on habitat conditions at Foothill Yellow-legged Frogs (*Rana boylii*) oviposition and tadpole rearing locations in eight study sites in the northern Sierra Nevada mountains, California. We evaluated both univariate (percentile-based and interval-based) and multivariate logistic regression techniques for creating suitability criteria. The transferability and predictive performance of the HSC were evaluated using validation data gathered from other rivers in the Sierra Nevada and applying the criteria in a two-dimensional (2D) hydrodynamic model. We evaluated conditions under which predictive performance was poor to discern the limitations of each technique. Multivariate logistic regression analyses classified the majority of the river as low suitability, and consequently produced overestimates of suitable area for egg masses and underestimates of highly suitable area for tadpoles. Univariate HSC performed well on rivers that had similar geomorphology to the study rivers. For small rivers and creeks with shallow depths and finer substrates, locally-derived HSC are needed. The percentile-based habitat suitability index (HSI) is recommended for regional habitat suitability criteria when the goal is to assess categorical levels of suitability. The interval-based HSI would be appropriate if further information on population outcomes (e.g., population trajectory, survival rates) could be quantitatively linked to fine scale gradients of suitability in hydraulic conditions. The univariate HSI are easily applied in 2D hydrodynamic models, which can provide information on oviposition and tadpole rearing conditions under various flow regimes. Managers can use HSC to make flow recommendations beneficial to *R. boylii* during the hydropower relicensing process.**

Key Words.—2D modeling; Foothill Yellow-legged Frog; habitat association; instream flow modeling; river management.

INTRODUCTION

River environments are some of the most highly modified ecosystems in the world. Dams, channelization, and water diversions disrupt ecological interactions and connectivity (Ligon et al. 1995; Power et al. 1996; Ward et al. 1999). Altered flow regimes and consequent changes to downstream aquatic habitats can have negative impacts on endemic aquatic populations (Lind et al. 1996; Freeman et al. 2001; Marchetti and Moyle 2001). In western North America, a variety of amphibians use streams and rivers for oviposition and larval development, including the Western Toad (*Anaxyrus boreus*) and Arroyo Toad (*A. californicus*), California (*Taricha rivularis*), Rough-skinned (*T. granulosa*), and Sierra (*T. sierrae*) newts, and the Foothill Yellow-legged Frog (*Rana boylii*). These species have reproductive cycles that are adapted to the natural flow regime and thus can be particularly vulnerable to altered flows in managed rivers. Conservation of these species therefore depends in part on understanding the impacts of regulated flow regimes on instream physical habitat conditions and whether habitat remains suitable during critical reproductive and growing seasons.

The Foothill Yellow-legged Frog reproduces exclusively in stream environments and its life history has evolved to take advantage of the wet (winter/spring) and dry (summer) seasonality of the Mediterranean climate (Kupferburg 1996; Yarnell et al. 2010). Because of this close association with flowing water and its status as a California State Species of Special Concern, *R. boylii* is a focal species during relicensing of hydroelectric dams in California under the Federal Energy Regulatory Commission (FERC). Adults breed and deposit egg masses in the spring as high flows begin to recede, and tadpoles grow and develop during stable low flows in the summer. Metamorphosis occurs in early fall with froglets remaining in the margins of the river or nearby riparian areas, springs, or small tributary streams through the following spring. Over the last half century, *R. boylii* has declined dramatically, most notably in streams below dams (Lind 2005; Kupferberg et al. 2012). Altered stream flow regimes, changes in sediment supply and instream habitat, and establishment of non-native species are some of the primary factors contributing to this decline (Lind et al. 1996; Kupferberg 1997; Yarnell 2000; Kupferberg et al. 2009).

Rana boylii is not adapted to withstand flow disturbance that occurs outside of the natural flow regime and thus can be negatively affected by aseasonal high and low flows common in regulated rivers (Kupferburg et al. 2009, 2011; Yarnell et al. 2010). Egg masses are typically deposited in shallow, low-velocity areas, on the downstream side of cobble and boulders (Kupferberg 1996; Lind 2005; Yarnell 2005). Flow fluctuations can have detrimental effects on the survival of egg masses via scour or stranding (Kupferburg et al. 2012; Yarnell et al. 2012), and even minor velocity increases during summer, which displace tadpoles, can have negative effects on population trajectories (Kupferberg et al. 2009). Instream flow habitat modeling for the obligate aquatic life stages of *R. boylii* (egg masses and tadpoles) is one method that can be used to assess the impacts of altered flow regimes (Ahmadi-Nedushan et al. 2006; Huckstorf et al. 2008). Similar to analyses conducted for fish, instream flow modeling can precisely quantify local changes in depth and velocity at oviposition and tadpole rearing locations and thus provides a valuable tool for assessing impacts to habitat suitability under a range of flow conditions (Yarnell et al. 2012). Instream flow modeling can provide information beyond weighted usable area estimates; it can be used to identify the potential risk to egg masses and tadpoles posed by stranding or scouring under various flow regimes (Yarnell et al. 2012).

Instream flow models require input of habitat suitability criteria (HSC) so that an index of suitability can be assigned based upon the range of hydraulic habitat conditions (i.e., water depth, water velocity, and substrate) used by a focal species. Several methods are used to develop HSC for instream flow models, with a key underlying assumption that greater frequency of use of certain hydraulic conditions equates to higher habitat suitability (Guay et al. 2000; Ahmadi-Nedushan et al. 2006). Currently the HSC developed for *R. boylii*, and used with instream flow models during flow evaluations, have been based on river-specific habitat use data or expert opinion on habitat preferences (PG&E 2007; PCWA, 2010. Instream flow full report. Available from http://relicensing.pcwa.net/html/science/padreportaquatic.php [Accessed 15 March 2010]). Habitat suitability criteria based upon multi-watershed use data have not been developed and transferability among watersheds at a regional scale is unknown (Yarnell et al. 2012). Having HSC that are transferable to multiple rivers would allow evaluation of instream flow models when local field data are sparse or new data cannot be collected. Data that quantify the aquatic habitat associations of *R. boylii* also contribute to evaluation of flow impacts on this species at a broader, regional scale. For example, HSC based on data from Sierra Nevada rivers provide insight into the breeding ecology of *R. boylii* throughout this region.

Our objectives were to quantify key hydraulic habitat conditions for *R. boylii* in rivers of the Sierra Nevada (California, USA) to evaluate methods of developing HSC, and to determine the transferability of these criteria to other rivers in the same region. To meet these objectives, we used three standard univariate and multivariate techniques to develop HSC for egg masses and tadpoles. We evaluated HSC transferability using data from other rivers and a 2D hydrodynamic flow model within this region.

Materials And Methods

Study sites.—We located study sites on eight rivers ranging across the northern Sierra Nevada, California (Fig. 1), and we conducted all field work in the spring and summer of 2009. Selected to represent typical geographic and hydrologic conditions in the northern Sierra, four of the rivers were regulated, primarily as diversion reaches, and four were unregulated. We located two of the study sites in drainages > 2000 km^2 (North Fork [NF] and Middle Fork [MF] Feather); two study sites were in drainages < 300 km^2 (Middle Fork [MF] Yuba and North Fork Middle Fork [NFMF] American). We located the other four sites in intermediate sized watersheds ranging from 400 to 1200 km^2. Elevation among the study sites ranged from 350 m at the North Fork (NF) American to 930 m at the South Fork (SF) American, with most of the sites located 400−500 m. Each study site had channel morphology typical of northern Sierran rivers, with stream gradients ranging from 0.8% to 4.4%, cobble and boulder dominated substrates, and repeating riffle-pool-run habitat sequences. Study sites were 500 m to 1 km long and were located at known *R. boylii* breeding locations where high numbers of individuals had been documented in previous studies for at least 2 y.

Egg mass and tadpole habitat use.—We conducted visual encounter surveys in May and June and collected data on hydraulic conditions at egg mass locations. Two surveyors walked along each side of the river, manually searching under larger substrates for egg masses (Heyer et al. 1994). In addition, we used mask and snorkel to detect egg masses in deeper water. We completed surveys once per week at each of the eight study sites until no new egg masses were found on subsequent surveys. At each egg mass, we measured total depth

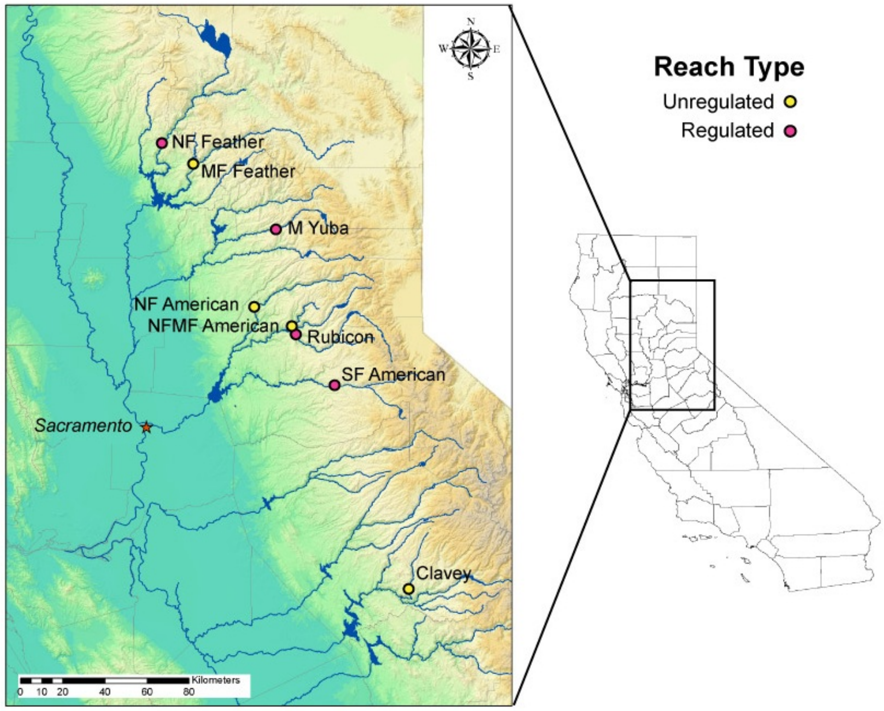

FIGURE 1. Location of the eight study sites for Foothill Yellow-legged Frogs (*Rana boylii*) in the northern Sierra Nevada range of California, USA.

with a wading rod and mid-column velocity using a Marsh McBirney Flow Meter (Hach Company, Loveland, Colorado, USA). We recorded egg mass attachment substrate as a categorical variable based on grain size diameter of the median axis: silt/fine sand (< 2 mm), gravel (2−64 mm), cobble (64−256 mm), boulder (> 256 mm), and bedrock (Harrelson et al. 1994). We recorded geographic coordinates for each egg mass using a handheld GPS unit, which were overlaid on 10-m resolution orthophoto imagery using a Geographic Information System (ArcGIS 9.0, ESRI, Redlands, California, USA).

We began tadpole surveys one month after the last egg mass was found, visiting each site once per month from July through September. Surveyors waded along the margins of the channel or snorkeled in deeper water, visually searching for tadpoles and turning over rocks to search the interstitial spaces. At each tadpole location the same hydraulic data were collected as described for the egg mass microhabitat conditions, including a GPS location for spatial analysis of tadpole distributions. When tadpoles occurred in close proximity to one another (less than 5 cm) and experienced the same microhabitat conditions, a single measurement was taken for each hydraulic variable to represent the group. If visual confirmation of tadpole developmental structures was feasible, life-stage categories were assigned as: Stage 1 (no rear limbs present or only small limb buds), Stage 2 (rear legs present), Stage 3 (rear legs with toes and front limb buds present), or Stage 4 (front limbs developed, tail still visible).

Habitat availability.—To quantify the available habitat for *R. boylii* during oviposition and tadpole rearing, we conducted habitat availability assessments at six of the eight study sites during each visual encounter survey. At the two study sites where availability data were not collected (Clavey and SF American), we surveyed a longer reach for egg masses and tadpoles. Within each of the six study sites, we used a random start point within the study reach and established a series of systematic transects to collect cross-sectional data. We oriented transects perpendicular to streamflow and at least one transect was placed in each mesohabitat type, based upon the classification of Hawkins et al. (1993), to cover the full range of depths, velocities, and substrate present. We collected hydraulic data at measurement points spaced at 1.5 m increments along each transect (2.0 m spacing at NF Feather site). At each survey point, we measured total depth, mid-column velocity, and dominant substrate type using the same methods described for egg mass and tadpole locations. If the water depth or velocity was such that it was unsafe to wade (depth > 1.10 m or velocity > 1 m s^{-1} during high flows in the spring), we used a range finder to determine the total wetted width of each cross section to account for points we could not survey.

Habitat suitability criteria development.—We assessed three types of HSC commonly used to define suitable instream habitat of aquatic species: (1) a composite habitat suitability index (HSI) created from combining interval-based univariate suitability indices (SI; Guay et al. 2000; Vismara et al. 2001; Guay et al. 2003); (2) a composite HSI created from combining percentile-based univariate SI (Amy Lind and Sarah Yarnell, unpubl. report); and (3) a multivariate habitat suitability index using a logistic regression approach (Guay et al. 2000; Rashleigh et al. 2005; Dixon and Vokoun 2009). For each technique, we used three hydraulic variables, total depth, mid-column velocity, and dominant substrate (attachment substrate for egg masses and dominant microhabitat substrate for tadpoles) to define suitable microhabitats. We pooled the egg mass data across all eight study sites to develop region-wide HSC. We used availability data from the spring survey in which the largest numbers of new egg masses were found, because it was representative of the river conditions during the peak of breeding season. Tadpole use data were also pooled across all eight study sites and we defined two developmental stage groups. The majority of tadpoles we found during the first survey (July) were Stage 1. On the second and third surveys (August-September) tadpoles were primarily Stages 2−3 with some Stage 4. We split the tadpole data into ‘early-stage’ (July) and ‘late-stage’ (August-September) groups according to survey month. Designating tadpole stages by survey month also had the advantage of more directly applying to regulated river flow management schedules, which are typically implemented on a monthly basis. We categorized the tadpole availability data as either early-stage or late-stage (combined August and September surveys) according to the month of survey and data from the six availability sites were pooled.

Suitability indices (SI) for hydraulic variables are commonly adjusted to represent a proportion of use relative to the proportion available by dividing the percentage of use by the percentage of available habitat for established ranges of each variable (Guay et al. 2000; Vismara et al. 2001; Maki-Petays et al. 2002). This approach is used because highly used conditions may not represent true habitat selection if they are also highly available. *Rana boylii* uses a narrow range of habitat conditions that are typically available, but they also avoid highly abundant habitat such as deep depths and high velocities (Kupferberg 1996; Lind 2005). We were concerned that values for frequently used habitats would be adjusted to express lower selectivity because these hydraulic conditions may be readily available. In contrast, less frequently used habitats would be misrepresented and overly classified as suitable if they were less abundant (Bovee and Bartholow 1996). Due to these concerns, we did not adjust the SI for availability and the univariate HSC are based upon use data only.

We created interval-based SI by converting each continuous variable to a series of intervals: 0.10 m increments for total depth (ranging from 0.00 to 1.10 m), and 0.05 m s^{-1} increments for mid-column velocity (ranging from 0.00 to 1.90 m s^{-1}). Attachment substrate for egg masses and dominant substrate at each tadpole or tadpole group was treated as an ordinal variable (range of 1−6) based on increasing size of median axis diameter. We calculated the frequency of use for each interval of the three hydraulic variables and normalized data from 0 to1 by dividing by the highest frequency of use. The resulting criteria represent the relationship between suitability (ranging from 0 to 1) and the range of each hydraulic variable.

To create suitability indices based on broader percentiles of use, we assigned ranges of observed mid-column velocities, total depths, and attachment substrates to one of two categories. We considered hydraulic conditions in which 90% of observed use occurred ‘high suitability’ and we assigned the range of the hydraulic variable a suitability value of 1.0. Conditions of ‘low suitability’ encompassed the remaining 10% of observations and we assigned a suitability of 0.1. We assigned all values outside of these ranges of use an SI of 0.0.

For both the interval and percentile approaches, we used the geometric mean to combine the three univariate SI (depth, velocity, and substrate) into a single habitat suitability index (HSI). This method allows for high suitability for one condition to compensate for low suitability of another by finding the central tendency of all SI values (Ahmadi-Nedushan et al. 2006). However, zero suitability for any variable yields an overall HSI of zero no matter how highly suitable the other two variables are.

The use of logistic regression has become increasingly prevalent in habitat selection studies for a variety of species, particularly in instream flow studies (Thomas and Taylor 2006). We used logistic regression modeling to simultaneously evaluate use and availability and to incorporate all three hydraulic variables in a single regression equation. The actual probability of use for any given egg mass and tadpole location is extremely small compared to the number of non-used locations available in a river environment. Thus, we regarded availability points in this dataset as non-use points and we used a case-control type logistic regression to evaluate use points to an equal number of random non-use points (Thomas and Taylor 2006). We used data from the six sites in which both use and availability data were collected, excluding the South Fork American and Clavey from this analysis. Velocity was square root transformed because it was highly skewed toward lower values, and quadratic polynomial terms were included for depth and substrate to reflect the unimodal relationship of use over the range of these variables. We performed the logistic regression in NCSS statistical software (NCSS, LLC, Kaysville, Utah, USA) and we assessed significance of parameters using $\alpha = 0.05$.

***HSC transferability.*—**We used a validation dataset to evaluate the transferability of the three habitat suitability criteria and their ability to predict occupied *R. boylii* habitats in other rivers. This validation data set consisted of egg mass and tadpole data from previous years and other rivers of the region. We gathered these data from hydropower relicensing studies and other unpublished data. Data were collected during visual encounter surveys (Heyer et al. 1994) completed between 2002 and 2009, where at each egg mass and tadpole location the same three hydraulic variables (depth, mid-column velocity, and substrate type) were measured (Placer County Water Agency, unpubl. report; Nevada Irrigation District, unpubl. report; PG&E, unpubl. reports; Yarnell 2005). The validation dataset was comprised of 393 egg mass locations, 300 early-stage and 288 late-stage tadpoles from six new river or creek sites and two rivers from our study but from different survey years (Middle Yuba in 2008; Rubicon in 2007 and 2008).

We assigned suitability values to the new data points using the three HSC we had already developed. Based on the values of total depth, mid-column velocity, and substrate type of each new egg mass and tadpole, we computed an associated HSI value ranging from 0 to 1. For the univariate HSC, we used the defined boundaries of the intervals and percentiles to assign numerical SI values for each hydraulic variable, which were then combined using the geometric mean. We used the parameter coefficients from the logistic regression model to compute HSI using the logistic function equation.

To assess the transferability of our HSC, we compared the distribution of the HSI output for the validation datasets for each HSC (i.e., interval, percentile, logistic). To simplify interpretation, we defined four categories of HSI values for the validation dataset: high suitability (> 0.66), moderate suitability (0.33−0.66), low suitability (0.01−0.33), and unsuitable (< 0.01). We considered the HSC we developed transferable if (1) most or all of the validation egg mass and tadpole data were classified as suitable, and (2) the majority of validation data were classified as moderate to highly suitable.

***Application within a 2D hydrodynamic model.*—**We used a two-dimensional (2D) hydrodynamic model (River2D) to predict depths, mid-column velocities, and dominant substrate types for egg masses and tadpoles at one "case-study" site (Rubicon River). To evaluate how well the HSC classified occupied and unoccupied areas of a river based on local hydraulic conditions, we used a representative river reach. This reach was selected because R. *boylii* oviposition and tadpole areas, as well as unoccupied areas, were known from previous work.

River2D is a depth-averaged finite element model freely available and used by the California Department of Fish and Wildlife, U.S. Fish and Wildlife Service, and others in fish habitat evaluation studies (Steffler and Blackburn 2002; Tiffan et al. 2002; Mark Gard, unpubl. report). The 2D model for the Rubicon study site was developed within the instream flow study for the Placer County Water Agency (PCWA) Middle Fork American hydropower relicensing project (FERC #2079) for use in evaluating potential project effects on instream flow conditions. Details on the calibration of the model, including information on the input topography, mesh density, and model error can be found online (PCWA, 2010. Instream flow full report. Available from http://relicensing.pcwa.net/html/science/padreportaquatic.php [Accessed 15 March 2010]). The calibrated model was provided for use in this study by PCWA.

We input each of the three types of HSC (interval, percentile, and logistic regression) to the 2D model and we mapped habitat suitability ranging from 0 to 1 across the modeled river reach. We then overlaid point locations for egg masses and tadpoles (late-stage only) surveyed in the modeled reach in 2008 onto the habitat suitability maps. The number of egg mass and tadpole locations that fell within one of four HSI categories were counted and plotted for comparison. We defined HSI categories as stated above (high, moderate, low, unsuitable). Similar to our approach with the validation data, we expected that useful (or good) HSC would always or nearly always classify oviposition and tadpole rearing habitat as moderate-highly suitable, and unoccupied areas would be classified as unsuitable. We evaluated how each HSC classified unoccupied areas of the river by assessing the extent to which areas of the river were classified in each HSI category. We evaluated habitat suitability at the modeled flows that were observed when the egg mass and tadpole data were collected; 1.5 $m^3 s^{-1}$ and 1.0 $m^3 s^{-1}$, respectively.

RESULTS

***Habitat use by life stage.*—**We found 147 egg masses at the eight study sites between 12 May 2009 and 19 June 2009 (Fig. 2), with approximately one-third (50 of 147) occurring at the NF Feather site. The timing of egg mass deposition and the duration of the breeding season varied widely among sites. The start of the breeding season ranged from 12 May 2009 (NF Feather) to 24 June (SF American) and the duration ranged from 3.5 weeks at the NF Feather to only 6 d at the SF American (Fig. 2). We collected three availability datasets at each

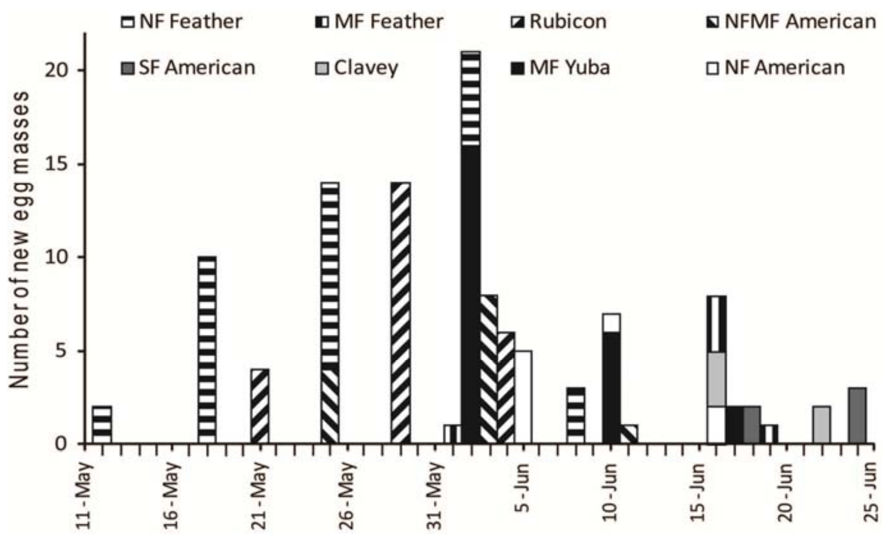

FIGURE 2. New egg masses of Foothill Yellow-legged Frogs (*Rana boylii*) found on each visual encounter survey in the spring of 2009. Because more than one site was surveyed on a single day the bars overlap for some dates (e.g., june 2 shows stacked data for both NF Feather and MF Yuba), the top of the bar represents the total for that site. The survey date on which the greatest number of new egg masses was found was considered the peak of breeding for that site (e.g., 20 new egg masses on June 2 for NF Feather).

of six availability census study sites and five availability datasets at the NF Feather due to the extended duration of breeding. We selected the habitat availability dataset corresponding to the peak of the breeding season on each river for further analysis (e.g., 29 May for Rubicon; Fig. 2).

At all eight river sites, R. boylii selected a subset of available habitat conditions for oviposition, depositing egg masses in areas of moderate depth and low velocities and attached to course substrate (Fig. 3). Oviposition sites had a mean total depth of 0.39 m (± [SD] 0.16) and mean mid-column velocity of 0.05 m s^{-1} (± 0.06). The deepest egg mass observed at any site was at 0.87 m (MF Yuba) and the highest mid-column velocity was 0.13 m s^{-1} (MF Feather). Boulder (63%) and cobble (35%) were the most frequently used attachment substrates and there were no egg masses attached to silt, sand, or gravel (Fig. 3). Because significant portions of the center of the river channel could not be surveyed during spring flows, the habitat availability data reflect depths that could be surveyed up to 1.1 m and velocities < 1.9 m s^{-1} (Fig. 3). However, greater depths and velocities existed in the river during the breeding season. Thus, the availability data underestimated the actual amount of deeper water and faster velocities that occurred during the breeding season.

We collected habitat data on 694 early-stage and 638 late-stage tadpoles. Early-stage tadpole rearing sites had an average total depth of 0.26 m (± 0.20), whereas late-stage tadpoles were found in shallower depths (0.18 m ± 0.22). All tadpole stages used microhabitats with low velocities, although mean mid-column velocity was lower for late-stage tadpoles (0.03 m s^{-1} ± 0.04) compared to early-stage tadpoles (0.05 m s^{-1} ± 0.07; Fig. 3). The most frequently used dominant substrate was cobble for both early- and late-stage tadpoles (79% and 63%, respectively; Fig. 3).

We collected three availability datasets at each of six availability study sites. We used the July habitat availability data set for comparison with early stage tadpoles and we pooled the August and September availability data sets for late-stage tadpoles. Similar to egg mass habitat selection, early- and late-stage tadpole habitat selection did not appear to be limited by the wide range of conditions available in the river.

***Interval-based habitat suitability index.*—**Egg mass interval-based suitability indices (interval SI) were unimodal for total depth and substrate type, but highly skewed toward lower values for mid-column velocity (Fig. 4). These SIs reflect the most frequent use in extremely low mid-column velocities (≤ 0.05 m s^{-1}) and moderately shallow depths (0.20–0.50 m; Fig. 4). Suitability values dramatically declined with increasing mid-column velocity and depth, such that velocities > 0.30 m s^{-1} and depths > 0.90 m were defined as unsuitable (SI = 0) due to lack of use. Fine substrates with no egg mass use (silt, sand, and gravel) had SI values of zero, while suitability increased with increasing attachment substrate size to an optimum value of 1.0 for boulders.

The interval SI for early- and late-stage tadpole rearing habitats were skewed toward lower values for total depth and mid-column velocity and were unimodal

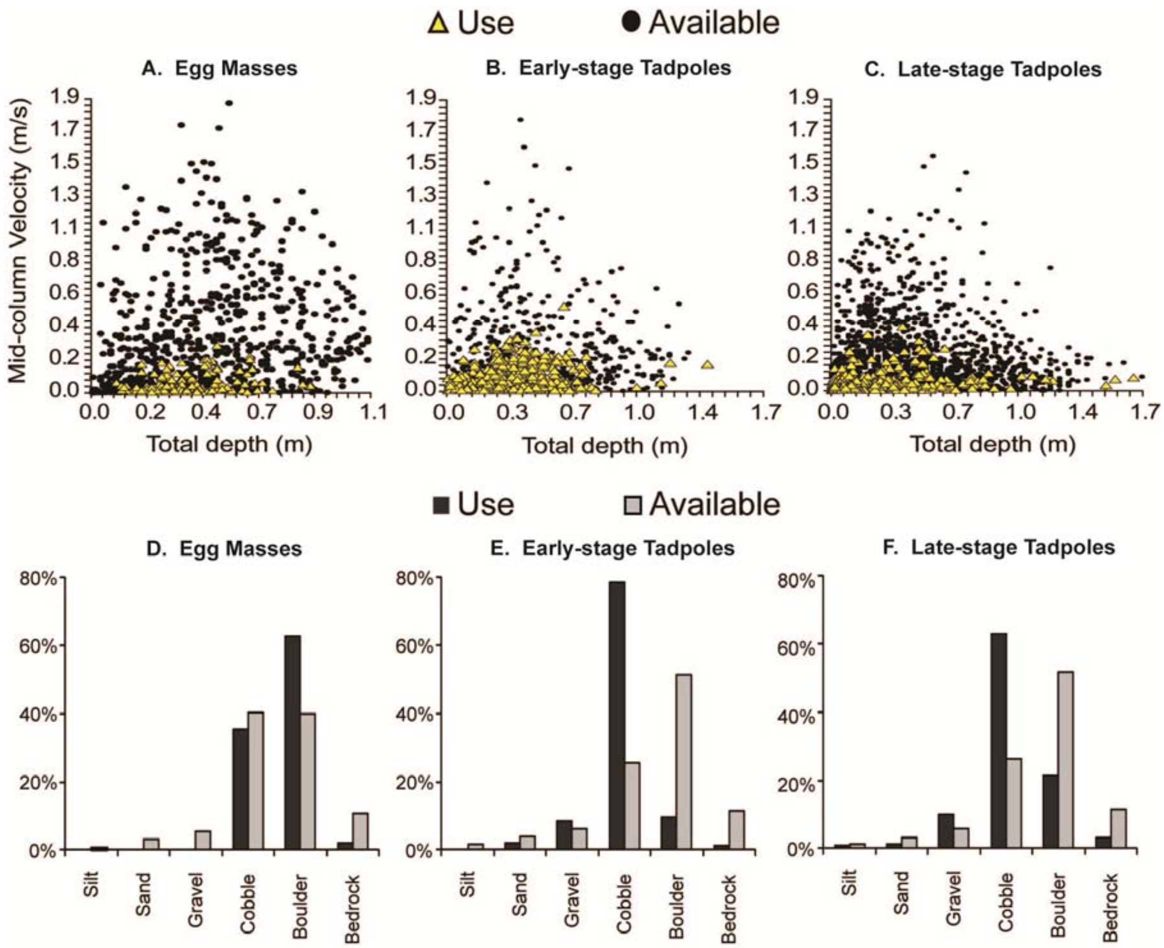

FIGURE 3. Hydraulic variables measured at egg mass and tadpole locations of Foothill Yellow-legged Frogs (*Rana boylii*) and available points. Top figures show the relationship between total depth and mid-column velocity at both use and available locations for (A) egg masses, (B) early-stage, and (C) late-stage tadpoles across all eight study sites. Lower figures are the frequency of used and available substrate types for (D) egg masses, (E) early-stage, and (F) late-stage tadpoles.

for substrate size (Fig. 4). For both tadpole stages, SI values for depth were highest in shallow water (0.01−0.10 m) and decreased as depth increased to 0.8 m. Suitability values oscillated between very low and zero within the range of 0.8 m and 1.7 m for both tadpole life stages.

Because we independently assigned each 0.1 m increment of depth an SI value based on use within that interval, depths in the range of 0.8−1.0 m and 1.2−1.3 m had no use and thus a suitability of zero, whereas depths in the range of 1.0−1.2 m and 1.3−1.4 m had very low use and a suitability of 0.01. Velocity SI values were similar for both tadpole life stages, with the highest values occurring between 0.00 m s^{-1} and 0.05 m s^{-1} and dramatically declining with corresponding increases in velocity to 0.55 m s^{-1}. Cobble and boulder substrates had the highest suitability values for both early- and late-stage tadpoles, whereas finer substrates and bedrock had low suitability values.

Percentile-based habitat suitability index.— Percentile-based suitability indices (percentile SI), defined by the extremes of use, had only three suitability index values: 1.0 for high suitability, 0.1 for low suitability, and 0.0 for unsuitable (Table 1). For each SI, the central 90% of observations defined the high suitability category; the remaining 10% of observations at the tail(s) of the use curves defined the low suitability category. Unlike the interval SI, all values up to the maximum observed use value were assigned a positive SI value (> 0.0), regardless of whether use was observed at the intermediate values. Similar to the egg mass interval SI, low mid-column velocities up to 0.15 m s^{-1} were categorized as highly suitable, whereas velocities up to 0.30 m s^{-1} were categorized as low suitability (Table 1, Fig. 5). The smallest grain sizes (silt, sand, and gravel) were not used for oviposition and thus were classified as unsuitable (Table 1, Fig. 5). Cobble and boulder were used most frequently (94%) and classified

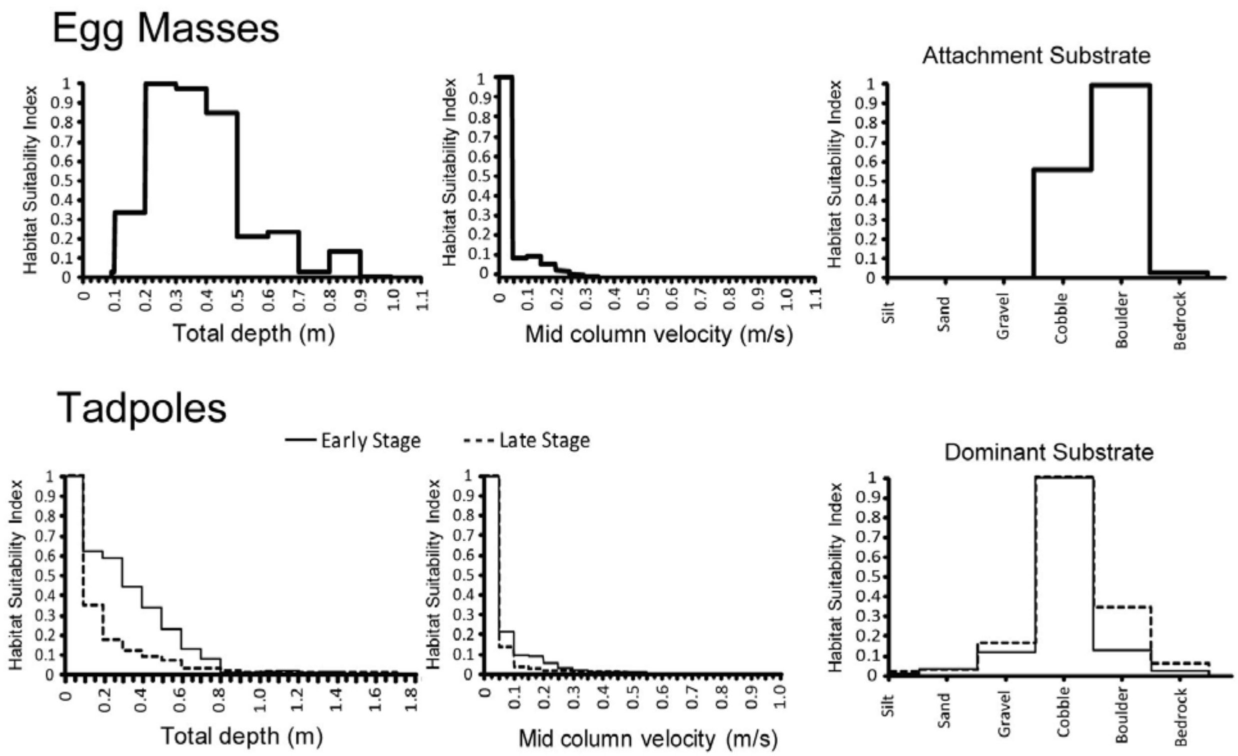

FIGURE 4. Interval-based univariate suitability indices by life stage of Foothill Yellow-legged Frogs (*Rana boylii*) for each hydraulic variable: total depth, mid-column velocity and substrate type. Each increment of the hydraulic variables was assigned a suitability index ranging from 0 to 1 based upon the relative frequency of use across all study sites.

as highly suitable for egg mass attachment, but only 6% of egg masses were attached to bedrock.

The percentile SI for both tadpole life stages were similar to the interval SI with the exception that the low suitability category for depth fully encompassed moderate depths between 0.55 m and 1.66 m (Table 1). The range of suitable velocities was slightly higher for early-stage tadpoles than late-stage tadpoles, but the distributions were similar with a strong skew to lower velocities (< 0.15 m s^{-1}). Early-stage tadpoles used all substrate types, except silt, and cobble and boulder were classified as highly suitable. Late-stage tadpoles used all substrate types with a shift to smaller sizes such that gravel, cobble, and boulder were assigned a high suitability.

Logistic regression habitat suitability criteria.—Three logistic regression models were developed, one for each *R. boylii* life stage (Table 2). In each logistic model the hydraulic parameters were significant (P < 0.001), but estimates of parameter coefficients differed among life stages. For oviposition sites and early-stage tadpole locations, there was a positive coefficient associated with depth and a negative coefficient with the quadratic depth term, describing the unimodal relationship between use and water depth. Late-stage tadpoles had greater use in shallower habitats indicated by the negative coefficient associated with depth and positive coefficient with the quadratic depth term. All life stages had negative mid-column velocity coefficients that decreased in value across progressive life stages from egg mass to late-stage tadpoles. A unimodal relationship between use and substrate size occurred for all life stages with positive substrate and negative quadratic substrate coefficients. The value of both substrate coefficients decreased progressively across life stages from egg masses to late-stage tadpoles as use of finer substrates increased through developmental stages.

Egg mass HSC transferability.—The three HSC classified the validation data differently overall and for specific rivers (Fig. 6). Across all seven validation datasets, the percentile HSI classified 61% of egg masses locations as high suitability (HSI > 0.66) compared with the interval HSI and the logistic model, which classified 40% and 46%, respectively. The logistic model classified the most validation dataset egg masses (32%) as moderate suitability (HSI = 0.33−0.66) compared with the interval and percentile HSI (21% and 16%, respectively). The interval HSI and logistic model classified more egg masses (20% and 18%, respectively) as low suitability (HSI < 0.33), whereas the percentile

TABLE 1. Foothill Yellow-legged Frog (*Rana boylii*) egg mass and tadpole rearing habitat suitability criteria based upon 90th and 10th percentiles of use cut-off values. Ranges of the hydraulic variables were assigned suitability values: 0 = not suitable, 0.1 = marginally suitable, 1 = suitable.

		Total depth (m)			Velocity (m s^{-1})			Substrate type		
Lifestage	n	0	0.1	1.0	0	0.1	1.0	0	0.1	1.0
Egg mass	147	< 0.10; > 0.87	0.10–0.13; 0.68–0.87	0.14–0.67	≥ 0.31	0.16–0.30	0.00–0.15	Silt/clay; sand; gravel	Bedrock	Cobble; boulder
Early-stage tadpole	694	< 0.01; > 1.40	0.55–1.40	0.01–0.54	≥ 0.56	0.17–0.55	0.00–0.16	Silt	Sand; gravel; bedrock	Cobble; boulder
Late-stage tadpole	638	< 0.01; > 1.65	0.52–1.65	0.01–0.51	≥ 0.42	0.13–0.41	0.00–0.12		Silt; sand; bedrock	Gravel; cobble; boulder

HSI only classified 4% as low suitability. The interval and percentile HSI both classified 19% of all the validation dataset egg masses as unsuitable (HSI = 0.00), but the logistic model classified only 4% as unsuitable.

All three HSC classified the majority of egg masses as either high or moderate suitability for four of the river validation data sets (Rubicon, Middle Yuba, West Branch Feather, Pit; Fig. 6). These rivers are characterized as large, high gradient, boulder and bedrock dominated rivers, similar to the rivers from which the HSC were developed. With the exception of the South Yuba, the percentile HSI classified the majority (> 60%) of the validation dataset egg masses as highly suitable on each river, whereas the logistic regression model classified the least number of egg masses as unsuitable on each river. Each of the HSC classified a portion of validation dataset egg masses at the South Yuba as occurring in unsuitable conditions due to deep water depths (> 0.90 m).

The interval and percentile HSI classified the largest number of egg masses as unsuitable on Butte Creek and Shady Creek, the two smallest streams in the validation datasets (Fig. 6). At Butte Creek, 18 % of validation dataset egg masses were attached to substrates smaller than cobble and 40% occurred in depths less than 0.10 m, resulting in HSI values of zero for both HSC. Similarly, 95% of egg masses at Shady Creek were in locations as highly or moderately suitable (52% and 42%, respectively), with only 3% classified as unsuitable. The interval HSI and logistic model classified 29% and 24%, respectively, of validation dataset tadpole observations as highly suitable across all sites, and 4% and 8%, respectively, as unsuitable. The percentile HSI classified 85% of all late-stage tadpoles as occurring in highly suitable habitats, whereas the interval HSI and the logistic model classified 43% and 37%, respectively, as highly suitable. None of the very shallow depths (< 0.10 m) and consequently were suitability, and only egg masses located on bedrock, regardless of depth, were classified as unsuitable.

TABLE 2. Parameter estimates for the logistic regression model used to predict habitat suitability for each life stage of Foothill Yellow-legged Frogs (*Rana boylii*). All coefficients were significant predictors of *R. boylii* use at α = 0.05 and all *P*-values were < 0.001 except the value for B_1 ($P = 0.01$) in the Early tadpoles model.

		Depth	$Depth^2$	Velocity	Substrate	$Substrate^2$
	Intercept	B_1	B_2	B_3	B_4	B_5
Egg masses	-31.02	16.21	-15.93	-8.00	13.49	-1.47
Early tadpoles	-13.02	3.15	-5.43	-10.55	7.96	-1.07
Late tadpoles	-3.32	-4.53	2.21	-12.97	3.51	-0.51

Tadpole HSC transferability.—Across all five rivers in the early-stage tadpole validation dataset, the percentile HSI classified the majority of rearing validation dataset late-stage tadpole observations were classified as unsuitable by the percentile and interval HSI, and the logistic model classified only 1% of late-stage tadpoles as unsuitable. Distinctions in transferability between large rivers and small creeks for the tadpole HSC were less evident than for the egg mass HSC. The interval and percentile HSI transferred well to other rivers for both tadpole stages, classifying few early-stage tadpole locations and none of the late-stage tadpole locations as unsuitable in any site (Fig. 6). Those tadpole observations that were classified as unsuitable occurred either in silt substrates (Butte Creek) or in depths greater than 1.4 m (South Yuba, WB Feather). The logistic model classified slightly more tadpole observations as unsuitable on Butte Creek, WB Feather, and South Yuba due to either deep depths or a combination of high depth or velocity with silt or bedrock.

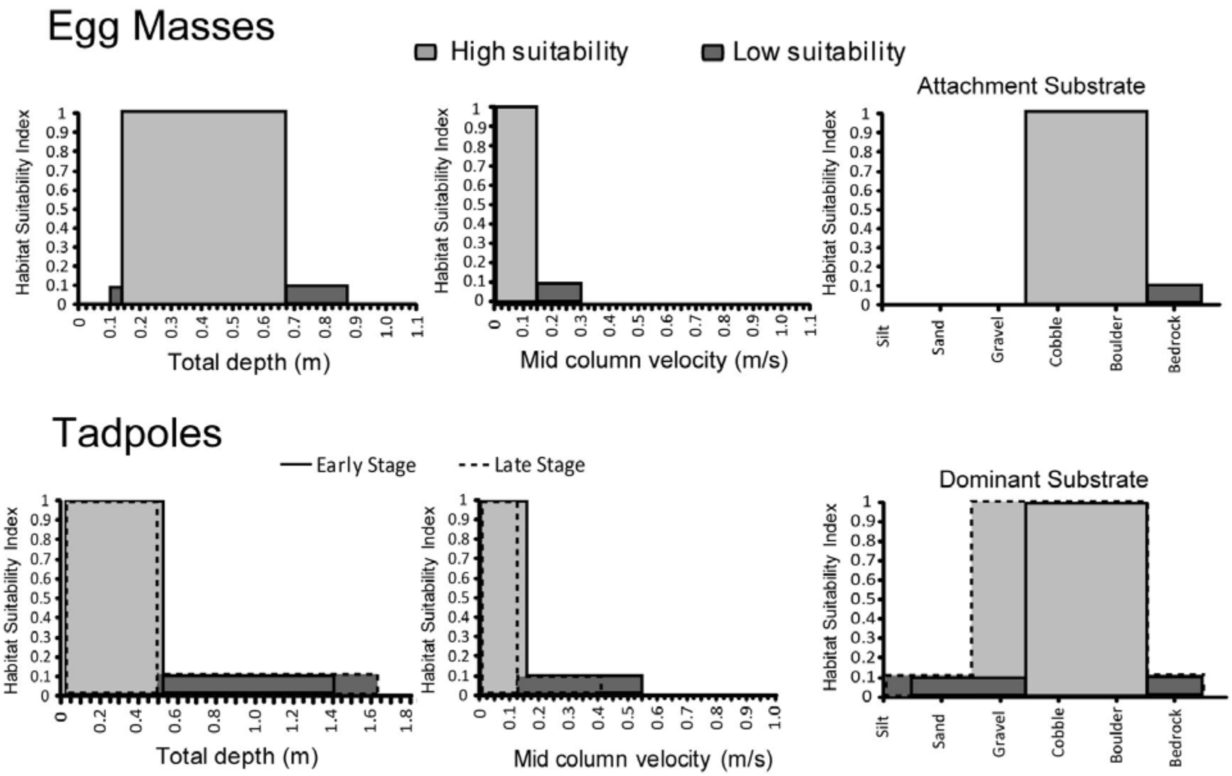

FIGURE 5. Percentile suitability indices by life stage of Foothill Yellow-legged Frogs (*Rana boylii*) for each hydraulic variable: total depth, mid-column velocity and substrate type, calculated from the frequency distribution of use data pooled across all study sites. Boxes delimit the boundaries of suitability categories based on 90th (light gray, high suitability = 1.0) and 10th (dark gray, low suitability = 0.1) percentiles of use. Ranges of variables with no observed use were categorized as unsuitable (0.0).

Application within a 2D hydrodynamic model.—At a typical late spring flow when egg masses were observed (1.5 m^3 s^{-1}), the HSC classified modeled depths, mid-column velocities, and dominant substrate types at egg mass locations in a similar fashion to the classifications within the validation datasets (Fig. 7). The percentile HSI classified the majority (56%) of actual egg mass locations as highly suitable, while the interval HSI and logistic model classified 13% and 19%, respectively, of egg mass locations as highly suitable. The logistic model classified the least number of egg mass locations as unsuitable (19%), whereas the interval and percentile HSI each classified 31% of observed egg masses as occurring in unsuitable habitat.

For a typical spring flow level at the scale of the entire modeled reach, the HSC classified unoccupied areas of the modeled river reach differently, thus these HSC would produce different results if used to calculate the amount of unsuitable habitat present under a variety of flow scenarios (Fig. 7). The interval HSI classified the least area of river as highly suitable (7%), whereas the percentile HSI classified the greatest portion as highly suitable (19%), reflecting differences in how each method assigns HSI values to generally suitable habitats. The interval and percentile HSI also classified twice the area of river as unsuitable for oviposition as the logistic model (62% versus 27%), primarily due to differences in how the HSC incorporated substrate suitability and high mid-column velocities. The interval and percentile HSI assigned an SI value of zero to gravel-dominated substrate, whereas the logistic model assigned a low but suitable value if the other hydraulic variables were suitable. In addition, the logistic model classified areas in the river with high mid-column velocities (> 0.30 m s^{-1}) as low suitability, rather than unsuitable. As a result, the logistic model classified the majority of the river as low suitability habitat.

At a typical late summer flow when tadpoles were observed (1.0 m^3 s^{-1}), the late-stage tadpole HSC performed well in the 2D model, classifying all modeled depths, mid-column velocities, and dominant substrate types at actual tadpole locations as suitable (Fig. 8). The percentile HSI classified 95% of tadpole locations as highly suitable, while the interval HSI classified 66% of locations as highly suitable. The remaining tadpole locations were classified as moderate suitability by the percentile HSI or moderate and low suitability (31% and 3%, respectively) by the interval HSI. The logistic model did not classify any tadpole locations as unsuitable, but only 3% were designated as highly

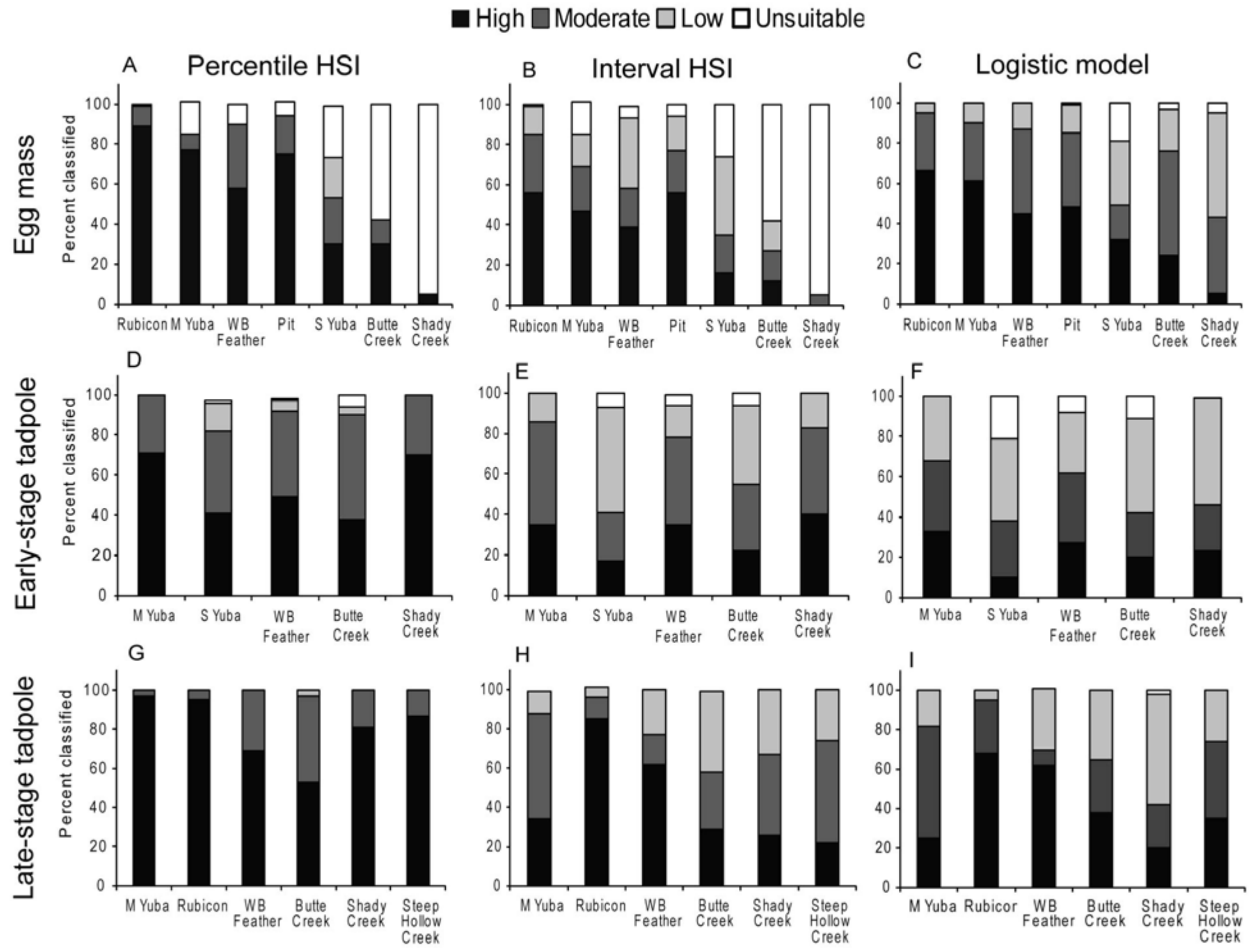

FIGURE 6. Output from three HSC models classified into unsuitable (0.0), low (< 0.33), moderate (0.33–0.66) and high (> 0.66) suitability categories for (A–C) egg masses, (D–F) early-stage, and (G–I) late-stage tadpoles of Foothill Yellow-legged Frogs (*Rana boylii*).

suitable, and 76% were assigned a moderate suitability. The remaining 21% of tadpole locations were classified as low suitability by the logistic model, a greater proportion than either of the other HSC.

At the whole reach scale, for a typical late summer flow, the majority of river habitat was classified as suitable by each of the late-stage tadpole HSC (Fig. 8). Each HSC classified a similar proportion (18−28%) of the area of river as unsuitable for tadpole rearing; however, the distribution of HSI values in suitable habitat varied widely among methods. Similar to the egg mass HSC the logistic model classified the majority of river habitats as low suitability for tadpole rearing, whereas the percentile HSI classified the majority of habitat as highly or moderately suitable. The interval HSI classified suitable habitat in a similar spatial pattern to the percentile HSI, but assigned values in a manner more similar to the logistic model. The logistic model classified the least area of river as highly suitable (8%), whereas the interval HSI classified 13% as highly suitable and the percentile HSI classified 35% as highly suitable.

DISCUSSION

We quantified hydraulic habitat conditions for the aquatic life stages (egg masses and tadpoles) of *Rana boylii* in the Sierra Nevada of California. Based on this information, we developed and evaluated three types of HSC that exhibited significant differences in the potential transferability to other rivers and predictive abilities in instream flow modeling. These differences are mainly attributable to methodological disparities. Specifically, the univariate HSI (both interval and percentile based) had distinct bounds on suitability based upon observed use and thus did not allow extrapolation beyond the range of data from which they were constructed. As a result, the univariate HSI appear to be readily transferable to large rivers, similar to those used to create the HSC, but not to smaller creeks. In terms of

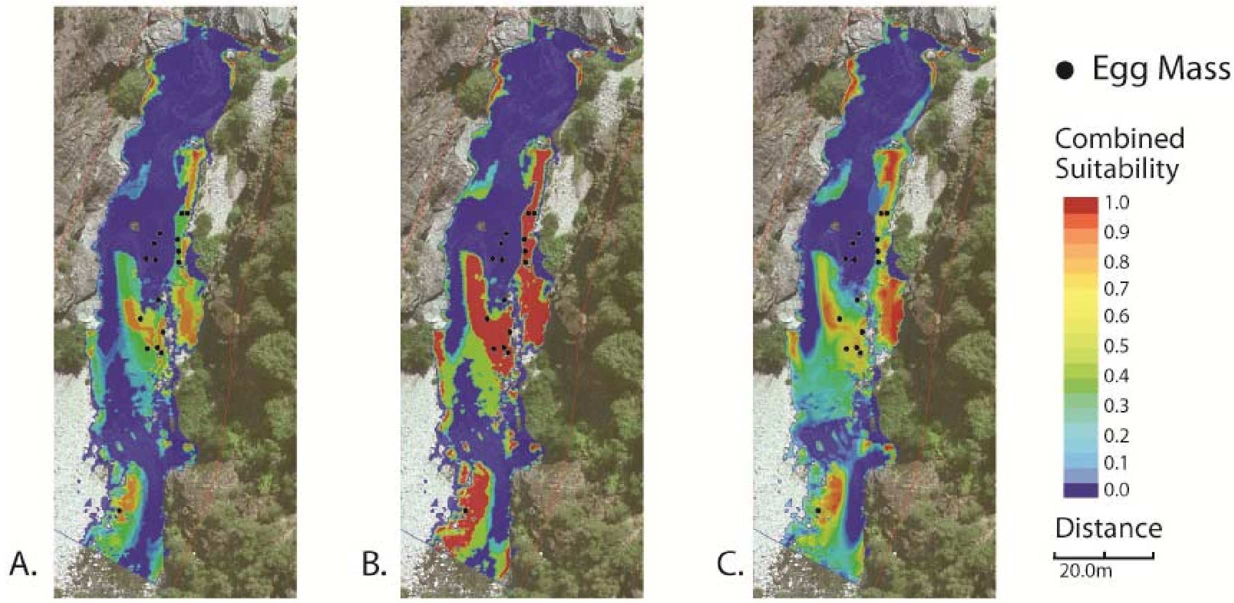

FIGURE 7. Modeled oviposition habitat suitability of Foothill Yellow-legged Frogs (*Rana boylii*) at Rubicon site using (A) interval HSI, (B) percentile HSI, and (C) logistic regression model. Dots represent surveyed locations of egg masses in spring, 2008; color bands represent habitat suitability values ranging from 0 to 1.

predictability, the univariate HSC were more accurate in predicting tadpole locations for the modeled river reach than they were for egg masses, indicating that the bounds for one or more of the hydraulic variables may be too narrow for the egg mass life stage. In contrast, the logistic regression model inferred potential suitability beyond the range of observed data based on trends in those data, and subsequently, the majority of the modeled river reach was classified as low suitability (rather than unsuitable). For this same reason, the logistic model showed higher transferability to both river and creek validation datasets. This characteristic of the logistic model may be appropriate for some aquatic species such as fish that use a broader range of available river habitat (Guay et al. 2003), but not for species that may be limited by a critical threshold in habitat conditions. Kupferberg et al. (2009, 2011) showed that velocities in the range of 0.3–0.4 m s^{-1} had a high likelihood of scouring *R. boylii* egg masses and/or washing out tadpoles and therefore may be a critical velocity beyond which conditions are unsuitable for either life stage. Thus, the logistic model, which assigned portions of the river with velocities greater than 0.3 m s^{-1} as low suitability, over-represented suitable habitat throughout the river reach.

The differences we identified in transferability between large rivers and small creeks, especially for the univarite HSI, are likely due to local availability of hydraulic conditions. Rivers in the validation dataset were of a similar size and geomorphology to the ones used to construct the HSC and likely had a similar range of water depths, velocities, and substrates, whereas the small creeks offered a narrower range of conditions. In the validation datasets from the small creeks, egg masses were more frequently attached to finer substrates and in shallower depths; thus, the univariate HSI with distinct bounds were not as transferable to these types of streams. Although the logistic model categorized the least number of validation dataset observations as unsuitable on rivers of all sizes, the model classified large areas of the modeled river reach as unsuitable for tadpoles contrary to field observations, and designated areas outside of known tolerance limits as suitable for egg masses.

The more continuous output of the interval HSI allowed for a finer degree of resolution in the habitat suitability values, ranging fully from 0 to 1. However, the interpretability of each suitability value is limited by a current lack of data on the relationships among gradients of habitat conditions and suitability, frog densities, and population outcomes (e.g., population trajectory, stability, life stage-specific survival rates). This research need has also been identified for other aquatic taxa (Lancaster and Downes 2010a; Moyle et al. 2011). Another concern with the interval HSI is that a variety of combinations of habitat conditions can result in the same HSI value (e.g., two highly suitable variables and one low suitability variable combine to equal the combination of three moderately suitable variables). In contrast, the geometric mean combination of only three SI values (0, 0.1, or 1.0) for the percentile HSI results in one of four categorical HSI values (i.e., the possible overall suitability values are 0, 0.22, 0.46, 1.0), which provides a relatively simple system for understanding

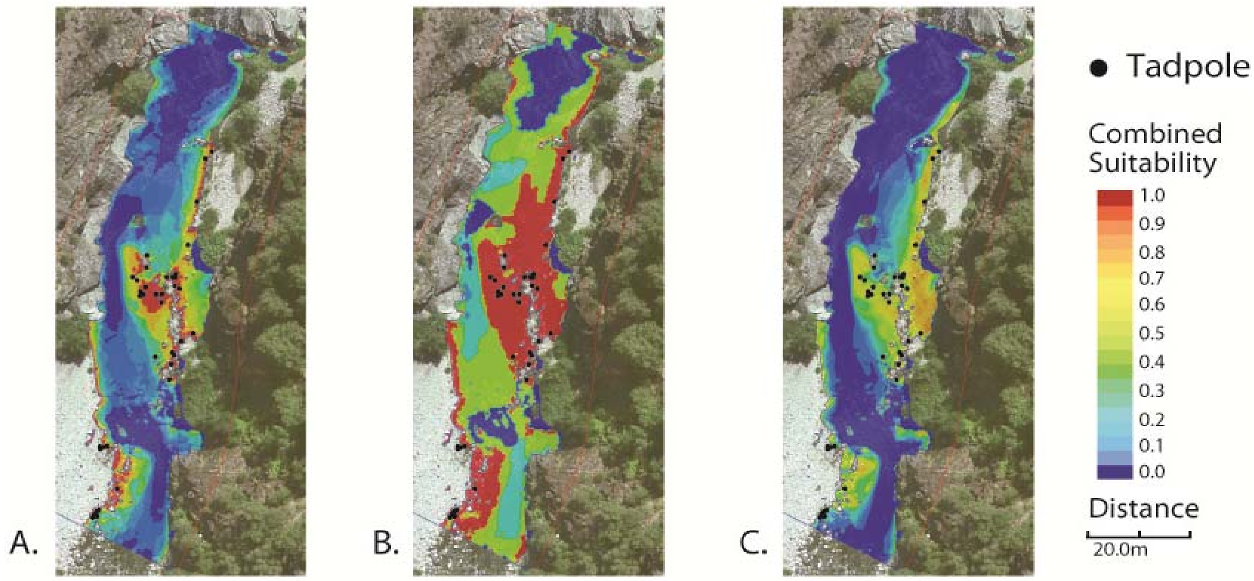

FIGURE 8. Modeled late-stage tadpole habitat suitability at Rubicon site using (A) interval HSI, (B) percentile HSI, and (C) logistic regression HSI. Dots represent surveyed locations of tadpoles in August 2008; color bands represent habitat suitability values ranging from 0 to 1.

how many hydraulic variables contribute to each overall suitability value.

Based on the ease of interpretation and the higher degree of transferability across rivers of similar size and geomorphology to those used in the HSC development, we recommend the percentile HSI be used as region-wide HSC for *R. boylii* in the northern Sierra Nevada. For smaller creeks and streams, with typically shallower water depths and smaller substrates, locally-derived HSC should be developed following the percentile HSI methodology. As relationships between habitat conditions and population outcomes for *R. boylii* become better understood, the interval HSI methodology may allow for assessments of finer gradients of habitat suitability for varying streamflows, and thus should be reassessed in the future for use in regional HSC for *R. boylii*.

The primary assumption of these HSC is that a greater frequency of use is equivalent to higher habitat suitability. Habitat suitability criteria based on frequency of use have been criticized because density may not necessarily reflect conditions that optimize survival and fitness (Lancaster and Downs 2010a). In addition, density can be influenced by a variety of non-habitat factors and thus may not accurately represent the breadth of habitat requirements for a species (Van Horn 1983; Huckstorf et al. 2008). The extent that assumptions about species area-environment relationships influence instream flow modeling outcomes and the need to more explicitly integrate ecological relationships (e.g., food availability, competition, predation pressure) and demographic outcomes (e.g., survival, population growth rates) into instream flow habitat modeling is an area of active debate (Lancaster and Downes 2010a; Lamouroux et al. 2010; Moyle et al. 2011). We offer several biological examples that support these assumptions for *R. boylii* and describe how the percentile HSI method represents tolerance limits for hydraulic conditions with ecological relevance.

For *R. boylii,* greater frequency of use of certain hydraulic conditions may reflect habitat selection that optimizes survival of egg masses and tadpoles. Egg masses are fragile and therefore vulnerable to detachment with even minor increases in velocity, and tadpoles have limited mobility (Kupferberg 1996; Lind et al. 1996; Kupferberg et al. 2011). Previous research has also shown that changes in summer streamflows and resulting changes in water depth and velocity can alter tadpole behavior, flush them from shallow stream margins, and affect survival indirectly via growth rates (Kupferberg et al. 2011). As reflected by the high frequency of course substrates used for oviposition, egg masses require an attachment surface that will remain stable during periodic spring flow fluctuations (Kupferberg 1996). Finally, stream flow events that negatively affect the early life stages of *R. boylii* have strong effects on the overall population growth rate (Kupferberg et al. 2009, 2012). The high use of shallow, low velocity habitats and large substrates that we observed in our Sierra Nevada study rivers is consistent with previous habitat work from the Coast Ranges of California (Fuller and Lind 1992; Kupferberg 1996; Lind 2005), and selection of these environments has a direct effect on survival of aquatic life stages. In addition, *R.*

boylii exhibits a lek-type mating system in which males establish calling territories, but females choose specific oviposition sites that are typically outside of a male's territory, indicating that male competition for oviposition sites is not a strong driver in habitat use (Wheeler and Welsh 2008).

Another concern presented by Lancaster and Downs (2010a) is that ecohydraulic models predict population level consequences associated with changes in use within gradients of suitability, rather than at or around critical thresholds. The percentile HSI, which we recommend, is a method that uses broad definitions of high suitability and includes quantitative tolerance limits for unsuitable conditions for egg mass and larval life stages of *R. boylii*. This approach is in line with ecohydraulic modeling methods that set biologically relevant limits of suitability, rather than an artifact of mathematical manipulation (Lancaster and Downes 2010b). In addition, HSC do not predict future densities of populations under varying flow conditions, but only the availability of habitats suitable for occupation. Therefore, these models can be used to predict the quantity and distribution of suitable hydraulic conditions for a species and to assess what flows may potentially limit or enhance reproductive output.

Riverine species with reproductive cycles adapted to the natural flow regime, such as *R. boylii*, can be negatively affected by altered flows (Poff et al. 1997; Kupferberg et al. 2012). In regulated rivers, water managers often use instream flow modeling to determine whether suitable instream habitat is available for aquatic species. These techniques rely on validated habitat suitability criteria that accurately predict the area and spatial distribution of habitats used by focal species. These criteria are necessarily simple; they do not account for non-hydraulic factors such as temperature, riparian conditions, food availability, and channel morphology (Lind 2005; Yarnell 2005; Yarnell et al. 2012). However, in the case of *R. boylii*, the hydraulic characteristics of velocity, depth and substrate exhibit a relatively narrow range of use compared to other habitat characteristics, and changes (especially aseasonal changes) in hydraulic conditions directly affect survival and ultimately population trajectory (Kupferberg 1996; Kupferberg et al. 2009, 2012). Therefore, we conclude that validated habitat suitability criteria can accurately quantify the amount and spatial distribution of suitable instream physical habitat available under different streamflow regimes for *R. boylii* (Yarnell et al. 2012). In addition, a broad-based suitability index, such as the percentile HSC recommended here, can be applied to assess instream habitat conditions for *R. boylii* in other river systems in the Sierra Nevada region where habitat use data is lacking.

Instream flow modeling of river habitats is a method that has been commonly used to assess flow impacts on fish for decades. *Rana boylii* is the first amphibian species for which the method has been used (Yarnell et al. 2012). Many amphibian species use edgewater and backwater habitats of managed rivers. These shallow, low velocity areas may quickly become unsuitable for egg deposition and larval development if flows are raised or lowered during the breeding season. Developing validated HSC for other river-dwelling amphibians will provide a tool for water managers to quantify changes in viable habitats required by critical life stages under varying flows.

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CHERYL A. BONDI is a Ph.D. student at the College of Environmental Science and Forestry, State University of New York. She received a Master's degree in Biology from Humboldt State University and a B.S. in Biology from Salem State University. Her primary research interests are amphibian ecology and conservation, with a focus on the distribution and habitat relationships of species in the context of a changing environment. Research projects she has worked on include the spatial ecology of Western Pond Turtles (*Actinemys marmorata*) in response to changes in flow regime and the current status of the species' distribution in northern California; Cascade Frog (*Rana cascadae*) population monitoring in the southern Cascade Mountains; and the breeding ecology of the Foothill Yellow-legged Frog (*R. boylii*) in Sierra Nevada rivers. Her current research investigates how calcium leaching in forest soils subject to acid deposition may affect the leaf litter community in northeastern forests. She is studying the role of soil calcium on the distribution and trophic interactions of the Redback Salamander (*Plethodon cinereus*) in northern hardwood forests. (Photographed by Monty Larson)

SARAH M. YARNELL is an Assistant Project Scientist at the Center for Watershed Sciences at UC Davis. Her studies focus on integrating the traditional fields of hydrology, ecology and geomorphology in the river environment. She is currently conducting research that applies understanding of river ecosystem processes to managed systems in the Sierra Nevada, with a focus on the development and maintenance of riverine habitat. She is a recognized expert in the ecology of the Foothill Yellow-legged Frog, a California species of special concern, and she is the first researcher to apply sediment transport and two-dimensional hydrodynamic modeling techniques to the evaluation of instream amphibian habitat. More recently, her experience has expanded to include consultation as a technical expert for various hydroelectric power relicensing projects (Big Creek Project, Desabla-Centerville Project, Middle Fork American Project, Yuba-Bear/Drum-Spaulding Project), where she has worked closely with government resource agencies and the private sector to assess the impacts of environmental flows on aquatic biota. (Photographed by Jeff Mount)

AMY J. LIND recently began a position as the hydroelectric coordinator for the Tahoe and Plumas National Forests in California. Prior to that she was a wildlife biologist with the USDA Forest Service, Pacific Southwest Research Station in Davis, California. She has a Ph.D. in Ecology from the University of California, Davis and a Master's degree in Wildlife from Humboldt State University. She has worked for the Pacific Southwest Research Station since 1986, conducting research on land and water management activities relative to California amphibians and reptiles and their habitats. Current research projects include livestock grazing effects on Yosemite toads (*Anaxyrus* [*Bufo*] *canorus*); responses of Foothill Yellow-legged Frogs to altered water flow regimes; riverine algal communities in regulated and unregulated rivers and consequences for aquatic grazers; natural and snow-melt recession hydrology in regulated and unregulated rivers - geomorphology and aquatic species responses. In addition to research activities, she also provides technical consulting for several National Forests on Federal Energy Regulatory Commission (FERC) hydropower relicensing studies and post-license monitoring plans. (Photographed by unknown)