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DYNAMIC FLOW MODELLING OF RIVERINE AMPHIBIAN HABITAT WITH APPLICATION TO REGULATED FLOW MANAGEMENT

S. M. YARNELL,[a]* A. J. LIND[b] and J. F. MOUNT[c]

[a] *Center for Watershed Sciences, University of California, Davis, CA, USA*
[b] *Sierra Nevada Research Center, United States Forest Service, Davis, CA, USA*
[c] *Center for Watershed Sciences, University of California, Davis, CA, USA*

ABSTRACT

In regulated rivers, relicensing of hydropower projects can provide an opportunity to change flow regimes and reduce negative effects on sensitive aquatic biota. The volume of flow, timing and ramping rate of spring spills, and magnitude of aseasonal pulsed flows have potentially negative effects on the early life stages of amphibians, such as the Foothill yellow-legged frog (*Rana boylii*). Two-dimensional hydrodynamic modeling is one method to evaluate potential effects of flow variation on frog egg masses and tadpoles. We explored the usefulness of this technique by modeling habitat suitability under several pulsed flow scenarios in two river reaches in northern California, USA. We conducted analyses beyond simple weighted usable area calculations, such as quantifying the risk of scour or stranding, in order to quantify potential loss under different flow scenarios. The modeling results provided information on potential susceptibility to flow fluctuations as well as the influence of channel morphology on habitat suitability. Under each flow scenario, low percentages of suitable habitat remained suitable or were 'buffered' from the pulse, creating high potential for scour of egg masses or tadpoles. However, due to differences in channel morphologies, the wide, shallow study site provided 2-3 times the buffering capacity of the entrenched study site.

Additional analyses suggested that limited buffering capacity and lack of connectivity between suitable egg mass and tadpole habitats may explain why some hydraulically suitable habitats are unoccupied. This type of model-based analysis would be useful for managing foothill yellow-legged frogs or similar aquatic species in regulated river systems. Copyright © 2010 John Wiley & Sons, Ltd.

KEY WORDS: instream flows; two-dimensional hydrodynamic modelling; River2D; regulated rivers; foothill yellow-legged frog; *Rana boylii*; pulsed flows

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INTRODUCTION

The foothill yellow-legged frog (*Rana boylii*) is one of a few native California amphibians whose complete life cycle is associated with fluvial environments. Dramatic declines in the last half century, thought to be primarily caused by hydrologic alteration (Lind, 2005), have resulted in a listing of the foothill yellow-legged frog as a California Species of Special Concern (Jennings and Hayes, 1994; Jennings, 1996), thus warranting management consideration during relicensing of hydropower projects by the Federal Energy Regulatory Commission (FERC). Previous studies have shown that the instream habitat preferences of foothill yellow-legged frogs are strongly associated with hydraulic and geomorphic conditions (Yarnell, 2000; Yarnell, 2008; Kupferberg, 1996) and that the fully aquatic egg and tadpole life stages are particularly vulnerable to velocity increases (Kupferberg *et al*., 2009; Lind *et al*., 1996). Instream habitat modelling, such as that done for fisheries management, may provide an analytical tool for water resource managers to assess how changes in flow may affect foothill yellow-legged frogs and their habitat.

Like many native California species, the life history of the foothill yellow-legged frog is synchronized with the predictable cycle of wet winters and dry summers that occurs across their range (Van Wagner, 1996; Lind, 2005). In spring, as snowmelt and winter flood waters recede, adults attach egg masses to the lee side of coarse substrates along the margins of wide and shallow shaped channel sections (Kupferberg, 1996; Yarnell, 2000). In summer and fall, natural low flow conditions provide stable, warm stream margin habitats suitable for tadpole growth and metamorphosis prior to fall precipitation and winter flow increases. In regulated rivers, alterations to the timing, magnitude and duration of discharge can be out of synch with natural seasonal runoff. The abrupt onset of a high volume spill in spring can scour previously laid egg masses, while the rapid cessation of a spill event can result in dewatering and stranding of egg masses laid during high flows. Summer pulsed flows can create small increases in local velocity that affect tadpole growth and survival or large increases in

*Correspondence to: S. M. Yarnell, Center for Watershed Sciences, University of California, Davis One Shields Avenue, Davis, CA 95616, USA. E-mail: smyarnell@ucdavis.edu

velocity that cause displacement or stranding (Kupferberg *et al*., in review). These negative impacts from rapid flow changes can result in high mortality and large population declines (Kupferberg *et al*., 2010).

Instream flow modelling is one of the most widely used tools for determining how hydraulic conditions vary between discharges (Bovee, 1982; Milhous *et al*., 1989). Two-dimensional (2D) hydrodynamic modelling, in particular, is a potentially useful method for evaluating hydraulic habitat data commonly collected for instream flow studies (e.g. water depth, water velocity, substrate size) in relation to the observed utilization and tolerances of the fully aquatic life stages of foothill yellow-legged frogs. In comparison to one-dimensional (1D) models, 2D models offer a finer scale approach that can better predict hydraulics in near-shore habitat and across large-scale roughness features, such as point bars (Osborne *et al*., 1988; Jowett *et al*., 1991; Ghanew and Hicks, 1992; Waddle *et al*., 2000), that are commonly utilized by foothill yellow-legged frogs. Because 2D models calculate both longitudinal and cross-sectional velocity distributions, they can more accurately predict water velocities and depths at local scales (Crowder and Diplas, 2000). For foothill yellow-legged frogs, this is particularly important as breeding and rearing sites are generally located within a few meters of shore. When combined with knowledge of the biological response and physical tolerances of egg and tadpole life stages, 2D modelling may also provide quantitative data on the impacts of proposed flow regimes on individuals. For example, hypothetical flow scenarios can be created specific to the types of conditions that might occur during a seasonal or aseasonal pulsed flow, and the results can be evaluated in a variety of ways that inform managers of the potential risks or benefits of a particular flow prescription.

As part of a larger comprehensive study exploring the effects of pulsed flows on foothill yellow-legged frogs (Kupferberg *et al*., 2009), we used a 2D hydrodynamic model, River2D (Steffler and Blackburn, 2002), to explore several flow scenarios that are considered during hydropower relicensing proceedings: (1) changes in suitable breeding and rearing habitat availability and connectivity as flows fluctuate, (2) the effects of a spring spill on breeding habitat and (3) the effects of an aseasonal pulse flow on tadpole rearing habitat. We combined the modelling results with data on the physical tolerances of each lifestage to quantify the potential negative effects from scour on individuals. Our goal was to evaluate the usefulness of 2D modelling for quantifying suitable hydraulic habitat and for providing information beyond classic weighted usable area analyses (Bovee, 1982) that may be more pertinent to foothill yellow-legged frog conservation.

METHODS

Using a 2D hydrodynamic model and field data from two study sites in Northern California, we designed a series of modelling scenarios to explore changes in suitable foothill yellow-legged frog habitat as flows fluctuated. At each study site, we simulated pulsed flow events by modelling flow increases from baseflow or low flow up to a typical high spring flow or summer hydropeaking or boatable flow. In regulated rivers, hydropeaking flows are produced to generate electricity. Under some hydropower licenses, pulsed flows are produced outside of, or in addition to, main power generation periods (e.g. on weekends) to provide recreational whitewater boating opportunities. At each stepped increment in flow, we determined the availability of suitable egg mass and tadpole habitat, examined the connectivity of habitats between steps, and assessed the changes in velocity within suitable habitat to determine the potential for scour of egg masses or tadpoles.

Study sites

We selected two study sites in Northern California, each representative of the hydrologic and geomorphologic conditions common to northern Coast Range rivers (South Fork Eel River [SF Eel], Mendocino County) and Sierra Nevada rivers (North Fork Feather River [NF Feather], Butte County) (Figure 1). The SF Eel study site has a smaller drainage area and lower mean annual discharge than the NF Feather site, but elevations are similar (Table I). Annual flows on the SF Eel illustrate a natural runoff hydrograph typical of unmanaged northern Coast Range rivers, while flows on the NF Feather reflect a pattern common to regulation of snow-melt driven Sierra Nevada rivers—large magnitude steeply peaked winter storm pulses overlying a flat minimum instream flow (Figure 2). Both study sites were located at established breeding (egg-laying) areas where previous surveys routinely documented high numbers of breeding and rearing individuals (Kupferberg, 1996; Kupferberg *et al*., 2009), and where habitat types occur that are similar in character to other known breeding and rearing areas.

Habitat types at the two study sites were similar, each including a run, riffle and pool in sequence; however, the channel morphology differed in that the typical cross-sectional shape of the NF Feather was deep, narrow and slightly entrenched, while the SF Eel was wide, shallow and slightly asymmetric (Figures 3–4). On the SF Eel study site, foothill yellow-legged frog breeding areas were located along the shallow margin of the run (Figure 3b) and on the shallow upstream end of the cobble bar adjacent to the riffle (Figure 3c) (Kupferberg, 1996). Breeding areas in the NF Feather study site also occurred in the shallow

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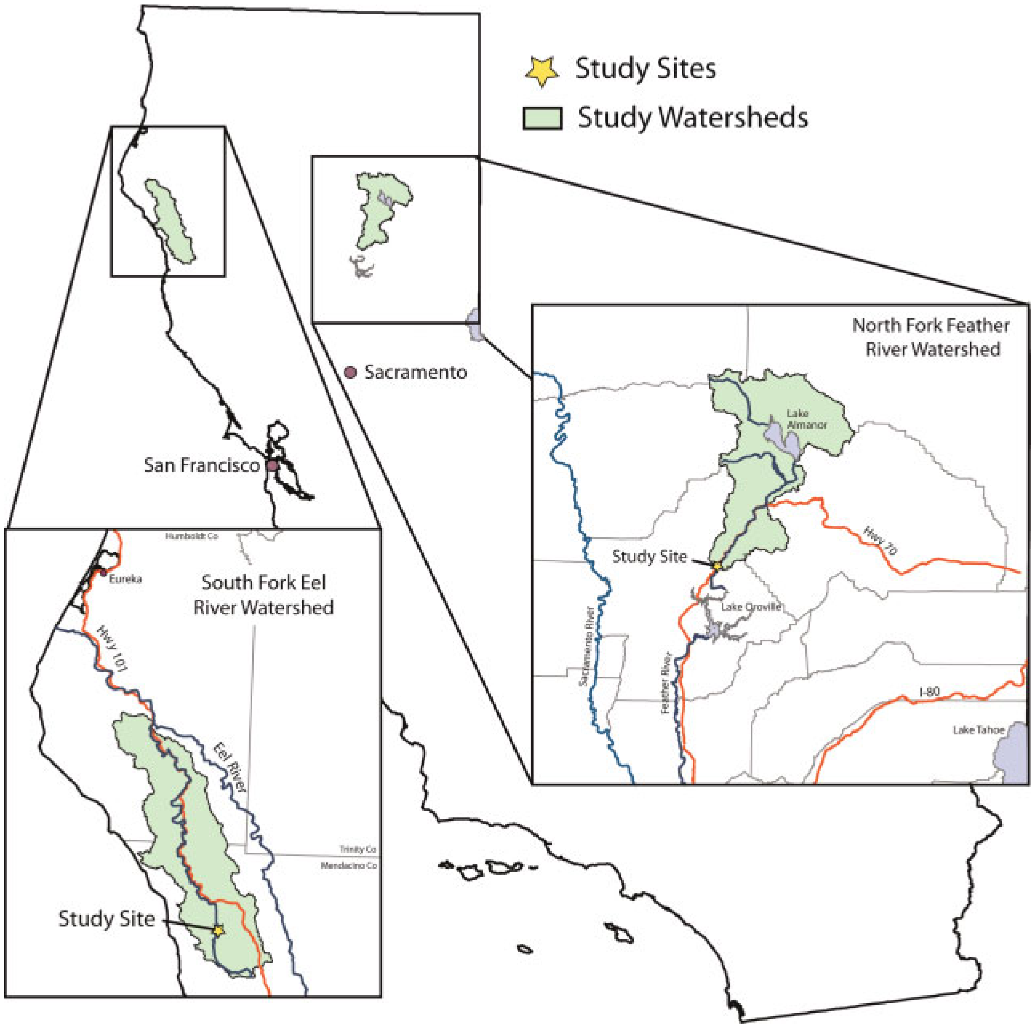

Figure 1. Location of study sites in Northern California, USA. This figure is available in colour online at wileyonlinelibrary.com

Table I. Hydrologic and geomorphic characteristics for each study site

	South Fork Eel River	North Fork Feather River
Nearest USGS gauge number	11475500	11404500
Drainage area[a] (km^2)	114	5078
Elevation (m)	390	415
Mean annual discharge[b] ($m^3\ s^{-1}$)	4.88	25.9
5-year recurrence discharge[b] ($m^3\ s^{-1}$)	163	752
Average summer baseflow[c] ($m^3\ s^{-1}$)	0.11	2.06
Channel bed slope	0.0067	0.0063
Study reach length (m)	110	150
Mean bankfull width (range) (m)	21.5 (16.4–25.4)	56.2 (45.6–77.0)
Dominant substrate	Bedrock overlain with cobbles, boulders	Bedrock overlain with cobbles, boulders
Dominant channel morphology	Riffle-pool	Riffle-pool

[a]Area upstream of the gauging station, data from USGS.
[b]Based on the following years of record: NF Feather, 1980–2006; SF Eel, 1968–2006.
[c]Average 30-day minimum flow.

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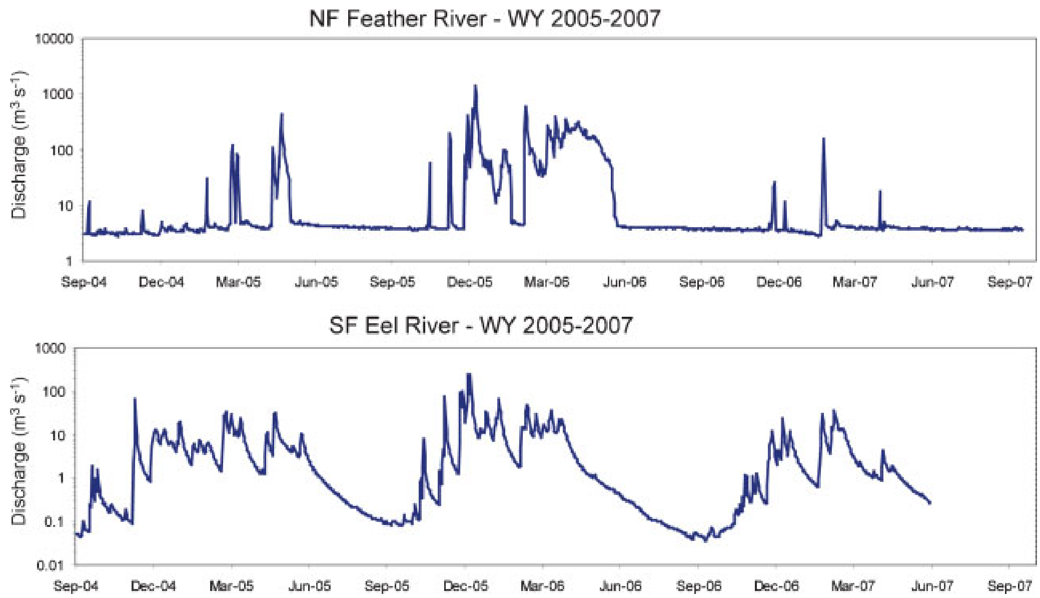

Figure 2. Mean daily discharge ($m^3 s^{-1}$) for water years 2005–2007 in the NF Feather (top) and SF Eel (bottom). This figure is available in colour online at wileyonlinelibrary.com

margins of the run (Figure 4c) and along the upstream end of the large cobble bar (Figure 4b). Substrates at both study sites ranged from small cobbles in the runs to boulders on the bars; however, large boulders also occurred in the deeper main channel on the NF Feather, while portions of the stream banks of the SF Eel study site were dominated by bedrock. Sedges lined the water's edge at both study sites, but common riparian vegetation such as willows and alders was limited at the SF Eel and abundant on the NF Feather.

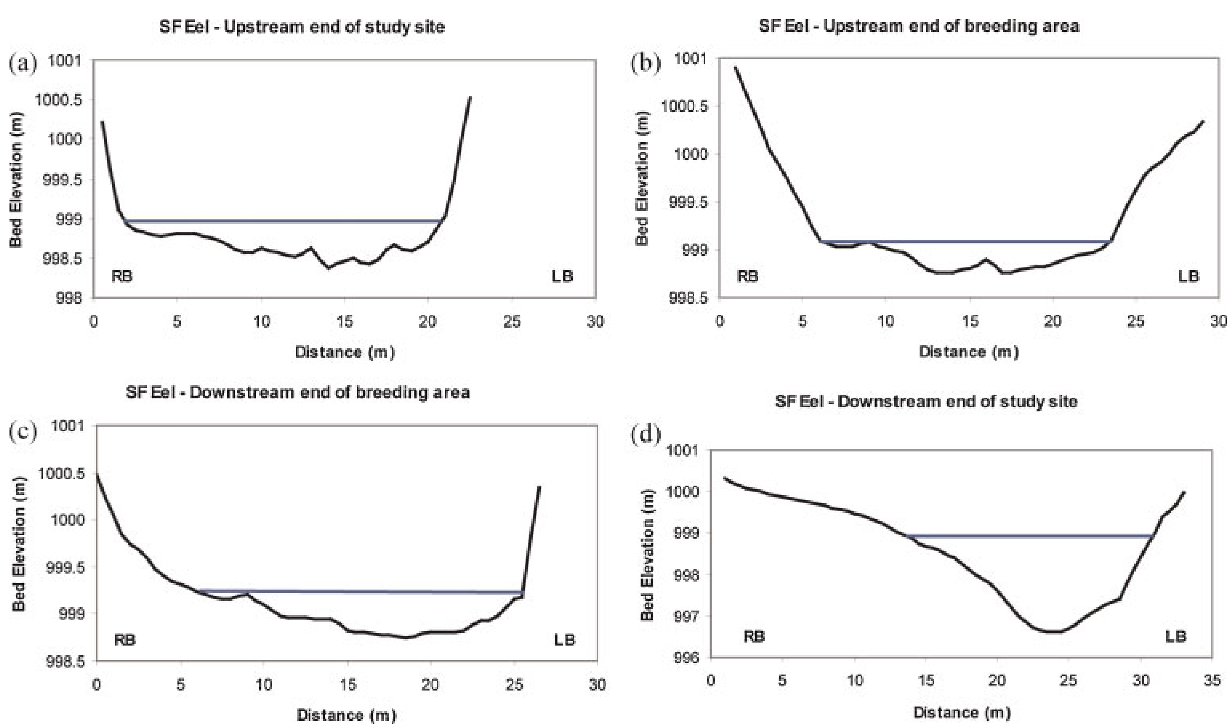

Figure 3. Representative cross-sections for the SF Eel study site ranging from most upstream (a) to downstream (d). Horizontal line represents depth at $1.45\,m^3 s^{-1}$, the discharge at breeding in 2006. This figure is available in colour online at wileyonlinelibrary.com

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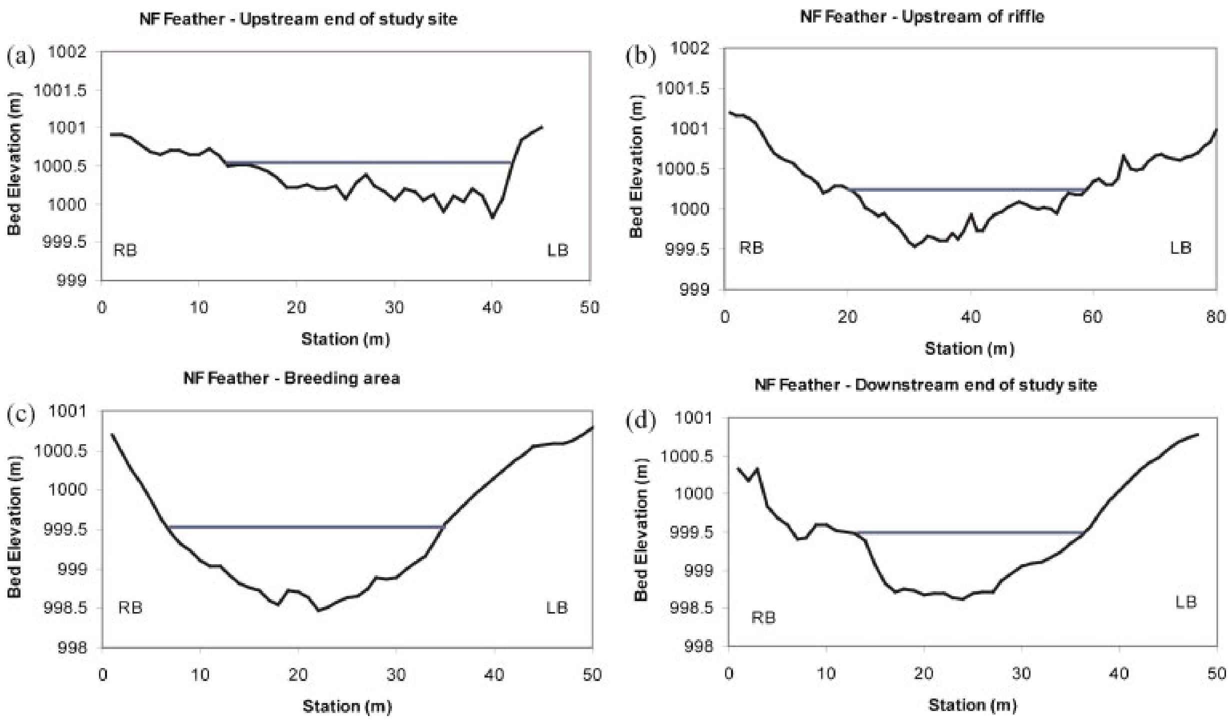

Figure 4. Representative cross-sections for the NF Feather study site ranging from most upstream (a) to downstream (d). Horizontal line represents depth at baseflow ($4.4\,m^3\,s^{-1}$), the discharge at breeding in most years. This figure is available in colour online at wileyonlinelibrary.com

Data collection and hydrodynamic modelling

Topographic surveys of each study site were completed in fall 2005 and winter 2006 using a robotic total station and a Global Positioning System—Real Time Kinematic (GPS-RTK) survey system (Topcon models GTS-802A and Hiper Lite Plus, respectively). Surveys were completed in a grid format at resolutions ranging from approximately $2\,m \times 2\,m$ in simple mid-channel or high floodplain areas to $0.25\,m \times 0.25\,m$ in the near-shore and channel margin areas where egg and tadpole habitats typically occur. In locations where large boulders or other flow-influencing features existed, the density of survey points increased (up to $0.10\,m \times 0.10\,m$) to reflect the topography of the feature. A total of 4847 points were surveyed across $3832\,m^2$ in the SF Eel study site, resulting in an average density of $1.3\,pts\,m^{-2}$. In the NF Feather study site, 7602 points were surveyed across $12\,596\,m^2$, resulting in an average density of $0.6\,pts\,m^{-2}$. An average substrate roughness in the form of roughness height, k_s, was estimated in the field for each primary geomorphic feature (e.g. pool, bar, riffle) and then assigned to each survey point on that feature. Roughness values ranged from 4.5 on the cobble/boulder bars to 2.0 in the pools for both survey reaches.

Hydrologic calibration and validation data were collected for the model at each site at low or base flows in fall, at high winter flow in January and February and at spring flow in May and June when egg masses were present in the channel. On the SF Eel, we surveyed water surface elevations and sampled hydraulic data at three discharges (0.15, 1.45 and $2.5\,m^3\,s^{-1}$), and collected hydraulic data at egg mass locations at $1.45\,m^3\,s^{-1}$ for comparison with predicted hydraulic conditions. On the NF Feather, we surveyed water surface elevations and sampled hydraulic data at two discharges, baseflow ($4.4\,m^3\,s^{-1}$) and a moderate flow ($15.7\,m^3\,s^{-1}$). However, due to unusual late-season high flows, hydraulic data could only be collected for validation purposes at four egg locations at baseflow.

The hydrodynamic modelling was completed using River2D, a two-dimensional, depth-averaged finite element model that is freely available and used by the California Department of Fish and Game, U.S. Fish and Wildlife Service and others in fish habitat evaluation studies (Steffler and Blackburn, 2002; Tiffan *et al*., 2002; Hanrahan *et al*., 2004; Gard, 2005). The inputs to the model included comprehensive reach-scale topographic surveys, detailed roughness parameters, inflow discharge and downstream boundary conditions in the form of water surface elevation (Steffler and Blackburn, 2002). Field measurements of water surface elevation, depth and velocity taken at low- and high-flows provided data for calibration purposes.

Flow simulations were run for each study reach at each of the discharges listed above. Simulations required downstream boundary conditions from a stage-discharge relation-

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ship that was either empirically derived (NF Feather site) or calculated from known water surface elevations (SF Eel site). A triangular finite element mesh with a node density ranging from approximately 0.1 to 0.25 m^2 was used to simulate hydraulic conditions at each study site. Output files from the flow simulations containing data on geographic location (local nodal coordinates) predicted depth, and velocity were input into a spreadsheet for analysis.

In general, simulated hydraulic conditions agreed well with measured values. Mean error in predicted depths and velocities in near-shore locations was low, with slightly greater variation in predicted velocities (e.g. 0.04 ± 0.08 m and 0.04 ± 0.13 m s^{-1}, respectively). A number of factors likely contributed to differences in measured and simulated values, including coarse resolution of the surveyed bed topography, field measurement error both due to the surveyor and the precision of the instrument and the natural variability of instantaneous velocity through time. In locations where substrates were poorly sorted and the resolution of the surveyed topography was not fine enough to delineate protruding cobbles and boulders, the model under-predicted depth and over-predicted velocity. At point egg mass locations, typically located on the lee sides of larger cobbles and boulder, modelled predictions of depth and velocity had a mean error of 0.03 ± 0.04 m and -0.04 ± 0.04 m s^{-1}, respectively, with velocity over-predictions ranging up to 0.10 m s^{-1} for 90% of the data (Figure 5). As a result, precise predictions of velocity at point egg mass locations downstream of protruding boulders were subject to a degree of error, but general hydraulic conditions throughout the near-shore environment were accurate.

For the focus of this study, we used the calibrated model at each study site to run flow simulations at a series of discharges ranging from base or low summer flows to winter flood flows. The goal was to encompass a range of flows typical of each study site in an average year. Output files from the flow simulations containing data on predicted depth and velocity were input into a Geographic Information System (GIS) for analysis.

At the SF Eel study site, data collected at egg locations during the spring discharge calibration flow (1.45 $m^3 s^{-1}$) in 2006 were used for validation of modelled habitat suitability conditions. On the NF Feather, due to unusual late-season high flows, frogs did not begin breeding at base flow or a moderate spring flow as in previous years, but laid eggs at a high discharge several days before flows were steeply reduced to base flow by upstream project operations. This resulted in a loss of half the egg masses due to desiccation and collection of egg mass location data only when flows had returned to base flow. Surveyed egg locations, including desiccated sites, were used to verify modelled habitat suitability conditions at both base flow and the simulated high spring discharge.

Habitat suitability criteria

Currently, validated habitat suitability criteria for foothill yellow-legged frogs do not exist, although new research is underway that aims to establish habitat criteria reflective of preference and unbiased by habitat availability. As a result, the habitat suitability criteria used in these model simulations are based on data reviewed and obtained within Kupferberg *et al.* (2009) and collected directly at the study sites. For egg masses, habitat suitability criteria were based on observed habitat use data collected at the SF Eel study site during the spring calibration flow in 2006 ($n = 73$). Suitable water depths were defined as 0.0–0.5 m and suitable water velocity was defined as 0.0–0.10 m s^{-1}, reflecting the range of hydraulic conditions observed at egg mass locations.

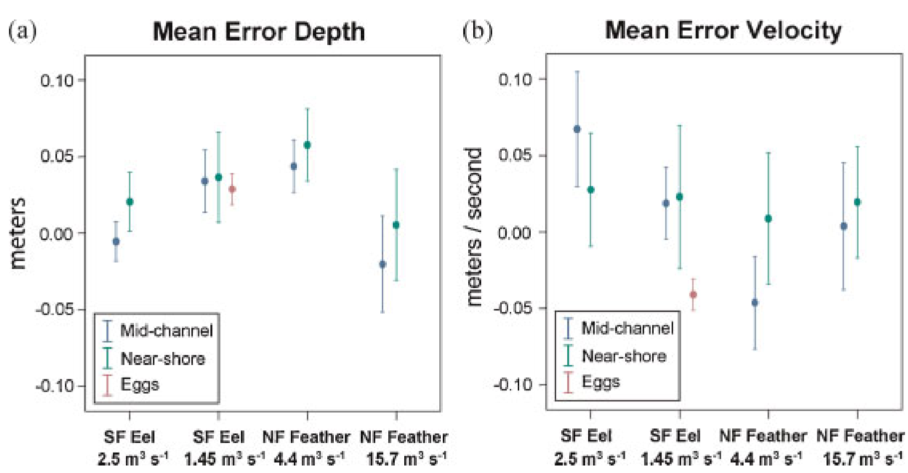

Figure 5. Mean error in surveyed versus modeled (a) depths and (b) velocities within various environments at each survey site at calibration and validation discharges. Points represent mean error and bars represent +/−2 standard errors. This figure is available in colour online at wileyonlinelibrary.com

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For tadpoles, suitable depth habitat was similarly defined as 0.0–0.5 m based on habitat use data from previous studies reported in Kupferberg *et al.* (2009). Experimental data from Kupferberg *et al.* (in review) showed suitable velocities for tadpoles ranged from 0.0–0.05 m s^{-1}, while velocities from 0.05–0.10 m s^{-1} precluded 'normal' behaviour and forced tadpoles to seek refuge in the substrate. Although the mean error in modelled velocity at each study site was low by typical hydrodynamic modelling standards, the model in some near-shore locations may not be sensitive enough to discern subtle differences in point habitat conditions such as 0.03 m s^{-1} versus 0.07 m s^{-1}. Therefore, in order to encompass the mean error in modelled velocity in the near-shore environment, suitable velocity for tadpoles was defined as 0.0–0.10 m s^{-1} with the knowledge that over longer periods (hours to days), tadpoles in higher local velocity locations are subject to higher predation risk and have lower growth rates than those in lower velocity locations (Kupferberg *et al.*, in review).

For both egg mass and tadpole lifestages, suitable substrate was defined categorically as cobble and boulder based on observations of habitat use at each study site in 2006. All depths, velocities and substrates defined as 'suitable' were assigned a suitability criteria value of 1.0, while all other values were assigned a suitability of zero. These individual habitat criteria were multiplied together to create a combined suitability index in River2D.

Hydrodynamic modelling scenarios

Combining derived habitat suitability criteria for the foothill yellow-legged frog with the flow simulations, it was possible to assess: (1) the overall area of available egg mass and tadpole habitat at different discharges and (2) the spatial connectivity of suitable habitats for discharges that represent typical changes from spring high flows to summer low flows. In addition, two flow scenarios representing specific issues that often arise during relicensing of hydropower projects were evaluated: (1) potential effects of spring spills on egg mass habitat conditions and (2) potential effects of aseasonal (e.g. summer) pulsed flows on tadpole habitat conditions.

Suitable habitat availability and connectivity as discharge changes. Seasonal changes (typically increases) to minimum instream flows are a common outcome of hydropower relicensing processes. Thus, we were interested in modelling suitable habitat area across a range of flows at each study site. Polygons of suitable habitat were delineated at each flow based on the modelled depth and velocity conditions at each node and summed across the reach. At both study sites, large areas of suitable habitat occurred that did not contain egg masses or tadpoles, so a subset of the total suitable nodes was also delineated as 'occupied' for comparison. Occupied suitable habitat was defined as all nodes between the furthest upstream and downstream egg locations in the longitudinal direction and all nodes between the minimum and maximum flow boundaries in the cross-sectional direction.

Several metrics for evaluating spatial relationships have been shown to be useful in previous studies exploring habitat connectivity such as nearest neighbour analysis and contingency analyses (Johnston, 1998). However, these metrics generally provide a measure of connectivity across a complex landscape at a single point in time. Temporal changes in habitat type across a landscape can be evaluated using a variety of change analyses; however, these techniques focus on changes through time at a specific spatial location. Simple techniques to quantify connectivity across both space and time are lacking. However, connectivity of suitable habitats as flows fluctuate through the season can be assessed qualitatively. While River2D cannot explicitly model standing water that is disconnected from the main channel flow, it models variations in wetting and drying in shallow areas by incorporating groundwater equations. A visual assessment of the locations of suitable habitat as discharge changed (viewed discretely in a series of snapshots in a GIS) was completed to provide information on which areas within the survey reach remain connected throughout the season.

Effects from spring spills. To determine the potential impact of sudden increases in flow on breeding habitat, a series of spring pulses was simulated for both study sites. On the NF Feather, the lowest three modelled flows (4.4, 7.1, and 10.0 $m^3 s^{-1}$) were each increased to 30.0 $m^3 s^{-1}$. The lowest flow, 4.4 $m^3 s^{-1}$, was the minimum baseflow required by the upstream project license in 2006, and was the discharge at which breeding occurred in most years, since monitoring began in 2000. On the SF Eel, spring egg-laying discharges for the last decade ranged from 0.7 to 11.0 $m^3 s^{-1}$ (S. Kupferberg, personal communication). Three of the lower modelled flows within this range (1.0, 1.45 and 2.0 $m^3 s^{-1}$) were selected, and each was increased to 7.0 $m^3 s^{-1}$, a typical high spring discharge.

For each simulated pulse, the risk of scour within egg mass habitats was determined. The change in velocity between the low and high flow was calculated at each modelling node within suitable habitat, then velocity increases were grouped into one of three categories associated with scour rates. Categories were based on observed rates of egg scour during an instream flow study in a previous relicensing project (Kupferberg *et al.*, 2009): velocity increases up to 0.1 m s^{-1} had 10% of eggs cumulatively scour, increases up to 0.4 m s^{-1} had approximately 45% cumulative scour and velocities increases greater than 0.4 m s^{-1} had approximately 50% and potentially greater cumulative scour. The per cent of

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modelling nodes within suitable egg mass habitat falling into each velocity category during each pulsed flow scenario was calculated.

Effects from aseasonal pulsed flows. To assess the impact of an aseasonal pulsed flow on suitable tadpole habitat, an increase in discharge from each of the three modelled low flows (same discharges as in spring scenario) to a representative high flow suitable for power generation or recreational boating (7.0 $m^3 s^{-1}$ on SF Eel, 30.0 $m^3 s^{-1}$ on NF Feather) was modelled at each site. Similar to the spring spill scenario, the change in velocity from low to high flow at each modelling node within suitable tadpole habitat was determined, and velocity increases were grouped into three categories associated with scour rates. Categories were based on an experimental study that showed the cumulative frequency of tadpole loss versus critical velocity when tadpoles fatigue (Kupferberg *et al.*, in review): velocity increases up to 0.1 $m s^{-1}$ had approximately 25% loss, increases of 0.1–0.25 $m s^{-1}$ had approximately 50% loss and velocity increases greater than 0.25 $m s^{-1}$ had approximately 75% and greater loss. The per cent of modelling nodes within suitable tadpole habitat falling into each velocity category during each pulsed flow scenario was calculated.

Based on experimental results in Kupferberg *et al.* (in review), most tadpoles responded to velocity increases by swimming straight down into the substrate rather than laterally to another potentially suitable patch. Therefore, as velocities increased at the higher discharge in the modelling scenarios, it was assumed that tadpoles either remained in their initially suitable habitats or were swept downstream and lost. Any modelling nodes that were initially unsuitable or dry, but became suitable as flow increased were not included in the assessment.

RESULTS

Habitat availability and connectivity as discharge changes

At the SF Eel study site, both suitable and occupied suitable habitat increased from the lowest to next higher modelled flow, but then decreased at successively higher discharges (Figure 6a). A similar pattern occurred with occupied suitable habitat in the NF Feather study site, although the initial increase in habitat was very small and habitat decreased in larger proportions as flow increased (Figure 6b). Availability of suitable habitat in the NF Feather site was highest at baseflow, and similarly declined at successively higher discharges. While the NF Feather study site has proportionally twice the cobble bar area (calculated as per cent of total reach with exposed cobble and small boulder deposits at low flow) as the SF Eel site (41% vs. 20% of the total study area, respectively), it provided roughly half the suitable habitat area at all modelled discharges (Figure 7).

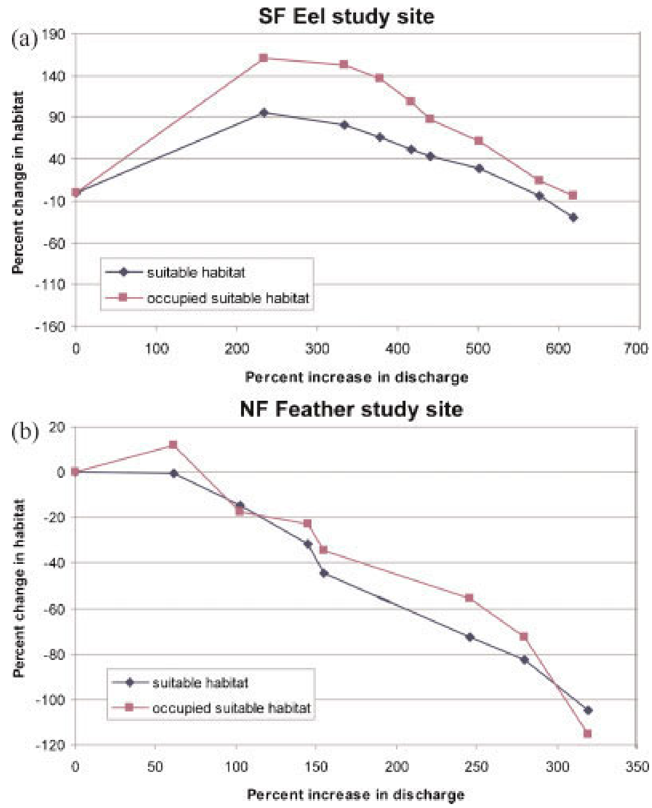

Figure 6. Per cent change in suitable and occupied suitable habitat as flow increases from base flow to each modeled flow for (a) SF Eel study site and (b) NF Feather study site. Per cent increase at each point is calculated as $\%\Delta Q = (((Qtest-Qbase)/Qbase)^{*}100)$ and $\%\Delta H = (((Htest-Hbase)/Hbase)^{*}100)$. This figure is available in colour online at wileyonlinelibrary.com

Figure 8 shows suitable habitat increasing at the SF Eel study site as modelled flows decrease from 1.45 $m^3 s^{-1}$ (2006 egg-laying discharge) to low summer baseflow (0.15 $m^3 s^{-1}$). In general, the majority of suitable habitat remained connected along the water's edge as flows decreased. Suitable habitat adjacent to the steep riffle at the river right (facing downstream) edge of the cobble bar was patchy where individual microhabitats were intermittently suitable depending on the flow. The patch of suitable habitat where the eggs were located on the river right bank adjacent to the run upstream of the riffle maintained connectivity to suitable habitat as flow decreased, and directly connected to the largest patch of suitability habitat at the lowest flow. Two additional large patches of suitable habitat at 1.45 $m^3 s^{-1}$, at the upstream river right end of the survey reach and along the river right cobble bar adjacent to the pool at the downstream end, also remained connected to suitable habitat as flows decreased; however, they connected to smaller patches of suitable habitat at the lowest modelled flow.

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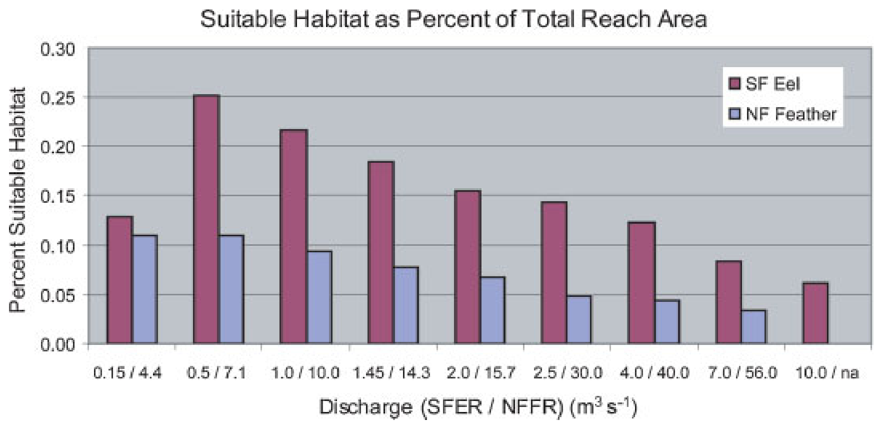

Figure 7. Suitable habitat in each study reach at each modeled flow expressed as a per cent of the total reach area. This figure is available in colour online at wileyonlinelibrary.com

At the NF Feather study site flows are regulated to a minimum instream baseflow throughout the late spring and summer; however, high spring runoff can occasionally occur into the breeding season forcing individuals to lay eggs above baseflow discharge, as was the case in 2006. Figure 9 shows suitable habitat increasing as modelled flows decrease from $30.0\,m^3\,s^{-1}$ (discharge at which all egg masses along river right bank were laid) to the baseflow of $4.4\,m^3\,s^{-1}$ (discharge at which four egg masses on the river left bank were laid). In general, the majority of the suitable habitat along the main channel below the riffle remained connected in a narrow band along the water's edge as flows decreased; however, suitable habitat upstream of the riffle along both banks was patchy and intermittent. The habitat on the river right bank where most of the eggs were laid maintained connectivity as flows decreased, and was connected to the largest patch of suitable habitat downstream of the riffle at baseflow. At moderate discharges, a large patch of suitable habitat appeared along the river left bank at the upstream end of the cobble bar and remained suitable as flows decreased to baseflow. Eggs were not laid in this location in 2006, but the area was utilized in 2007 when discharge at breeding was $4.3\,m^3\,s^{-1}$.

Effects from spring spills

To determine the potential impact of sudden increases in flow on breeding habitat, a series of spring pulses was simulated for both study sites. Figure 10 summarizes the change in velocity, grouped into categories associated with

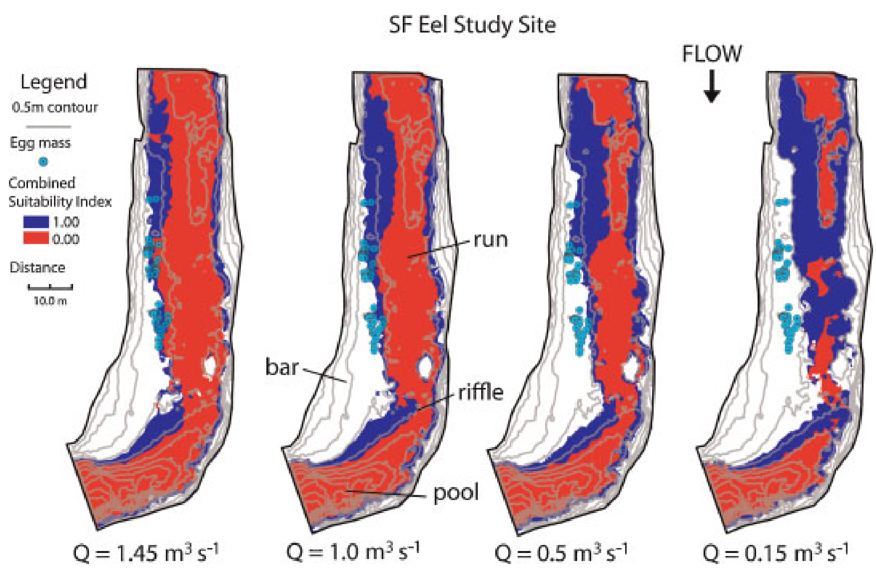

Figure 8. Suitable habitat at the SF Eel study site as modeled flows decrease from (a) $1.45\,m^3\,s^{-1}$ (2006 egglaying discharge) to (b) $1.0\,m^3\,s^{-1}$, (c) $0.5\,m^3\,s^{-1}$, and (d) $0.15\,m^3\,s^{-1}$ (low summer flow). Upstream is at the top of each inset figure. Background shows 0.5 m bed elevation contours; Overlaid colours depict the extent of flow and habitat suitability [suitable in blue (dark grey) and unsuitable in red (light grey)]; Encircled dots indicate egg locations. This figure is available in colour online at wileyonlinelibrary.com

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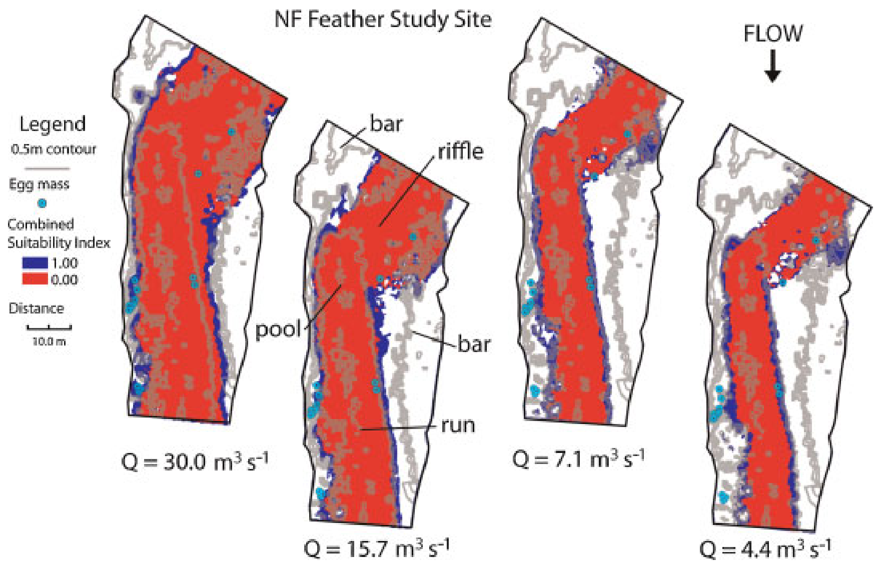

Figure 9. Suitable habitat at the NF Feather study site as modeled flows decrease from (a) 30.0 $m^3 s^{-1}$ (2006 egg-laying discharge) to (b) 15.7 $m^3 s^{-1}$, (c) 7.1 $m^3 s^{-1}$, and (d) 4.4 $m^3 s^{-1}$ (baseflow). Locations of eggs in 2006 are shown as light blue encircled dots; eggs laid along the river right bank (left side of inset figures) were laid at 30.0 $m^3 s^{-1}$, while the four eggs laid on the river left bank were laid at 4.4 $m^3 s^{-1}$. Upstream is at the top of each inset figure. Background shows 0.5 m bed elevation contours; Overlaid colours depict the extent of flow and habitat suitability [suitable in blue (dark grey) and unsuitable in red (light grey)]. This figure is available in colour online at wileyonlinelibrary.com

rates of scour, within suitable egg mass habitats as discharge increased from three representative low flows to a high flow. At both study sites all simulated pulses showed the majority of suitable breeding habitat became unsuitable with velocities greater than 0.1 $m s^{-1}$ and was associated with moderate to high rates of scour. At the SF Eel study site, only 23–35% of the breeding habitat remained suitable or was 'buffered' from higher velocities during the pulses. At the NF Feather study site, <5% of the breeding habitat was buffered from velocity increases. At both sites, the highest modelled low flows had the largest 'buffering capacity', defined as the highest per cent of suitable nodes with little to no change in velocity (velocity category with lowest rate of scour). 'Buffering capacity' could also be quantified in a less conservative manner as the per cent of suitable nodes remaining below 0.4 $m s^{-1}$ (low to moderate rates of scour). Using this definition, the highest low flow (10.0 $m^3 s^{-1}$) at the NF Feather study site and the mid-level low flow (1.45 $m^3 s^{-1}$) at the SF Eel study site provided the greatest buffering capacity because these flows resulted in the lowest relative per cent of nodes falling into the highest velocity category (>0.4 $m s^{-1}$): 46.04 and 10.73, respectively.

The spatial distribution of velocity changes associated with the middle initial discharge of the spring pulse scenario for each study site is shown in Figure 11. At the SF Eel study site, egg masses are primarily located in locations with moderate to high velocity increases, or moderate to low buffering capacity. Conversely, at the NF Feather study site,

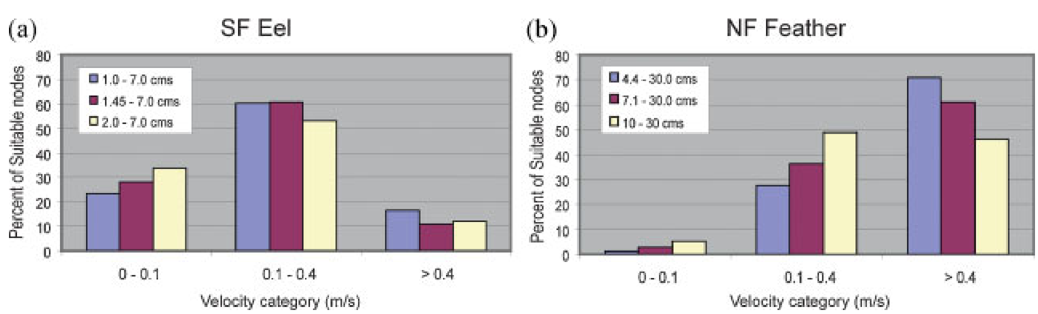

Figure 10. Per cent of modeling nodes in suitable breeding habitat at each low spring flow for (a) SF Eel study site and (b) NF Feather study site that fall within each velocity category when flow is increased to a high spring discharge. Velocity categories represent ranges associated with observed scour of egg masses from a previous study (Kupferberg *et al.*, 2009): <0.1 $m s^{-1}$ = ~10% cumulative loss of eggs; 0.1–0.4 $m s^{-1}$ = ~45% cumulative loss; >0.4 $m s^{-1}$ = ≥50% cumulative loss. For example, on the SF Eel site, 60% of suitable nodes at 1.0 $m^3 s^{-1}$ show an increase in velocity from <0.1 $m s^{-1}$ to 0.1–0.4 $m s^{-1}$ at 7.0 $m^3 s^{-1}$, and thus are associated with moderate rates of scour. This figure is available in colour online at wileyonlinelibrary.com

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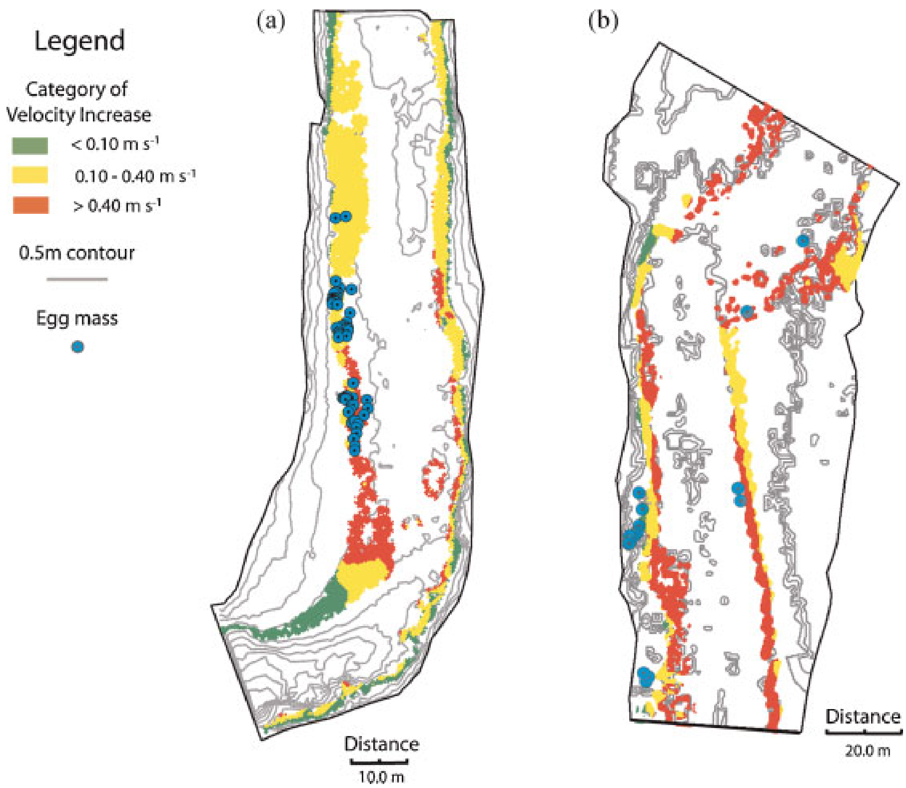

Figure 11. Spatial distribution of suitable breeding nodes differentiated by category of velocity increase during a modeled spring pulse scenario. (a) SF Eel study site; discharge increased from 1.45 $m^3 s^{-1}$ to 7.0 $m^3 s^{-1}$; (b) NF Feather study site, discharge increased from 7.1 $m^3 s^{-1}$ to 30.0 $m^3 s^{-1}$. Upstream is at the top of each inset figure. Background shows 0.5 m contours. Overlaid colours depict the category of velocity increase, where each category is associated with a rate of scour. Locations of eggs in 2006 are shown as light blue encircled dots. This figure is available in colour online at wileyonlinelibrary.com

the majority of the egg masses on river left are located in a small area of high buffering capacity (green shading overlain by blue shaded circles).

Effects from aseasonal pulsed flows

To determine the potential effects of an aseasonal pulsed flow on tadpoles, a series of flows that increased from a low flow (same discharges as assessed in spring scenario) to a representative high flow analogous to a hydropeaking or recreational boating flow were modelled; the subsequent velocity increases within suitable tadpole habitats were then evaluated. Similar to the spring spill scenario, the highest initial discharges had the lowest velocity increases when discharge was increased (Figure 12). However, the difference between the two study sites of the per cent

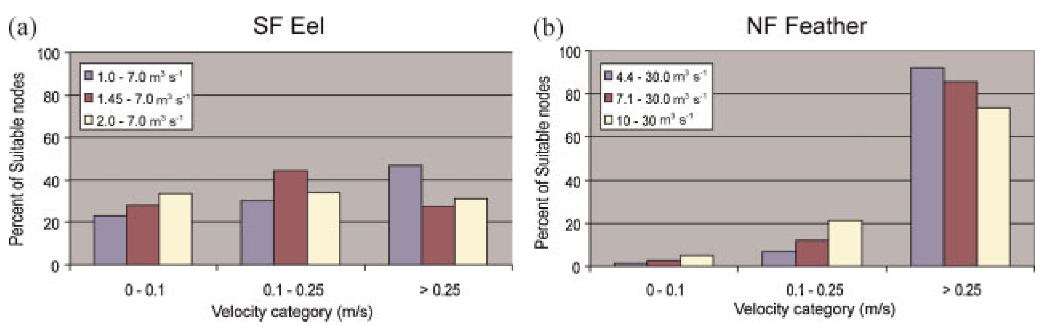

Figure 12. Per cent of modeling nodes in suitable tadpole habitat at each low summer flow for (a) SF Eel study site and (b) NF Feather study site that fall within each velocity category when discharge is increased to a summer hydropeaking or boatable discharge. Velocity categories represent ranges associated with observed loss of tadpoles in field and flume experiments (Kupferberg *et al*., 2011Kupferberg *et al*., in review): <0.1 $m s^{-1}$ = ~25% loss of tadpoles; 0.1–0.25 $m s^{-1}$ = ~50% loss; >0.25 $m s^{-1}$ = ~75% loss. For example, on the SF Eel site, 30% of suitable nodes at 1.0 $m^3 s^{-1}$ show an increase in velocity from <0.1 $m s^{-1}$ to 0.1–0.25 $m s^{-1}$ at 7.0 $m^3 s^{-1}$, and thus are associated with a 50% loss of tadpoles. This figure is available in colour online at wileyonlinelibrary.com

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of suitable nodes falling into the highest velocity category (increases $>0.25\,\mathrm{m\,s^{-1}}$) was much more pronounced. While only 25–45% of suitable nodes at the SF Eel study site became highly unsuitable with increases $>0.25\,\mathrm{m\,s^{-1}}$ (associated with >75% tadpole loss), 75–90% of the suitable nodes at the NF Feather site became highly unsuitable. Although both study sites showed velocity increases at most nodes, the NF Feather site had larger magnitude increases.

DISCUSSION

An assessment of whether results from a 2D model can adequately predict habitat suitability depends in part on how broadly or narrowly suitability is defined. In the broadest sense, 'habitat suitability' is the extent to which a habitat patch provides the correct abiotic conditions and biotic factors for a particular species or life stage to survive, grow and/or successfully reproduce. These factors and conditions are nested in a hierarchy from small to large spatial and temporal scales (Frissell *et al*., 1986; Power *et al*., 1988; Imhof *et al*., 1996), where multiple interacting variables can influence the success of a particular species. In modelling the relationship between instream flow conditions and specific lotic taxa, however, 'habitat suitability' is narrowly defined in terms of the hydraulic characteristics of water depth, water velocity and substrate (Bovee, 1982; Stalnaker *et al*., 1995). Local hydraulic conditions have been shown to be key selective factors for foothill yellow-legged frog sub-populations among creeks in the Yuba River watershed (Yarnell, 2005), and frog population fluctuations appear linked, at least in part, to flow-related effects on survival and recruitment (Kupferberg *et al*., 2010). Therefore, use of a 2D hydrodynamic model to describe how hydraulic habitat suitability for egg and tadpole life stages varies with discharge can provide information relevant to foothill yellow-legged frog population trajectories and conservation. In particular, analyses beyond simple weighted usable area calculations, such as quantifying the risk of scour or stranding, can provide pertinent information regarding potential mortality, a factor of concern for management of this species.

Our 2D modelling results provided information on both the potential susceptibility of early frog life stages to flow fluctuations and the influence of channel morphology on habitat suitability. The differences in trends in habitat availability between the two study sites were primarily a reflection of differing channel morphology. The SF Eel study site had wide, shallow or slightly asymmetrical channel shapes that provided more stable depth and velocity conditions across at least a subset of flow fluctuations (Figure 3). The NF Feather site had steeply faced banks along the water's edge that created less total shallow, low velocity edgewater habitat (Figure 4). When discharge fluctuated within the main low-flow channel of the NF Feather, only small changes in width could occur, resulting in large changes in depth and velocity. As a result, regardless of the initial low flow discharge, the SF Eel study site provided a greater inherent buffering capacity against velocity increases than the NF Feather study site as flows increased. For both eggs in spring and tadpoles in summer, the ability of the channel to buffer against significant velocity increases is an important component in limiting potential loss from flow fluctuations (Kupferberg, 1996; Kupferberg *et al*., in review).

One possible reason for the differing channel morphologies between study sites may be hydrologic regime. A comparison of the annual hydrographs for each study site (Figure 2) shows that the NF Feather is dominated by flat baseflows (i.e. minimum flows required by license agreements in regulated rivers) through the summer and large peak magnitude storms with steep recession limbs in the winter and early spring. Intermediate flows that promote cobble bar scour and gradual redeposition of sediment as flows slowly recede are lacking on the NF Feather, but present on the SF Eel. The presence of an annual gradually declining spring recession may contribute to the asymmetry in channel bar shape observed on the SF Eel (Yarnell *et al*., 2010). The differing flow regimes may also contribute to the differences in vegetation distribution observed on each study reach. While both study sites had a similar variety of riparian species along the stream margins, the lack of moderate to high flows and dominance of a flat baseflow on the NF Feather may have contributed to the observed encroachment of vegetation into the main channel. The encroached vegetation may be stabilizing the cobble bars, further focusing flows into the main channel and promoting the entrenched channel shape (Hadley and Emmett, 1998; Brandt, 2000). Alternatively, regional factors, such as local geology, land use history and sediment supply, may contribute to the differences in channel morphology between study sites (Ligon *et al*., 1995; Kondolf *et al*., 2002).

While validation of the modelling results with observed egg mass locations supported the habitat suitability modelling, it also provided insight to other potential factors influencing foothill yellow-legged frog habitat suitability. There are a variety of reasons why habitats with suitable depth, velocity and substrate conditions may be unoccupied, including unstable hydraulic conditions as flows fluctuate (Kupferberg, 1996), lack of connectivity across flows, spatial distribution and habitat association of predators, presence of heavy vegetation or canopy cover that limits direct sunlight and affects algal food availability (Kupferberg, 1997), life history strategies that encourage site fidelity and aggregate breeding (Wells, 1977; Wheeler, 2007) or simply that habitat is not a limiting factor (Kupferberg *et al*., 2010). Results from the 2D modelling suggest several of

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these factors may be relevant at our study sites. In particular, buffering capacity from velocity increases and connectivity between suitable egg mass and tadpole habitats during recession of high flows appear to be key factors. At the NF Feather study site, the highest density of observed occupied suitable habitat overlapped with one of only two locations with high buffering capacity (lowest velocity change category in Figure 11). Although regulated, high spring pulses due to spill occur with moderate frequency on the NF Feather and protection from high velocities may increase egg mass survival. This location is also connected to a large area of suitable tadpole habitat in the summer. Conversely, the area of suitable but unoccupied habitat with high buffering capacity at the base of the riffle did not connect to suitable tadpole habitat. While the large area of suitable but unoccupied habitat in the eddy upstream of the cobble bar on river left provided moderate buffering capacity and connected to suitable tadpole habitat, a large overhanging tree provided dense shade throughout much of the day. At the NF Feather study site, both buffering capacity and connectivity may be important in differentiating occupied from unoccupied suitable habitat.

At the SF Eel study site, buffering capacity was not associated with occupation of suitable habitat. The occupied suitable habitat along the right bank upstream of the riffle showed low to moderate buffering capacity with velocities increasing from 0.1 to $0.4\,\mathrm{m\,s^{-1}}$ and greater than $0.4\,\mathrm{m\,s^{-1}}$ during the simulated spring pulse (Figure 11). However, this location directly connected to the largest area of suitable tadpole habitat in the summer (Figure 8). Additionally, the locations with the lowest change in velocities were primarily in eddies adjacent to the deep downstream pool and the upstream scour pool. While both these eddy locations provided suitable habitat in terms of flow, other non-flow related factors, such as the presence of predators (fish) in the large downstream pool or shading by overhanging vegetation (a large redwood tree) in the upstream eddy, may limit suitability for tadpole rearing. On the unregulated SF Eel where high spring pulses are infrequent, connectivity to suitable tadpole habitat may be more important for breeding site selection than buffering capacity.

A spatial evaluation of how hydraulic conditions change as flows fluctuate that includes habitat connectivity, buffering capacity, the position of riparian vegetation and other potentially influential environmental features, may help to resolve the question of why some suitable sites are unoccupied, and thus provide a broader context for what defines ‘suitable habitat’ for foothill yellow-legged frogs. While not conclusive due to limitations in time and space, the modelling results from this study elucidate the primary hydraulic habitat factors that define suitable foothill yellow-legged frog habitat conditions and point to additional ecological factors that could be examined in future studies.

CONCLUSIONS

The use of 2D hydrodynamic modelling as an assessment tool for flow-related impacts on foothill yellow-legged frogs appears promising. 2D modelling offers the ability to explore discrete quantifications of changes in hydraulic habitat, a key characteristic known to influence frog populations (Yarnell, 2005; Kupferberg *et al*., 2010). A variety of flow scenarios can be assessed, specific to questions of interest for management, and results can be explored in the larger context of general habitat suitability.

In this study, several modelled flow scenarios were conducted reflecting typical flow regimes prescribed in hydropower project relicensing proceedings. During hypothetical pulsed flow scenarios, low percentages of suitable habitat at each study site remained suitable or were ‘buffered’ from the pulse, creating high potential for scour of egg masses or tadpoles. However, differences in channel morphologies resulted in the wide, shallow SF Eel site providing two to three times the buffering capacity of the entrenched NF Feather site. Occupied suitable habitat overlapped with locations of high buffering capacity at the NF Feather site, but not at the SF Eel site.

Analyses of habitat connectivity across modelled flows provided additional insight to factors that may relate to whether suitable habitat is occupied. At both study sites, high density occupied suitable breeding habitat connected to large areas of suitable tadpole rearing habitat. Additional non-flow related environmental factors such as presence of predators and degree of shading may also influence general habitat suitability, contributing to the lack of occupation of some hydraulically suitable habitats.

One limitation of a 2D modelling approach for assessing impacts on foothill yellow-legged frogs from various flow regimes is the necessity of incorporating compatible hydraulic habitat suitability criteria for each life stage. If the question of interest requires defining habitat suitability at a scale finer than the precision of the model (e.g. suitability of $0\text{–}0.05\,\mathrm{m\,s^{-1}}$ in a model with resolution of $+/-0.05\,\mathrm{m\,s^{-1}}$), a different methodology should be used. Likewise, different definitions of suitability might provide different results. For example, in the spring pulse modelling scenario, if a larger range of velocities (e.g. $0.0\text{–}0.15\,\mathrm{m\,s^{-1}}$) had been determined to provide suitable habitat, discrete quantifiable results such as available habitat area and the per cent of habitat falling within a suitable velocity category would change. However, relative changes between flows and the degree of impact comparatively between flows would remain the same. The habitat suitability criteria used in this study were determined to be acceptable for these specific study sites, but they may not be applicable in other river reaches or watersheds. Validated habitat suitability criteria for the foothill yellow-legged frog are needed.

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In regulated rivers, the timing, magnitude, and rate of change of discharge are critical characteristics that can be managed to reduce impacts to native aquatic biota and enhance diversity in instream habitat (Yarnell *et al*., 2010). There is a unique opportunity through the process of hydropower project relicensing to consider and potentially alter flow management operations in regards to sensitive aquatic taxa, such as the foothill yellow-legged frog. Based on the results of this study, setting limits on the timing and magnitude of controlled pulsed flow events, providing appropriately slow ramping rates during a return to baseflow following uncontrolled spill events, and setting minimum instream flows at discharges conducive to maintaining habitat connectivity should spills occur may reduce potential negative impacts to foothill yellow-legged frogs and their habitat.

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