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Modeling potential river management conflicts between frogs and salmonids

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Abstract: Management of regulated rivers for yellow-legged frogs 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.

Gestion des cours d'eau réglementés pour les grenouilles à pattes jaunes 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 mainstems (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 produce flows high enough to wash out FYF eggs and tadpoles can significantly 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. 2011a, 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. 2010). 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. 2014).

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. 2014) 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. 2010), and basic research on how variables such as temperature and velocity affect various life stages (Kupferberg et al. 2011a, Catenazzi and Kupferberg 2013, Wheeler et al. 2014).

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 which emerge directly from the two key individual behaviors included in the model. We then analyze the model's sensitivity to parameter values, in five 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, instead of its unmanaged flows and water temperatures, those from a nearby river that is controlled by an upstream reservoir and managed primarily for salmonids.

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. 2014). 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 (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).

143 **Egg masses and tadpoles are at risk from both decreasing and increasing flows.**
144 Decreases in flow that expose egg masses or tadpoles to air and sun cause rapid mortality via
145 desiccation. Increases in flow and water velocity expose these life stages to the risk of being
146 washed downstream and into habitat where survival is presumably low (Kupferberg 1996); we
147 refer to this risk as scouring. Egg masses are especially at risk because they cannot move, and
148 because even moderate velocities (local velocities well below 0.5 m/s) can cause gradual
149 disintegration and scouring. However, tadpoles are poor swimmers and their swimming ability
150 decreases as they develop more frog-like bodies; hence they are also vulnerable to both
151 desiccation and scour (Kupferberg et al. 2011a).
152 **Breeders place egg masses in habitat that provides a balance between the risks of**
153 **desiccation and scour.** FYF typically oviposit in places where depth is adequate to prevent
154 desiccation during "normal" rates of spring flow decreases, while also avoiding velocities high
155 enough to cause scouring (Kupferberg 1996). They also appear to avoid habitat with near-zero
156 velocities, presumably because some water movement is needed to provide oxygen to, and carry
157 metabolic wastes from, egg masses. Oviposition sites typically include moderately shallow
158 stream margins (with eggs masses attached to cobbles or the downstream side of larger substrate)
159 and deeper locations protected from high velocities (Bondi et al. 2013).
160 **Egg development rates are temperature-dependent, while tadpole development rates**
161 **depend on multiple factors that interact with temperature.** The time between oviposition and
162 hatching of eggs decreases as water temperature increases (Kupferberg et al. 2011b). Tadpole
163 growth and development also appear temperature-dependent, with time to metamorphosis into
164 froglets inversely related to water temperature. However, tadpole development also depends on
165 other factors such as quantity and quality of algae and diatom food (Catenazzi and Kupferberg

166 2013, Furey et al. 2014), water velocity, and predator-avoidance behavior (Kupferberg et al.
167 2011a,b). Because the mechanisms controlling tadpole development are complex and not all
168 directly related to flow or temperature, we did not include them explicitly in the model.

169 **Model description**

170 We developed the Foothill Yellow-legged Frog Assessment Model (FYFAM), an
171 individual-based, spatially explicit, time-step simulation model. The model was designed to
172 contain the simplest useful representations of the processes causing the patterns identified above.
173 Here we provide a summary of the model's elements and processes[1].

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

184 "Reproductive success" here refers primarily to survival of eggs and tadpoles, from when
185 eggs are laid (oviposition) through the first summer of life. The endpoint of reproductive success

[1] Supplement A 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).

186 is metamorphosis from the aquatic tadpole to the amphibious froglet life stage, in the first
187 summer of life. The time at which metamorphosis occurs is a second important component of
188 reproductive success because froglets that metamorphose earlier have more time to attain larger
189 size and find suitable habitat, which makes them more likely to survive their first winter and,
190 hence, more likely to contribute to future breeding populations.

191 **Habitat entities, state variables, and scales.** Frog habitat is represented at two scales,
192 reaches and cells. FYFAM represents one "reach", a contiguous section of stream or river and
193 adjacent riparian habitat. A reach is the model's spatial extent, which can be from a few tens to
194 several hundred meters of stream length. A reach has a static variable *cell-size* for the width of
195 each of its cells and dynamic (time-varying) state variables *step-length*—length of the current
196 time step (in days), *flow*—stream flow (m^3/s), and *temperature*—water temperature (°C). The
197 flow and temperature variables represent averages over the time step. The temperature variable
198 represents water temperature in the channel edge habitat typically occupied by the frog life
199 stages in this model; Wheeler et al. (2014) found such channel edge temperatures close to mid-
200 channel temperatures at a daily time step in the river we study, so mid-channel temperatures
201 (which are much easier to measure or model) can suffice for this variable.

202 Cells are square habitat elements representing variation within the reach. Each cell has
203 static boolean (TRUE-FALSE) variables *breeder-suitable?* for whether it is suitable physical
204 habitat for breeders (e.g., rock substrate exposed to sun) and *has-shelter?* for whether it has
205 velocity shelter for egg masses. These cell variables are input that can be developed from field
206 observations. Cells also have dynamic variables updated each time step: *depth* and *velocity* for
207 water depth (m) and velocity (m/s), and the boolean *ovi-suitable?* for whether the cell has
208 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 ("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 a 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

231 until all simulated tadpoles have metamorphosed, typically near the end of the summer dry
232 season.

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

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

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

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

250 (3) Breeders ready for oviposition decide whether to oviposit. A ready breeder oviposits
251 on the next time step when water temperature is above a threshold of 10°C, the rate of change in
252 water depth is below a threshold of 0.03 m/d, and there is suitable oviposition habitat available
253 within the radius *oviposition-radius*.

(4) Breeders oviposit. Any breeder that decides to oviposit identifies the best cell within *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 (on the basis of field observations by Lind et al. (In press) 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 1 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 1 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 non-zero 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. 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 archived.

299 **Study site and model input**

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

308 Our simulation experiments used input from five years, 2009-13. These years included a
309 wide range of runoff patterns—flow magnitude and variability, illustrated below—that affect
310 FYF breeding in different ways. Daily mean flow input was synthesized by adjusting data from
311 the US Geological Survey gage upstream at Hyampom, California (USGS gage 11528700). The
312 adjustment used linear regression between four flows we measured at the site (ranging 0.64 to
313 14.5 m^3/s) and instantaneous flows reported by the USGS gage 1 hour before our measurements
314 ($R^2 = 0.997$). Daily mean water temperature input was assembled and synthesized from data we
315 collected at the site in April-August 2009 and since May, 2014; and from regression models
316 (separate models for each month) that predict water temperature from river flow and air
317 temperature observed at the nearby town of Willow Creek (US National Oceanic and
318 Atmospheric Administration station Willow Creek 1 NW CA).

319 We determined the availability of velocity shelter for egg masses in habitat cells using
320 field observations and GIS. The distribution of habitat providing velocity shelter was mapped
321 during field observations using a total station. Habitat patches of at least 75% by area of cobble

and boulder ≤ 25% 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 an average of 5.5 valid elevation points per m^2 (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/s. 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.

344 The FaSTMECH depth and velocity predictions were then exported to GIS and resampled onto
345 the 1-m square grid used by FYFAM.
346 Three discharge and WSE data sets measured at the site were used to calibrate the
347 hydrodynamic model, with two sparser sets of WSE measurements at higher flows used for
348 additional guidance. Initial and boundary conditions for simulated flows were estimated by
349 developing rating curves at the upstream and downstream reach boundaries from the cross-
350 sectional topography, the local channel slope, and estimated channel roughness for the local
351 substrate. The upstream and downstream ratings curves were also verified by WSEs observed
352 during field site visits.
353 The model was calibrated by varying two parameters, channel roughness and the lateral
354 eddy viscosity (LEV). Both of these parameters vary with water depth so different values were
355 used over the range of measured flows. Calibration at 5.0 and 14.5 m^3/s was achieved with the
356 same parameter values; calibration at 67 m^3/s was achieved by reducing channel roughness.
357 Roughness was defined by two polygons, a small polygon of mid-channel higher roughness to
358 represent the riffle at the upstream end of the reach and a larger polygon encompassing the rest
359 of the reach. The ratio of roughnesses in the two polygons remained the same over the range of
360 discharges simulated. In simulating uncalibrated flows, the roughness and LEV were varied with
361 flow to account for their variation with depth.

362 **Parameter sensitivity analysis**

363 We used a simple individual-parameter sensitivity analysis to better understand the model
364 and what it says about effects of flow and water temperature on FYF breeding. We analyzed all
365 of the model's 27 parameters with these exceptions: we included mean but not minimum and
366 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 2009-13 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.

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 (a) simply plotted results and (b) determined, for each of the five 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.

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 mainstem 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 mainstem is complex and multi-objective, but intended primarily to restore and maintain anadromous salmonid stocks (USFWS 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-September of 2009-13; 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/s 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/s, 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 May 1.

As expected, FYFAM results differed strongly among the five 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 randomness in when breeders become ready to oviposit caused much of the stochasticity in froglet production (by affecting how many egg masses are present during scour and desiccation events) and almost all the stochasticity in metamorphosis date.

Simulated breeding success was low in 2009-11. Few froglets were produced and, in 2009-10, the froglets metamorphosed late (mostly in August). In 2012-13 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 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; in our simulations, most egg masses were in depths between 0.05 and 0.4 m and velocities less than 0.2 m/s. Bondi et al. (2013) found tadpoles concentrated in depths less than 0.5 m and velocities less than 0.2 m/s; our simulated tadpoles were all in depths less than 0.5 m and almost all in velocities less than 0.2 m/s.

Parameter sensitivity

Results of the parameter sensitivity analysis were complex and variable[2]. Many parameters had significant effects (linear regression between scaled parameter value and model

[2] Complete sensitivity analysis results are in Supplement B.

454 output with $p \leq 0.1$) in some years but not others (Section 2 of Supplement B). Only 1 parameter
455 had no significant effects on either froglet production or median metamorphosis date in any year:
456 the rate at which eggs die of desiccation when their cell becomes dry. This rate was unimportant
457 because once a cell dried during decreasing flows, it rarely became wet again before all the eggs
458 died, whether the mortality rate was low or high.

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

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

473 Another important tradeoff apparent from the sensitivity analysis was between the
474 number of froglets produced and the time at which they metamorphose. Parameters controlling
475 the rate at which eggs and tadpoles develop (those relating egg development to temperature, and
476 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).

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 to the more natural South Fork (Fig. 3), the mainstem 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, though the eggs hatched late (Fig. 11). The high froglet production years (2010-12) 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 five 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 (an average over all years and replicates of 29,100, compared to 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 to 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 September 3) compared to South Fork simulations (July 22).

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* sp.) are especially prominent (Fitch 1941), while aquatic macroinvertebrates, fish, newts (*Taricha* sp.), birds, and otters have all been observed eating eggs and tadpoles. Flow and water temperature management can affect predation indirectly, e.g., by affecting tadpole growth and size and by inducing behaviors (e.g., sheltering from high velocities; Kupferberg et al. 2011a) 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 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 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.

543 Despite the limited extent to which it has been validated, FYFAM is still useful for
544 understanding and predicting effects of river management on river-breeding frogs. The model
545 encodes the relationships and understandings we have from extensive field studies, and tells us
546 their consequences for breeding success in specific situations. Sensitivity analysis of the model is
547 useful for developing a mechanistic understanding of site-specific breeding success. While
548 detailed simulation models for management of river fish, especially salmonids, have been
549 available for many years, FYFAM is one of the very few similarly powerful tools for assessing
550 effects on other taxa. Increasing breeding success can be effective for reducing the probability of
551 extinction for small and declining frog populations (Kissel et al. 2014), so FYFAM may be
552 useful for developing conservation strategies for imperiled populations where flows and
553 temperatures can be controlled.
554 Both our parameter sensitivity analyses and our simulations of five hydrologically
555 different years illustrate how FYF breeding is a gamble in which no strategy succeeds
556 consistently. Placing eggs in deeper habitat may prevent them from being desiccated if flow
557 decreases rapidly but puts them at higher risk of scouring if flow increases. Waiting longer to
558 breed increases the probability that eggs and tadpoles survive scour and desiccation, but gives
559 the surviving froglets less time to establish and grow on an arthropod-based diet before winter
560 and, hence, a lower probability of contributing to the breeding population.
561 Simulating FYF breeding success under the flow and temperature regime of the mainstem
562 Trinity River, which is managed primarily to restore and enhance salmonid habitat via variable
563 flows and cold water temperatures, indicated that salmonid management is not inherently bad for
564 frog breeding success but that there is definitely a high potential for conflicts. In years when
565 reservoir operations stabilized flows or limited their rate of change during the breeding season,

566 there were undoubtedly benefits in reduced scour and desiccation of egg masses and tadpoles.
567 However, spring flow releases that started after the onset of frog breeding had strong negative
568 effects. The model therefore indicates that when frog breeding starts, relative to spring flow
569 pulses, is a critical factor determining river management effects on FYF; this relation could
570 strongly select for breeding strategies that compensate for changes in flow timing (e.g., delayed
571 oviposition). The extent to which breeding starts before the spring flow releases was, in our
572 simulations, highly dependent on water temperatures. While we use water temperature as the
573 model's trigger for the onset of breeding, adult frogs may also use air temperature as a cue for
574 breeding, and the difference between air and water temperatures is typically higher below a
575 reservoir than in unregulated rivers (Olden and Naiman 2010). Careful studies of what triggers
576 the onset of breeding may be important for understanding the extent to which the current spring
577 flow schedule affects FYF and the extent to which the species could adapt to it.

578 The most consistent negative effect of salmonid management in our simulations was
579 delayed metamorphosis. Under the reservoir-controlled mainstem temperature regime, frog
580 metamorphosis occurred weeks later than with natural temperatures; the actual effect would
581 probably be even greater because FYFAM neglects effects of temperature on tadpole
582 development rates and survival (Catenazzi and Kupferberg 2013, Wheeler et al. 2014). Delayed
583 metamorphosis reduces the opportunity for froglets to grow before winter, and reduced size and
584 body condition of froglets may have longer-term and demographically important effects such as
585 reduced survival of the first winter, decreased post-metamorphic growth rates, smaller size at
586 maturity, and lower reproductive success (Smith, 1987; Berven, 1990; Goater, 1994; Altwegg
587 and Reyer, 2003).

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

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725 ## Supplemental Material

726 **Supplement A**

727 Complete description of FYFAM: model processes and parameters and their justification,
728 inputs, and software use.

729 **Supplement B**

730 Complete parameter sensitivity analysis results.
731

Figure captions

Figure 1. Conceptual diagram of breeder habitat selection. Breeders not yet ready for oviposition (the 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 left-most 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 tradeoff between the risks of scouring and desiccation.

Figure 2. Hydraulic simulation results: mean depth, velocity, and area of wetted cells at flows ranging from 0.5 to 100 m^3/s in increments of 0.1.

Figure 3. Temperature (a) and flow (b) input for the 2009-13 foothill yellow-legged frog breeding seasons, at the South Fork Trinity River (unregulated) site.

Figure 4. 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 value, and the black square represents the median replicate.

Figure 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 due to 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 egg mass' last tadpole hatches.) Fate of tadpoles (right panels) include the number hatched, desiccated, scoured, and successfully metamorphosed.

Figure 6. Simulated habitat use by yellow-legged frog egg masses and tadpoles. Each dot 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.

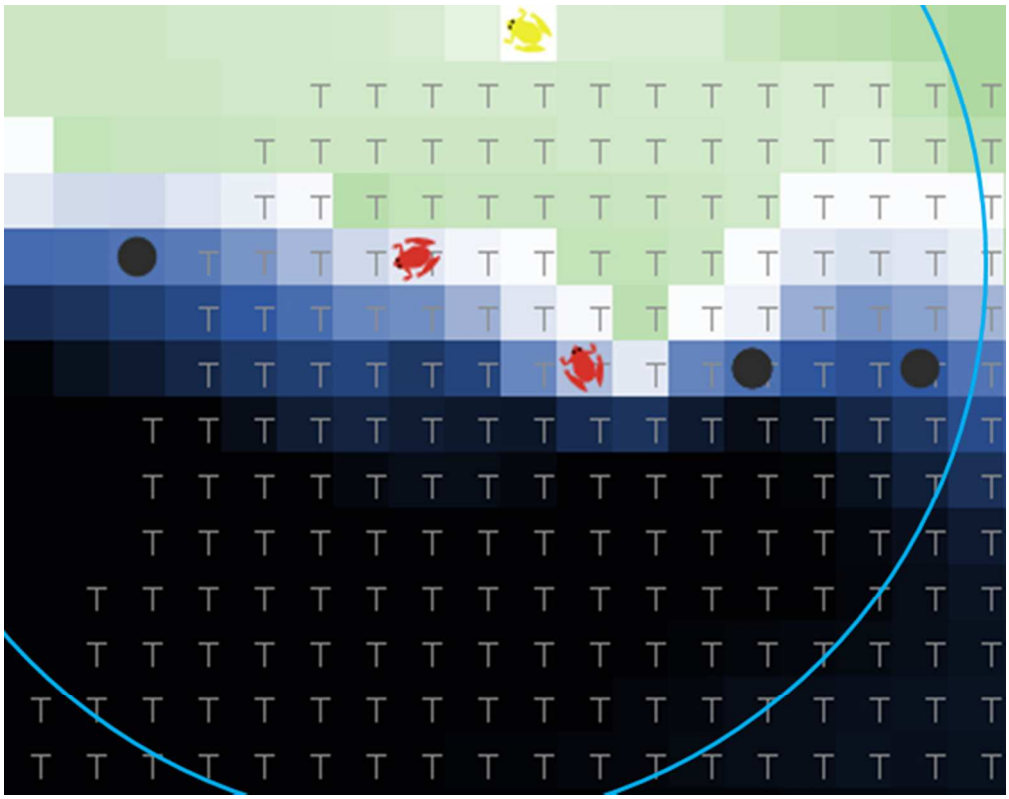
Figure 7. Sensitivity of the simulated number of froglets produced to *expected-incubation-time*, the time horizon that simulated yellow-legged frog breeders use in predicting whether a potential oviposition cell will become dry before eggs can hatch. This parameter's value was varied from 10 to 30 days, 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.

Figure 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).

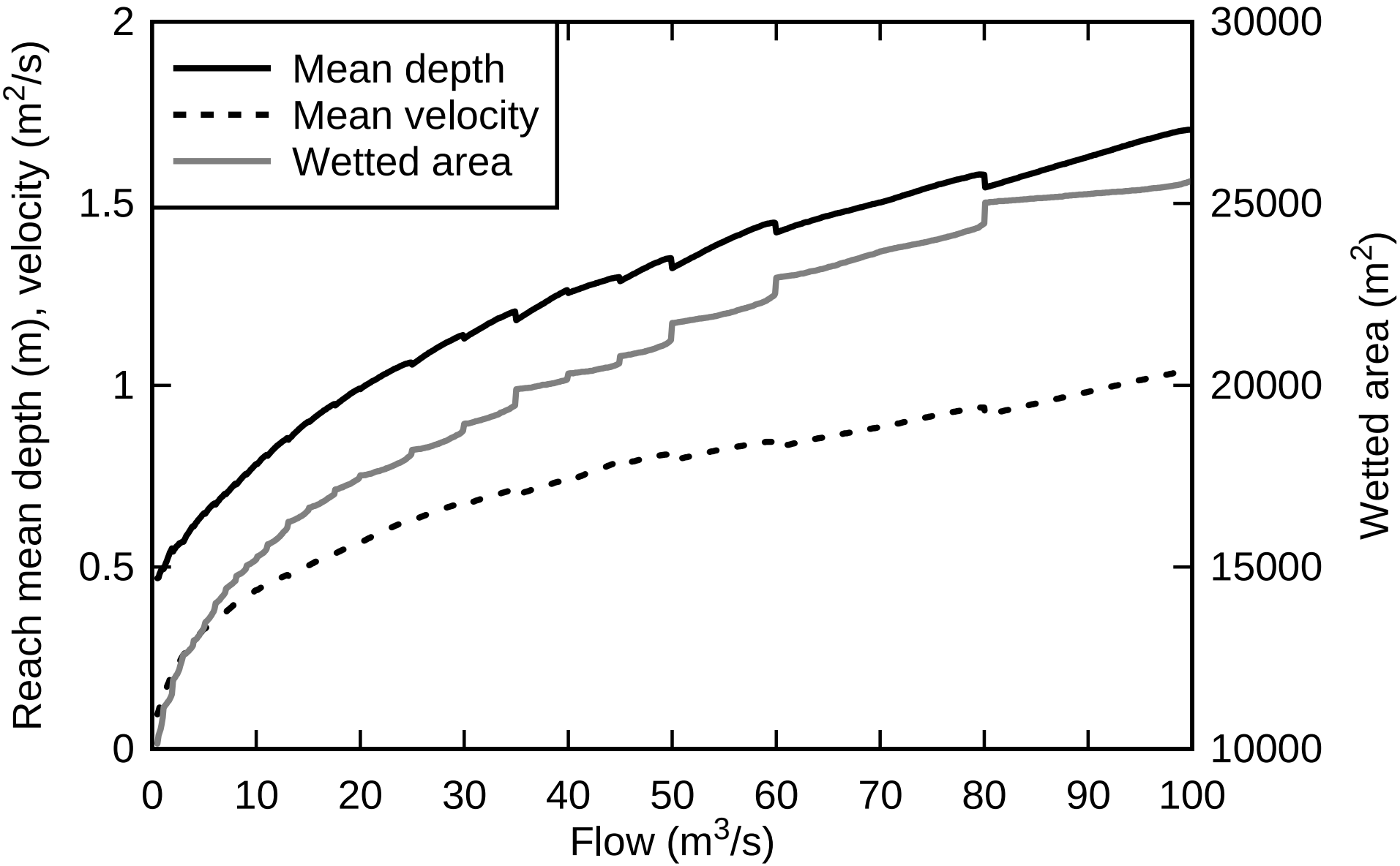
Figure 9. Temperature (a) and flow (b) input representing the mainstem (regulated) Trinity River below Lewiston Reservoir (USGS gage 11525854 at Douglas City, California).

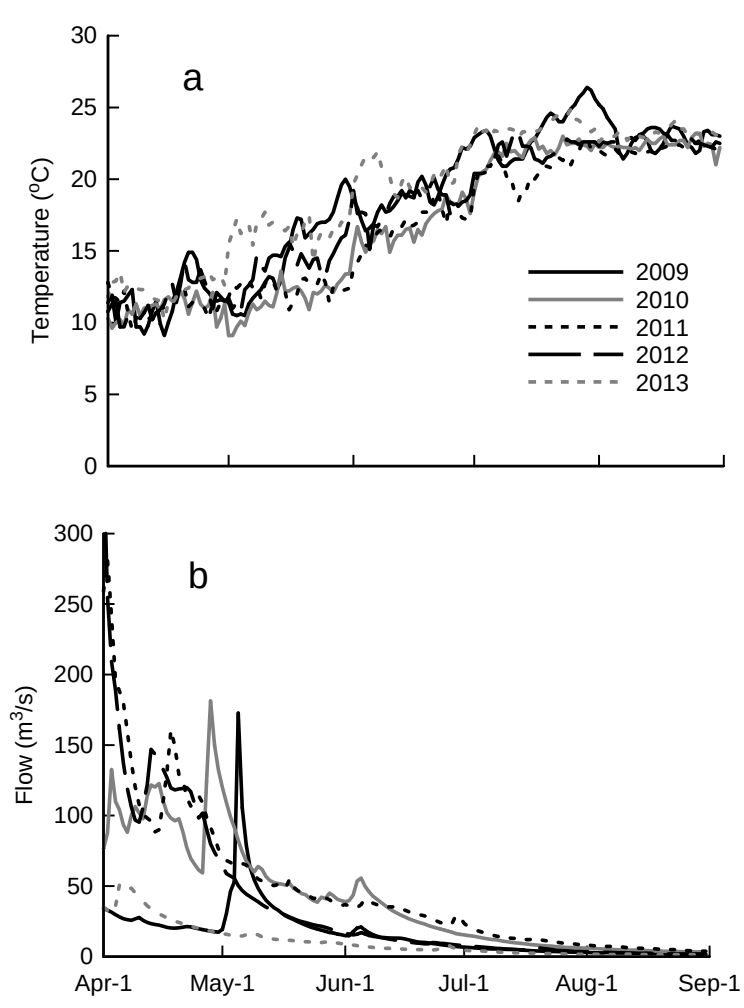
Figure 10. Results for mainstem Trinity River temperature (a) and flow (b) patterns, in the same format as Fig. 4, which presents comparable results for South Fork temperatures and flows. In the highest 2010 replicate, 41,500 froglets were produced. The wide range among replicates in 2013 metamorphosis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

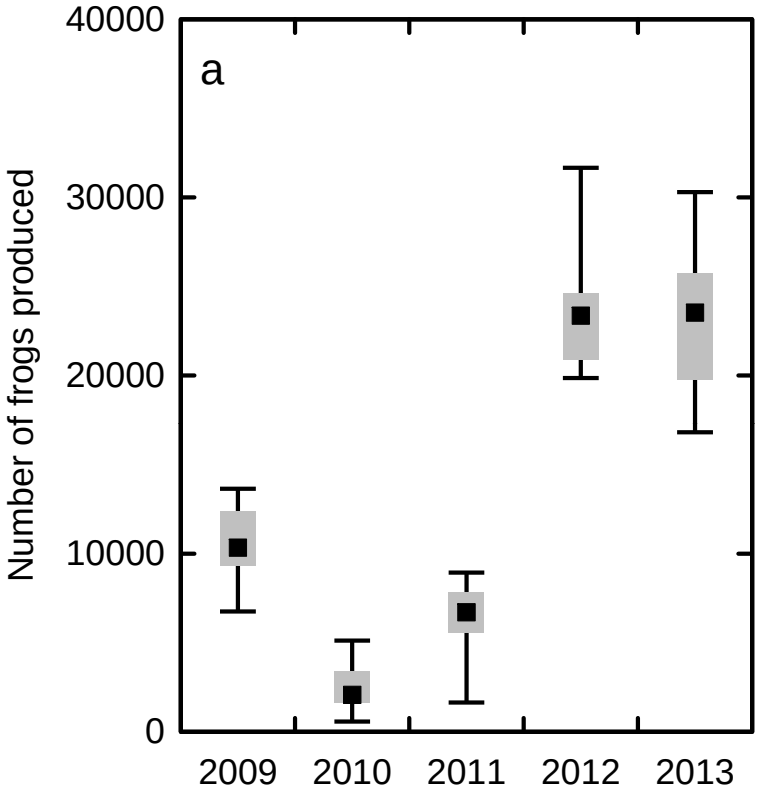
777 Figure 11. Egg mass fates (sum of five replicates) in simulations with 2009 mainstem Trinity
778 River temperatures and flows. Curves represent the cumulative number of egg masses that
779 were created via oviposition, died due to desiccation and scour, and hatched successfully
780 into tadpoles.

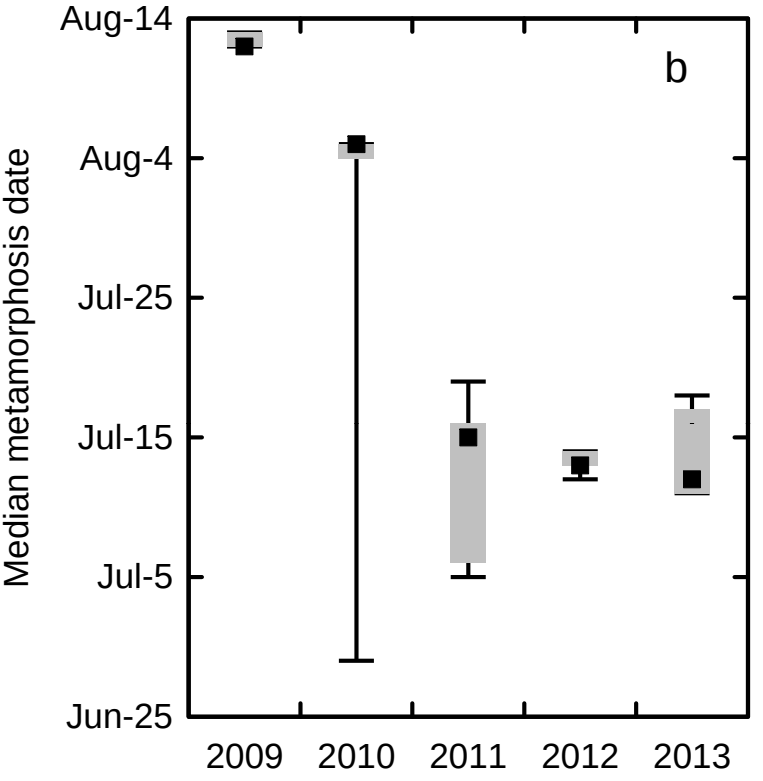


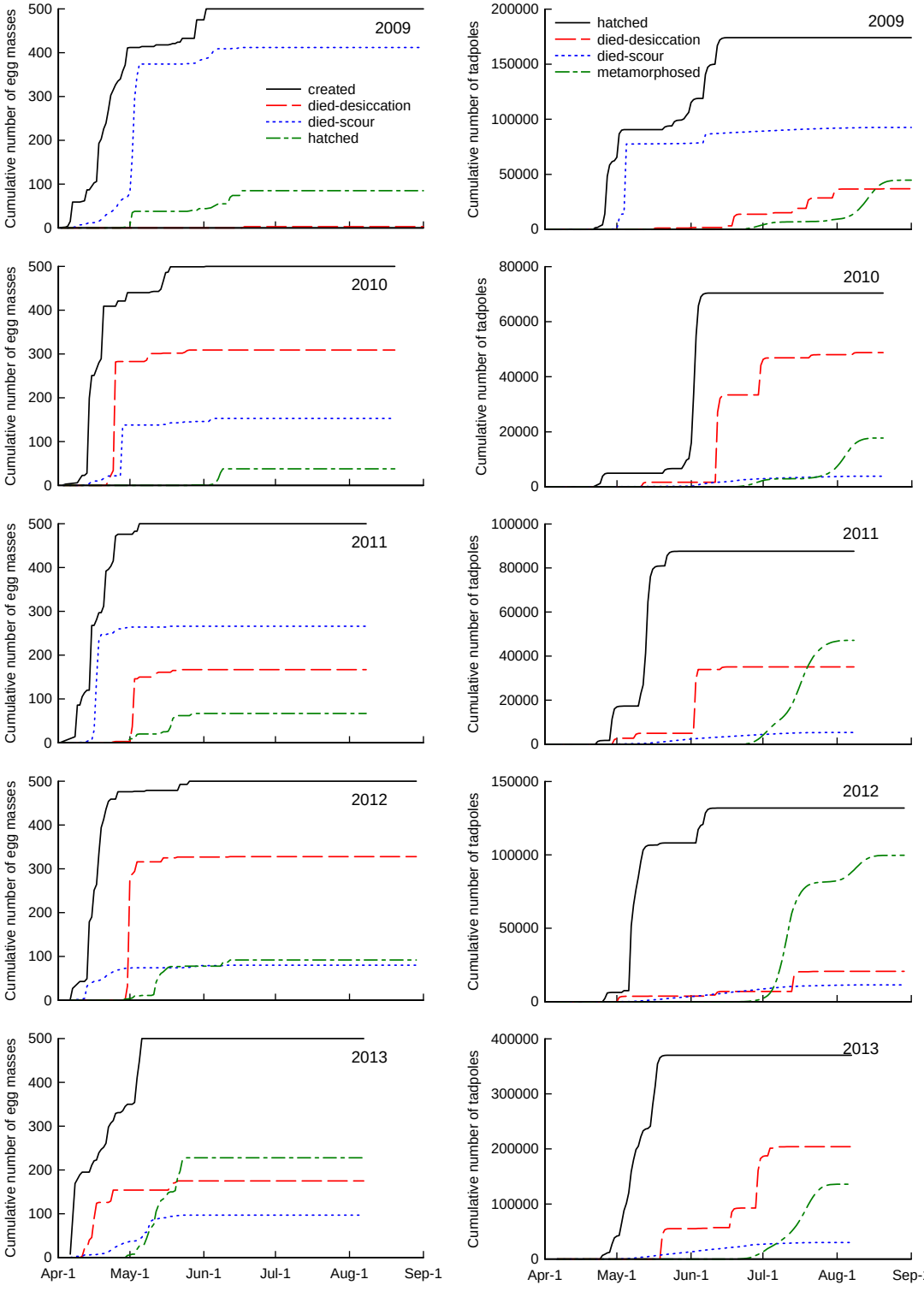
Conceptual diagram of breeder habitat selection. Breeders not yet ready for oviposition (the upper light-shaded frog) wait away from the water's edge. Breeders ready to oviposit (the darker-shaded frogs) select habitat at the water's edge. (Wet cells are shaded by depth, deeper cells being darker.) As flow changes, breeders move to cells that are within a radius of 10 m (shown for the left-most 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 tradeoff between the risks of scouring and desiccation.
186x146mm (96 x 96 DPI)

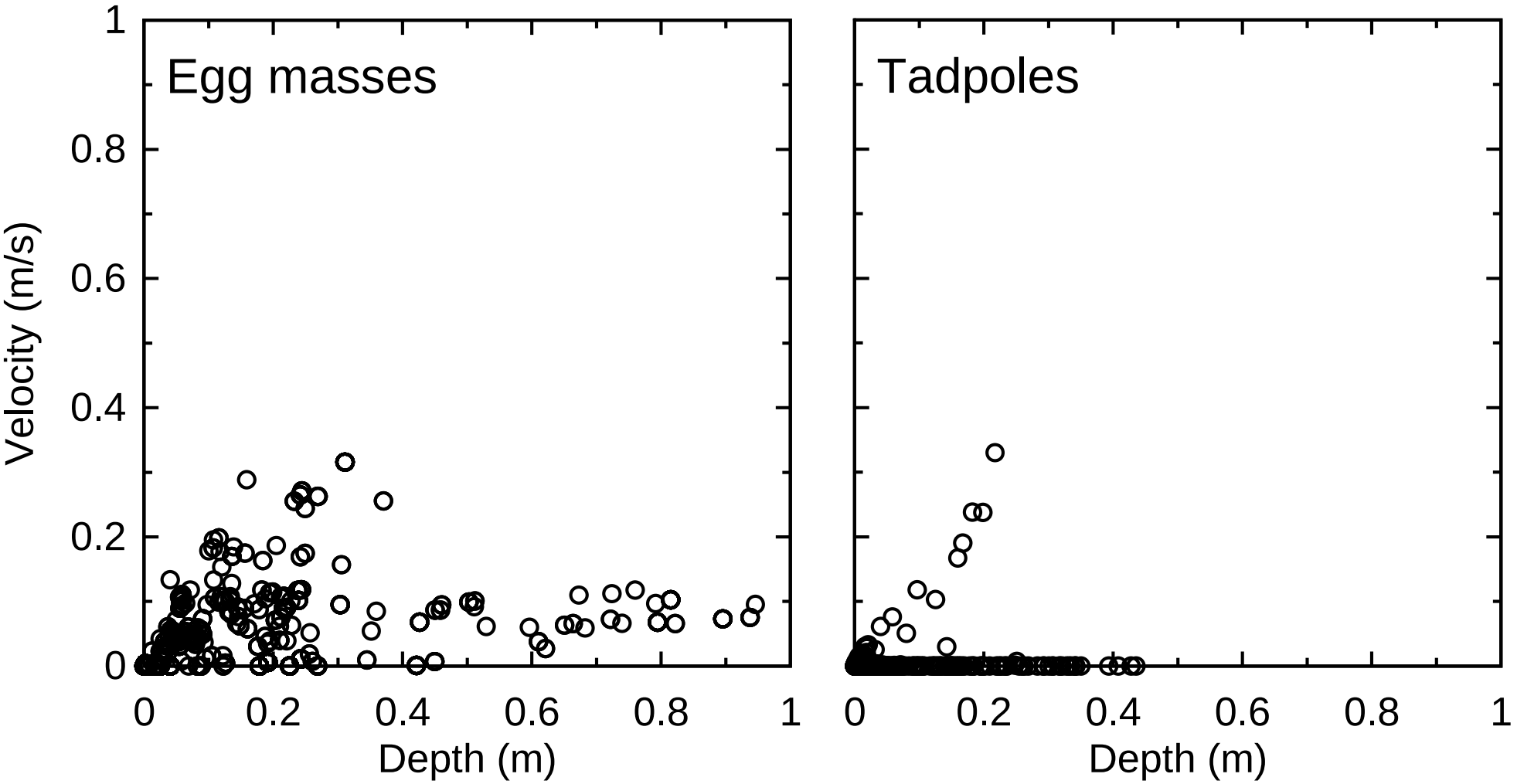

Mean depth
Mean velocity
Wetted area
Reach mean depth (m), velocity (m2/s)
Wetted area (m2)
Flow (m3/s)
0
0.5
1
1.5
2
10000
15000
20000
25000
30000
0
10
20
30
40
50
60
70
80
90
100

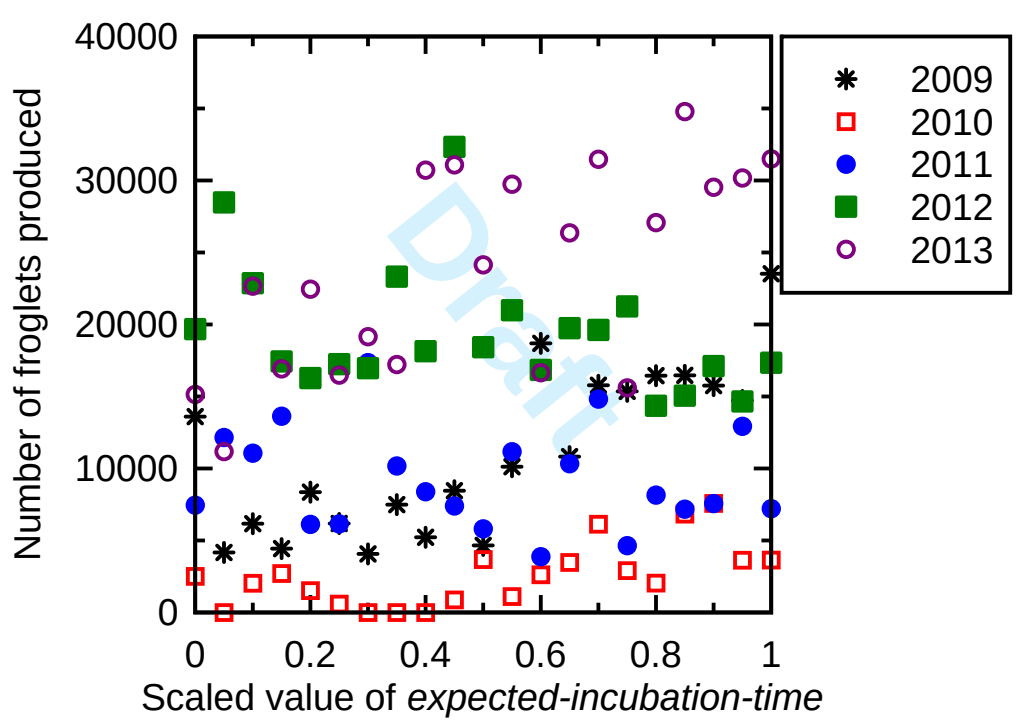

a
Temperature (°C)
30
25
20
15
10
5
0
2009
2010
2011
2012
2013
b
Flow (m³/s)
300
250
200
150
100
50
0
Apr-1
May-1
Jun-1
Jul-1
Aug-1
Sep-1

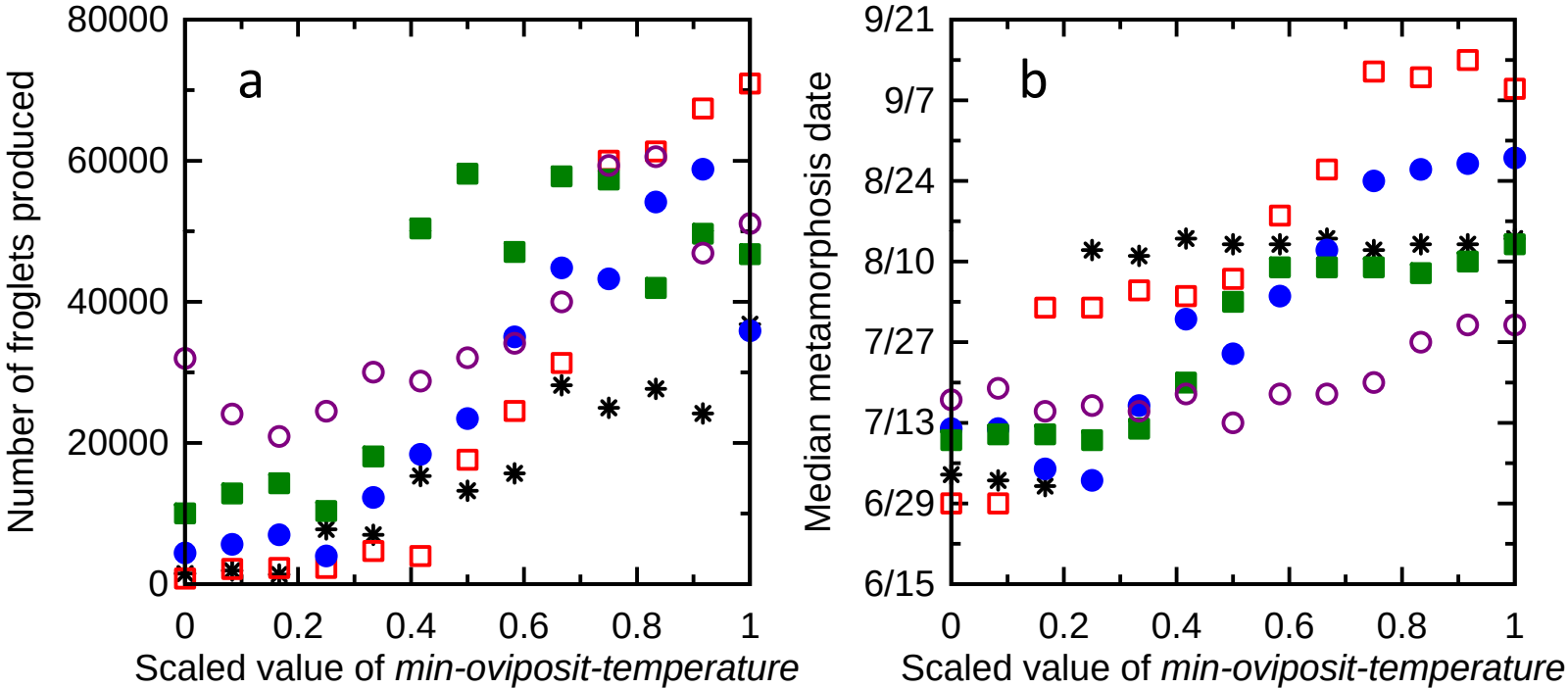

a
Number of frogs produced
40000
30000
20000
10000
0
2009
2010
2011
2012
2013

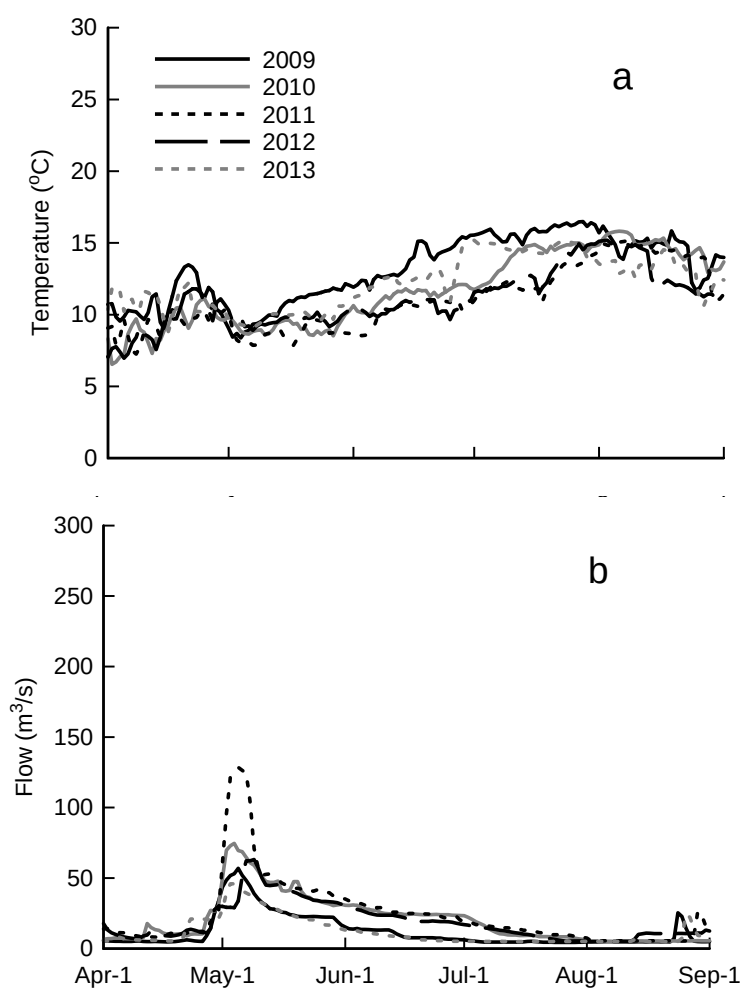

b
Median metamorphosis date
Aug-14
Aug-4
Jul-25
Jul-15
Jul-5
Jun-25
2009
2010
2011
2012
2013

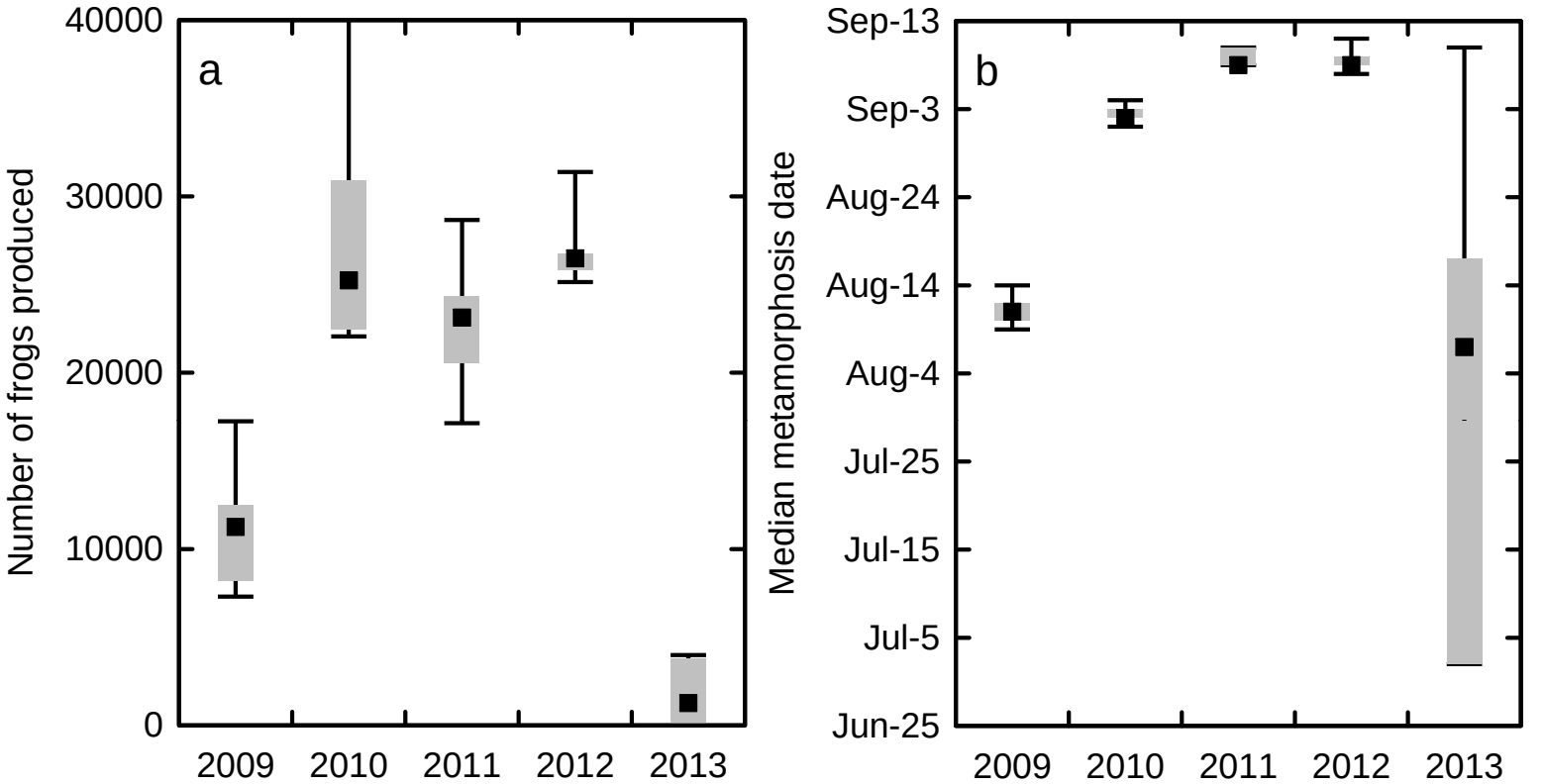

2009
created
died-desiccation
died-scour
hatched
Cumulative number of egg masses
Cumulative number of tadpoles
2010
2011
2012
2013
Apr-1
May-1
Jun-1
Jul-1
Aug-1
Sep-1

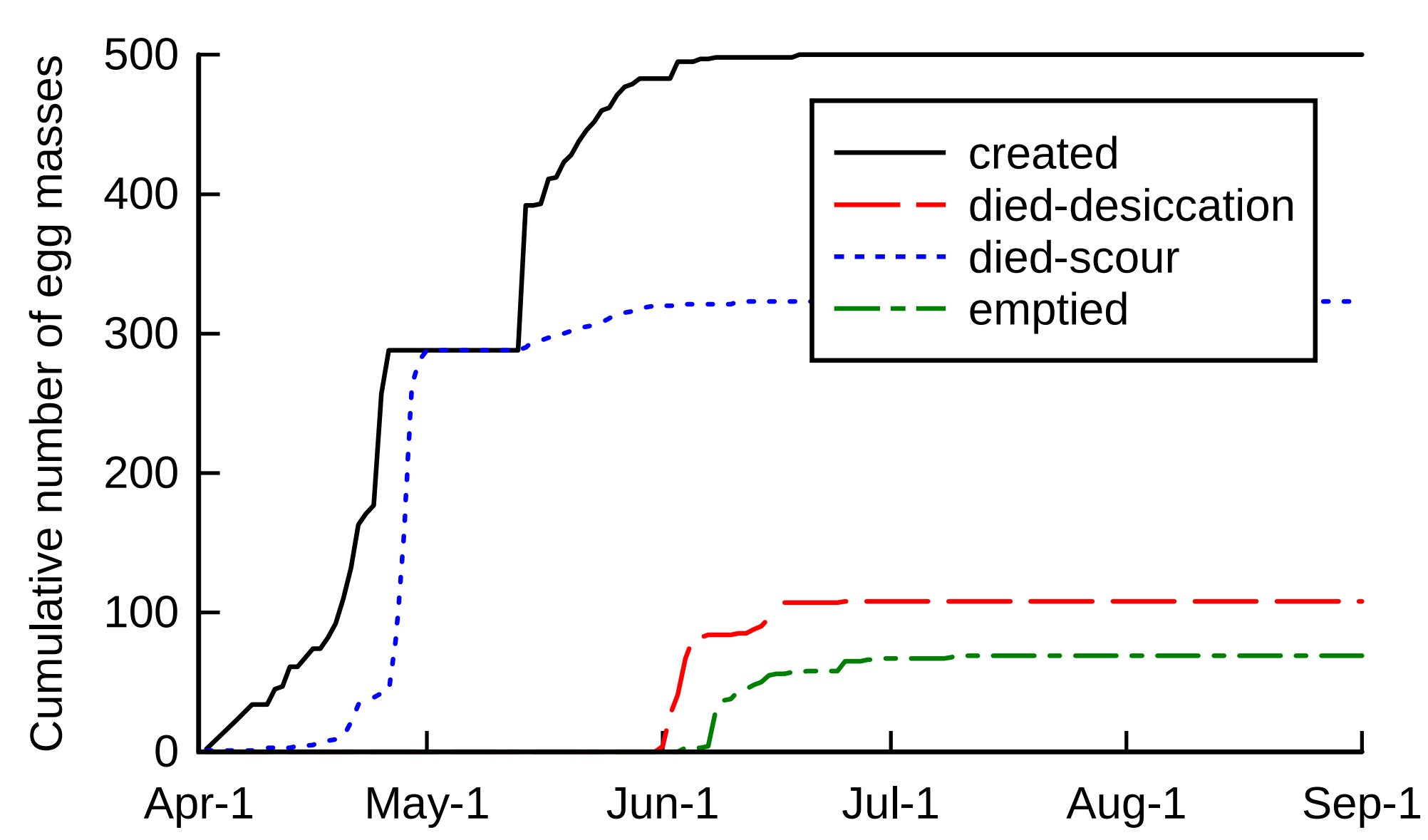

Egg masses
Tadpoles
Velocity (m/s)
Depth (m)
Depth (m)
0
0.2
0.4
0.6
0.8
1


Number of froglets produced
40000
30000
20000
10000
0
0
0.2
0.4
0.6
0.8
1
Scaled value of *expected-incubation-time*
2009
2010
2011
2012
2013
Draft


a
b
Number of froglets produced
Median metamorphosis date
80000
60000
40000
20000
0
9/21
9/7
8/24
8/10
7/27
7/13
6/29
6/15
0
0.2
0.4
0.6
0.8
1
Scaled value of *min-oviposit-temperature*
Scaled value of *min-oviposit-temperature*


a
2009
2010
2011
2012
2013
Temperature (°C)
30
25
20
15
10
5
0
b
Flow (m3/s)
300
250
200
150
100
50
0
Apr-1
May-1
Jun-1
Jul-1
Aug-1
Sep-1


a
b
Number of frogs produced
Median metamorphosis date
40000
30000
20000
10000
0
Sep-13
Sep-3
Aug-24
Aug-14
Aug-4
Jul-25
Jul-15
Jul-5
Jun-25
2009
2010
2011
2012
2013


Cumulative number of egg masses
500
400
300
200
100
0
Apr-1
May-1
Jun-1
Jul-1
Aug-1
Sep-1
created
died-desiccation
died-scour
emptied

Supplement A:

Foothill Yellow-legged Frog Assessment Model (FYFAM) Description

April 22, 2015

Steven F. Railsback

Bret C. Harvey

Contents

Figures

1 Report Objective

This report documents the foothill yellow-legged frog assessment model (FYFAM). It follows the ODD model description format of Grimm et al. (2010). In this document the word "frog" and any references to frogs (e.g., "egg mass", "tadpole") refer only to the foothill yellow-legged frog (FYF; *Rana boylii*).

2 Model Description

2.1 Purpose

FYFAM is intended for stream and river management support. 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. The model is intended, for example, to use results of flow and temperature models to predict the effects on frogs of alternative flow release policies at a dam. Such flow policies can control both base flows (e.g., mean daily or monthly flows) and high-flow releases for objectives such as recreation and sediment management.

"Reproductive success" here refers primarily to survival of eggs and tadpoles, from oviposition (creation of egg masses by breeding females) through the first summer of life. The endpoint of reproductive success is metamorphosis from tadpole to amphibious froglet life stages, which is assumed to occur 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 accumulate energy and select habitat for survival of their first winter.

The habitat variables considered by FYFAM are stream flow and temperature regimes, channel shape, and the distribution of substrate types important to FYF reproduction.

2.2 Entities, state variables, and scales

2.2.1 Habitat entities, 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 a few 10s of m to 100s of m in stream length. Reaches normally include the full channel width but do not necessarily have to; habitat clearly not usable by frogs can be excluded. A reach has a static variable *cell-size* for the width of each of its cells (all cells are assumed to have the same size) and dynamic (time-varying) state variables *step-length*—length of the current time step (in days), *flow*—stream flow (m^3/s), and *temperature*—water temperature (°C). The flow and temperature variables represent averages 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. (2014) found channel-edge temperatures to be very close to mid-channel temperatures.

Cells represent habitat variation within the reach. Cells are square but can provide a fully two-dimensional representation of habitat via techniques such as "warped grids" or simply representing a grid of points on a two-dimensional space. Each cell has static boolean (TRUE-FALSE) variables *breeder-suitable?* for whether it is suitable habitat for breeders and *has-*

shelter? for whether it has velocity shelter for egg masses. Cells also have dynamic variables *depth* and *velocity* for their depth (m) and velocity (m/s), and the boolean *ovi-suitable?* for whether it has hydraulic conditions suitable for oviposition. Cell depth and velocity are functions of the reach's flow, typically obtained via hydrodynamic modeling.

Cell size (width) is FYFAM's spatial resolution. Cell size is not fixed, but must be selected in preparing input for each site. Cell size should ideally be just small enough to capture important gradients in hydraulic conditions in the shoreline habitat used by frogs.

2.2.2 Frog entities and variables

The model represents three life stages of FYF as three kinds of entity.

"Breeders" represent the pairs of adults that create egg masses (oviposit). Breeders are included only as a way to model when and where oviposition occurs; they execute behaviors that in reality are attributed to either male or female frogs. Breeders know their location (the cell they currently occupy), and have a boolean variable *ready?* for whether they are ready to breed and oviposit.

"Egg masses" represent the mass of eggs 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 they contain (*eggs-in-mass*) and for the development state of the eggs: *egg-development* is set to zero when an egg mass is created, and eggs are ready to hatch into tadpoles when *egg-development* reaches 1.0.

When eggs hatch, each egg 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) between hatching and metamorphosis into froglets.

2.2.3 Time scales

The temporal extent of a FYFAM simulation is from mid-spring through late summer of one 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 is normal run until a date after all simulated tadpoles have metamorphosed near the end of the summer dry season.

(The exact start and end of a simulation is set by the user, via the parameters `start-time` and `end-time`. The model starts at the first time in the time-series input file that is at or after `start-time`, and stops at the last time in the file that is before or at `end-time`.)

The temporal resolution (time step length, reach variable *step-length*) is variable and determined by the flow and temperature input. The model simply executes one time step for each time in the flow and temperature input file (Sect. 3.3.4), and each such time step represents the time until the next time in the file. Flow and temperature values in the file represent conditions from the time associated with them in the input file until the next time step starts. For this example input file, if simulations start on April 1:

```
Time,flow,temperature
4/1/2000 00:00,0.38,5.5
4/2/2000 00:00,0.5,5.8
4/2/2000 07:00,10.0,5.8
4/2/2000 17:00,0.5,5.8
4/3/2000 00:00,0.46,6.4
4/4/2000 00:00,0.83,7
4/5/2000 00:00,0.78,6.2
```

the model's first time step will represent April 1, from midnight to midnight, with a flow of 0.38 m^3/s. On April 2, a mid-day flow pulse is represented; the model's second time step represents midnight to 7:00 a.m. at a flow of 0.5, the third step represents 7:00 to 17:00 at a flow of 10.0, and the fourth represents the rest of the day at 0.5 m^3/s. The remaining time steps are each one full day.

FYFAM time steps are typically one day, using daily mean flow and temperature as input. Daily values capture natural flow and temperature changes with sufficient resolution to model their effects on frog reproduction. However, one purpose of FYFAM is to assess effects of sub-daily flow pulses (or reductions), so such pulses can simply be inserted into the input file. The model can also use input at time steps longer than one day, e.g. weekly mean flows; however, some frog processes (e.g., development of eggs, especially at high temperature) occur relatively quickly compared to a week, so using time steps greater than a day could create uncertainty or error in results.

Time variables in FYFAM use units of days, unless otherwise noted.

2.3 Process overview and scheduling

FYFAM executes the following actions once per time step. Because the model assumes no hierarchies among frogs, the order in which individuals execute these actions is randomized each time step.

1. Habitat is updated. The time step's length is determined from input, and reach flow and temperature are updated. The depth and velocity of each cell is calculated from flow, using methods described in Sect. 2.7.1.
2. Breeders ready for oviposition select habitat, using methods in Sect. 2.7.3.
3. Breeders oviposit. The breeders that are ready for oviposition but have not previously oviposited determine whether to do so in the current time step, considering whether temperature is suitable and whether changes in water depth are suitably small (Sect. 2.7.4). If so, they select a cell for their egg mass (Sect. 2.7.5) and create it (Sect. 2.7.6).
4. Breeders not yet ready for oviposition decide whether they become ready (Sect. 2.7.2). This action is after oviposition because oviposition requires breeders to sense changes in water surface elevation since the previous time step; breeders are assumed unable to sense water elevation until they decide to become ready for oviposition.
5. Egg masses survival is determined. Egg masses are vulnerable to loss via scouring (being washed downstream and broken up during higher flows) and desiccation (mortality due to drying when dewatered by decreased flow). Frog egg masses are also subject to predation, which is not represented in FYFAM because predation is assumed (a) unaffected by the flow and temperature management issues the model is designed for and

(b) not interactive with other mortality sources. Survival of egg masses is described in detail in Sect. 2.7.7.

6. Egg masses develop at a temperature-dependent rate (Sect. 2.7.8), and hatch into tadpoles when development is complete (Sect. 2.7.9).
7. Tadpoles select habitat (Sect. 2.7.10).
8. Tadpoles survive (Sect. 2.7.11).
9. Tadpoles develop and metamorphose (Sect. 2.7.12).

2.4 Design concepts

This section describes the model using a set of standard concepts that capture essential characteristics of individual-based models (Grimm et al. 2010).

2.4.1 Basic principles

The adaptive behaviors of this model are based primarily on empirical rules and data, plus simple assumptions, about how habitat affects FYF reproductive success.

2.4.2 Emergence

Key results of this model are: the timing and location of oviposition, survival of egg masses, survival of tadpoles, and the timing of tadpole metamorphosis. These results emerge from channel shape and substrate distributions, flow and temperature regime, and physiological characteristics and behaviors of frogs.

2.4.3 Adaptation

The model includes several adaptive behaviors at different frog life stages. Breeders decide when to become ready to breed, using simple empirical rules that impose the observed dependence of the behavior on temperature and variability among individuals (Sect. 2.7.2). Breeders then select habitat in a way that imposes observed proximity to oviposition habitat (Sect. 2.7.3). Breeders then decide when and where to oviposit via rules that indirectly represent an important element of reproductive success: egg mass survival of both scouring and desiccation (Sects. 2.7.4 and 2.7.5). Tadpoles select habitat using rules that minimize velocity while avoiding dry cells, an indirect way of maximizing expected survival of scouring and desiccation (Sect. 2.7.10). Other events in the model (life history transformations including egg hatching and tadpole metamorphosis) are imposed to reproduce observed life-stage timing, not modeled as adaptive decisions.

2.4.4 Objectives

None of the adaptive behaviors include optimization of an explicit objective function.

2.4.5 Learning

No learning is represented.

2.4.6 Prediction

Breeders make one prediction in deciding where to oviposit: they predict whether the depth in a cell will fall below a minimum during the egg incubation period (Sect. 2.7.5).

2.4.7 Sensing

Breeders are assumed able to sense water temperature in their readiness decision. Breeders are also assumed to sense whether cells within a habitat selection radius have (a) suitable habitat for breeders, (b) non-zero depth, and (c) an adjacent non-dry cell. Breeders also sense depth changes in nearby oviposition habitat using an explicit process of identifying and sensing a particular cell's depth (Sect. 2.7.2). During oviposition, breeders are assumed able to sense habitat conditions in cells within a limited radius. During habitat selection, tadpoles are assumed able to sense velocities in their current cell and the cells within a limited radius (Sect. 2.7.10).

2.4.8 Interaction

There is little interaction among frogs in FYFAM. Interaction only occurs in breeder habitat selection, which includes an upper limit on the density of breeders at the cell level. No hierarchy is represented so the density limit acts merely to spread breeders out. For subsequent habitat selection behaviors (for egg masses and tadpoles) there are no such density limits or competition for resources.

2.4.9 Stochasticity

Key uses of stochastic rules are: (a) breeder readiness is a stochastic function of temperature, to impose a realistic level of variability in oviposition timing; (b) in habitat selection behaviors, if multiple cells offer equally good habitat then one is chosen randomly; (c) the number of eggs in each egg mass is randomly drawn from a normal distribution; and (d) survival of eggs and tadpoles is simulated as stochastic events with probabilities that are deterministic functions of habitat.

2.4.10 Collectives

Collectives are not represented. (Egg masses are represented as individual entities each containing multiple eggs, but the eggs are not treated as individuals.)

2.4.11 Observation

Model results important for testing and understanding the model include the timing of major life history events, and the number of tadpoles surviving until metamorphosis into frogs. Life history events including oviposition, egg hatching, mortality of egg masses and tadpoles, and metamorphosis can be observed via an output file that records the time and location of each such event for each individual. A summary output file reports population status over time. Spatial information is also provided by the model's animation display, which shows depth or velocity of each cell and the location of breeders, egg masses, and tadpoles.

2.5 Initialization

2.5.1 Habitat

Habitat initialization data are provided via input files and include, for each square cell: coordinates of the cell center (in any Euclidian coordinate system), elevation, the values of *breeder-suitable?* and *has-shelter?*, and lookup tables of depth and velocity as a function of flow (described in Sect. 2.7.1). These data must all be prepared by the user, typically using hydrodynamic models and geographic information systems.

2.5.2 Frogs

Breeders (adult frogs) are created when FYFAM is initialized; the number of breeders is specified by the user via the parameter `num-breeders`. Because breeders actually represent a mating pair that produces one egg mass (Sect. 2.2.2), the value of `num-breeders` should represent the number of females, not the total number of adults.

Breeders are not initially ready to breed and produce egg masses. Field observations of egg mass production over time (Kupferberg 1996, Welsh and Wheeler 2014) indicate that breeding adults do not arrive at breeding sites all at once. Therefore, at initialization each breeder is placed at an arbitrary location away from the water's edge, with its value of *ready?* set to FALSE. This arbitrary location is chosen by drawing a random X coordinate, and then randomly choosing either the minimum or maximum Y coordinate of all the cells. For irregularly shaped spaces, this initial location often will not be in one of the model's habitat cells. If a breeder's initial location is not in a cell, the breeder moves to a cell randomly chosen from among those on the edge of the simulated space (having at least one adjacent location that is not a cell) that also have the same X coordinate as the breeder's initial location; if there are no such cells the breeder stays in its initial location.

2.6 Input data

FYFAM is driven by two time-series inputs: stream flow and water temperature. The input file provides a mean flow and temperature for each time step.

2.7 Submodels

2.7.1 Interpolation of cell depth and velocity

The depth (m) and velocity (m/s) of each cell is updated daily as a function of the reach's flow. This update is conducted via interpolation from lookup tables provided by the user to FYFAM. These tables include a series of flows, spanning the range of simulated flows from low to high, and the depth and velocity of each cell for each flow. The lookup tables are typically generated by hydraulic modeling, though they could be produced directly from extensive field data.

On each simulated day, cell depths and velocities are calculated by interpolating linearly between values in the lookup tables. This interpolation is limited in several ways to deal with lookup table limitations.

First, each cell has a variable *flow-at-wetting* for the lowest flow at which its depth exceeds zero. This flow is identified by extrapolating downwards from the two lowest flows with non-zero depths in the lookup table. This extrapolation is subject to several conditions:

- If depth is non-zero at the lowest flow in the lookup table, *flow-at-wetting* is set to zero.
- If depth is zero at the highest lookup-table flow, *flow-at-wetting* is set to an arbitrary large number.
- If depth is non-zero only at the highest lookup-table flow, *flow-at-wetting* is arbitrarily set to halfway between the two highest flows in the depth lookup table. (In this case it is impossible to interpolate a value of *flow-at-wetting*. Setting *flow-at-wetting* to the highest lookup-table flow causes division by zero during interpolation.)

- If depth decreases instead of increases between the first and second flows with non-zero depths, then *flow-at-wetting* is set to zero but also subject to the next condition.
- If the extrapolated value of *flow-at-wetting* is lower than a lookup-table flow at which depth is zero, *flow-at-wetting* is set to the highest lookup-table flow with zero depth.

At a flow equal to or below *flow-at-wetting*, depth and velocity are set to zero. At a flow between *flow-at-wetting* and the lowest lookup-table flow with non-zero depth, depth and velocity are interpolated between *flow-at-wetting* and the lowest flow in the tables with non-zero values.For a flow above the lowest with non-zero depth in the lookup table, depth and velocity are interpolated linearly from values in the lookup table for the two flows just lower and higher than the flow.

The second limitation is made if the flow is less than the lowest flow in the lookup table (which should be avoided by including very low flows in the table). In this case, depth is extrapolated downwards from the depths at the two lowest flows in the table and set to zero if a negative value is produced; and velocity is interpolated from the velocity at the lowest table flow and zero velocity at zero flow, but set to zero if depth is zero. (In these cases, depth and velocity are still set to zero if flow is at or below the cell's flow at which depth reaches zero.)

Third, if the flow is higher than the highest flow in the lookup tables (also to be avoided by including higher flows in the lookup table) then both depth and velocity are extrapolated upward from their values at the two highest flows in the table. This extrapolation for higher flows does not allow cells dry at the highest flow in the lookup table to become wet at higher flows. It is possible for this extrapolation to produce negative depths or velocities, when a cell has a lower depth or velocity at the highest flow in the table than at the penultimate flow. In this case, negative depths are set to zero but negative velocities cause execution to stop; the problem must be solved by revising the lookup table.

To prevent the above interpolation methods from having strong and unrealistic effects, it is very important for the depth and velocity lookup tables to include many flows within the range in which egg masses and tadpoles are present. These flows should be concentrated in the range where oviposition through tadpole development typically occur. For example, the initial application of FYFAM uses 30 flows over a range of 0.5 to 300 m^3/s, with half of these flows less than 20 m^3/s.

2.7.2 Breeder readiness

The breeder readiness submodel simulates when individual breeders move to the stream edge and become ready to oviposit. Its assumptions are based on field observations of male breeders, which appear to select stream-edge habitat and attempt to attract females (via vocalizations) when conditions seem favorable for oviposition. These observations indicate that (a) FYF oviposition tends to start when mean daily water temperatures rise above 10° C (Kupferberg 1996, Wheeler et al. 2014), and (b) when conditions (temperature, flow; Sect. 2.7.4) for oviposition appear good, the distribution of new egg masses over time appears peaked over several weeks (Wheeler et al. 2014). Temperature is used to limit oviposition readiness (instead of, for example, day length or water levels) because temperature is physiologically important for breeding energetics and would not always be closely related to date because of factors such as elevation, shading, and weather (Sect. 2.7.4).

The submodel assumes that readiness of each breeder is a stochastic event, the probability of which increases linearly with the number of simulated days with mean water temperature above the threshold specified by the parameter `min-oviposit-temperature`, which has a value of 10° C. The slope of this linear relation is determined by the parameter `readiness-t-days`, the number of days with temperature above `min-oviposit-temperature` at which the probability of readiness reaches 100%.

The probability of a breeder becoming ready for oviposition on a time step is therefore simply equal to (*D* / `readiness-t-days`) × *step-length*, where *D* is the length of time (days) immediately preceding the current time step that had temperature equal to or above `min-oviposit-temperature`. However, breeders cannot become ready on any time step with temperature less than `min-oviposit-temperature`.

Because time steps are not necessarily one day in length, the value of *D* is updated in the following way. It is initially zero. At the start of each subsequent time step, the length of the previous time step is added to *D* if the temperature for the previous time step was above `min-oviposit-temperature`. If the temperature for the previous time step was below `min-oviposit-temperature` then *D* is reset to zero.

This submodel produces a distribution of breeder readiness over time that is peaked when temperature remains above `min-oviposit-temperature`. (The peak in the number of breeders becoming ready per day occurs because the probability of readiness increases as *D* increases, but the number of breeders still unready decreases.) With a value of 60 d for `readiness-t-days`, readiness peaks at the eighth day of suitable temperatures and 90% of breeders (on average) become ready within 21 days of suitable temperatures (Figure SA-1).

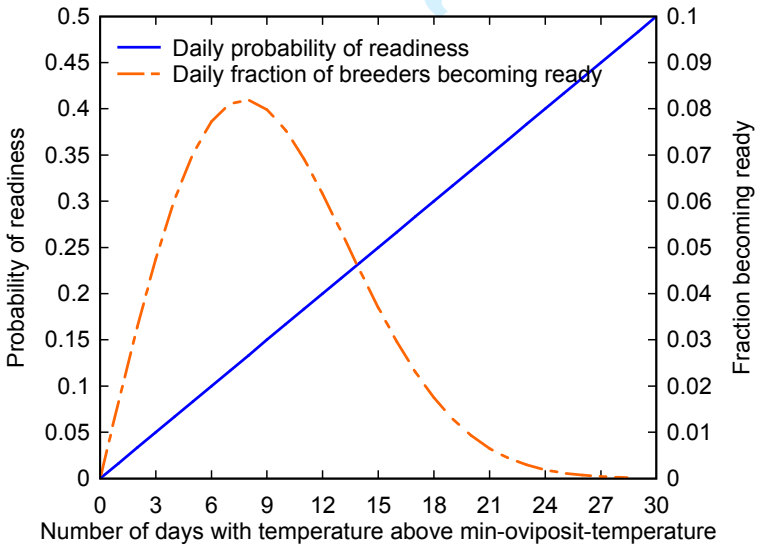


Figure SA-1. Distribution of readiness over time with `readiness-t-days` equal to 60 days.

When they become ready for oviposition, breeders move to the streamside. The initial locations of breeders can be important because these locations affect where the breeders place their egg

masses and, therefore, egg mass and tadpole survival. However, the breeder habitat selection action (Sect. 2.7.3) lets breeders adapt their location to changes in flow, proximity to oviposition habitat, and local breeder density. Upon reaching readiness, a breeder is simply placed in a cell that is usable breeder habitat at the water's edge. The initial cell of each breeder is chosen randomly from all cells meeting three criteria: (1) the cell variable *breeder-suitable?* (Sect. 2.7.3) is TRUE, (2) depth is greater than zero, and (3) at least one adjacent cell has zero depth. (If there are no such cells, the breeder instead remains unready for oviposition.)

To allow breeders to monitor water elevation, once they have moved to the water's edge they select a nearby cell, the depth of which they subsequently use to represent water level changes (Sect. 2.7.4). This "depth-cell" is simply the nearest cell with depth >= 0.2 m.

2.7.3 Breeder habitat selection

Habitat selection by breeders is important not because breeder locations are important model results but because those locations affect where egg masses are placed. Male FYF breeders appear to aggregate at the water's edge near good oviposition habitat, and call underwater to attract female breeders.

FYF breeders appear to select mating habitat over larger scales than they select oviposition sites (Kupferberg 1996); breeders can move long distances to aggregate in streamside areas of 10s to 100s of square meters. Factors that appear to affect FYF breeder habitat selection include availability of suitable oviposition habitat, exposure to the sun (presumably to provide warmth), presence of other breeders, presence of sparse vegetation, proximity to tributaries that provide adult habitat but not breeding habitat (Kupferberg 1996), and possibly "site fidelity": preference for sites used in previous years.

Many of these factors potentially affecting breeder habitat would be difficult to predict in a model but are relatively static and easy to observe in the field. Hence we combine factors such as exposure, vegetation, proximity to tributaries, and site fidelity into one habitat-cell variable, *breeder-suitable?*, that has a value of either TRUE or FALSE. Factors that are readily modeled—area of nearby oviposition habitat and density of other breeders—are treated explicitly.

One assumption about breeder interactions is a basis of this submodel. The male breeders that select habitat are assumed territorial, so FYFAM assumes a maximum local density of breeders. This maximum density is set by a breeder parameter `max-breeder-density` (number per m^2), with a value of $1.0/m^2$ estimated from the modelers' field observations. (A second kind of interaction, attraction of breeders to aggregations of other breeders, does not appear necessary for the model to reproduce such aggregations; aggregations result also from attraction to large areas of oviposition habitat.)

We assume a limited habitat selection radius, so breeders can move only relatively short distances (e.g., in response to flow changes) before they breed. Breeders are assumed able to evaluate and select cells within a distance between cell midpoints less than or equal to the parameter `breeder-selection-radius` (m). This parameter has a standard value of 10 m.

The breeder habitat selection submodel implements the above assumptions via two steps that each breeder executes. Because we assume no hierarchy among breeders, the order in which breeders execute the submodel is randomized each time step.

First, the breeder identifies potential destination cells, the cells that (a) are within the radius defined by `breeder-selection-radius`, (b) have a depth greater than zero but adjacent to at least one cell with zero depth (meaning the cell is submerged but at the stream margin), (c) have a density of breeders (including those that have and have not already selected habitat on the current time step) less than the value of `max-breeder-density`, and (d) a value of *breeder-suitable?* of TRUE. If there are no such cells, the second step is skipped and the breeder instead moves to the nearest cell (beyond the breeder selection radius) meeting these four criteria. In the (very unlikely) event that no cells at all meet the four criteria then the breeder does not move.

Next, the breeder identifies the potential destination cell with the most oviposition habitat nearby: the cell with the highest number of cells that are suitable for oviposition (using the methods in Sect. 2.7.5) within the distance `oviposition-radius` (Sect. 2.7.5). If multiple potential destination cells have the same highest number of suitable oviposition cells nearby (including zero), then one such cell is chosen randomly. The breeder then moves to that cell immediately (before any subsequent breeders execute their habitat selection).

2.7.4 Oviposition timing

This submodel represents the breeder decision of whether or not to oviposit in the current time step, once the breeder is ready and next to the stream. The decision is assumed driven by water levels and temperature. The submodel is based largely on analysis of field observations of water elevation, temperature, and egg masses in a range of streams and rivers of California's north coast (Kupferberg 1996, Welsh and Wheeler 2014, Wheeler et al. 2014). The data recorded by Welsh and Wheeler (2014) indicate that small increases in water elevation (<3 cm over 1-2 days) seem not to delay oviposition, while breeders appear not to oviposit during larger fluctuations. While not clear from the data, it is reasonable to assume breeders also avoid oviposition during rapidly decreasing flows, which would put egg masses at risk of stranding. The data also indicate that oviposition is rare at water temperatures below 10° C.

Considering these observations and mechanisms, FYFAM assumes breeders oviposit on time steps where the following criteria are met. (1) The water temperature is equal to or above the parameter `min-oviposit-temperature`, which is 10°. (2) The current rate of depth change is less than or equal to the parameter `max-oviposit-depth-rate`, which has a value of 0.03 m/d. This rate is calculated by subtracting the water depth at the previous time step from the current water depth, dividing that difference by the length of the previous time step, and taking the absolute value of the result. "Depth" here refers to depth of the cell chosen by the breeder to represent water elevations when it became ready for oviposition (Sect. 2.7.2). (If this depth evaluation cell has become dry so depth is zero, it is still used in this rate of depth change. However, in this case a new depth cell is chosen for use in the next time step, using the same methods used to select a cell described in Sect. 2.7.2.)

2.7.5 Oviposition habitat selection

This submodel describes where breeders place egg masses. The submodel is based on a few simple assumptions. First, we assume breeders select oviposition locations over a limited but

relatively large area. They appear to oviposit within a day or two of breeding and hence have limited time for exploring for oviposition sites, but egg masses have been observed up to 5 m from the water's edge where breeding is assumed to occur (Lind et al., In press).

The second assumption is that oviposition site selection has evolved in response to the typical decrease in flow during egg incubation. Hence, habitat selection considers that the depths and velocities experienced by the egg mass are likely highest at the time of oviposition and decrease during incubation.

Third, we assume that velocity within a few cm of the egg mass is a primary factor in oviposition habitat quality. The frogs are believed to select habitat with non-zero velocity (perhaps to avoid excessive temperatures, provide dissolved oxygen, and carry away waste), but exposure to even moderate velocities can scour egg masses (Sect. 2.7.7). For egg masses attached to cobbles and boulders that provide velocity shelter, the velocity to which an egg mass is exposed can be roughly half of the unobstructed velocity (Figure 4 of Kupferberg 1996).

Our fourth assumption is that while depth may be less important than velocity, breeders select oviposition habitat to at least avoid egg mass stranding. Because flows typically decrease during egg incubation, this assumption means that breeders must consider depth near the end of incubation, not just depth at the time of oviposition.

Fifth, we assume that the effect of substrate type on oviposition habitat selection—except for providing velocity shelter—is negligible. This assumption is based on the observations of Lind et al. (In press) that egg masses were found on pebble, cobble, boulder, and even vegetation substrates; and on the assumption that substrate stability is unlikely a problem during declining flows.

Finally, egg masses are commonly observed at high density (several per m^2), so no territoriality or limitation on distance among egg masses is assumed.

Implementing all these assumptions, we use the following rules for how breeders select a cell for their egg masses. (Note that it is possible for oviposition to occur when flows are increasing slightly, and that these rules do not consider the potential for future scour in this situation.)

- Cells are excluded if their distance from the breeder's cell (center to center) is more than a distance set by the parameter `oviposition-radius` (m). This parameter has a standard value of 5 m. (This parameter is separate from `breeder-selection-radius` because it represents how far a female breeder searches underwater for oviposition sites, whereas `breeder-selection-radius` represents movement above water to select mating sites.)
- Cells are excluded if their depth is expected to be less than the parameter `min-expected-ovi-depth` (m) by the end of egg incubation. Expected depth is calculated as the minimum of current depth and (current depth – (depth change rate × `expected-incubation-time`)), where depth change rate is the difference between the cell's previous depth and current depth, divided by the length of the previous time step. (Hence, a breeder's expected depth in a cell is based on the cell's rate of depth change, not on the rate of depth change at the breeder's depth cell used in oviposition timing; Sect. 2.7.4. This difference is used for computational reasons.) The parameter `expected-`

`incubation-time` represents a typical incubation time (d); a value of 20 d is reasonable. The parameter `min-expected-ovi-depth` should have a value just high enough to exclude stranding, e.g., 0.05 m.

- Cells are excluded if the velocity an egg mass would be exposed to is high enough to cause a daily probability of surviving scouring of less than 95%, using the scour probability method of Sect. 2.7.7. Scouring survival probability depends on cell velocity and presence of velocity shelter in the cell: if the cell has no velocity shelter, egg masses are exposed to the cell's mean velocity. If the cell has velocity shelter, the egg mass is exposed to a velocity of cell mean velocity × `velocity-shelter-factor`. The parameter `velocity-shelter-factor` is the fraction by which velocity at an egg mass is reduced by velocity shelter; its standard value is 0.5.
- If there are no unexcluded cells, the breeder does not oviposit on the current time step.
- If there are unexcluded cells, the breeder selects the one with an egg mass exposure velocity (considering velocity shelter) closest to an "optimal" value set by the parameter `oviposition-optimal-velocity`, set to 0.1 m/s. (This parameter value is higher than the mean velocity at egg masses observed by Lind et al. (In press), about 0.04 m/s, because velocity normally will decrease as incubation proceeds.)

2.7.6 Oviposition

Oviposition is the process of actually creating an egg mass. When a breeder oviposits, a new egg mass object is created in the cell selected in the oviposition habitat selection submodel. The egg mass's variable *egg-development* is set to zero.

The number of eggs in the egg mass (variable *eggs-in-mass*) is also set at oviposition. This number is randomly drawn from a normal distribution defined by the parameters `fecundity-mean` and `fecundity-SD`, defined as the mean and standard deviation in the number of viable eggs that would survive to hatching in the absence of mortality. However, to bound the number of eggs to realistic numbers (e.g., non-negative ones), if the random draw is below or above the range defined by parameters `fecundity-min` and `fecundity-max` then the fecundity is set to `fecundity-min` or `fecundity-max`, respectively.

The fecundity parameters were given values based on observations of Kupferberg et al. (2009; their Sect. 2.3.2), who estimated fecundity of *R. boylii* at sites on the South Fork Eel River, Alameda Creek, and North Fork Feather River. Kupferberg et al. (2009) estimated egg mass volume and counted the live tadpoles that emerged and the dead embryos. They found fecundity significantly higher at Alameda Creek than at the other two sites. Kupferberg et al. (2009; their Table 2.4) developed parameters for the number of female tadpoles per egg mass, assuming half the eggs are female. Doubling their values produces a mean (across 56 egg masses at three sites) of 1740 eggs and a standard deviation of 444. They also observed that 83% of eggs survived to hatching. From these values we set `fecundity-mean` to 1500 eggs/female and `fecundity-SD` to 440. We set the parameters limiting fecundity (`fecundity-min` and `fecundity-max`) to about two standard deviations below and above the mean: 500 and 2500.

The final step in the oviposition submodel is to remove the breeder executing it from the model. In reality frogs do not typically die when they breed, but the simulated breeders no longer have any effect on the model.

2.7.7 Egg mass survival

Egg masses are vulnerable to mortality due to predators such as fish and snakes, dislocation and crushing by people or animals, desiccation if exposed to air, and scouring by high velocities. Because FYFAM is focused on effects of flow management, it represents only the two mortality sources that are common and directly linked to flow (Kupferberg et al. 2009, their Sect. 2.2.1): desiccation and scouring.

Because egg masses dry out rapidly when exposed to air and direct sunlight, FYFAM assumes low survival when the cell containing an egg mass has a depth of zero. (Desiccation could begin when depths are slightly above zero, if the egg mass is above the mean bottom elevation of a cell, but we neglect that possibility.) Survival of desiccation is represented by assuming all eggs survive if depth is above zero; and when depth is zero, the number of eggs surviving (variable *eggs-in-mass*) is updated by multiplying it by the parameter `eggs-desiccation-survival` (daily survival rate when depth is zero) raised to the power *step-length*, and truncating the result to an integer. (A more stochastic approach such as drawing the number of surviving eggs from a Poisson distribution is not justified because desiccation mortality is rapid and consistent.) The value of `eggs-desiccation-survival` is estimated as 0.1 to reflect rapid mortality; this value causes 9% of eggs to die each hour out of the water.

Survival of scouring is modeled as a Bernoulli trial (stochastic true-or-false event) using the daily probability of an entire egg mass being lost by being dislodged from the substrate and washed downstream. This probability is assumed a logistic function of the velocity eggs are exposed to, considering velocity shelter provided by large substrate or being embedded among cobbles (Sect. 2.7.5). An egg mass is assumed entirely destroyed (*eggs-in-mass* set to zero) if a random number between zero and one is greater than the logistic function's value raised to the power *step-length*.

The logistic function for scouring survival represents the probability of an egg mass surviving for one day at a particular velocity. The function is defined by parameters `eggs-scouring-v01` and `eggs-scouring-v09`, the velocities at which the survival logistic has values of 0.1 and 0.9. To estimate values for these parameters we considered data on FYF egg masses reported by Bondi et al. (2013), which indicated no egg masses at mid-column velocities above 0.13 m/s. Our own observations indicated rapid scouring of egg masses on boulders at velocities approaching 0.5 m/s, but apparently stable egg masses embedded in cobble where the mid-column velocity was well above 0.5 m/s. Parameter values of 0.4 m/s for `eggs-scouring-v01` and 0.2 m/s for `eggs-scouring-v09` result in a high probability of egg mass survival at velocities less than about 0.15 m/s and low probability of survival for more than a day at velocities above 0.3 m/s (Figure SA-2).

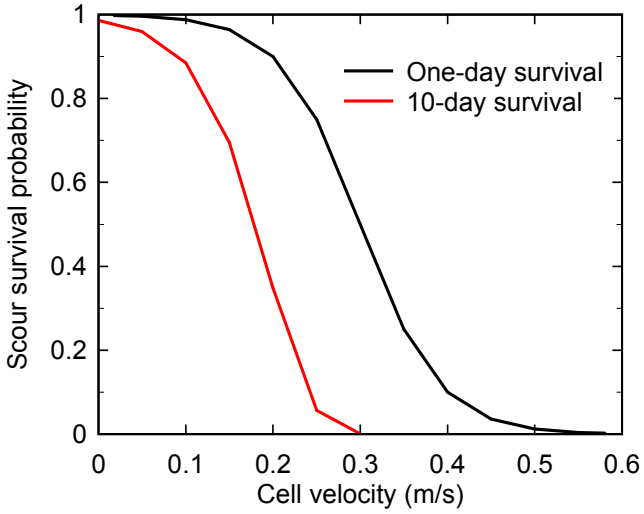


Figure SA-2. Egg mass scour survival function. The graph depicts both the probability of egg mass survival for one day and for 10 days at the same velocity.

2.7.8 Egg mass development

This submodel represents how development of eggs toward hatching depends on temperature. The submodel is based on data in McBain and Kupferberg (2012) cited as Kupferberg and Catenazzi (*unpublished data*). These data show the mean number of days for egg hatching declining relatively linearly with increasing temperature, from a maximum of about 21 days at temperatures around 11-12° C to a minimum of about 7 days at temperatures of 19° and higher. (The exact measure of temperature reported in these data is not clear; it appears to be daily mean temperature over the incubation period.)

The submodel calculates the amount by which the egg mass variable egg-development is incremented each time step. The value of this variable is increased by the amount step-length / days-for-hatching. Days-for-hatching is the number of days it would take an egg mass to hatch at the current temperature, calculated as: max[`eggs-min-devel-days`, (temperature × `eggs-devel-slope` + `eggs-devel-const`). The parameters are evaluated from the data presented by McBain and Kupferberg (2012): `eggs-min-devel-days` is 7 days, `eggs-devel-slope` is -1.66, and `eggs-devel-const` (the number of days to hatching at 0°) is 40. If the temperature is at or below 0° then days-for-hatching is set to `eggs-devel-const`.

2.7.9 Hatching

When an egg mass is fully developed, it creates new tadpoles. The tadpoles are not created all at once but over several days, to reproduce the variability in hatching observed in real tadpoles. The number of tadpoles created by an egg mass on a day that its value of egg-development equals or exceeds 1.0 is equal to the parameter `eggs-hatching-rate` times the time step length times eggs-in-mass (the number of eggs remaining in the egg mass), rounded up to an integer. A value of 0.7 for `eggs-hatching-rate` causes all eggs to hatch within five days, with 90% hatched in the first two days.

The number of tadpoles created is subtracted from the egg mass' value of eggs-in-mass. When eggs-in-mass reaches zero, the egg mass is removed from the model.

When tadpoles are created, their location is set to the patch containing the egg mass. Their age is set to 0 days, and a development time is drawn from a random normal distribution (Sect. 2.7.12).

2.7.10 Tadpole habitat selection

The tadpole habitat selection submodel represents movement among cells to find or maintain good rearing habitat. A variety of evidence indicates that tadpoles are capable of using only very low velocities and prefer low depths. Habitat selection observations by Kupferberg et al. (2011) and Bondi et al. (2013) found tadpoles using depths up to 1 m but velocities rarely above 0.3 m/s, with more mature tadpoles using lower velocities than younger ones. (As a tadpole matures, its tail becomes smaller compared to its body size, reducing swimming ability.) Kupferberg et al. (2011) observed poor swimming ability in tadpoles and an inability to return only 1-2 m to low velocity habitat when displaced into higher velocities. The habitat selection submodel based on the above evidence is simple. On each time step, each tadpole is assumed to evaluate the cells that are either (a) within a distance (cell center to center) equal to the parameter `tadpole-move-radius`, which has a value of 1.0 m, or (b) adjacent to their current cell. Hence, at minimum a tadpole evaluates its current cell and 8 surrounding cells (unless it is at the edge of the reach where there are fewer than 8 surrounding cells). The tadpole then simply selects and moves to the cell with lowest velocity and depth greater to zero. If there are no cells with depth greater than zero (due to a sharp decrease in flow), it does not move.

2.7.11 Tadpole survival

Like the egg mass survival submodel, tadpole survival focuses on two kinds of mortality directly affected by flow: desiccation and scour.

Survival of desiccation is modeled simply by assuming each tadpole has a low but not zero probability of survival in any time step when its cell's depth is zero. Survival is not zero when depth is zero because parts of a recently dewatered cell may remain submerged. The probability of survival when depth is zero is equal to the parameter `tadpole-desiccation-survival`, raised to the power *step-length*. The value of `tadpole-desiccation-survival` is 0.2.

Scour mortality represents tadpoles washed downstream and presumably to death when entrained in velocities too high for them to maintain or control position; Kupferberg et al. (2011) showed that tadpoles are easily washed downstream in even moderate velocities. The probability of surviving scour is defined by a logistic function of cell mean velocity. A tadpole's probability of surviving scour is equal to this logistic function raised to the power *step-length*. The logistic function is defined by the parameters `tadpole-scouring-v01` and `tadpole-scouring-v09`, the velocities at which the logistic function has values of 0.1 and 0.9. This submodel neglects the substantial decline in swimming ability as tadpoles develop as observed by Kupferberg et al. (2011).

The logistic function parameters were based on several observations. Bondi et al. (2013) measured velocities in habitat used by tadpoles in natural streams and found them almost always less than 0.3 m/s. Kupferberg et al. (2011) observed velocities in tadpole habitat to be almost always less than 0.1 m/s, and less than 0.02 m/s for tadpoles nearing metamorphosis; and most

tadpoles exposed to velocities of 0.1 to 0.2 m/s were washed downstream. Kupferberg et al. (2011) also measured critical swimming speeds (approximating a maximum sustainable swimming speed) in a laboratory and found values ranging among individuals from nearly zero to over 0.4 m/s, with values decreasing with increasing development. The parameters based on these observations are 0.3 and 0.15 m/s for `tadpole-scouring-v01` and `tadpole-scouring-v09` (Figure SA-3).

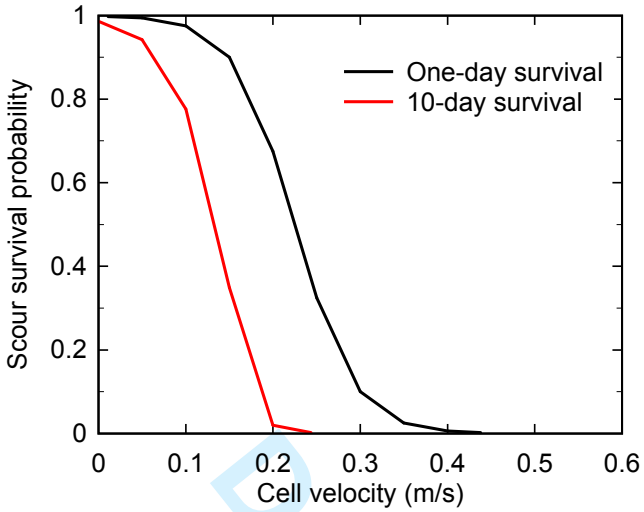


Figure SA-3. Tadpole scour survival function.

2.7.12 Tadpole development and metamorphosis

After hatching from eggs, tadpoles go through a number of development stages until they metamorphose into froglets that live primarily on land instead of in the stream. FYFAM stops simulating tadpoles when they reach this metamorphosis. This submodel determines when metamorphosis is reached.

The time between hatching and metamorphosis is variable and it is reasonable to assume the time depends on factors such as temperature and food availability. However, the field observations of Wheeler et al. (2014) indicated no significant effect of temperature. Wheeler et al. (2014) observed the average time to metamorphosis ranging from 7 to 10 weeks across 7 sites, with a mean of 9 weeks.

Because time to metamorphosis varies among and within sites but the causes of variation are not understood, we model this time stochastically using a distribution specified by parameters. The parameters `tadpole-devel-time-mean` and `tadpole-devel-time-SD` are the mean and standard deviation (days) of a normal distribution from which the development time for each tadpole is drawn when it hatches. The values of these parameters can be set to reflect productivity characteristics of each site if information exists. Values of 65 and 4 for these parameters cause an average of 95% of tadpoles to metamorphose between 57 and 73 days (8

and 10 weeks; this variability among individuals at a site is not comparable to variability among sites in average metamorphosis time reported by Wheeler et al. 2014).

The development and metamorphosis submodel therefore does the following for each tadpole. First, the tadpoles age is incremented by the value of *step-length*. Then, if the new age exceeds the development time the tadpole is counted as having successfully metamorphosed and removed from the model.

3 Software Guide

3.1 License

The FYFAM software is copyrighted and licensed under the GNU General Public License (GPL; https://www.gnu.org/licenses/gpl.html), which means it is free software that anyone can use, modify, and re-distribute; but it must remain free. A copy of the license is on the "Info" tab of the model's NetLogo file.

3.2 Installation

Installing FYFAM requires two simple steps: installing NetLogo and then copying the model files. FYFAM uses the NetLogo modeling platform (Wilensky 1999). NetLogo is free, easy to install, and available for all common operating systems. FYFAM therefore can be used on Windows, Macintosh, and Linux computers.

NetLogo is installed by downloading an installer from its web site at Northwestern University: http://ccl.northwestern.edu/netlogo/. FYFAM was developed using version 5.1.0 of NetLogo, but should work in any later version.

FYFAM itself is installed by simply copying (or unzipping) a directory containing the code file (typically named something like FYFAM.nlogo), its input files (described below), and a subdirectory containing the "time" extension to NetLogo that the model uses. (The time extension can alternatively be installed in NetLogo's code directory where the typical user will not see it, but it is not installed automatically with NetLogo.) The FYFAM directory can be copied anywhere.

FYFAM can then started by either (a) starting NetLogo (the same way any other installed software package is started) and using "File > open" in NetLogo to find and open the FYFAM code file, or (b) simply double-clicking on the code file.

3.3 Model files

FYFAM uses several input files, plus a file of parameter values. These files must all exist in the same directory as the FYFAM NetLogo code file. Examples of these files are distributed with the model, but users typically simulate new sites or management scenarios by creating new files.

All the input files are in plain text format; they can be created in spreadsheet software and then saved in either tab-separated or CSV (comma-separated value) format (as specified below for each file type). The files can all be edited with text editors such as Notepad.

All the input files except the parameter file (Sect. 3.3.5) have user-specified names. The names of these files must be provided in the parameter file: after creating or re-naming an input file, the user must edit the parameter file to provide the file name that the model is to use.

3.3.1 Cell geometry file

This file provides the coordinates of the centers of the habitat cells. The geometry must follow these conventions, which are based on UTM coordinates:

- Cell numbers must be positive integers. (0 is not a valid cell number.) However, cell numbers need not be continuous nor in any particular order.
- Coordinates must be in units of meters.
- For display, X coordinates increase from left to right (west to east) and Y coordinates increase from bottom to top (south to north).
- The cells must be a north-south, east-west grid of square cells (or the equivalent in an arbitrary coordinate system): their centers must be evenly spaced in both the X and Y dimensions.
- Cell size is unrestricted: the distance between cell centers can be any number.
- The cells do not need to make up a square space.

The format of the cell geometry file (Figure SA-4) is: three lines of header information that are ignored by the computer, followed by one line for each cell. These lines contain the cell number and the X and Y coordinates of the cell center. **These values must be separated by spaces or tab characters, not commas.**

```
FYFAM cell geometry input file
Example site. Coordinates are in meters.
CellNum     X      Y
1      210.53      70.31
4      210.53      73.31
2      210.53      71.31
3      210.53      72.31
...
```

Figure SA-4. Example cell geometry file.

3.3.2 Cell variables file

The cell variables file provides habitat variable values for each cell. Cells are references using the same cell numbers as in the cell geometry file. The format is similar to that of the geometry file: three header lines followed by one line per cell. These data lines contain:

- The cell number,
- Cell elevation (bed elevation, in meters, using any datum; used for display only),
- A zero (false) or one (true) representing the boolean variable *breeder-suitable?* (Sect. 2.2.1), and
- A zero or one representing the boolean variable *has-shelter?* (Sect. 2.2.1).

The data lines need not be in any particular order. **Values on each line must be separated by spaces or tab characters, not commas.**

```
FYFAM cell variables input file
Example site.
CellNum     Elevation (m)     Breeder-suitable? Has-shelter?
1           103.2       0     1
2           104.3       0     0
3           101.1       0     0
4           100.4       0     0
...
```

Figure SA-5. Example cell variables file.

3.3.3 Depth and velocity files

The depth and velocity files provide lookup tables of depth/velocity values for a range of flows, for each cell. These files are usually generated from output from a hydraulic model (see Sect. 2.7.1). The number of flows in the tables is not fixed, and the depth and velocity files can each use different flows and different numbers of flows.

The flows must be in units of cubic meters per second, depths in meters, and velocities in meters per second. **The values in the depth and velocity files must be separated by spaces or tabs, not commas.**

The two files have the same format (Figure SA-6):

- Three header lines that are ignored by the computer;
- One line that contains only a single (integer) number: the number of flows for which depths/velocities are provided;
- One line that contains each of the flows, in ascending order; and
- One line for each cell, containing the cell's depth or velocity for each of the flows.

```
Depth lookup table file, example site
Flows in m3/s, depth in m.
First the number of flows; one row of flows; then depths for each flow at each cell.
12
     0.04   0.06   0.08   0.1    0.15   0.2    0.3    0.4    0.5    0.6    0.8    1
1    0.08   0.1    0.1    0.12   0.13   0.13   0.15   0.16   0.18   0.2    0.21   0.22
2    0      0.02   0.02   0.04   0.05   0.05   0.07   0.08   0.1    0.12   0.13   0.14
3    0      0      0      0.01   0.03   0.04   0.07   0.09   0.15   0.2    0.26   0.35
4    0.01   0.03   0.03   0.05   0.06   0.06   0.08   0.09   0.11   0.13   0.14   0.15
...
```

Figure SA-6. Example depth file.

3.3.4 Flow and temperature time series file

One file provides the values of the time-series habitat variables that drive FYFAM: flow and water temperature. This file also specifies the model's time step and is explained more fully in Sect. 2.2.3. The file must contain values for the entire time period to be simulated; it can also contain times before and after the simulated period, which are ignored.

The time series input file is designed to be maintained in spreadsheet software and (unlike the other input files) uses CSV format. **Values in the data lines of this file must be separated by commas, not spaces or tabs.** (The file follows the format standards for time-series files used by the "Time" extension to NetLogo, https://github.com/colinsheppard/time. However, FYFAM uses a different date format than the time extension's default.)

The time series file (Figure SA-7) can start with as many header lines as desired, each starting with the semicolon character ";". These header lines are ignored by the computer. The next line must contain only the text "Time,flow,temperature". The remaining data lines each contain:

- A date and time, in the "m/d/yyyy h:mm" format (for example, midnight at the start of May 5, 2010 is: 5/5/2010 0:00. One p.m. on the same day is: 5/5/2010 13:00);
- The flow, in cubic meters per second; and
- The water temperature (C°).

```
;Time series input for FYFAM, years 2000-2004
; Contains flow (m3/s), temperature (C)
; DO NOT CHANGE variable names in row 3
; Times must be in m/d/yyyy h:mm format!
Time,flow,temperature
1/1/2000 0:00,0.38,5.5
1/2/2000 0:00,0.5,5.8
1/3/2000 0:00,0.46,6.4
1/4/2000 0:00,0.83,7
...
```

Figure SA-7. Example flow and temperature time series input file. This example uses daily values, assuming each flow and temperature represents a full day, starting at midnight.

3.3.5 Parameter file

The values of FYFAM's parameters are set in a file named `parameters.nls`. This file is actually part of the model's NetLogo code: the file contains a NetLogo procedure named `set-parameters` that sets the values of all the model's global variables. The file can be edited by itself, or from within NetLogo (via the "Includes" button on the Code tab).

The parameters file contains many lines with the same format:

```
set parameter-name value ; description.
```

Examples are:

```
set geom-file-name "BullCreek_Geom.txt"     ; Cell geometry file name

set num-breeders 100     ; Initial number of breeders
```

Parameter values can be changed by finding the parameter name in the file (see the list of parameters at Sect. 5) and editing its value. Parameter values that are file names must be in double-quotes. Text following semicolons are comments that are ignored by the computer.

3.4 Starting and controlling simulations

When FYFAM is opened in NetLogo, its graphical interface appears (Figure SA-8). The user controls the model and several options via this interface. (The interface is easily modified, so different versions of the model will likely have different controls and displays.)

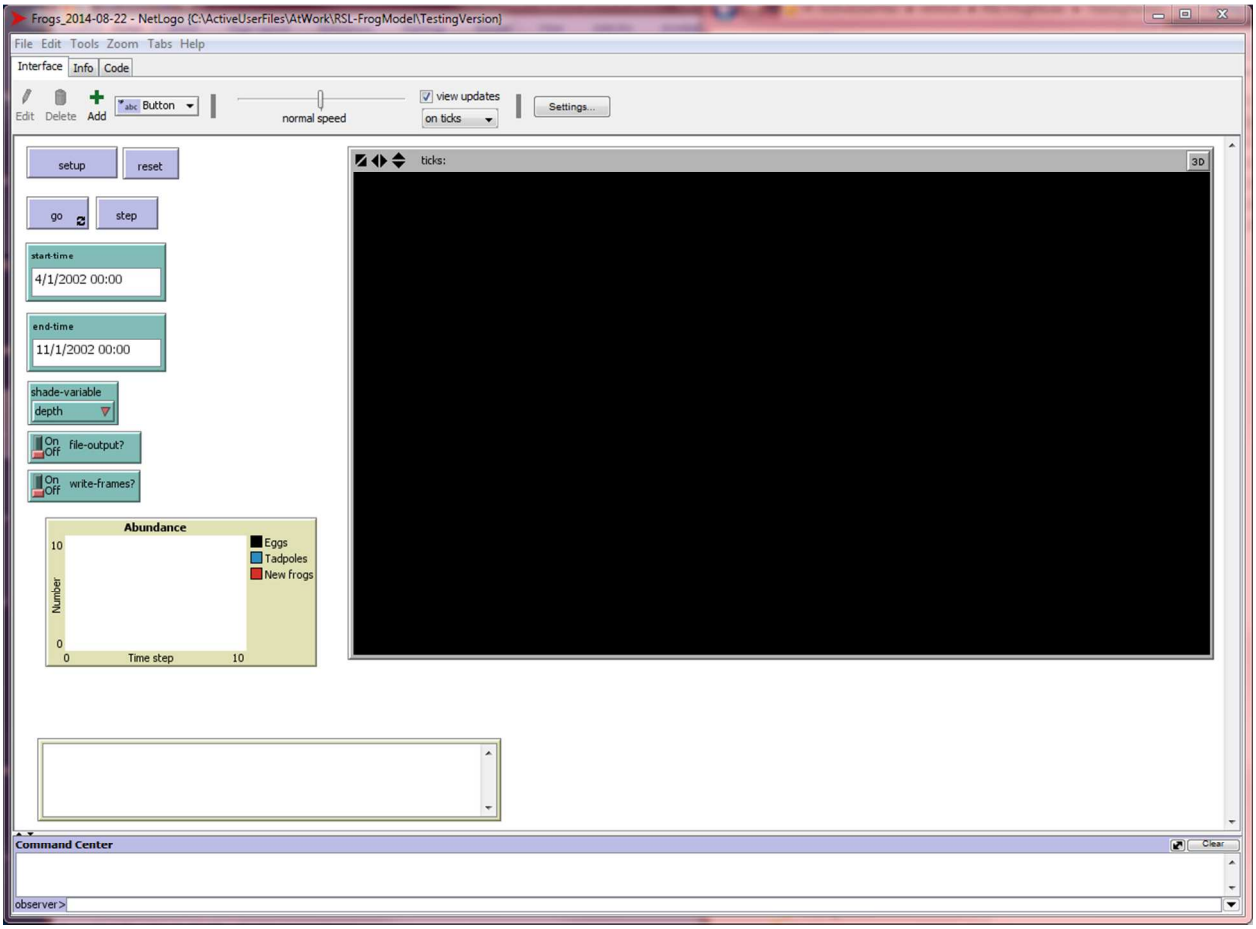


Figure SA-8. The FYFAM user interface before setup.

Common interface functions include:

- Click on the “setup” button to initialize the model: read input files, create the habitat and initial frogs, and prepare for execution to start. It normally takes several seconds for setup to complete; the button turns black while it is working.

- Click the “go” button to start model execution. Subsequent clicks on it pause, then re-start, execution.
- After the model is set up, or when it is paused, click the “step” button to execute just one time step.
- After a simulation has been completed or paused, click “reset” to re-initialize the model. “Reset” differs from “setup” because reset does not re-build the habitat from input files, and hence is much faster. (“Setup” must be used at least once before the first model run.)
- Set the parameters for model start and end times by editing their values in the green input boxes.
- Selecting the “shade-variable”, which determines whether the display colors submerged cells by their depth or velocity.
- Turning file output (Sect. 3.5) on or off. Output files are written only when turned on.
- Turning on or off the “write-frames” option, which saves the display to a graphics file (in PNG format) each time step. These files can be assembled into a movie of the display.

Once the model is set up and running (Figure SA-9), the animation display (the “world” in NetLogo terminology) shows habitat cells shaded by elevation when dry and by depth or velocity when below water. Breeders appear as yellow frogs, egg masses as grey circles (turning lighter grey with time), and tadpoles as small triangles.

Another control that users will likely need is setting the “patch size”, which is thesize of cells on the animation display. During setup, the model adjusts the dimensions of this display to match the simulated area represented in the cell geometry file. However, the size of the display depends on the computer screen resolution and the patch size as well as the habitat area. To adjust patch size, click the “Settings” button near the top the interface and edit its value in the dialog box that opens. To accommodate different site shapes and sizes, the whole NetLogo window can be stretched, and individual items on the interface can be selected (by dragging the cursor over them or by right-clicking on them) and moved.

Changes to the model interface (or parameters) can be made permanent by clicking on “File” and “Save”.

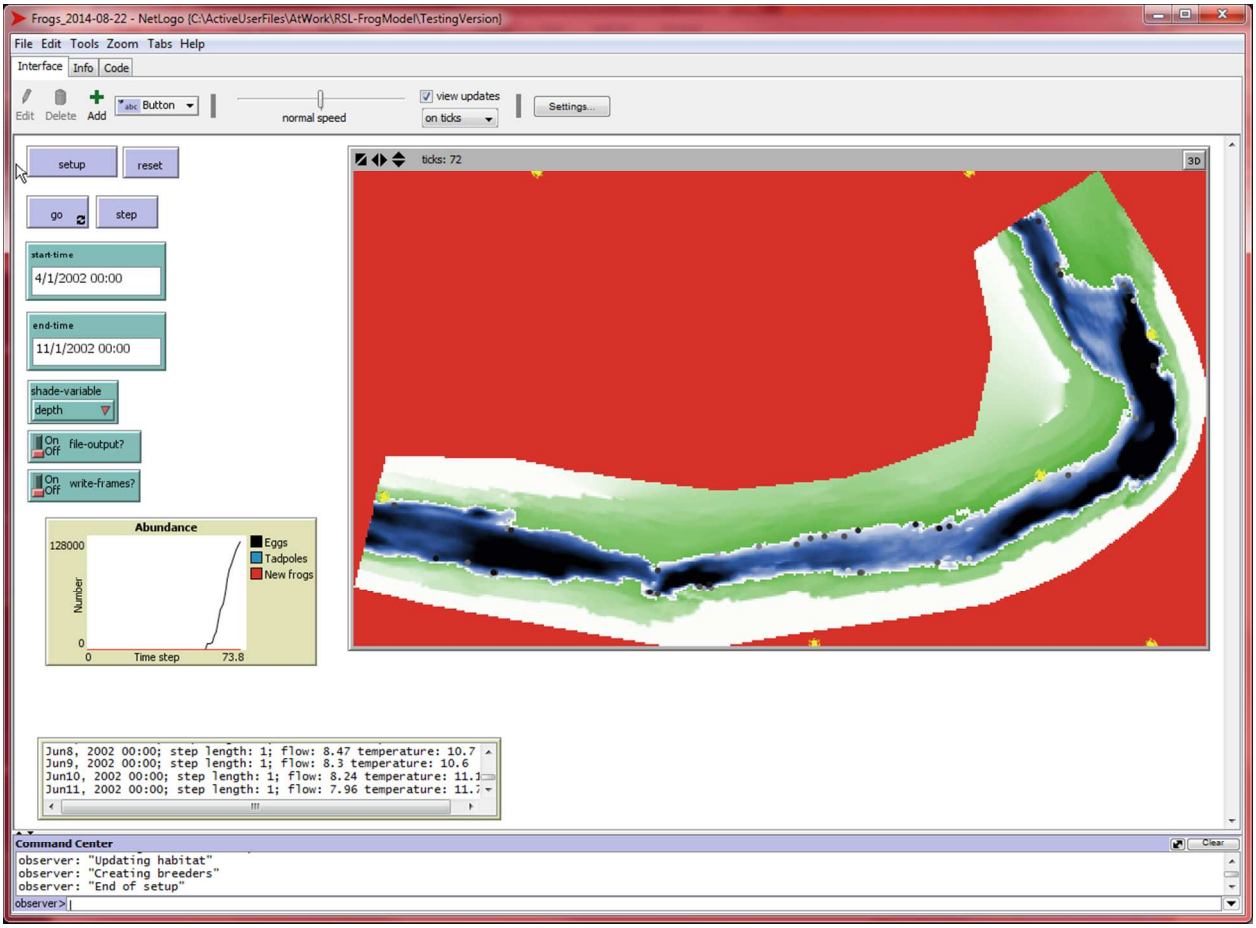


Figure SA-9. The model interface during execution.

3.5 Output files

When file output is turned on, FYFAM produces two output files. The output file names are generated by the code from the system date and time, so each model run produces unique output files. These files are in CSV format so they are easily opened in spreadsheet or statistical software.

The summary output file has a file name starting with the word “Output”, e.g., “Output-01-16-15.763PM21-Aug-2014.csv”. This file simply reports the number of breeders, egg masses, tadpoles, and new frogs alive at the end of each time step. Time steps are designated by the time at which they started.

The events output file has the same name as the summary output file but with the word “-Events” appended to it (e.g., Output-01-16-15.763PM21-Aug-2014-Events.csv). This file reports the time at which each individual in the model undergoes a transition event. The event types are:

- Breeders becoming ready to breed (Sect. 2.7.2; event label: “readied-to-breed”),

- Breeders ovipositing (Sect. 2.7.6; event label "oviposited"),
- Egg masses being created ("created"),
- Egg masses dying of desiccation ("died-desiccation"),
- Egg masses dying of scouring ("died-scour"),
- Tadpoles hatching from eggs ("hatched"),
- Egg masses emptying ("emptied"),
- Tadpoles dying of desiccation ("died-desiccation"),
- Tadpoles dying of scouring ("died-scour"), and
- Tadpole metamorphosing into new frogs ("metamorphosed").

The file contains one line per event, reporting the date and time at the start of the time step when the event occurred, the entity type (breeders, egg masses, tadpoles), the individual's unique identity number, the identity number of the individual's parent breeder, the X and Y coordinates of the cell where the event occurred (actual coordinates from the geometry file), and the event type.

4 References Cited

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5 Parameter Index

Supplement B

Foothill Yellow-legged Frog Assessment Model (FYFAM) Sensitivity Analysis Results

Prepared:

April 21, 2015

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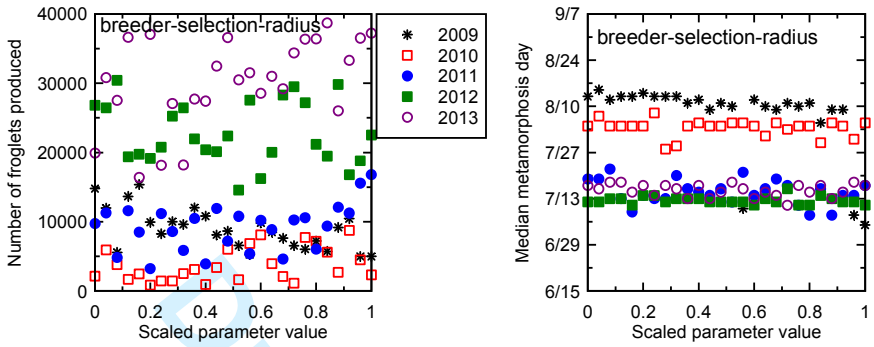
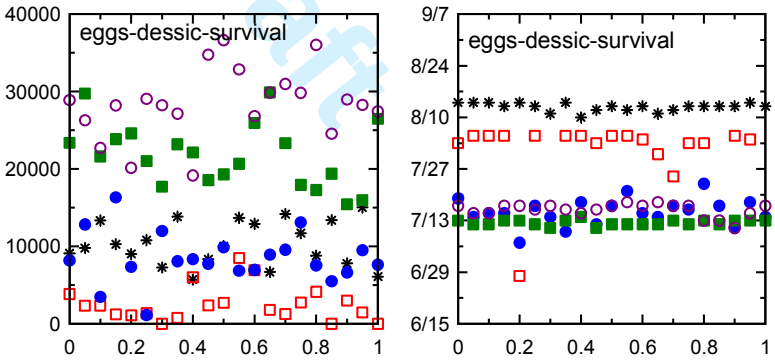
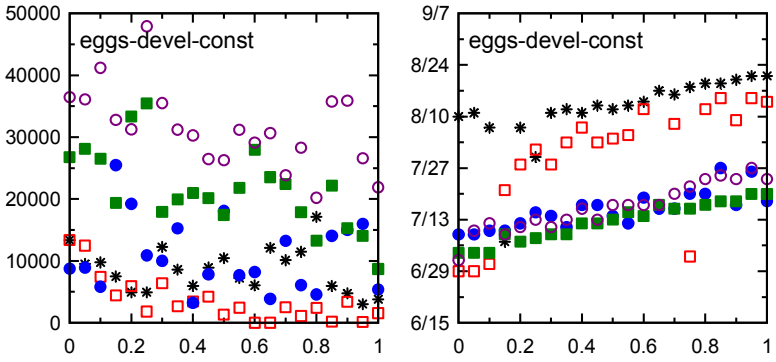
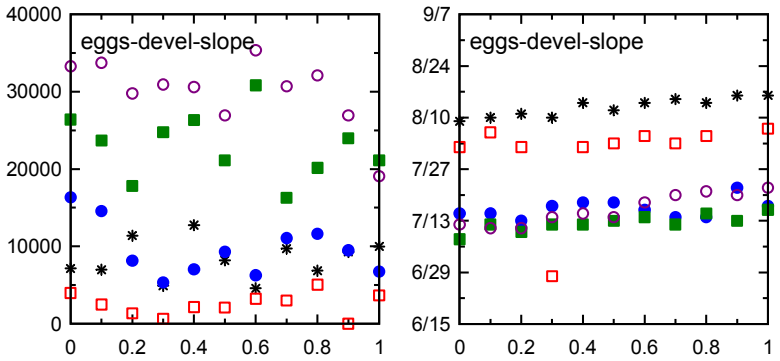
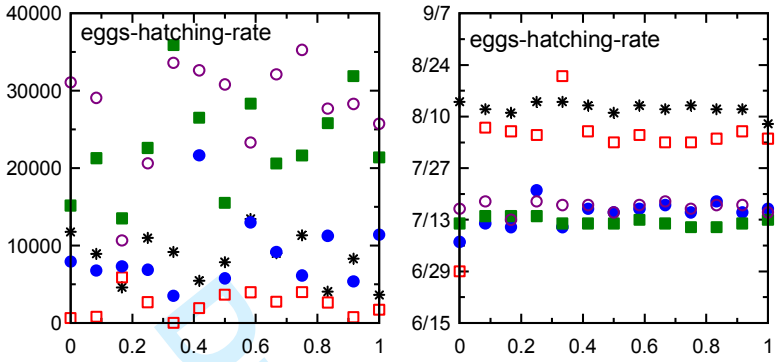
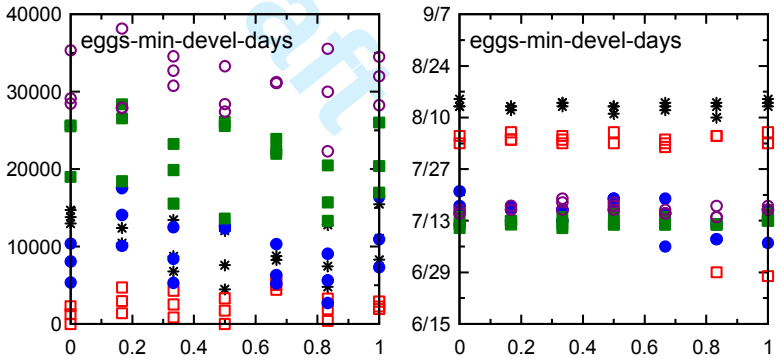
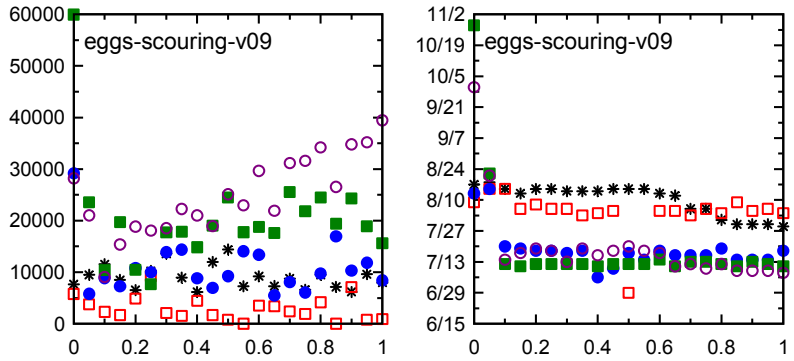
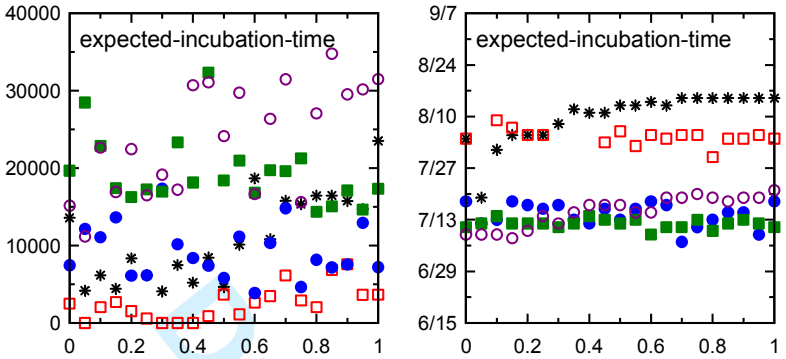
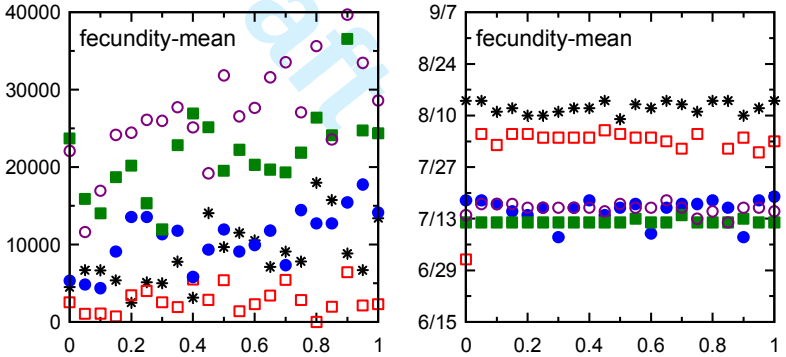
1 Graphical Results

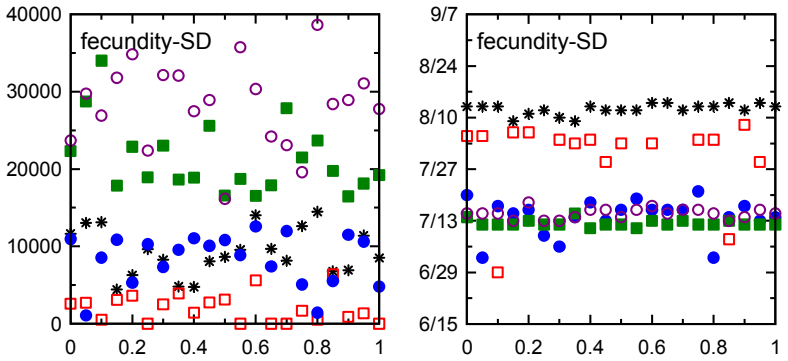
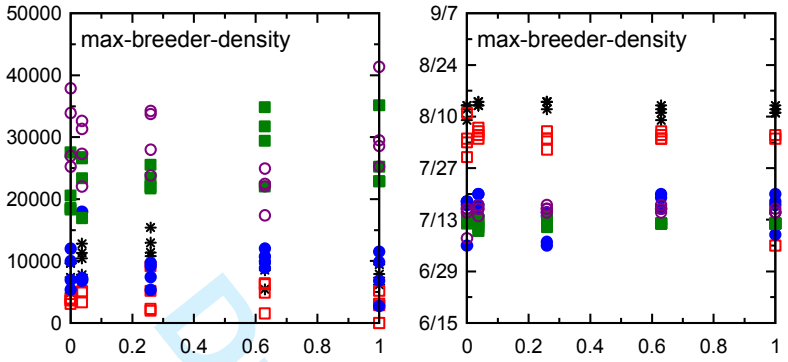
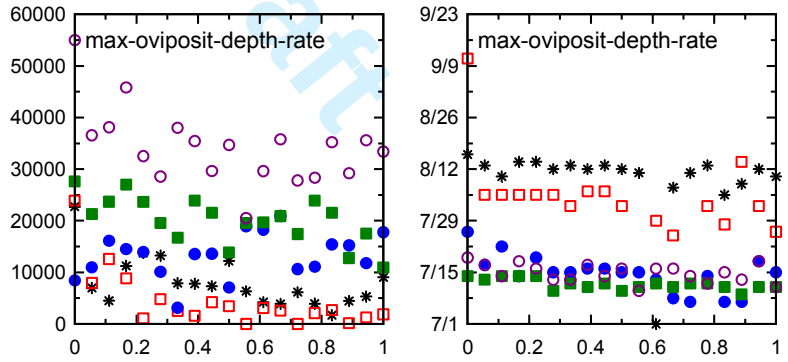
For each parameter in FYFAM, the left column describes the standard value (used in all other simulations) and the range of values examined in the sensitivity analysis. (Parameter definitions and units are in Supplement A.) The right column contains two graphs, displaying (left) number of new froglets created and (right) median metamorphosis date. The X axis of these graphs is the scaled parameter value, from 0 to 1, with 0 and 1 corresponding to the minimum and maximum parameter values examined. Results are presented separately for each simulated year.

Parameter name, standard value, values analyzed	**Graphical results**
breeder-selection-radius 20 From 5 to 30 by 1	
eggs-desiccation-survival 0.1 From 0 to 0.4 by 0.02	
eggs-devel-const 40 From 30 to 50 by 1	

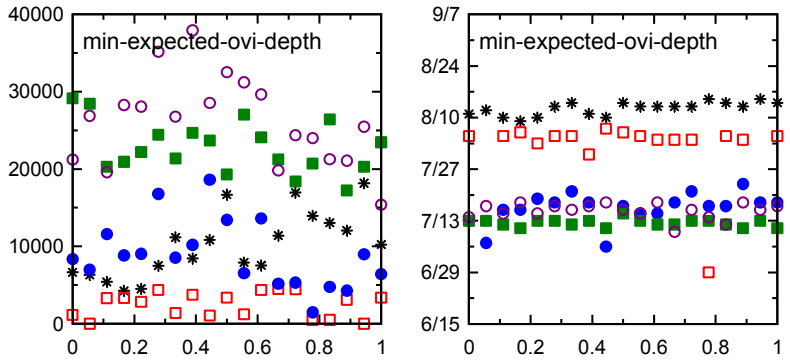
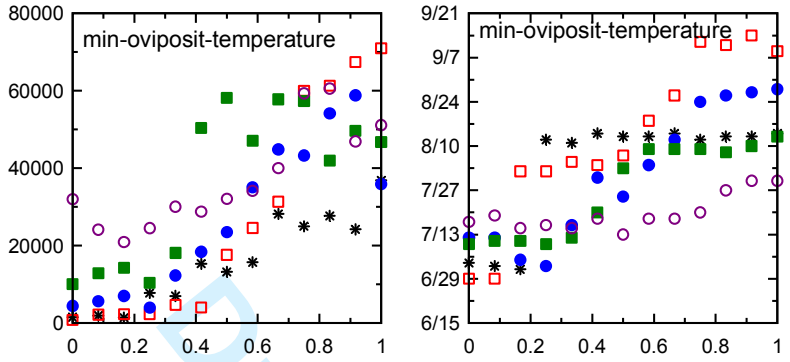
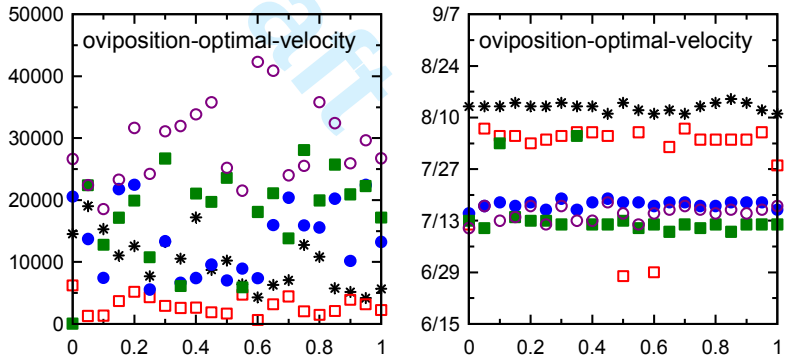
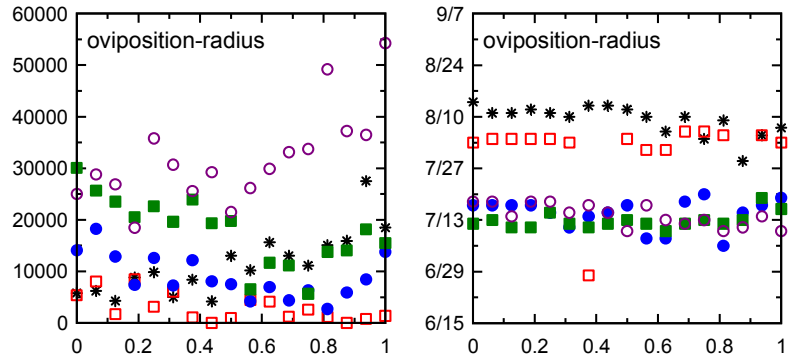
eggs-devel-slope -1.66 From -1.9 to -1.4 by 0.05	
eggs-hatching-rate 0.7 From 0.3 to 0.9 by 0.05	
eggs-min-devel-days 7 From 5 to 11 by 1	

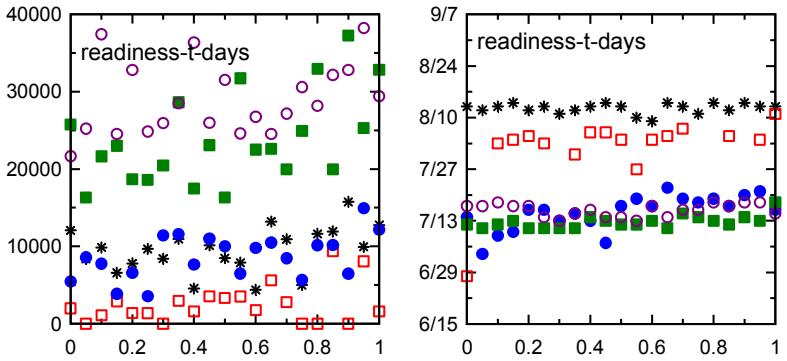
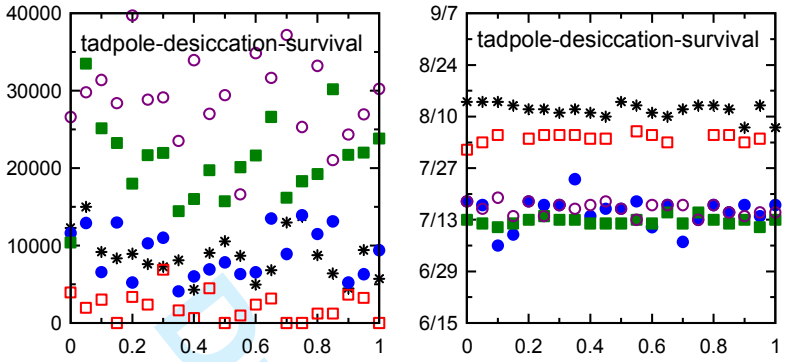
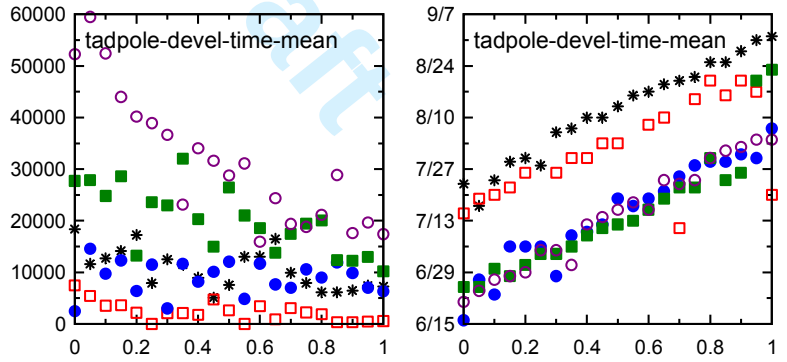
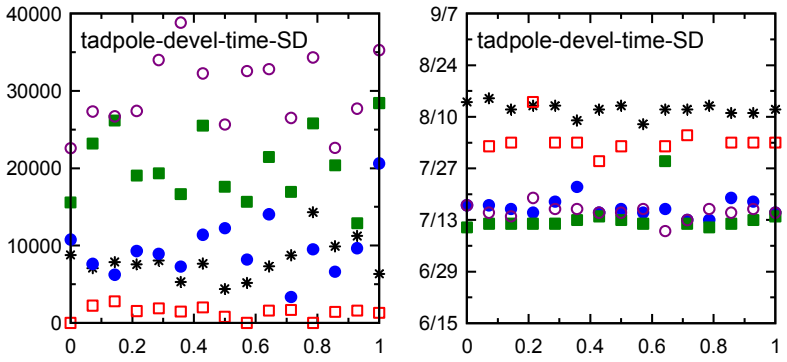
eggs-scouring-v09[1] 0.2 From 0.05 to 0.3 by 0.0125	
expected-incubation-time 20 From 10 to 30 by 1	
fecundity-mean 1500 From 1000 to 2000 by 50	

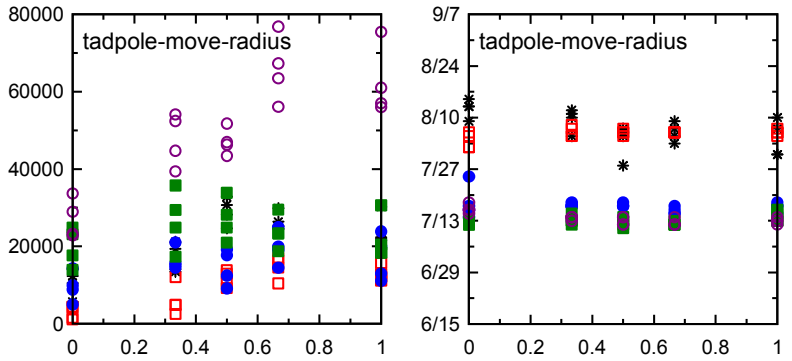
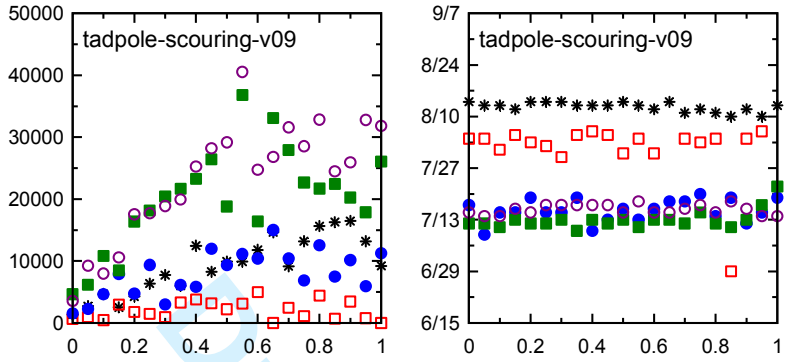
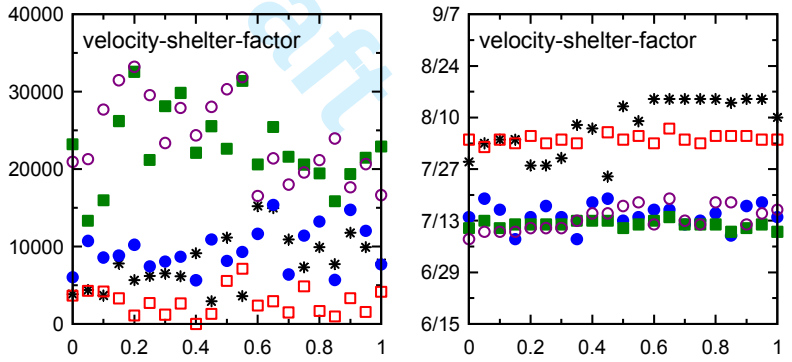
[1] The related parameter eggs-scouring-v01 was set to eggs-scouring-v09 + 0.2 in this analysis.

fecundity-SD 440 From 100 to 600 by 25	
max-breeder-density 1 0.3, 0.4, 1, 2, 3[2]	
max-oviposit-depth-rate 0.03 From 0.01 to 0.1 by 0.005	

[2] This parameter is discrete because it is evaluated for only one cell; therefore, only five values corresponding to 1, 1, 1, 2, and 3 breeders per cell were simulated. The experiment included four replicate simulations for each parameter value.

min-expected-ovi-depth 0.05 From 0.01 to 0.1 by 0.005	
min-oviposit-temperature 10 From 8 to 14 by 0.5	
oviposition-optimal-velocity 0.1 From 0 to 0.2 by 0.01	
oviposition-radius 5 From 2 to 10 by 0.5	

readiness-t-days 60 From 40 to 80 by 2	
tadpole-desiccation-survival 0.2 From 0.0 to 0.4 by 0.02	
tadpole-devel-time-mean 65 From 45 to 85 by 2	
tadpole-devel-time-SD 4 From 1 to 8 by 0.5	

tadpole-move-radius 1 1, 2, 2.5, 3, 4[3]	
tadpole-scouring-v09[4] 0.15 From 0.05 to 0.25 by 0.01	
velocity-shelter-factor 0.5 From 0.3 to 0.7 by 0.02	

[3] This parameter is discrete because the number of cells within a radius varies discretely with the radius. Therefore, five values were simulated (corresponding to 5, 13, 21, 29, and 49 potential cells to move to). The experiment included four replicate simulations for each parameter value.
[4] The related parameter tadpole-scouring-v01 was set to tadpole-scouring-v09 + 0.15 in this analysis.

2 Statistical Results

This table presents regression analysis of model results versus scaled parameter values. "Number of positive responses" is the number of years (out of five total) in which the model result had a significant ($p \leq 0.1$) correlation and positive slope with respect to scaled parameter value. "Number of negative responses" is the number of years in which the model result had a significant but negative correlation with scaled parameter value.

Parameter	Number of froglets produced		Median metamorphosis date	
	Number of positive responses	Number of negative responses	Number of positive responses	Number of negative responses
breeder-selection-radius	3	1	0	1
eggs-desiccation-survival	0	0	0	0
eggs-devel-const	0	3	5	0
eggs-devel-slope	0	1	3	0
eggs-hatching-rate	0	0	1	2
eggs-min-devel-days	0	0	0	2
eggs-scouring-v09	1	0	0	4
expected-incubation-time	3	1	2	1
fecundity-mean	4	0	0	0
fecundity-SD	0	1	1	0
max-breeder-density	1	0	0	1
max-oviposit-depth-rate	0	4	0	4
min-expected-ovi-depth	1	2	2	0
min-oviposit-temperature	5	0	5	0
oviposition-optimal-velocity	1	1	1	0
oviposition-radius	2	3	1	2
readiness-t-days	2	0	3	0
tadpole-desiccation-survival	0	0	0	2
tadpole-devel-time-mean	0	4	5	0
tadpole-devel-time-SD	0	0	0	0
tadpole-move-radius	4	0	1	2
tadpole-scouring-v09	4	0	1	1
velocity-shelter-factor	1	1	2	0