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ARTICLE

Modeling potential river management conflicts between frogs and salmonids

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Abstract: Management of regulated rivers for yellow-legged frogs (*Rana boylii*) and salmonids exemplifies potential conflicts among species adapted to different parts of the natural flow and temperature regimes. Yellow-legged frogs oviposit in rivers in spring and depend on declining flows and warming temperatures for egg and tadpole survival and growth, whereas salmonid management can include high spring flows and low-temperature reservoir releases. We built a model of how flow and temperature affect frog breeding success. Its mechanisms include adults selecting oviposition sites to balance risks of egg dewatering by decreasing flow versus scouring by high flow, temperature effects on development, habitat selection by tadpoles, and mortality via dewatering and scouring. In simulations of a regulated river managed primarily for salmonids, below-natural temperatures delayed tadpole metamorphosis into froglets, which can reduce overwinter survival. However, mitigating this impact via higher temperatures was predicted to cause adults to oviposit before spring flow releases for salmonids, which then scoured the egg masses. The relative timing of frog oviposition and high flow releases appears critical in determining conflicts between salmonid and frog management.

Résumé : Gestion des cours d'eau réglementés pour les grenouilles à pattes jaunes (*Rana boylii*) et les salmonidés illustre les conflits potentiels entre les espèces adaptées aux différentes parties des régimes d'écoulement et de température naturelles. Grenouilles à pattes jaunes pondent dans les rivières au printemps et dépendent de la diminution des flux et des températures de réchauffement de l'œuf et de têtard survie et la croissance. Tandis que la gestion des salmonidés peut inclure des flux de haute avec des températures faible pendant le printemps. Nous avons construit un modèle de la façon dont débit et la température affectent le succès de reproduction grenouille. Ses mécanismes comprennent les adultes sélections des sites de ponte d'équilibrer les risques de déshydratation d' œufs en diminuant l'écoulement par rapport à récurer en haut débit, effets de la température sur le développement, la sélection de l'habitat par les têtards, et de la mortalité par déshydratation et affouillement. Dans les simulations d'une rivière régulée gérées principalement pour les salmonidés, les températures plus faibles que les naturels températures retardées têtard métamorphose en petites grenouilles, ce qui peut réduire la survie hivernale. Cependant, atténuer cet impact par des températures plus élevées a été prédit pour provoquer les adultes pondent avant flux de printemps de presse pour les salmonidés, qui a ensuite écumé les masses d'œufs. La période relatif de grenouille ponte et d'écoulement des rejets importants apparaît essentiel dans la détermination des conflits entre les salmonidés et la gestion de la grenouille.

Introduction

River management for one objective, such as conservation of important fish populations, often has undesirable effects on other objectives and resources. In California, the foothill yellow-legged frog (FYF, *Rana boylii*) provides a particularly good illustration of this conundrum. Although this stream-dwelling frog naturally co-occurs with several species of salmonid fish (Hayes and Jennings 1988), the directions of spawning migrations are opposite. Salmonids often swim upstream to spawn in cool, shaded tributaries conducive to survival and growth of offspring, while adult FYF typically move downstream from tributaries to main stems (Bourque 2008) to congregate on the margins of broad, sunlit river segments where warm water and abundant periphyton allow grazing tadpoles to grow rapidly (Welsh et al. 2005; Catenazzi and Kupferberg 2013). Although salmonids and FYF both have life cycles adapted to the flow and water temperature regimes produced by California's Mediterranean climate (high winter flows followed by declining flows and increasing temperatures through summer and fall), the life-stage-specific flow and thermal requirements of the two taxa are quite different. Adult FYF mate in spring and attach eggs to rocks in shallow, slow-velocity habitat. Tadpoles hatch from eggs in 1–3 weeks and metamorphose into amphibious froglets prior to autumn rains. In contrast, salmonids display a broad diversity of migration and spawning patterns. On many salmon rivers in California, large water-supply dams make it impossible for salmon to reach their natural spawning habitat. Consequently, much of the relatively warm mainstem habitat that FYF are adapted to is instead now managed as the only remaining salmon spawning and juvenile rearing habitat. Thus, for FYF to co-exist, the requirements of early life stages of both frogs and salmonids must now be met in the same locations, when naturally they were separated in space or time, or both, within a watershed.

Its complex reproductive cycle and reliance on shallow, low-velocity habitats make FYF breeding success vulnerable to natural hydrologic events as well as to negative consequences of river management. Late-spring rain storms or spills from dams that

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produce flows high enough to wash out FYF eggs and tadpoles can substantially impair recruitment (Kupferberg 1996; Lind et al. 1996; Kupferberg et al. 2012), and rapid decreases in flow can dewater and desiccate eggs or tadpoles. Conspicuous examples of flow management actions with negative consequences to FYF have been aseasonal high reservoir releases to provide summer recreational whitewater boating and flow pulses for load-following hydropower generation (Kupferberg et al. 2011*a*, 2012). Over longer time scales, flow diversion and storage decrease winter floods, allowing channel incision and invasion of woody plants in the active channel (Ligon et al. 1995; Trush et al. 2000; Gordon and Meentemeyer 2006). Vegetation encroachment initiates morphological changes to stream channels, with banks stabilization by roots, sediment trapping, and berm building causing changes in bar shape, bank slope, and connectivity to floodplains. These changes reduce the availability of shallow, low-velocity habitat patches important to both juvenile fish (Trush et al. 2000) and frog breeding (Yarnell et al. 2012). Breeding success of FYF is also vulnerable to altered river temperatures. Lower temperatures resulting from hypolimnetic reservoir releases can slow the development of eggs and tadpoles, delaying metamorphosis and reducing size and body condition of both tadpoles and newly metamorphosed froglets (Catenazzi and Kupferberg 2013; Wheeler et al. 2015).

While widespread effects of river alteration has resulted in California listing FYF as a species of special concern, river management in much of its range is directed primarily at restoring and enhancing salmonid populations. Some typical salmonid management actions have the potential for affecting FYF reproductive success — either positively or negatively. For example, flow schedules that protect early life stages of salmonids from ill-timed flow fluctuations that cause redd dewatering, catastrophic displacement of emerging fry, and stranding (reviewed by Young et al. 2011; Nislow and Armstrong 2012) would likely also protect frog eggs and tadpoles. Other salmon management actions are likely to be detrimental to FYF and other warm-water-adapted amphibians and reptiles; examples are lowering summer water temperatures (e.g., by controlling the depth from which reservoir releases are made or by increasing flow rates; Wheeler et al. 2015) and releasing pulses of high flow at unnatural times.

A great deal of effort and technology has gone into models and procedures for designing and evaluating salmonid habitat restoration actions, from simple approaches similar to habitat selection modeling (Bovee 1982) to detailed individual-based models that predict population responses (Railsback et al. 2013). In contrast, tools for predicting effects of habitat alteration on FYF have been limited to habitat-selection-like models (Bondi et al. 2013), hydraulic models adapted to assess the risk of egg stranding and scour from flow and channel morphology (Yarnell et al. 2012), and basic research on how variables such as temperature and velocity affect various life stages (Kupferberg et al. 2011*a*; Catenazzi and Kupferberg 2013; Wheeler et al. 2015).

Our objective is to provide a quantitative assessment of how river management primarily for salmonids could affect reproductive success of FYF. The Trinity River of northwestern California is our example study site. We describe a new simulation model of the FYF breeding cycle and how it is affected by river flow and temperature regimes and channel characteristics. We apply the model to a site with unmanaged flows and temperatures and analyze how well the model reproduces observed patterns in the location of egg masses and tadpoles, patterns that emerge directly from the two key individual behaviors included in the model. We then analyze the model's sensitivity to parameter values, in 5 separate years with very different, though unregulated, flow patterns. We use the model first to examine how observed temperatures and flows affect FYF breeding success at the unmanaged site. Finally, we predict how breeding success would change if the same site had flows and water temperatures of a nearby river that is controlled by an upstream reservoir and managed primarily for salmonids, instead of its unmanaged flows and water temperatures.

Methods

Flow and water temperature effects on FYF breeding

Our first modeling step was to identify patterns from the literature and our own field observations in how river flow and temperature affect FYF breeding success. Processes believed to be the main drivers of these patterns were then included in the model.

Breeding activity is seasonal and apparently temperature-dependent

Observations at many sites indicate that FYF activity starts in the spring after water temperatures have begun warming (Kupferberg 1996; Garcia and Associates 2008; Wheeler et al. 2015). While the seasonality of breeding could be explained by other factors such as day length, a threshold water temperature generally explains the start of the breeding season (i.e., breeding becomes widespread only after river temperature warms to this threshold in spring).

Oviposition can be delayed by flow variation

Even when temperature is suitable for breeding, FYF appear to delay or interrupt oviposition when flow is not stable or does not provide suitable oviposition sites (Kupferberg 1996; Garcia and Associates 2008; Wheeler and Welsh 2008). This behavior makes evolutionary sense considering the flow-related risks to egg masses (below).

Egg masses and tadpoles are at risk from both decreasing and increasing flows

Decreases in flow that expose egg masses or tadpoles to air and sun cause rapid mortality via desiccation. Increases in flow and water velocity expose these life stages to the risk of being washed downstream and into habitat where survival is presumably low (Kupferberg 1996); we refer to this risk as scouring. Egg masses are especially at risk because they cannot move and because even moderate velocities (local velocities well below 0.5 $m \cdot s^{-1}$) can cause gradual disintegration and scouring. However, tadpoles are poor swimmers and their swimming ability decreases as they develop more frog-like bodies; hence, they are also vulnerable to both desiccation and scour (Kupferberg et al. 2011*a*).

Breeders place egg masses in habitat that provides a balance between the risks of desiccation and scour

FYF typically oviposit in places where depth is adequate to prevent desiccation during "normal" rates of spring flow decreases while also avoiding velocities high enough to cause scouring (Kupferberg 1996). They also appear to avoid habitat with near-zero velocities, presumably because some water movement is needed to provide oxygen to, and carry metabolic wastes from, egg masses. Oviposition sites typically include moderately shallow stream margins (with eggs masses attached to cobbles or the downstream side of larger substrate) and deeper locations protected from high velocities (Bondi et al. 2013).

Egg development rates are temperature-dependent, while tadpole development rates depend on multiple factors that interact with temperature

The time between oviposition and hatching of eggs decreases as water temperature increases (Kupferberg et al. 2011*b*). Tadpole growth and development also appear temperature-dependent, with time to metamorphosis into froglets inversely related to water temperature. However, tadpole development also depends on other factors such as quantity and quality of algae and diatom food (Catenazzi and Kupferberg 2013; Furey et al. 2014), water velocity, and predator-avoidance behavior (Kupferberg et al. 2011*a*, 2011*b*). Because the mechanisms controlling tadpole development are complex and not all directly related to flow or temperature, we did not include them explicitly in the model.

Model description

We developed the Foothill Yellow-legged Frog Assessment Model (FYFAM), an individual-based, spatially explicit, time-step simulation model. The model was designed to contain the simplest useful representations of the processes causing the patterns identified above. Supplement A[1] provides a complete description of the model, and the literature and knowledge it is based on, in the ODD format of Grimm et al. (2010). Here we provide a summary of the model's elements and processes.

Purpose

FYFAM is intended as a tool for river and watershed management. Its purpose is to predict how reproductive success of FYF is affected by habitat variables that are often controlled by management of water and forest resources, specifically, stream flow and temperature regimes, channel shape, and the distribution of substrate types important to FYF reproduction. The model is intended, for example, to use results of flow and water temperature models to predict the effects on frogs of alternative flow release policies at a dam. Such flow policies can control both minimum flows (e.g., daily or monthly minimum flow releases) and high-flow releases for objectives such as whitewater recreation, power production, and sediment management. FYFAM is not a population dynamics model because it does not include the full life cycle and because it does not include predation, a major source of mortality.

"Reproductive success" here refers primarily to survival of eggs and tadpoles, from when eggs are laid (oviposition) through the first summer of life. The endpoint of reproductive success is metamorphosis from the aquatic tadpole to the amphibious froglet life stage, in the first summer of life. The time at which metamorphosis occurs is a second important component of reproductive success, because froglets that metamorphose earlier have more time to attain larger size and find suitable habitat, which makes them more likely to survive their first winter and, hence, more likely to contribute to future breeding populations.

Habitat entities, state variables, and scales

Frog habitat is represented at two scales: reaches and cells. FYFAM represents one "reach", a contiguous section of stream or river and adjacent riparian habitat. A reach is the model's spatial extent, which can be from a few tens of metres to several hundred metres of stream length. A reach has a static variable cell size for the width of each of its cells and dynamic (time-varying) state variables: step length — length of the current time step (in days), flow — stream flow ($m^3 \cdot s^{-1}$), and temperature — water temperature (°C). The flow and temperature variables represent means over the time step. The temperature variable represents water temperature in the channel edge habitat typically occupied by the frog life stages in this model; Wheeler et al. (2015) found such channel edge temperatures close to mid-channel temperatures at a daily time step in the river we study, so mid-channel temperatures (which are much easier to measure or model) can suffice for this variable.

Cells are square habitat elements representing variation within the reach. Each cell has static boolean (TRUE–FALSE) variables "breeder-suitable?" for whether it is suitable physical habitat for breeders (e.g., rock substrate exposed to sun) and "has-shelter?" for whether it has velocity shelter for egg masses. These cell variables are input that can be developed from field observations. Cells also have dynamic variables updated each time step: water depth (m) and velocity ($m \cdot s^{-1}$) and the boolean "ovi-suitable?" for whether the cell has hydraulic conditions suitable for oviposition (low velocity; depth and rate of depth change unlikely to result in desiccation during egg incubation). Cell depth and velocity are functions of the reach's flow.

Cell size (width) is FYFAM's spatial resolution. Cell size can differ among sites; ideally, it should be just small enough to capture important gradients in hydraulic conditions in the shoreline habitat used by frogs. Here, we use 1 m cells.

Frog entities and variables

FYFAM represents three frog life stages as separate kinds of model entities. "Breeders" represent the pairs of adults that create (i.e., oviposit) egg masses. Breeders are included only as a way to model when and where oviposition occurs; they execute some behaviors that in reality are attributed to male frogs and some attributed to females. Breeders have variables for their location (the cell they occupy) and a boolean variable "ready?" for whether they are ready to breed and oviposit. "Egg masses" represent the egg clutches (clusters of eggs held together and attached to substrate by a gelatinous adhesive) that a breeder creates. Egg masses are immobile and have a static state variable for their location (the cell they occupy). Egg masses have dynamic variables for the number of live eggs (embryos) they contain (eggs-in-mass) and for the development state of the eggs; egg development is set to 0 when an egg mass is created, and eggs are ready to hatch into tadpoles when egg development reaches 1.0. When eggs hatch, each turns into a "tadpole" entity. Tadpoles have dynamic state variables for location (their cell) and age (days since hatching). Tadpoles also have a static variable for the time (days) it takes them from hatching to metamorphosis into froglets.

Time scales

The temporal extent of an FYFAM simulation is from mid-spring through late summer of 1 year. Simulations actually start before flow and temperature conditions are suitable for oviposition, as the date of oviposition is an important model result. The model runs until all simulated tadpoles have metamorphosed, typically near the end of the summer dry season.

The temporal resolution (time step length, reach variable step length) can vary but typically (including all simulations reported here) is 1 day. Shorter time steps, for example to represent within-day flow pulses for recreation or power generation, can be executed simply by including them in the flow and temperature input. Time-dependent variables such as survival probabilities and development rates are automatically adjusted for time step length.

Process overview and schedule

FYFAM executes the following actions once per time step. The order in which individuals execute these actions is randomized at each time step, so no individuals have a consistent advantage or disadvantage in access to resources.

(1) Habitat is updated. An input file provides the time step's flow and water temperature. The depth and velocity of each cell is calculated from flow using linear interpolation and lookup tables developed from an external hydraulic model (explained below).

(2) Breeders ready for oviposition select habitat (Fig. 1). Each breeder identifies potential destinations: the cells within a limited radius that are submerged but adjacent to at least one dry cell, have a TRUE value of "breeder-suitable?", and would not have breeder density exceeding the parameter representing maximum density. The breeder then selects and moves to the potential destination cell that has the highest number of cells with TRUE values of "ovi-suitable?" near it (within a radius equal to the parameter oviposition radius, set to 5 m).

(3) Breeders ready for oviposition decide whether to oviposit. A ready breeder oviposits on the next time step when water

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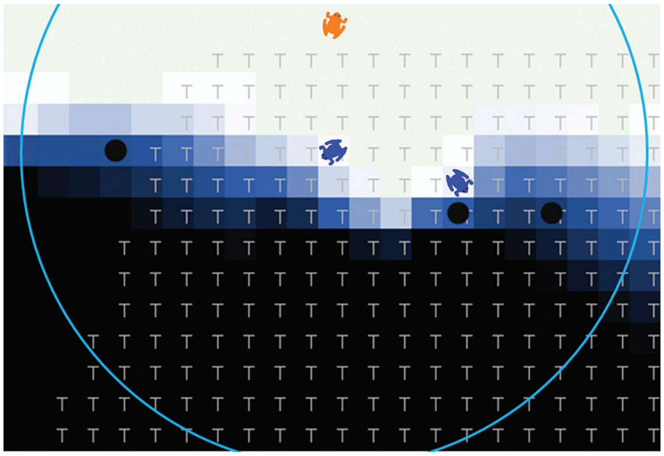
[1] Supplementary data are available with the article through the journal Web site at http://nrcresearchpress.com/doi/suppl/10.1139/cjfas-2015-0267.

Fig. 1. Conceptual diagram of breeder habitat selection. Breeders not yet ready for oviposition (upper light-shaded frog) wait away from the water's edge. Breeders ready to oviposit (the darker-shaded frogs) select habitat at the water's edge. (Wet cells are shaded by depth, deeper cells being darker.) As flow changes, breeders move to cells that are within a radius of 10 m (shown for the central breeder), submerged but adjacent to the water's edge, and have a value of TRUE ("T" in the diagram) for the variable representing whether they have conditions — sunlight, vegetation, substrate — suitable for breeders. Upon oviposition, each breeder creates one egg mass, represented by the circles, in a cell providing a good trade-off between the risks of scouring and desiccation. [Colour online.]



temperature is above a threshold of 10 °C, the rate of change in water depth is below a threshold of 0.03 m·day^{-1}, and there is suitable oviposition habitat available within the oviposition radius.

(4) Breeders oviposit. Any breeder that decides to oviposit identifies the best cell within the oviposition radius and creates an egg mass in it. Suitable oviposition sites are identified by excluding those with too-high velocities (daily probability of egg mass scouring mortality >0.05 at the current flow) and too-low depths (expected depth at the end of incubation, calculated from current depth and current rate of depth change, <0.05 m). The best cell is chosen from those meeting these criteria as the one with velocity nearest an "optimal" value set to 0.1 m·s^{-1} (on the basis of field observations by Lind et al. (2015) of velocities at egg masses). The breeder creates a new egg mass in the selected cell and sets its value of eggs in mass to a fecundity drawn from an empirical distribution and is then removed from the model (we assume females produce only one egg mass per year).

(5) Breeders not yet ready for oviposition decide whether they become ready. This decision is stochastic (to spread breeding out over a realistic time), with the daily probability of becoming ready increasing in proportion to the number of days that water temperatures have been above a threshold; breeders do not become ready if this threshold is not met on the current day.

(6) Egg masses survive or die. FYFAM represents egg mass mortality due only to flow-related mechanisms. The probability of scouring (an entire egg mass being washed downstream and broken up) increases with velocity. Desiccation is represented as a fraction of the egg mass's eggs dying on any time step when depth is 0.

(7) Egg masses develop. The development rate increases with temperature, and egg masses hatch into tadpoles (create one new tadpole object for each egg) when development is complete.

(8) Tadpoles select habitat. Each tadpole identifies the cells within a limited radius (here, the eight surrounding cells) with nonzero depth and moves to the one with lowest velocity.

(9) Tadpoles survive or die. As with egg masses, scouring and desiccation are the only kinds of mortality represented.

(10) Tadpoles develop and metamorphose when development is complete. Even though tadpole development rates are dependent on water temperature and other factors such as food quantity and quality, we chose to neglect this complexity and be aware that the model may underestimate effects of temperature on metamorphosis date. The time tadpoles take to develop into froglets is drawn from a normal distribution with mean and standard deviation of 65 and 4 days, respectively. When that time is reached, the tadpole is considered a successful froglet and removed from the model.

Initialization

At the start of a simulation, a fixed number of breeders (100 in simulations used here) is created. (We use the same number of breeders each year because FYFAM is not a population model in which the number of breeders one year could be determined from simulation of previous years. Instead, creating 100 breeders each year makes the model's results an index of breeding success that is comparable across years.) The breeders are given locations randomly selected from the cells along the margins of the simulated reach (away from the water's edge, where adult frogs are prior to breeding) and their variable "ready?" is set to FALSE.

Implementation

FYFAM is implemented in version 5.1 of NetLogo (Wilensky 1999), which provides a powerful programming language for individual-based models, visualization of simulations, and automated execution of simulation experiments (Railsback and Grimm 2012). The program was tested via several methods recommended by Railsback and Grimm (2012), including independent reimplementation (in Excel) of all major processes, and the tests were archived.

Study site and model input

For this study, we applied FYFAM to a reach of the South Fork Trinity River approximately 1600 m above its confluence with the mainstem Trinity River, on the border between Humboldt and Trinity counties, California. While undoubtedly affected by water withdrawals (Bauer et al. 2015), the South Fork Trinity River has no reservoir and relatively natural flow and water temperature regimes. It supports a robust population of FYF (Lind et al. 1996). The simulated reach is approximately 580 m in length, with a total surface area of 42 121 m^2, about 40% of which is submerged at a typical spring flow of 20 m^3·s^{-1}.

Our simulation experiments used input from 5 years: 2009–2013. These years included a wide range of runoff patterns — flow magnitude and variability, illustrated below — that affect FYF breeding in different ways. Daily mean flow input was synthesized by adjusting data from the US Geological Survey gage upstream at Hyampom, California (USGS gage 11528700). The adjustment used linear regression between four flows we measured at the site (ranging 0.64 to 14.5 m^3·s^{-1}) and instantaneous flows reported by the USGS gage 1 h before our measurements (R^2 = 0.997). Daily mean water temperature input was assembled and synthesized from data we collected at the site in April–August 2009 and since May 2014 and from regression models (separate models for each month) that predict water temperature from river flow and air temperature observed at the nearby town of Willow Creek (US National Oceanic and Atmospheric Administration station Willow Creek 1 NW CA).

We determined the availability of velocity shelter for egg masses in habitat cells using field observations and GIS. The distribution of habitat providing velocity shelter was mapped during field observations using a total station. Habitat patches of at least 75% by area of cobble and ≤25% of boulder embedded in finer substrate were assumed to provide velocity shelter for egg masses. We overlaid the map of habitat providing velocity shelter on the grid of habitat cells; all habitat cells containing velocity shelter were given a “has-shelter?” value of TRUE.

We assigned values for “breeder-suitable?” using aerial photography and GIS. Cells on the sun-exposed north side of the channel and adjacent to run habitat were given a value of “breeder-suitable?” of TRUE. To account for variation in streamflow, cells in the wetted channel adjacent to those streambanks out to the center of the stream were also assigned “breeder-suitable?” = TRUE.

Hydraulic habitat modeling

The depth and velocity lookup tables for each model cell were developed via two-dimensional hydrodynamic modeling. The hydrodynamic model was based on a detailed topographic survey made in June–July 2014. This survey combined high-resolution sonar sweeps in the wetted channel with conventional GPS and total station surveys in dry and shallow areas. The survey observed a mean of 5.5 valid elevation points per square metre (total points divided by total area).

Two-dimensional predictions of depth and velocity were produced for 30 different steady flows, ranging from 0.5 to 300 $m^3 \cdot s^{-1}$. We used the FaSTMECH model (Nelson and Smith 1989; Nelson et al. 2003) operated within the International River Interface Cooperative (I-IRIC 2.2.4.4109) platform. FaSTMECH inputs are flow, initial water surface elevation (WSE), downstream boundary WSE, channel topography, and channel bed roughness. The simulations assumed steady flow; thus, each discharge was simulated discretely. All simulations used the same curvilinear–orthogonal grid created within FaSTMECH from the study site survey data. The FaSTMECH depth and velocity predictions were then exported to GIS and resampled onto the 1 m square grid used by FYFAM.

Three discharge and WSE datasets measured at the site were used to calibrate the hydrodynamic model, with two sparser sets of WSE measurements at higher flows used for additional guidance. Initial and boundary conditions for simulated flows were estimated by developing rating curves at the upstream and downstream reach boundaries from the cross-sectional topography, the local channel slope, and estimated channel roughness for the local substrate. The upstream and downstream ratings curves were also verified by WSEs observed during field site visits.

The model was calibrated by varying two parameters, channel roughness and the lateral eddy viscosity (LEV). Both of these parameters vary with water depth, so different values were used over the range of measured flows. Calibration at 5.0 and 14.5 $m^3 \cdot s^{-1}$ was achieved with the same parameter values; calibration at 67 $m^3 \cdot s^{-1}$ was achieved by reducing channel roughness. Roughness was defined by two polygons, a small polygon of mid-channel higher roughness to represent the riffle at the upstream end of the reach and a larger polygon encompassing the rest of the reach. The ratio of roughnesses in the two polygons remained the same over the range of discharges simulated. In simulating uncalibrated flows, the roughness and LEV were varied with flow to account for their variation with depth.

Parameter sensitivity analysis

We used a simple individual-parameter sensitivity analysis to better understand the model and what it says about effects of flow and water temperature on FYF breeding. We analyzed all of the model’s 27 parameters with the following exceptions: we included mean but not minimum and maximum breeder fecundity; and the two parameters used to relate scour mortality to velocity were varied together, for both egg masses and tadpoles. For each parameter, we estimated low and high values that span the range of feasible values. We executed FYFAM for approximately 20 parameter values across that range. To capture how parameter effects can differ among runoff conditions, the sensitivity experiments were run for each of the 2009–2013 input years. Two measures of simulated breeding success were examined: the total number of successfully metamorphosed froglets and the median date at which metamorphosis occurred.

Fig. 2. Hydraulic simulation results: mean depth, velocity, and area of wetted cells at flows ranging from 0.5 to 100 $m^3 \cdot s^{-1}$ in increments of 0.1 $m^3 \cdot s^{-1}$.

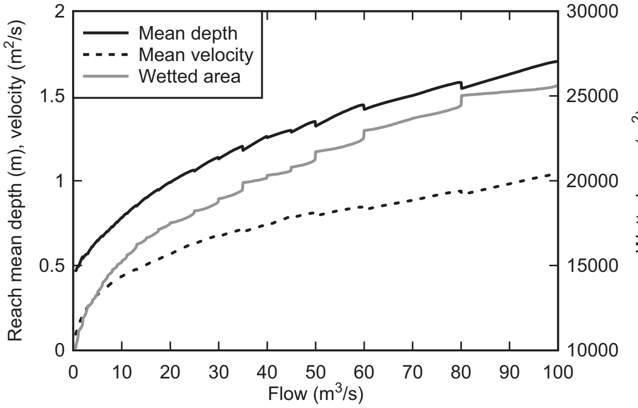
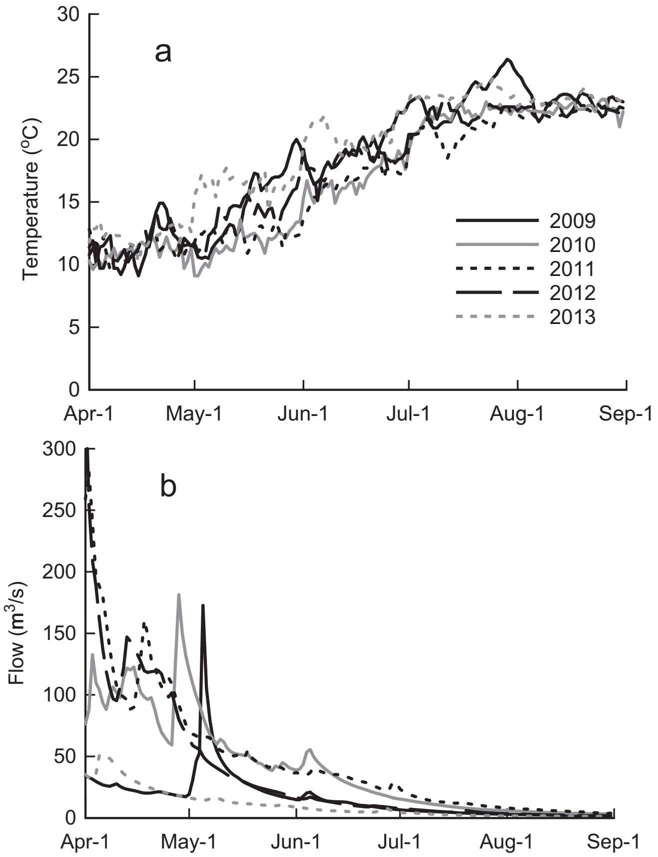
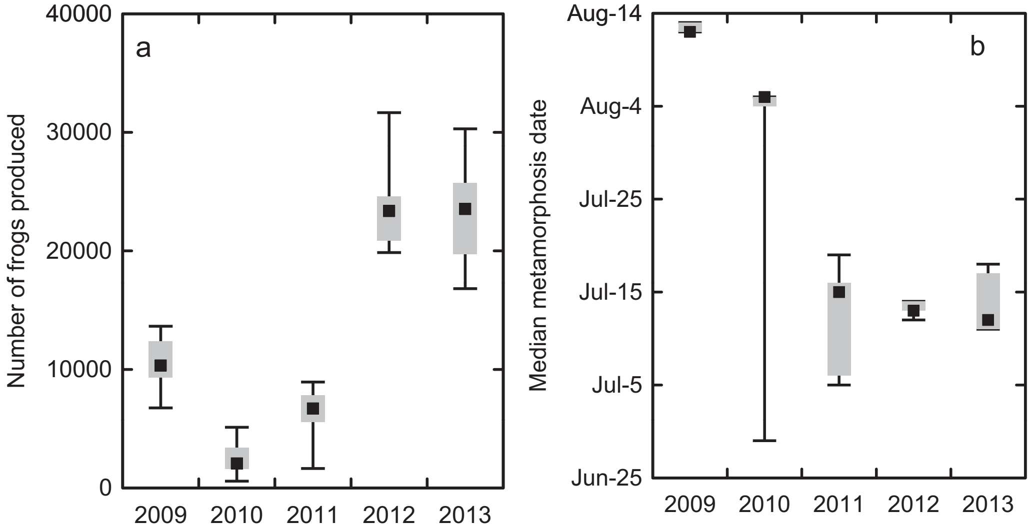


Fig. 3. Temperature (*a*) and flow (*b*) input for the 2009–2013 foothill yellow-legged frog breeding seasons, at the South Fork Trinity River (unregulated) site.



For analysis, we scaled the values of all parameters from 0.0 to 1.0 by subtracting the minimum value and then dividing by the range of values. Because the model’s responses to many parameters were nonlinear and different among years, we did not attempt to reduce results to a single sensitivity index for each parameter. Instead, we (*i*) simply plotted results and (*ii*) determined, for each of the 5 simulated years, whether each parameter produced a significant positive or negative response (defined as a linear regression p value ≤ 0.1) in either of our two measures of frog breeding success.

Fig. 4. Foothill Yellow-legged Frog Assessment Model (FYFAM) results for five replicate simulations of the baseline scenario: 2009–2013 with South Fork Trinity River input. Results are number of froglets produced (*a*) and median date that new frogs metamorphosed (*b*). The whiskers represent the lowest and highest value among the replicates, the ends of the grey box represent the second- and fourth-highest values, and the black square represents the median replicate.



Analysis for conflicts with salmonid management

Our final model analysis examined potential conflicts between river management for salmonid restoration and FYF breeding success. We conducted the analysis by comparing results from our South Fork Trinity River site to model results using the same channel but with flow and temperature regimes of the nearby mainstem Trinity River. The main stem is largely controlled by releases from Trinity and Lewiston reservoirs (a large storage reservoir and small re-regulation reservoir). Flow and temperature management of the main stem is complex and multi-objective, but intended primarily to restore and maintain anadromous salmonid stocks (USFWS and HVT 1999).

To represent mainstem flow and temperature regimes, we used data from the Douglas City gage (USGS 11525854), which is near the upstream-most known site where FYF currently breed on the mainstem Trinity River. Flow data from this gage were adjusted by multiplying each daily value by the ratio of South Fork to mainstem median flow from April to September of 2009–2013; this ratio was 0.36. Daily mean water temperatures from the gage were used directly; these temperatures are strongly influenced by hypolimnetic releases from Trinity Dam.

Results

Habitat simulation

The cell depths and velocities we simulated at 30 flows, combined with FYFAM's methods for interpolating between those flows, produced hydraulic habitat conditions illustrated in Fig. 2. Our lookup table and interpolation approach is flexible and computationally feasible (alternative approaches such as hydraulic modeling every daily flow would be very cumbersome); however, it does produce artifacts that can affect model results. Interpolation has limited ability to predict the exact flow at which each channel margin cell changes between submerged and dry, and this ability is least at higher flows and along shallowly sloped channel margins. (Interpolation ability also depends on the spatial resolutions of the hydraulic model and the FYFAM simulation.) As flow decreases through one of the flows in the lookup table, a number of margin cells can become dry at once instead of gradually (e.g., at 50, 60, and 80 $m^3 \cdot s^{-1}$ in Fig. 2). Because egg masses and tadpoles typically inhabit the very margin of river channels, this artifact can exaggerate the risk of desiccation mortality. However, this exaggeration appears small at flows below 30 $m^3 \cdot s^{-1}$, which include 75% of the days in our simulations.

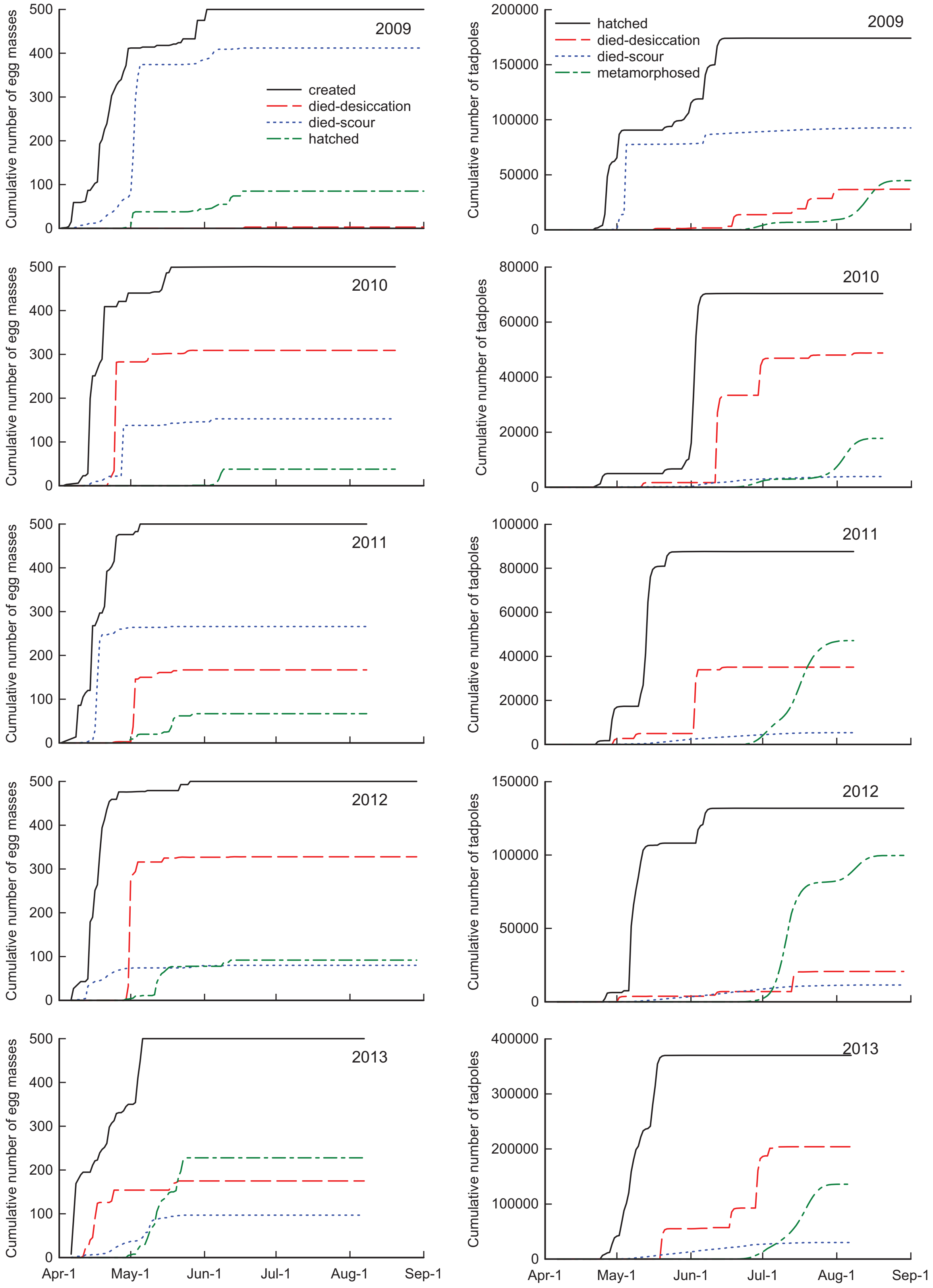
Baseline scenario

The five breeding seasons we simulated were similar in temperature but not flow (Fig. 3). Years 2009 and 2010 exemplify one of the worst situations for FYF breeding: a period of declining flow that induces breeding, followed by a spike in flow (from atypically late rainstorms) that scour egg masses and tadpoles (Kupferberg 1996). In contrast, 2013 had what appear to be very good breeding conditions: gently declining flows and relatively high temperatures. The other years had some flow variability early in the breeding season but no major flow events after 1 May.

As expected, FYFAM results differed strongly among the 5 years (Fig. 4). In addition, model results — especially for numbers of froglets produced — are relatively stochastic, as indicated by the substantial variation among replicate simulations illustrated in Fig. 4. ("Replicates" are simulations differing only in the random numbers used to represent stochastic events.) To understand the causes of stochasticity in results, we conducted experiments that removed stochasticity from parts of the model, one part at a time. These experiments revealed that much of the stochasticity in froglet production results from the randomness in the dates at which breeders become ready to oviposit, which affects how many egg masses are present during scour and desiccation events.

Simulated breeding success was low in 2009–2011. Few froglets were produced, and in 2009–2010, the froglets metamorphosed late (mostly in August). In 2012–2013, success was much higher, with many more froglets produced and most of them metamorphosed before mid-July. The details of what happened to egg masses and tadpoles (Fig. 5) illustrate the model's mechanisms. In 2009, most breeders had oviposited when a high-flow event at the beginning of May scoured most egg masses and tadpoles; the survivors then experienced relatively little mortality. In 2010, steeply declining flows followed by a high-flow event desiccated or scoured most egg masses. Of the few tadpoles produced, many died of desiccation during June's unusually steep flow decline. The relatively low breeding success in 2011 was mainly due to flow variation in April, which both scoured and desiccated many egg masses. Steep flow

Fig. 5. Detailed results for the baseline years 2009–2013: sum of five replicates, each starting with 100 yellow-legged frog breeders. Fate of egg masses (left panels) are the cumulative number (over time) that were created via oviposition, died because of desiccation and scour, and hatched successfully into tadpoles. (Each egg mass produces up to 2500 tadpoles; “hatched” in the left graphs represents the day on which the last tadpole hatches from the egg mass.) Fate of tadpoles (right panels) include the number hatched, desiccated, scoured, and successfully metamorphosed.



decreases in late April 2012 caused desiccation of most egg masses, but survival of eggs and tadpoles was high for the rest of the season. The unusually low and steady flows of 2013 produced only moderate desiccation and scour of both eggs and tadpoles, with high overall survival. High water temperatures early in 2013 caused oviposition to start earlier than in other years, and many of the early egg masses were lost to desiccation in April.

Our FYFAM simulations produced realistic placement of egg masses and habitat use by tadpoles. To illustrate this, we simulated a weekly survey of habitat use, having each egg mass and tadpole in the model output its depth and velocity. Habitat use in the model (Fig. 6) was comparable to that observed for real FYF (e.g., by Bondi et al. 2013). Bondi et al. (their fig. 4) observed egg masses concentrated in depths between 0.1 and 0.5 m and velocities <0.1 m·s^{-1}; in our simulations, most egg masses were in depths between 0.05 and 0.4 m and velocities <0.2 m·s^{-1}. Bondi et al. (2013) found tadpoles concentrated in depths <0.5 m and velocities <0.2 m·s^{-1}; our simulated tadpoles were all in depths <0.5 m and almost all in velocities <0.2 m·s^{-1}.

Parameter sensitivity

Results of the parameter sensitivity analysis were complex and variable. (Complete sensitivity analysis results are in Supplement B[1].) Many parameters had significant effects (linear regression between scaled parameter value and model output with $p \leq 0.1$) in some years but not others (Section 2 of Supplement B[1]). Only one parameter had no significant effects on either froglet production or median metamorphosis date in any year: the rate at which eggs die of desiccation when their cell becomes dry. This rate was unimportant because once a cell dried during decreasing flows, it rarely became wet again before all the eggs died, whether the mortality rate was low or high.

Only six parameters had significant and consistent (all positive or all negative) effects on froglet production in at least 4 of the 5 years (Section 2 of Supplement B[1]); these parameters represent mean fecundity of breeders, maximum rate of depth change for oviposition, minimum oviposition temperature, mean tadpole development time, tadpole habitat selection radius, and the relation between water velocity and tadpole scouring mortality. There were five parameters with significant and consistent effects on median metamorphosis date; they represent temperature effect on egg development, the relationship between cell velocity and egg scour probability, maximum rate of depth change for oviposition, minimum oviposition temperature, and tadpole development time.

Many parameters had opposite effects in different years. Six parameters had significant positive effects on froglet production in some years and significant negative effects in others, and five parameters had such effects on metamorphosis date. Parameters representing the trade-off between desiccation and scouring risks — placing eggs in shallower versus deeper water — were among these (e.g., Fig. 7), because each strategy's success depends on the flows each year.

Another important trade-off apparent from the sensitivity analysis was between the number of froglets produced and the time at which they metamorphose. Parameters controlling the rate at which eggs and tadpoles develop (those relating egg development to temperature, as well as the mean tadpole development time) had strong effects on both; more rapid development results in earlier metamorphosis and hence higher survival to metamorphosis. But parameters that control when breeding starts (e.g., for the minimum temperature for oviposition) had conflicting effects on the two outputs. Delayed breeding produced more froglets, because scouring and desiccation are more severe early in the season, but resulted in later metamorphosis (Fig. 8).

Fig. 6. Simulated habitat use by yellow-legged frog egg masses and tadpoles. Each circle represents the cell depth and velocity of one egg mass or tadpole. Results are 674 observations of egg masses and 637 000 of tadpoles from one simulation each of years 2009–2012.

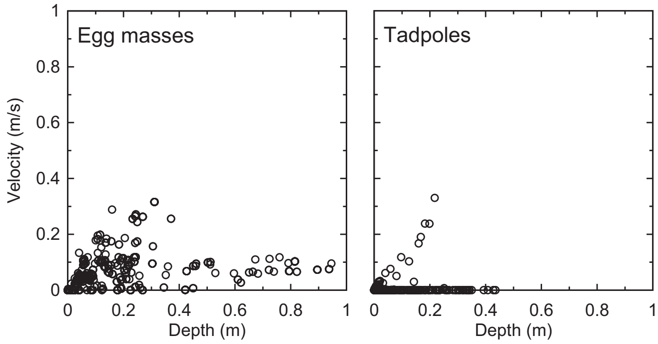
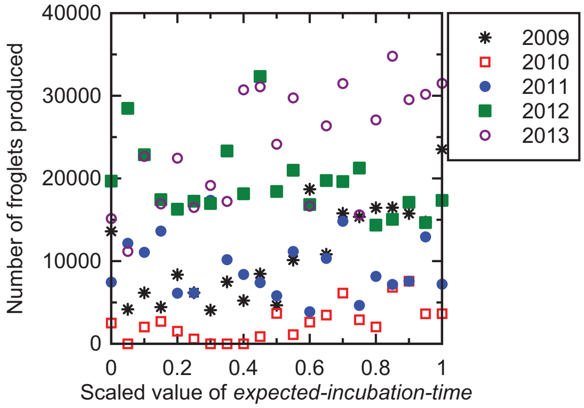


Fig. 7. Sensitivity of the simulated number of froglets produced to "expected incubation time", the time horizon that simulated yellow-legged frog breeders use in predicting whether a potential oviposition cell will become dry before eggs can hatch. This parameter's value was varied from 10 to 30 days, with higher values usually causing oviposition in deeper cells. The relation between scaled parameter value and froglet production was significantly positive in 2009, 2010, and 2013 and significantly negative in 2012 ($p \leq 0.1$).



Management analysis

We simulated FYF breeding success with flow and water temperature regimes from the mainstem Trinity River, where reservoir releases are managed primarily for salmonids (Fig. 9). Compared with the more natural South Fork (Fig. 3), the main stem has temperatures that start lower in April and increase little during the summer. Mainstem flows differ in being relatively low and steady until late April and May, with controlled peaks (which we refer to as "May high flows") that are lower and later. After the May high flows, mainstem flow tends to attenuate more gradually and less variably than in the unregulated South Fork. The May high flows are reservoir releases designed, in part, to maintain the complex alluvial channel morphology that provides habitat for both salmonids and frog breeding (USFWS and HVT 1999).

The overall numbers of froglets produced with mainstem input were comparable to those obtained from South Fork flows and temperatures (Fig. 10). However, two major differences are apparent: with mainstem input, metamorphosis dates are much later, and the pattern among years in froglet production is very different from that of the South Fork. In the mainstem simulations, low froglet production years (2009, 2013) had warmer temperatures early, causing breeders to oviposit before the May high flows. Those high flows destroyed the egg masses. Breeders that waited until after the high flows to oviposit had some of their egg masses survive,

Fig. 8. Sensitivity analysis results for the minimum temperature for oviposition, varied from 8 to 14 °C: number of froglets produced (*a*) and median metamorphosis date (*b*). See Fig. 7 for symbol legend.

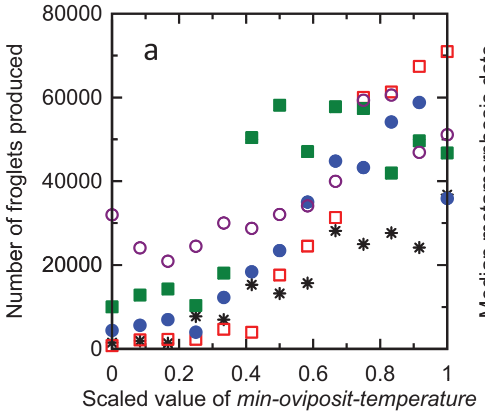
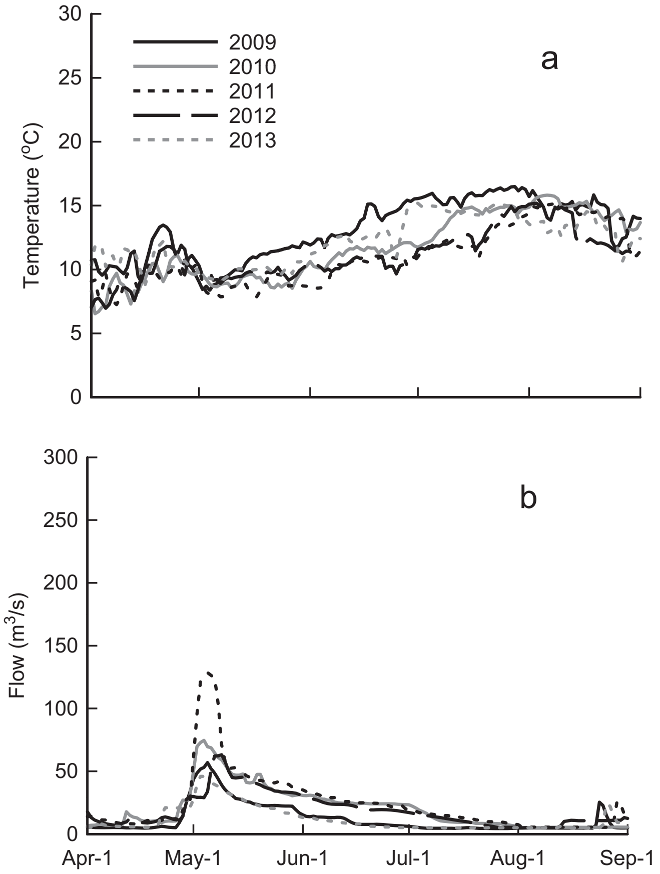


Fig. 9. Temperature (*a*) and flow (*b*) input representing the mainstem (regulated) Trinity River below Lewiston Reservoir (USGS gage 11525854 at Douglas City, California).



though the eggs hatched late (Fig. 11). The high froglet production years (2010–2012) were when breeders waited until after the May high flow to oviposit, so egg and tadpole survival was higher but metamorphosis was still late.

We also conducted simulations to examine the effects of the mainstem's flows and temperatures separately. Simulations using the mainstem's regulated flows and the South Fork's warmer temperatures produced very low breeding success; no years produced more than 10 000 froglets and in eight of the 25 simulations (five replicates of the 5 years) no froglets were produced. (Complete breeding failure never occurred in simulations using South Fork flows and temperatures.) The warm temperatures caused almost all breeders to oviposit before the May high flows, so their egg masses rarely survived. Simulations using the South Fork's unregulated flows and the mainstem's lower temperatures produced more froglets than any other scenario (a mean over all years and replicates of 29 100, compared with 13 300 for the South Fork simulations). This scenario produced high numbers of froglets in 2010 (a mean among replicates of 44 900), in contrast with the baseline simulations (mean of 2600); colder temperatures caused breeders to oviposit only after the May high flows that caused extensive desiccation and scour in other simulations. However, this combination produced much later metamorphosis (median of 3 September) compared with South Fork simulations (22 July).

Discussion

This modeling analysis indicates that there are indeed both mutual benefits and potential conflicts in managing rivers for salmonids and protecting other species of interest, such as river-breeding amphibians. The effects of salmonid management on species such as FYF emerge from complex interactions among channel shape, flow and water temperature regimes, and breeding phenology, so they are not simple or easily predicted without models such as FYFAM.

Like all models, FYFAM is an intentional simplification. We chose not to include potential effects of temperature on tadpole development because of the uncertainties in doing so. Other factors likely to limit tadpole development rates include the limited quantity and quality of algal and diatom food (Catenazzi and Kupferberg 2013; Furey et al. 2014) and competition among tadpoles (Kupferberg 1997); if food competition is strong, high oviposition and egg incubation success could result in later metamorphosis and smaller froglets. We also chose not to include predation mortality. FYF eggs and tadpoles are highly vulnerable to many terrestrial and aquatic predators. Garter snakes (*Thamnophis* spp.) are especially prominent (Fitch 1941), while aquatic macroinvertebrates, fish, newts (*Taricha* spp.), birds, and otters have all been observed eating eggs and tadpoles. Flow and water temperature management can affect predation indirectly, for example by affecting tadpole growth and size and by inducing behaviors (e.g., sheltering from high velocities; Kupferberg et al. 2011*a*) that can increase vulnerability to some predators. However, these mechanisms are indirect and complex, so we did not include them.

Our ability to validate FYFAM was limited to confirming that its key individual behaviors, breeders placing egg masses and tadpoles selecting habitat, produced realistic habitat use and also limited to illustrating that the model contains the mechanisms through which flow and temperature are believed to affect survival and metamorphosis timing most strongly. Because the model does

Fig. 10. Results for mainstem Trinity River temperature (*a*) and flow (*b*) patterns, in the same format as Fig. 4, which presents comparable results for South Fork temperatures and flows. In the highest 2010 replicate, 41 500 froglets were produced. The wide range among replicates in 2013 metamorphosis date was because only in one replicate did any of the early-oviposited egg masses survive May high flows.

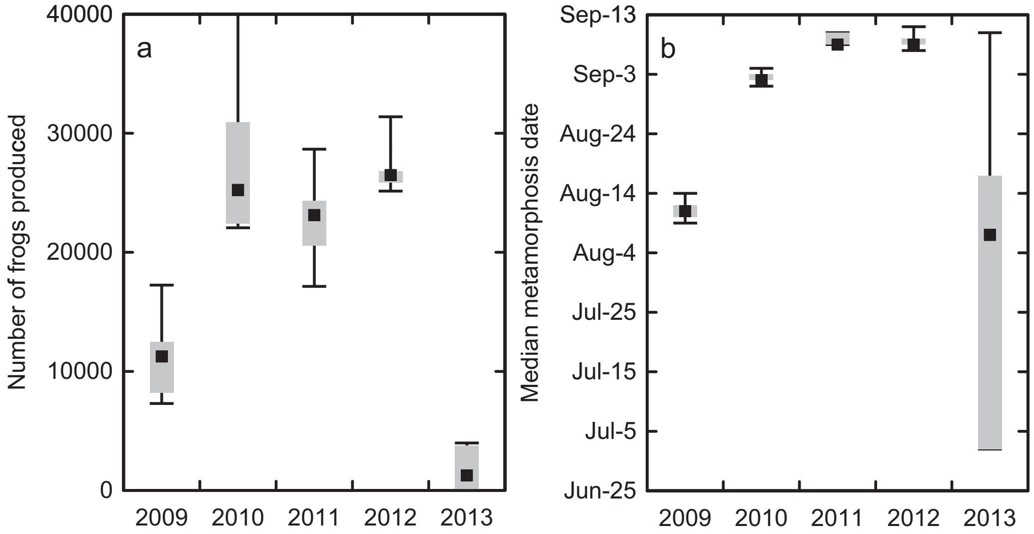
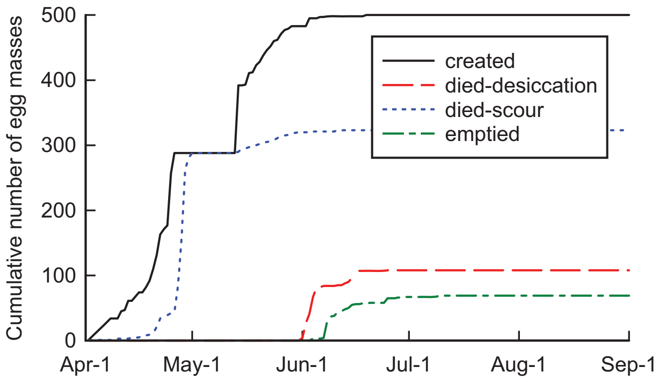


Fig. 11. Egg mass fates (sum of five replicates) in simulations with 2009 mainstem Trinity River temperatures and flows. Curves represent the cumulative number of egg masses that were created via oviposition, died because of desiccation and scour, and hatched successfully into tadpoles.



not represent the full life cycle nor important population-regulating processes such as predation mortality and competition among individuals, it cannot be expected to make testable predictions about population dynamics. We have not yet tested the model against observed effects of flow and temperature, in part because of the challenges of observing and quantifying the effects of scouring and desiccation events and distinguishing their effects from those of predation.

Despite the limited extent to which it has been validated, FYFAM is still useful for understanding and predicting effects of river management on river-breeding frogs. The model encodes the relationships and understandings we have from extensive field studies and tells us their consequences for breeding success in specific situations. Sensitivity analysis of the model is useful for developing a mechanistic understanding of site-specific breeding success. While detailed simulation models for management of river fish, especially salmonids, have been available for many years, FYFAM is one of the very few similarly powerful tools for assessing effects on other taxa. Increasing breeding success can be effective for reducing the probability of extinction for small and declining frog populations (Kissel et al. 2014), so FYFAM may be useful for developing conservation strategies for imperiled populations where flows and temperatures can be controlled.

Both our parameter sensitivity analyses and our simulations of five hydrologically different years illustrate how FYF breeding is a gamble in which no strategy succeeds consistently. Placing eggs in deeper habitat may prevent them from being desiccated if flow decreases rapidly but puts them at higher risk of scouring if flow increases. Waiting longer to breed increases the probability that eggs and tadpoles survive scour and desiccation, but gives the surviving froglets less time to establish and grow on an arthropod-based diet before winter and, hence, a lower probability of contributing to the breeding population.

Simulating FYF breeding success under the flow and temperature regime of the mainstem Trinity River, which is managed primarily to restore and enhance salmonid habitat via variable flows and cold water temperatures, indicated that salmonid management is not inherently bad for frog breeding success but that there is definitely a high potential for conflicts. In years when reservoir operations stabilized flows or limited their rate of change during the breeding season, there were undoubtedly benefits in reduced scour and desiccation of egg masses and tadpoles. However, spring flow releases that started after the onset of frog breeding had strong negative effects. The model therefore indicates that the timing of oviposition, relative to spring flow pulses, is a critical factor determining river management effects on FYF; this relation could strongly select for breeding strategies that compensate for changes in flow timing (e.g., delayed oviposition). The extent to which breeding starts before the spring flow releases was, in our simulations, highly dependent on water temperatures. While we use water temperature as the model's trigger for the onset of breeding, adult frogs may also use air temperature as a cue for breeding, and the difference between air and water temperatures is typically higher below a reservoir than in unregulated rivers (Olden and Naiman 2010). Careful studies of what triggers the onset of breeding may be important for understanding the extent to which the current spring flow schedule affects FYF and the extent to which the species could adapt to it.

The most consistent negative effect of salmonid management in our simulations was delayed metamorphosis. Under the reservoir-controlled mainstem temperature regime, frog metamorphosis occurred weeks later compared with with natural temperatures; the actual effect would probably be even greater because FYFAM neglects effects of temperature on tadpole development rates and survival (Catenazzi and Kupferberg 2013; Wheeler et al. 2015). Delayed metamorphosis reduces the opportunity for froglets to grow before winter, and reduced size and body condition of froglets may have longer-term and demographically important effects, such as reduced survival of the first winter, decreased postmetamorphic growth rates, smaller size at maturity, and lower reproductive success (Smith 1987; Berven 1990; Goater 1994; Altwegg and Reyer 2003).

Declining flows in spring and low flows and warm temperatures in summer are natural and ecologically important characteristics of salmonid-bearing rivers with Mediterranean flow regimes (Gasith and Resh 1999; Power et al. 2008). Managing reservoir-controlled rivers for mainstem-spawning salmonids can have negative consequences for warm-water-adapted taxa (Ashton et al. 2015). Finding flow and water temperature regimes that adequately support both warm- and cold-water taxa — for example, ways to manage the mainstem Trinity River to obtain the benefits of spring high flows without strong impacts on FYF breeding — will require the use of novel modeling tools such as the one we present here.

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