Foothill Yellow-legged Frog Assessment Model (FYFAM) Description

Version 2

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Figures

1 Report Objective and Revision History

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*).

Version 2 of FYFAM, which this report documents, includes changes made after the original version published as Supplement A of Railsback et al. (in press). These changes include consideration of egg mass elevation above the cell bottom in desiccation mortality (Sect. 2.7.7) and temperature effects on tadpole development (Sect. 2.7.12).

The original documentation of Version 2 was dated September 1, 2015.

The version dated December 3, 2015 describes changes in software (also dated December 3, 2015) that do not affect the model formulation. These changes include changing the parameter and rules defining when a simulation stops (Sect. 2.2.3), modifying the summary output file format (Sect. 3.5), and the addition of a recommended configuration for automated simulation experiments (Sect. 3.6).

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.

While FYFAM is intended for assessment of water temperature effects on frog development rates, it does not represent direct effects of temperature on frog survival. For example, mechanisms such as heat stress and parasitism by which high temperatures affect survival of FYF (discussed by Catenazzi and Kupferberg 2013) are not included in FYFAM.

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: *eggs-frac-developed* is set to zero when an egg mass is created, and eggs are ready to hatch into tadpoles when *eggs-frac-developed* reaches 1.0.

When eggs hatch, each egg turns into a "tadpole" entity. Tadpoles have dynamic state variables for location (their cell), age (days since hatching), and development status (*tadpole-frac-developed*). 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 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 `run-duration`. The parameter `start-time` is a date and time variable; the model starts at the first time in the time-series input file that is at or after `start-time`. The value of `run-duration` is the maximum number of days that the simulation lasts; the model stops at the last time in the file that is before or at `run-duration` days after `start-time`. However, simulations also automatically stop when no more breeders, egg masses, or tadpoles are alive; hence a high value of `run-duration` (e.g., 300 days) causes simulations to stop as soon as no more useful output is produced.

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 flows equal toor below *flow-at-wetting*, depth and velocity are set to zero. At flows between *flow-at-wetting* and the lowest lookup-table flow with non-zero depth, depths and velocities are interpolated between *flow-at-wetting* and the lowest flow in the tables with non-zero values.

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 1).

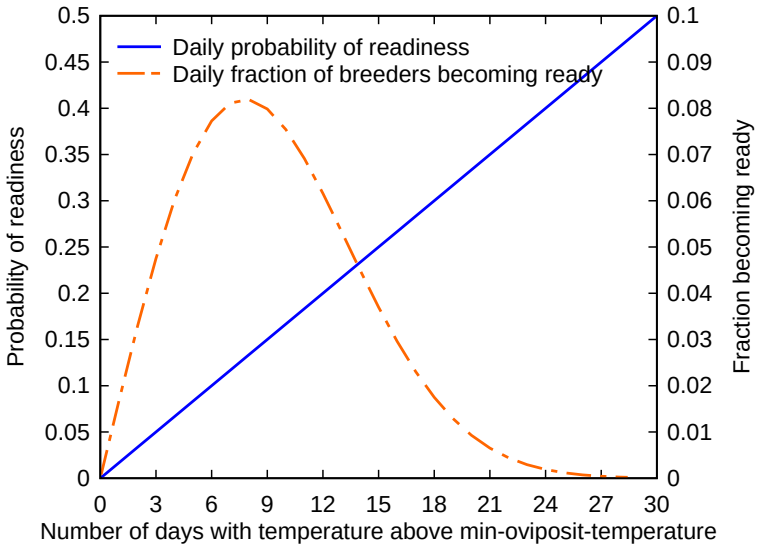

Figure 1. Distribution of readiness over time with `readiness-t-days` equal to 60 days.

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 four criteria: (1) the cell variable *breeder-suitable?* (Sect. 2.7.3) is TRUE, (2) depth is greater than zero, (3) at least one adjacent cell has zero depth, and (4) the density of breeders (number of other breeders already in the cell, divided by cell area) does not exceed the maximum specified by parameter `max-breeder-density` (the definition of this parameter and some cautions about breeder density are in Sect. 2.7.3). 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.)

It is very important to understand that the maximum breeder density is applied only at the individual-cell scale: a breeder can use a cell only if the number of other breeders there, divided by cell area, is less than `max-breeder-density`, no matter how big the cells are or how many breeders are in nearby cells. In a simulation with, for example, 0.25 m^2 cells and `max-breeder-density` set to 0.5 frogs/m^2, a breeder could use an empty cell even if it were surrounded by occupied cells such that the number of other breeders within a 1-m^2 area was greater than 0.5. Consequently, unless its value is greater than 1 / *cell-size* the only effect of `max-breeder-density` is preventing more than one breeder per cell.

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 and Welsh *submitted*).

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 and Welsh (submitted) 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.
- 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 and Welsh *submitted*, 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.

Egg masses dry out rapidly when exposed to air and direct sunlight, so FYFAM assumes an egg mass has low survival when the water level in its cell declines below the elevation of the egg mass. Starting with Version 2 of FYFAM, the relation between cell depth and water level at the egg mass is controlled by the parameter `eggs-elevation-above-cell`, the typical vertical distance (m) of an egg mass above the cell's bottom elevation.

Survival of desiccation is represented by assuming all eggs survive if depth at the egg mass (*depth* - `eggs-elevation-above-cell`) is above zero; and when this depth is zero or negative, 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.

Good values of `eggs-elevation-above-cell` depend on whether there are vertical structures (usually, large rocks) that frogs typically attach egg masses to. In habitat where such structures are absent (e.g., where frogs oviposit in gravel and cobble), `eggs-elevation-above-cell` should be set to zero.

Where vertical structures are used by frogs, `eggs-elevation-above-cell` can be estimated from field observations of egg masses. Such estimations need to keep in mind that this parameter does not represent the difference in elevation from an egg masses to the lowest point in a cell, but to the characteristic cell elevation used in hydraulic modeling. Typically, this elevation can be thought of as the average elevation across the cell's bed.

In California's North Fork Mokelumne River, unpublished observations by Garcia and Associates (for Pacific Gas & Electric) indicate that FYF egg masses were placed in cells with depths of 0.40 to 1.24 m, but with egg mass attached to rocks at depths of 0.33 to 1.12 m. The difference between mean cell depth and mean egg mass depth was 0.10 m. Hence, a value of 0.1 m may be appropriate for `eggs-elevation-above-cell` in such habitat.

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*. However, if the egg mass is above the cell's water level (*depth* - `eggs-elevation-above-cell` is zero or negative) then no scouring mortality is simulated.

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 2).

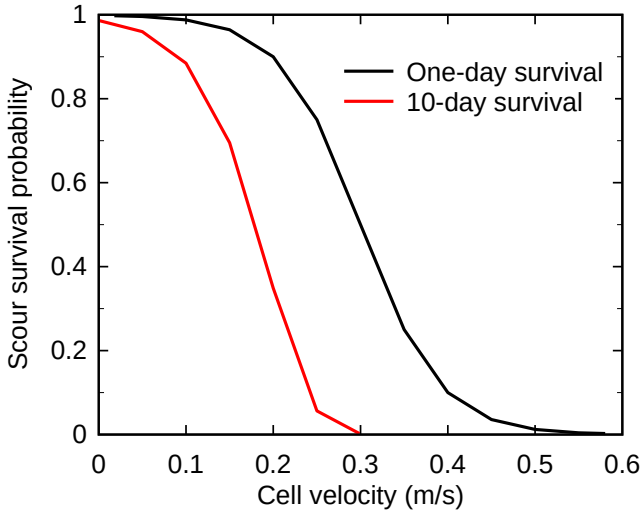

Figure 2. Egg mass scour survival function. The graph depicts both the probability of egg mass survival for one day and for 10 days at the same velocity.

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 linear relation between temperature and egg mass development time allows us to model development each time step as a function of temperature. The daily rate of egg mass development (fraction, between zero and 1.0, of of full development from oviposition to hatching) is modeled as:

$$\textit{eggs-daily-development} = \min[(1 / (m\mathrm{T} + b), (1 / c)].$$

In this equation m is the slope of the relation between temperature and development time (parameter `eggs-devel-slope`, d/°C), b (parameter `eggs-devel-constant`, d) is the constant from the same relation, and c (parameter `eggs-min-devel-days`, d) is the minimum number of days for hatching.

The egg development model is implemented via the egg mass variable *eggs-frac-developed*. On each time step, the above equation is used to calculate *eggs-daily-development*. The value of *eggs-daily-development* is multiplied by the value of *step-length* and the result added to each egg mass's value of *eggs-frac-developed*. This variable is then used in the hatching submodel (Sect. 2.7.9) to determine when eggs hatch into tadpoles.

The parameters for egg mass development can be evaluated from the data presented by McBain and Kupferberg (2012), which suggest values for `eggs-min-devel-days` of 7 days, `eggs-devel-slope` of -1.66, and `eggs-devel-const` (the number of days to hatching at 0°) of 40.

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 *eggs-frac-developed* 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 each individual's value of *frac-developed* is set to zero.

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 3).

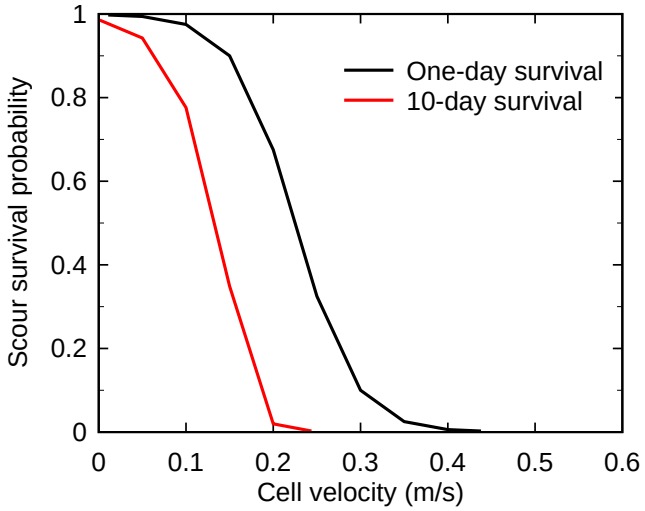

Figure 3. Tadpole scour survival function.

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 first version of FYFAM modeled the time from hatching to metamorphosis as simple stochastic process independent of environmental variables. That

assumption was based on observations such as those by Wheeler et al. (2014) that average time to metamorphosis ranging from 7 to 10 weeks across 7 sites, with no clear effect of temperature.

Version 2 of FYFAM treats tadpole development as a temperature-dependent process, on the basis of new analysis of field observations by Catenazzi and Kupferberg (2013). Catenazzi and Kupferberg made weekly observations of development status of FYF eggs and tadpoles throughout the incubation and development periods, at multiple sites in four streams across a range of temperatures. They also measure the temperature continuously and supplemented the supply of algae food for some frogs. We analyzed their data to estimate, for each cohort used as a treatment, the mean date of hatching into tadpoles, the mean date of front leg emergence, and the mean temperature between hatching and front leg emergence. We assumed an additional 10 days for complete metamorphosis (tail absorption).

This analysis produced a relatively strong and clear relation between temperature and time between hatching and front leg emergence (Figure 4).

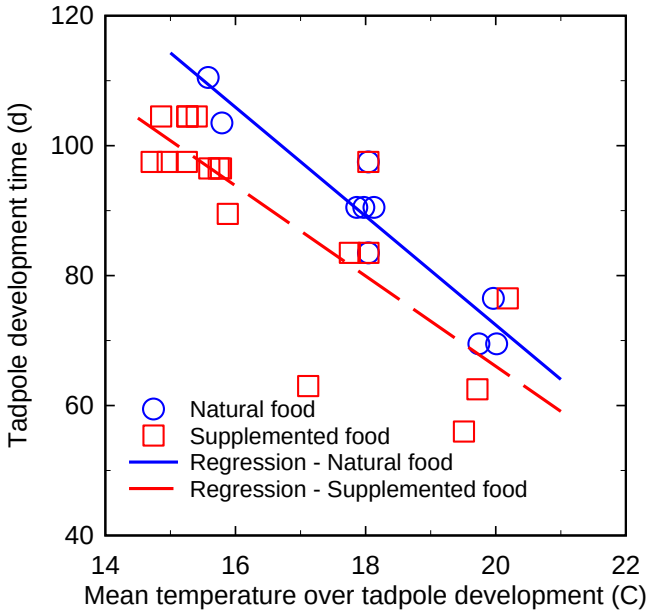

Figure 4. Tadpole development time vs. temperature from data of Catenazzi and Kupferberg (2013). The Y axis is development time defined as the number of days from hatching to front leg emergence. The X axis is the mean temperature over that period. Results are indicated separately for treatments with and without supplementation of the natural food supply.

The model of tadpole development is similar to that for egg masses (Sect. 2.7.8). We represent daily tadpole development (fraction of development from hatching to metamorphosis) as:

$$\textit{tadpole-daily-development} = 1 / (mT + b).$$

In this equation m is the slope of the relation between temperature and development time (parameter `tadpole-devel-slope`); the relation for natural food in Figure 4 suggests a value of -8.38 d/°C. The variable b (parameter `tadpole-devel-constant`) is the constant from the same

relation. The value of `tadpole-devel-constant` can be estimated as 250 d, from the y-intercept of the relation for natural food in Figure 4 (240 d) plus an estimated 10 d between emergence of front legs (the endpoint of the experiment by Catenazzi and Kupferberg) and full metamorphosis.

This model of tadpole development is implemented via the tadpole variable *tadpole-frac-developed*. On each time step, the above equation is used to calculate *tadpole-daily-development*. The value of *tadpole-daily-development* is multiplied by the value of *step-length* and the result added to each tadpole's value of *tadpole-frac-developed*. If a tadpole's new value of *tadpole-frac-developed* exceeds 1.0, it is counted as having successfully metamorphosed and removed from the model.

Example results of the tadpole development submodel are shown in Figure 5, for (left) a site with relatively cool temperatures and (right) a warmer site.

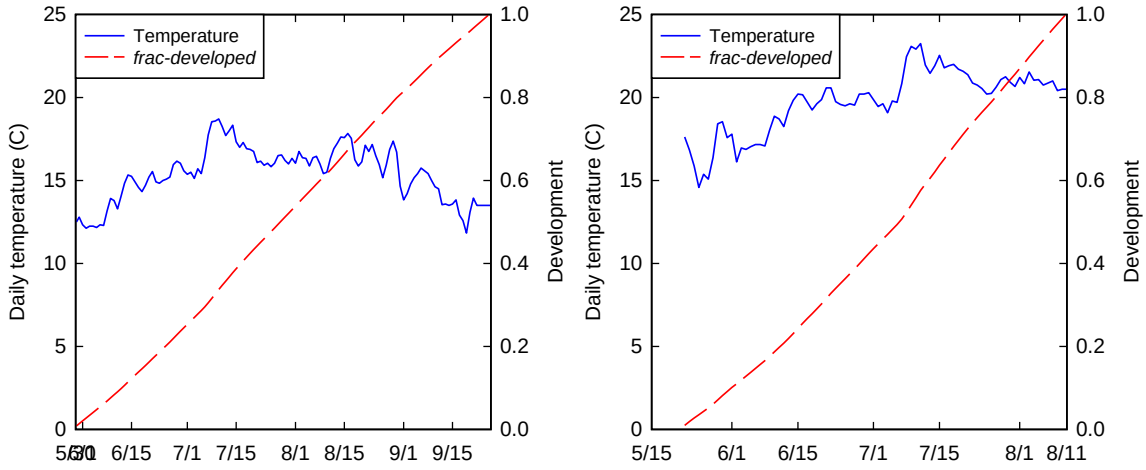

Figure 5. Example tadpole development results, with values of 250 and -8.34 for parameters `tadpole-devel-constant` and `tadpole-devel-slope`. The dashed line represents the fraction of complete development, starting on the day the tadpole is hatched. Note the difference in X axis dates. Temperature data are from baskets 23 and 55 of Catenazzi and Kupferberg (2013).

Figure 4 indicates that good values for the parameters `tadpole-devel-slope` and `tadpole-devel-const` can depend on food availability: the treatments with food supplementation had development times about 10 days shorter and slightly less dependent on temperature.

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/. Version 2 of FYFAM was developed using version 5.2.0 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 6) 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 6. 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 7. 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 8):

- 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 8. 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 9) 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 9. 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 10). 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.)

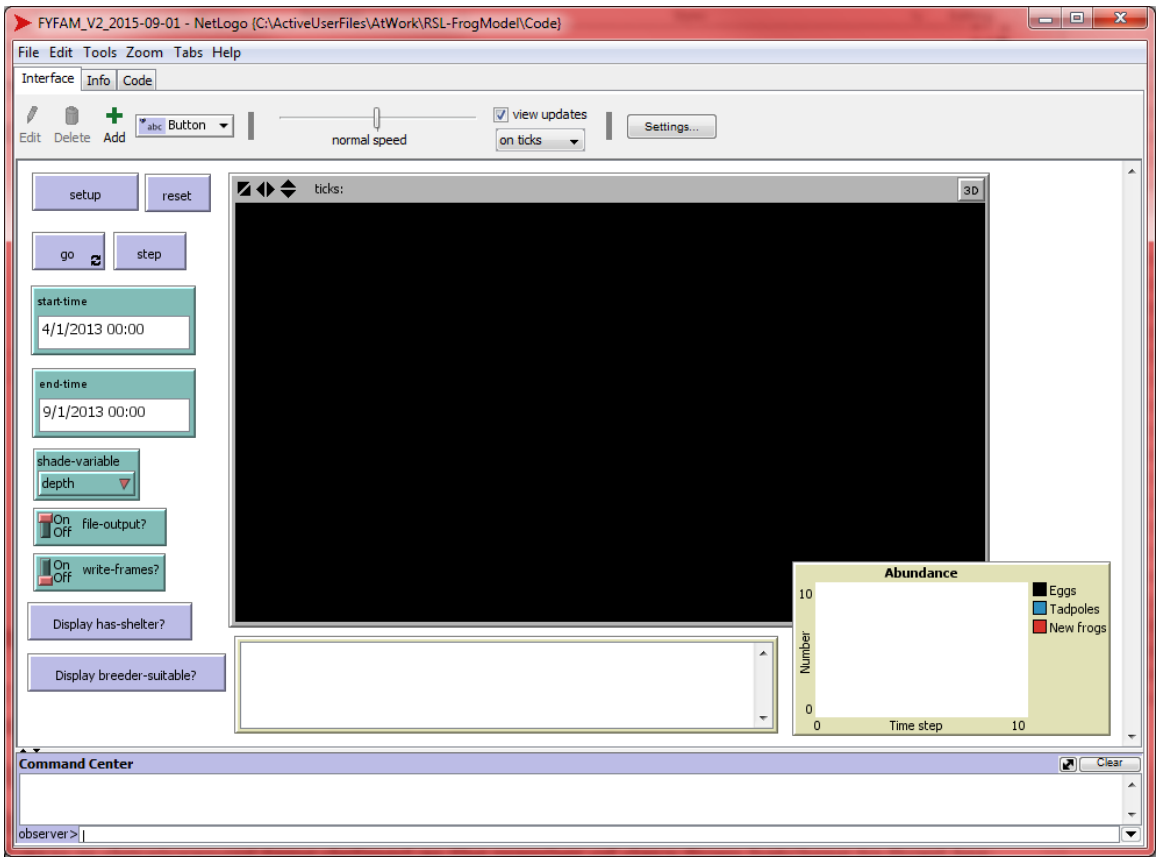

Figure 10. The FYFAM user interface before setup.

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 11), 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".

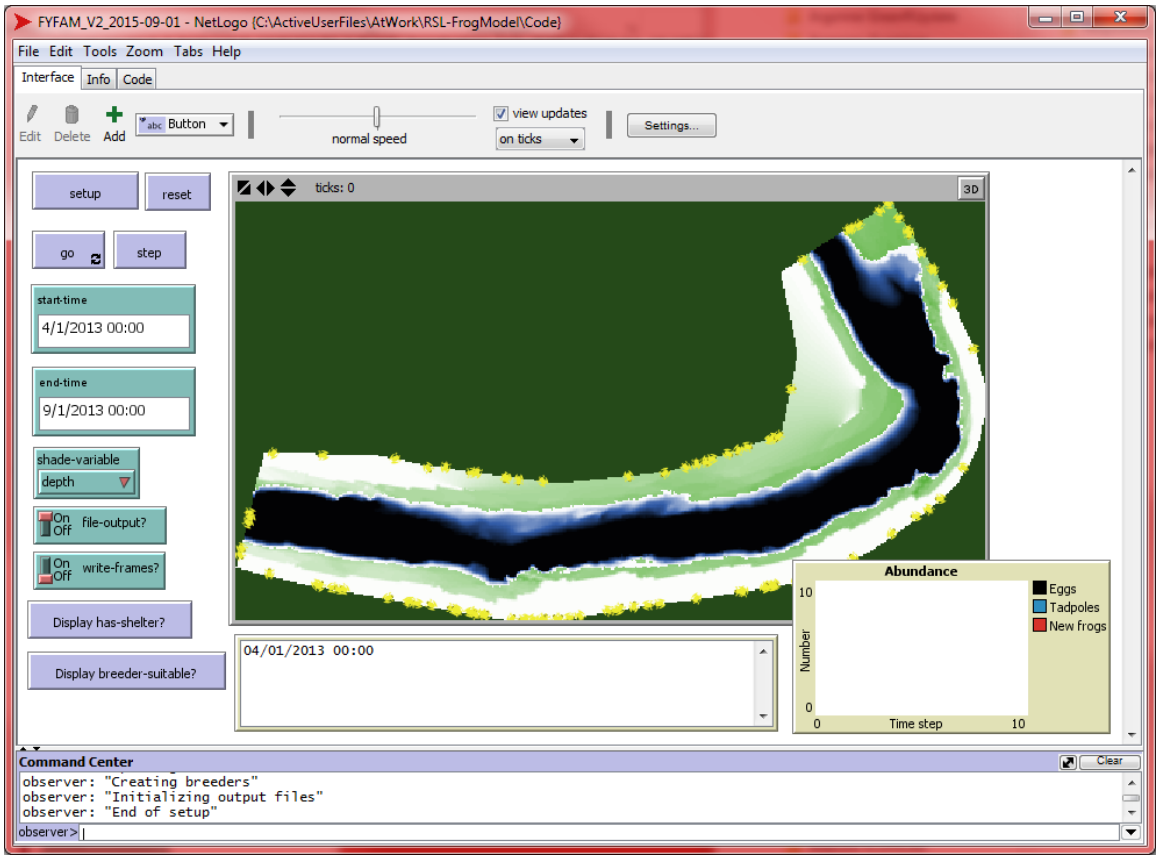

Figure 11. The model interface during execution.

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 reports one line of output for each time step, each line reporting the following information.

Column label	Output
Start of time step	Date and time at the start of the time step
Flow Temperature	The flow and temperature on the current time step
Breeders Egg masses Tadpoles	The numbers of breeders, egg masses, and tadpoles alive at the end of the time step
New frogs	The total (cumulative) number of new froglets metamorphosed by the end of the time step
Median metamorph date	The median date of froglet metamorphosis so far; the value is meaningful only after all tadpoles have metamorphosed and is set to 1 January when no tadpoles have metamorphosed yet
eggmasses-created eggmasses-died-desic eggmasses-died-scour eggmasses-emptied	The total (cumulative) number of egg masses created, died of desiccation, died of scour, and emptied (hatched into tadpoles) by the end of the time step
tadpoles-hatched tadpoles-died-desic tadpoles-died-scour	The total (cumulative) number of tadpoles hatched (created from eggs), died of desiccation, and died of scour by the end of the time step

The summary output file therefore makes it easy to produce time-series plots of flow and cumulative mortality (desiccation and scour of eggs and tadpoles), which are very helpful for understanding how flow regimes affect frog reproduction.

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.

3.6 Automated simulation experiments with BehaviorSpace

NetLogo includes a very powerful tool for setting up and executing simulation experiments; this tool is called BehaviorSpace. BehaviorSpace is quite simple and intuitive to use, and comprehensive instructions for using it are provided by Railsback and Grimm (2012).

BehaviorSpace is accessed via NetLogo's "Tools" menu, and is menu-driven: users fill out a menu defining what simulation experiments are to be executed and what output is to be saved from them. Each experiment configuration ("Experiment") can be saved as part of the model's NetLogo file. FYFAM is packaged with an example parameter sensitivity experiment (Figure 12), which users should duplicate and modify for their own experiments. This experiment configuration produces the same output as FYFAM's summary output file (Sect. 3.5), so file output can be turned off when using it.

BehaviorSpace users should note:

- The recommended BehaviorSpace configuration in Figure 12 does not repeat the very slow `setup` procedure between model runs. That means (a) `setup` must be executed manually before a BehaviorSpace experiment is started, and (b) each experiment can only run on one processor. In some cases it may be preferable to use `setup` instead of `reset` as BehaviorSpace's "Setup commands" so that multiple processors can be used to execute runs in parallel.
- The variables that can be varied in the experiment are any global variables on the model interface or set in the `set-parameters` procedure.

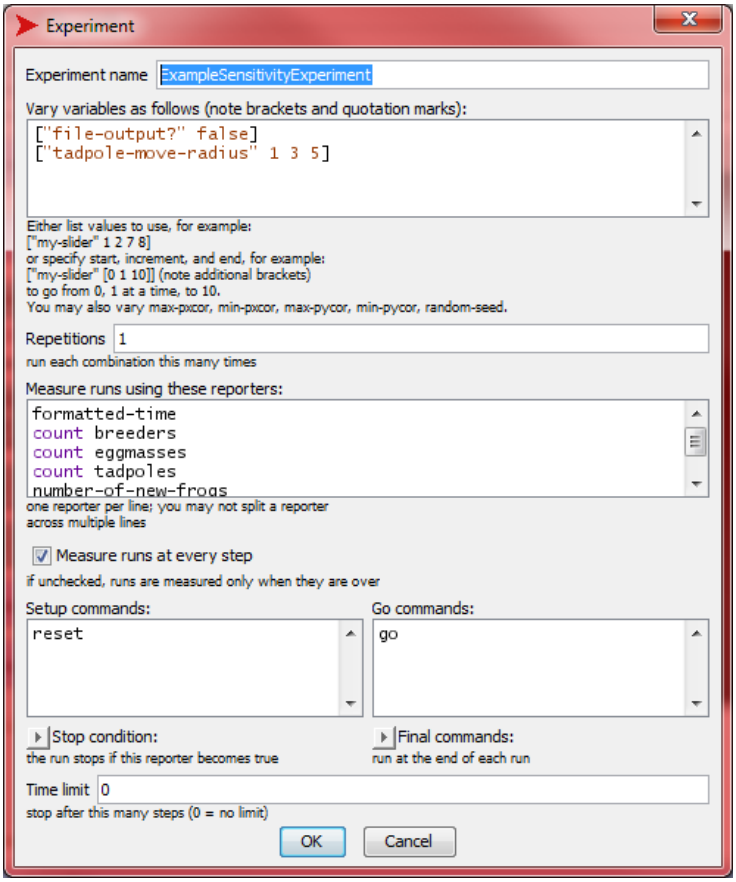

Figure 12. Example BehaviorSpace setup.

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5 Parameter Index