Arnold Schwarzenegger

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# PULSED FLOW EFFECTS ON THE FOOTHILL YELLOW-LEGGED FROG (*RANA BOYLII*): POPULATION MODELING

PIER FINAL PROJECT REPORT

*Prepared For:*

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# Pulsed Flow Effects on the Foothill Yellow-Legged Frog (*Rana boylii*): Population Modeling

## FINAL REPORT

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# Preface

The Public Interest Energy Research (PIER) Program supports public interest energy research and development that will help improve the quality of life in California by bringing environmentally safe, affordable, and reliable energy services and products to the marketplace.

The PIER Program, managed by the California Energy Commission (Energy Commission), annually awards up to $62 million to conduct the most promising public interest energy research by partnering with Research, Development, and Demonstration (RD&D) organizations, including individuals, businesses, utilities, and public or private research institutions.

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What follows is a final report detailing results for the hydropower pulsed flow program (contract number PFP-03) conducted by the University of California, Davis and its affiliates. The report is entitled *Pulsed flow effects on the Foothill Yellow-Legged Frog (Rana boylii): population modeling approaches.* The information from this project contributes to PIER's Energy-Related Environmental Research program.

For more information on the PIER Program, please visit the Energy Commission's website www.energy.ca.gov/pier/reports.html or contact the Energy Commission at (916) 654-4628.

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# Abstract

The decline of the river breeding foothill yellow-legged frog (*Rana boylii*) has been attributed to the altered flow regimes and habitat fragmentation associated with water storage and hydropower dams. Recent research has provided insight into potential mechanisms for these declines, confirming that early life history stages (embryos and tadpoles) are negatively affected by altered hydrology, especially pulses in water flows during spring and summer which change water velocities and depths in oviposition and rearing habitats. To evaluate whether such early life stage impacts could ultimately affect *R. boylii* population dynamics, we developed a 30-year stochastic matrix population model (Reference model) and explored a range of possible hydrologic and demographic perturbations to these virtual populations. While most female *R. boylii* appear to reach maturity at age 3, there is evidence that some Central Coast populations may reach maturity at age 2. To account for this potential regional life-history difference, we also developed a "two year to maturity" reference model, and explored a subset of relevant hydrologic scenarios. For each reference model, *R. boylii* life-stage specific survival rates were collected by new field efforts and assembled from existing data provided by other researchers and the literature for populations in hydrologically un-regulated rivers. To incorporate variability and uncertainty in these rates, distributions of possible values for each vital rate were described based on multiple data sources, and these distributions served as the basis for stochastic projections. Thirty different perturbations to the reference models were evaluated, with each scenario based on expected effects of altered hydrology for single or multiple life stages. The 30-year probability of extinction increased substantially (relative to the reference models) with small starting population sizes and in scenarios with high levels of stranding and/or scouring of egg masses or tadpoles. Multivariate sensitivity analysis confirms that egg mass scouring, and tadpole, juvenile, and adult survival are key factors influencing overall population dynamics. Modeled populations were unable to persist with multiple artificial pulsed summer flows or combinations of hydrologic stressors suggesting that the fate of early life stages can be critical to *R. boylii* population persistence in hydrologically altered rivers. A key observation stemming from this modeling effort is the need for better demographic data collection for *R. boylii*, especially annual tadpole and juvenile survival, and a functional understanding of how specific changes in hydrology affect particular life stage survival rates. Until such data are collected and incorporated into a similar modeling effort, the results reported here should be interpreted as preliminary and predictions made about real *R. boylii* populations under altered hydrologies will remain highly uncertain.

**Key Words**: matrix population model, hydrologic scenarios, sensitivity analyses

# Executive Summary

## Project Objective and Problem Statement

Hydrologic alteration of many California rivers has resulted in population declines and local extinctions of native species. *Rana boylii*, the Foothill Yellow-legged Frog, exemplifies this phenomenon, having declined dramatically over the last half century, especially in Southern California and the Southern Sierra Nevada mountains. It is a California Species of Special Concern and has disappeared from over 50% of known historic sites, with absences being more common in close proximity to large dams. During California's era of hydroelectric dam construction 30-40 years ago, habitats were destroyed and fragmented as river channels were converted to reservoirs. The persisting populations are small relative to those in unregulated rivers and are being adversely affected by aseasonal pulsed releases of water. The altered hydrologic regimes do not match a key adaptation of *R. boylii* to avoid flood induced mortality – synchrony of reproductive timing with the predictable seasonality of discharge.

A conservation challenge for *R. boylii* is to predict how negative effects on specific life stages from altered flow regimes will influence a population as a whole. Population viability analysis using life stage specific demographic rates offers a method to assess the probability that a population will persist when the survival of one or more stages is changed. Such a mathematical model requires compiling the probabilities of surviving from one life stage to the next in a life table. Outcomes are then forecast by using the life table values in combination with a defined starting population size and extinction threshold. The aim of this study is to construct the model and develop it as a tool to address a focal question; how are the population dynamics of *R. boylii* influenced by the frequency, timing, and magnitude of pulsed flow induced mortality of early life stages?

## Methods: Model Construction and Population Viability Analysis

Life table values were estimated using: (1) breeding censuses conducted at three focal watersheds to determine starting population sizes; (2) analyses of existing capture-recapture data on adult frogs to estimate the time to reproductive maturity and annual survival; (3) field enclosures of egg masses to quantify the number of offspring per female and embryo survival; (4) field experiments on tadpole survival; and (5) mark-recapture of young of the year frogs in the fall and following spring to assess the survival of tadpoles to metamorphosis and survival through the first winter. Missing rates were derived from the literature or data on related species. Once vital rates were compiled into a reference (unregulated river) model, scenarios were developed to assess the effects of hydrologic stressors on one or more life stages, and the population as a whole. The population was projected 30 years into the future and 10,000 simulations were done for the reference models and each scenario. Results were evaluated based on the probability of extinction and the average population growth rate.

Thirty scenarios of altered hydrology were explored. Each was a virtual manipulation of population or hydrologic factors: starting population size, the definition of 'virtual' extinction, spring and summer flow effects on egg mass and tadpole survival, thermal effects on tadpole survival, and combinations of factors. The impact of each scenario was compared to the dynamics of hypothetical unregulated populations of *R. boylii* in Northern or Central California (3 and 2 years to maturity, respectively). To assess the relative influence of each life stage on overall population outcomes, a multivariate sensitivity analysis was conducted.

## Population Modeling Results and Discussion

We found that *Rana boylii* populations in regulated rivers were at greater risk of extinction by virtue of their low abundance, even before the effects of hydrologic stressors were considered. Compared to the Reference Model which assumed a starting population of 32 breeding female frogs / km (unregulated average), regulated river populations (with an average of 4.6 females / km, or at the low end 2.1 / km) had a four to thirteen-fold increase in the 30-year risk of extinction. Simulated populations experiencing rapid flow fluctuation causing egg mass stranding and scouring led to 2.2-4.6 fold increases in extinction risk. The compounding effects of rapid flow fluctuation on egg survival were explored based on the observation that large females, which produce larger egg masses, breed earlier. Clutches laid later in the spring, which escape stranding and scouring, contain many fewer offspring. When this difference was accounted for, extinction risk was 17 times greater than in the reference model. Similarly, the joint effects of summer hydrologic stressors were greater than the sum of the component impacts. Extinction risk more than doubled with the tadpole mortality caused by annually recurring summer pulsed flows. Notably, extinction risk increased ten-fold when considering the food scarcity caused by the export of algal food during a pulsed flow. Multiple pulsed flows increased extinction risk twenty fold.

When the effects of spring *and* summer hydrologic alteration on *R. boylii* populations were considered, the relative increases in extinction above the Reference Model were very large. A hypothetical decline history for *R. boylii* was modeled by subjecting a robust starting population size to worst case scenario levels of stranding and scouring in the spring and then an annual summer pulsed flow as might have occurred historically due to scheduled maintenance of hydropower projects. The results indicated that a population would have very small chances of surviving these joint effects. When the seasonal trends in numbers of offspring produced were taken into account, extinction risk was >19 times greater than the Reference Model. The potential for recovery of small populations in regulated rivers, was explored by combining small starting population size with a background rate of stranding and scouring typical of regulated rivers as the sole hydrologic stressor. The resulting fifteen fold increase in extinction risk relative to the Reference Model indicated that recovery potential of such populations is low.

## Conclusions and Recommendations

Conservation of *R. boylii* in regulated rivers will depend on management that minimizes altered flows during the spring breeding and summer tadpole rearing seasons. In unregulated rivers, *R. boylii* populations appear to be self-sustaining under natural levels of hydrologic variation. When spring pulses that represent spill events and recreational boating flows were simulated, the 30-year risk of extinction was doubled. Similarly for the tadpole life stage, summer pulsed flows increased the risk of extinction three to five fold over the reference model. Combinations of hydrologic stressors that reflect real-world situations resulted in compounded increases in extinction risk.

These model results confirm the importance of the synchrony between the *R. boylii* life cycle and the seasonality of low flows typical of Mediterranean climates in spring and summer. When flow regimes deviate from this natural seasonal timing of flow fluctuation, locally adapted communities of organisms, including *R. boylii*, are likely to be threatened. Although model simulations were not intended to predict the actual dynamics of any one *R. boylii* population, the results correspond to trends in time series data collected at the SF Eel River, Alameda Creek, and NF Feather River.

While the overall results generated from the reference model and scenarios are well-supported, several uncertainties remain. The top priorities for follow-up investigation are to improve estimates of tadpole survival, over winter survival, and juvenile survival. As more detailed demographic data become available, these results and modeling scenarios may need to be revised. With that caveat, management recommendations are:

- Eliminate manufactured pulsed flows once frog breeding begins in the spring and suspend such flows through the early fall when metamorphosis occurs.
- Recognize synergisms and indirect effects among various hydrologic changes.
- Gather data on key birth and death rates during dam relicensing and use this model as a starting point for Population Viability Analyses of specific *R. boylii* populations.
- Improve long-term monitoring programs for *R. boylii* in both regulated and unregulated (reference) river systems, especially in the Sierra Nevada.
- Appropriate State and/or Federal agencies should elevate the protection status of *R. boylii* under the California or Federal Endangered Species Act.

## Benefits to California

During adaptive management of dam operations and the relicensing of hydropower projects, there are often discussions of the possible ecological effects of alternative base flows, pulsed flows, and other hydrologic conditions. If early life-stages of *R. boylii* are likely to be affected by the flow regime attribute under consideration, our results provide support that these actions may directly affect the status of adult populations. This connection between the dynamics of early life-stages and the adult population provide an important biological context for evaluating competing flow proposals. Future applications of these models may also aid in the assessment of risk for other sensitive species with similar reproductive timing and ecological niches.

# 1.0 Research Problem Statement

## 1.1. Hydrologic Alteration, *Rana boylii* Conservation, and the Need for Population Projection Models

Hydrologic alteration has reduced the abundance and imperiled the status of a wide array of riverine species (Richter et al 1997; Rosenberg et al. 2000; Bunn and Arthington 2002). *Rana boylii*, the foothill yellow-legged frog, exemplifies this phenomenon, having declined dramatically over the last half century, especially in Southern California and the Southern Sierra Nevada mountains. It is absent from over 50% of known historic sites (Davidson et al. 2002, Lind 2005) and is a California Species of Special Concern (Jennings and Hayes 1994; Jennings 1996; California Department of Fish and Game 2008). Absences from historic localities are more common in close proximity to large dams (Lind 2005). During California's era of hydroelectric dam construction 30-40 years ago, habitats were destroyed and fragmented as river channels were converted to reservoirs. The populations that persist are small relative to those in unregulated rivers and are being adversely affected by aseasonal pulsed releases of water (Kupferberg et al. 2008).

For *R. boylii*, the general problem in regulated rivers is that the altered timing, duration, and magnitude of discharge do not match its key adaptation for evading mortality from flow fluctuation, synchronizing reproductive timing and life stage transitions with the seasonality of discharge (Table 1.1). A thorny challenge for conserving a riverine species with a complex life cycle is predicting how flow regime effects on a particular life stage will influence the population as a whole. As regulators and utilities negotiate new license conditions for hydropower projects, there is an urgent need for tools that can link a specific change in discharge timing or magnitude to a desired conservation outcome. Population viability analysis (PVA) using life-stage specific demographic rates offers a method to assess the likelihood that a population will persist for a given period of time, when changes are made to the survival of one stage. The first step in conducting such a PVA is to define the relevant stages and transitions among stages.

**Table 1.1. Overview of potential and documented impacts to *Rana boylii* in regulated rivers.**

| Project Operations | Short-term impacts | Long-term impacts |
|---|---|---|
| Intentional aseasonal flows (power generation, recreation, outmigration of salmonid smolts); Unintentional spill of water over dam | - scour and/or desiccation of egg masses[1,2] / tadpoles[3]<br>- export spring and summer algal productivity[4,5], reduced resources for tadpoles, reduced insect abundance[5], food web repercussions | - discharge decoupled from environmental cues (e.g. rainfall, air temperature) triggering inappropriate behavioral responses by adults, juveniles, delayed onset of breeding[1,6]<br>- smaller population sizes[1,2] |
| Intentional de-watering of stream channels for rescue operations | - desiccation of egg masses / tadpoles | Unknown |
| Unintentional powerhouse outages resulting in rapid increase in flows in bypass reaches, followed by rapid decrease in flows | - changes to margin water temperature, depth, and velocity,<br>- scouring/desiccation of eggs/tadpoles, depending on ramping rate, magnitude of change, channel shape | Unknown |
| Reduced winter/spring flows | - absence of scouring/depositional flows that prevent riparian encroachment<br>- reduced breeding habitat, greater distances between breeding sites[3] | - vegetation encroachment, altered channel morphology, reduced breeding habitat<br>- population loss/fragmentation[3], reduced gene flow, altered metapopulation dynamics |
| Altered summer baseflows | - lower water temperatures<br>- change in available habitat (channel shape) | - promotes habitats that support non-native predatory fish, amphibians, and invertebrates, increased predation on eggs, tadpoles |
| Movement of water among river basins | - potential for increased disease and parasite transmission | Unknown |

*References*: 1. Garcia and Associates (GANDA) 2008; 2. Kupferberg et al. 2008; 3. Lind et al. 1996; 4. Spring Rivers 2002; 5. GANDA 2006; 6. Borque 2008

## 1.2. *Rana boylii* Life Cycle and Demographic transitions

For the purposes of building the population model, the following demographic rates, or transition probabilities are designated during *Rana boylii's* life cycle. (1) **Fecundity** (eggs/female). Fecundity is the number of eggs produced by each female when the breeding adults move out of tributaries (unaffected by flow regulation) to spawning sites on main-stem channels (which are subject to dam related flow fluctuation). Frogs spawn at the margins of relatively wide and shallow channel sections, in habitats that protect their immobile progeny from moderate flow variation. Females attach their single clutch of eggs in low velocity locations behind, and sometimes under, rocks which provide relatively stable depth and velocity conditions across a range of discharge volumes (Kupferberg 1996; Yarnell 2005; Lind 2005). (2) **Embryo scour rate.** Under a natural flow regime, there are low recurrence-interval wet springs with spates, in which some egg masses are lost due to scour. (3) **Embryo stranding rate**. In dry springs, rapidly receding shorelines can strand egg masses (Kupferberg 1996, see Figure 9, Kupferberg et al. 2008). In most years however, spawning occurs in synchrony with the receding limb of the spring hydrograph such that embryos and recently hatched larvae avoid flood or desiccation mortality. (4) **Embryo survival rate**. For those eggs that remain wetted and attached to substrate, not all hatch. Some may not have been fertilized, and some die prior to hatching into tadpoles. (5) **Tadpole survival to metamorphosis**. In addition to being prey for numerous consumers in stream food webs, tadpoles are susceptible to hydrologic sources of mortality. The larvae do not have morphological flow adaptations such as a ventral suctorial disc used for adhesion, as occurs in anurans whose larvae inhabit turbulent habitats or endure unpredictable flooding (Altig and Johnston 1989; Richards 2002). (6) **First over winter juvenile (young of the year) survival**. There is scant information about autumn movements of young of the year frogs (the young of the year life stage extends from metamorphosis through the first winter). They may move upland away from main stem channels (Twitty et al. 1967; Palen pers. obs. at SF Eel), to off-channel seeps (Rombough 2006), and caves (Peek and Kupferberg pers. obs. at SF American), or may over-winter in tributaries. (7) **Juvenile survival** and **(8) juvenile to adult survival.** Frogs must continue to survive for one or two more years (depending on location specific growth rates) before reaching the transition to reproductive maturity. The juvenile life-history stage is largely a mystery, and how these transition probabilities may relate to flow regime, either directly or via carry-over effects related to larval growth history are topics requiring additional research. (9) **Adult survival**. Adult numbers do not appear to be influenced by main-stem winter peak discharges (Kupferberg et al. 2008) and radio-telemetry data indicate that adults over-winter in tributaries and are able to cross wide channels to access breeding sites even at high flows (GANDA 2008). Given this multi-staged natural history, the basic question addressed in this study is: **What are the consequences of changes to a particular life-stage's vital rate to the persistence of the whole frog population through time?**

## 1.3. Focal Watersheds (Alameda Creek, South Fork Eel River, North Fork Feather River, Hurdygurdy Creek)

For estimation of demographic rates and time to maturity, data were collected within several different California watersheds (Figure 1.1. The three primary study areas where new data were collected are: the unregulated South Fork Eel River (SF Eel) in the University of California Angelo Reserve (Mendocino Co.); two regulated reaches (Poe and Cresta) of the North Fork Feather River (NFFR) on the Plumas National Forest (Butte Co.); an unregulated reach of Alameda Creek (Alameda) in the Sunol-Ohlone Regional Wilderness of the East Bay Regional Park District (Alameda Co.). Alameda Creek flows into the San Francisco Bay. A pre-existing data set for a population of *R. boylii* at Hurdygurdy Creek, a tributary of the South Fork Smith River (Del Norte Co.), was provided by Clara Wheeler. Each watershed has hydrologic, geomorphic and habitat characteristics typical of *R. boylii* localities in its respective region, the north coast, the Sierra Nevada, and the central coast (Table 1.2). For detailed habitat descriptions see Appendix A. These study sites correspond with three genetically distinct clades, or branches, in the evolutionary tree developed for *R. boylii* (Lind 2005). However, it is not known if these genetic differences translate to phenotypic differences in timing of breeding or other life history traits that may be differentially influenced by hydrologic variation. These locations were chosen because they have ongoing monitoring of frog populations and good hydrologic records.

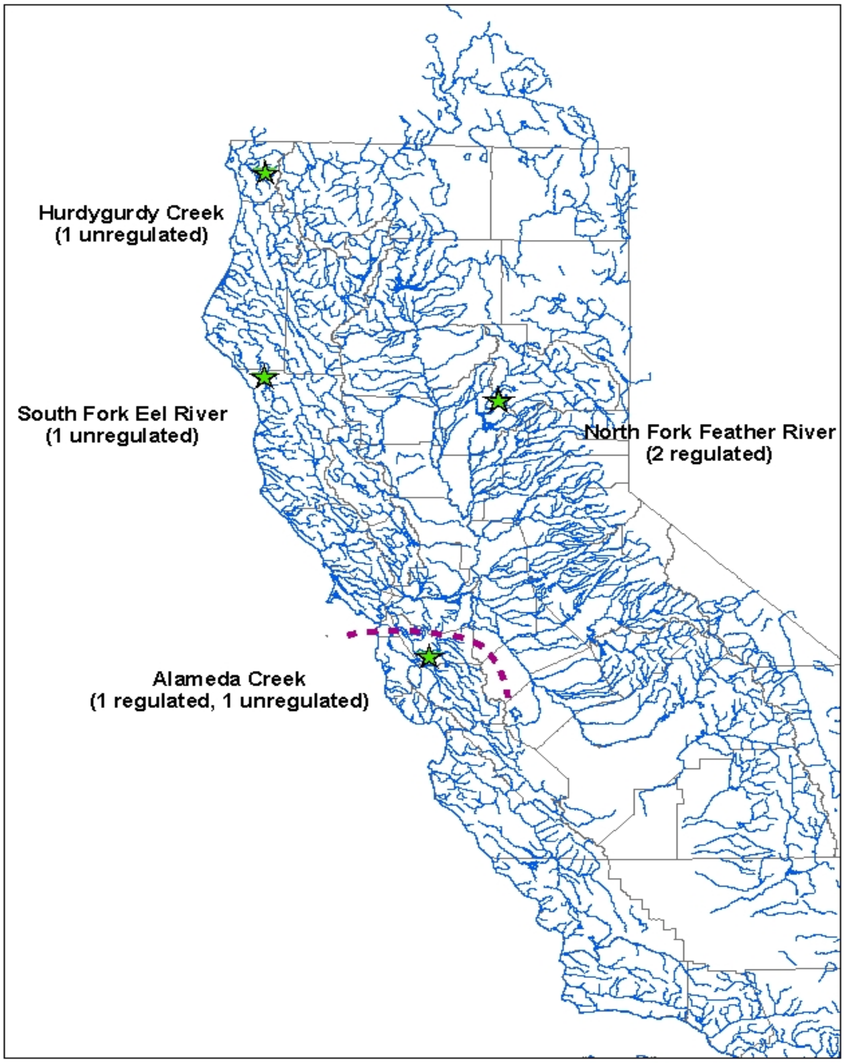


**Figure 1.1. Location of the study watersheds in northern and central California. The number of regulated or unregulated river reaches is listed for each watershed.**

**Populations south of the dashed purple line are hypothesized to reach maturity in 2 years; populations north and east of the line reach maturity in 3 years.**

The character of the pulse flows in the three focal watersheds with stream gaging is distinct (Figure 1.2). Annual hydrographs for the SF Eel illustrate natural seasonal runoff, with peak discharges in winter and occasional spring spates caused by rainfall. The regulated reaches have periodic late spring and summer pulsed flows that are aseasonal. The NF Feather reaches have large magnitude peak flows during winter and spring in wet years when the dams spill at the peak of snowmelt and when rain on snow events occur. The hydrograph is flat during the summer and fall, unless pulsed flows are manufactured as they were in the Cresta reach for whitewater boating (2002-2005, once per month June-Oct). The Alameda Creek regulated reach has a hydrograph that, while somewhat natural in shape, has reduced magnitude base flows, with occasional disproportionately high-magnitude peaks associated with flood spills and plateaus associated with continued releases. Since 2001, due to seismic safety concerns about Calaveras Dam, the maximum allowable reservoir height is 40% of capacity. Water is released to maintain that level (SFPUC 2007). By comparison, the unregulated Camp Ohlone reach on Alameda Creek has pulse magnitudes and durations directly coupled to rainfall. The magnitude of peak flows there is expected to decline under climate change scenarios (Klausmeyer 2005).

The frog population trends in rivers where these different types of hydrologic regimes predominate motivate the scenarios presented in this report. Generally populations are sparse and / or in decline in regulated rivers, while they are more abundant, stable, or increasing in free-flowing locations (Table 2.12, Figure 2.8). Specifically, at the SF Eel time series data indicate stable and increasing populations respectively (Kupferberg et al. 2008). In the NF Feather, frog population trends between the Poe and Cresta reaches are divergent, with Poe increasing and Cresta decreasing after new license conditions were instituted for Cresta Dam (increased base flow and summer white water boating flows). In Alameda Creek, populations are increasing in the Camp Ohlone reach, under natural hydrologic conditions, whereas downstream of the confluence with Calaveras Creek, *R.boylii* populations have decreased after consecutive years with high discharge conditions in the spring. This more southern population may be governed by different biological processes, such as faster growth rates and earlier age at reproductive maturity. The hydrologic stressors faced may be determined more by drinking water and irrigation needs than by power generation and recreational demands, and have different seasonal timing.

**Table 1.2. General characteristics of the focal river systems' topography, hydrology, geomorphology, and vegetation.**

| River / Creek | Reach and Nearest USGS Gage # | Regulation | Drainage Area[1] ($km^2$) | Mean±1 s.d. Annual Discharge[2] (cms) | Elevation (m) | Dominant Channel Morphology | Upland Vegetation | Riparian Vegetation | Dominant Substrate |
|---|---|---|---|---|---|---|---|---|---|
| NF Feather | Cresta 11404330 | Cresta Dam | 4976 | 22.5±25.6 | 488-424 | Riffle-pool | Chaparral and Mixed Conifer Forest | Willow, Alder, blackberry, sedge | Bedrock overlain by boulders and cobbles |
| | Poe 11404500 | Poe Dam | 5078 | 25.9±27.4 | 424-287 | Riffle-pool | | | |
| Hurdygurdy | Not currently gaged | none | ~ 80 | ~ 1 (summer)<br>100-140 (winter)[5] | 760 | Riffle-pool | Hardwood / Douglas Fir Forest | Alder, willow | Bedrock, overlain by boulders and cobbles |
| SF Eel | Branscomb[3] 11475500 | none | 114 | 4.88±1.70 | 427-365 | Riffle-pool | Douglas Fir Forest | Alder, sedge | Bedrock overlain by boulders and cobbles |
| Alameda | Camp Ohlone 11172945 | none | 88 | 0.77±0.42 | 380-365 | Riffle-run | Oak Woodland, Grassland | Sycamore, Mulefat, Alder, sedge | Bedrock, Cobble, gravel |
| | Sunol[4] 11173510<br>11173575 | Calaveras Dam | 273 | 1.17±1.07 | 134-122 | Riffle-run | | | |

1. Area upstream of the gaging station, data from USGS for all but Hurdygurdy. Hurdygurdy data is the area above the creek mouth.

2. Based on the following years of record: NF Feather Poe, 1980–2006, Cresta, 1986-2006; SF Eel, 1946-1970 and 1991–2006, synthetic record derived from Leggett data; Alameda, above diversion 1995–2006, below confluence with Calaveras 1999-2006

3. Branscomb gage USGS 1946-1970, re-established by Dietrich and Power 4/1990, USFS 2004

4. Alameda Creek, high flow discharges from gage near Welch Ck., approximately 5 km downstream of survey reach, gage below Calaveras confluence is a low-flow only gaging station

5. Estimated from previous gage data, no current active gage.

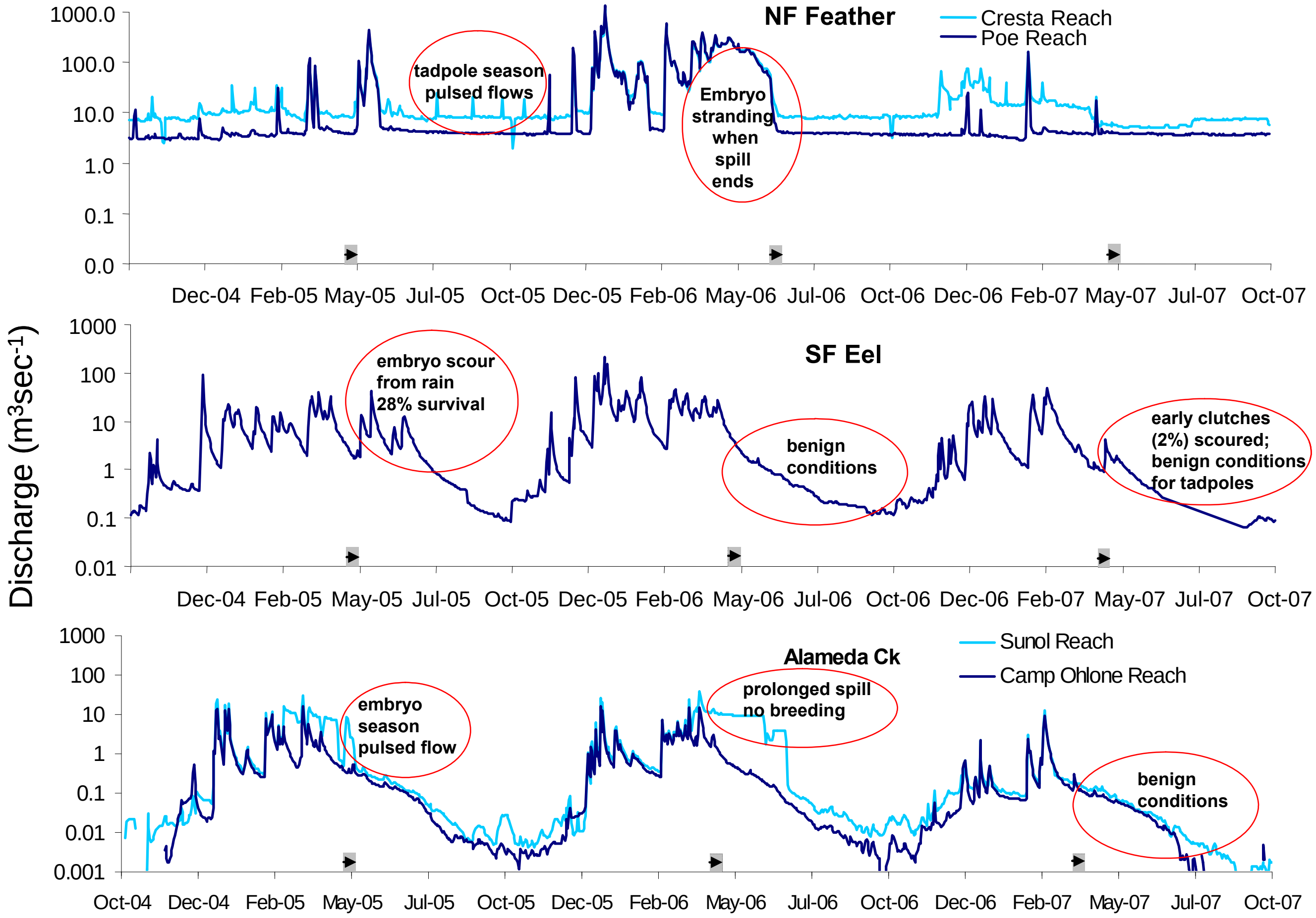


**Figure 1.2. Mean daily discharge ($m^3sec^{-1}$) for water years 2005-2007 in one regulated and one unregulated reach of Alameda Creek (bottom), the unregulated SF Eel (middle) and two regulated reaches of the NF Feather (top). Circled regions of hydrographs indicate periods and events important to the survival of early life stages of *Rana boylii*. Small arrows along the x-axes indicate dates when the oviposition and tadpole rearing seasons began in each river system.**

## 1.4. Project Objectives and Report Organization

The purpose of this project is to investigate the demographic processes contributing to patterns of frog decline associated with river regulation during the times of year when early life stages are vulnerable to flow induced mortality. The population level consequences of extreme fluctuation in water discharge volume during atypical times of the year are evaluated using a stochastic projection matrix model that relies on estimation of demographic rates for early multiple life stages.

*R. boylii* demography and populations dynamics were examined by combining: (1) count data from breeding censuses conducted at three focal watersheds; (2) analyses of existing mark-recapture data on adult frogs to assess time to reproductive maturity and yearly survival rates; (3) field enclosures of egg masses to quantify fecundity and embryo survival; and (4) mark-recapture of young of the year frogs in the fall and following spring to assess tadpole survival to metamorphosis and first winter survival. This report has six sections and two appendices. Section 2 presents the methods, section 3 the results, and section 4 the discussion and synthesis. Sections 5 and 6 contain references and a glossary. Specific objectives are:

Section 2: Model Statement, Life Table Construction, Estimation of Survival Rates, Development of Population Model, and Descriptions of Modeled Scenarios

- Construct a generalized life table (life stage based summary of fecundity, longevity, survival, and mortality factors) for *R. boylii* by compiling data from several northern and central California populations.
- Define the relationships between hydrologic disturbance and probability of transitioning from one life stage to the next.
- Conduct field enclosure studies to assess fecundity and embryo survival.
- Compile data on egg mass scouring and stranding rates during natural and artificial flow fluctuations during the spring and summer breeding and rearing periods.
- Conduct capture-recapture study on young of the year frogs in fall and then again in the following spring to develop young of the year frog population estimates and determine first year over-winter survival rate.
- Develop a matrix population projection model that will allow prediction of population and life stage effects under a variety of hydrologic regimes (both human-controlled and natural).

Section 3: Results and Discussion of Model Runs and Sensitivity Analyses

- Evaluate risk of extinction under different scenarios of starting population size and hydrologically driven mortality events
- Conduct sensitivity analyses to determine which life stages are critical for conservation.

Section 4: Conclusions and Recommendations

- Provide an overall synthesis and conclusions based on sections 2 and 3.
- Recommend future research and direction for FERC studies with the aim of collecting data to fill gaps in knowledge of the vital rates of stages that have large influence on population persistence
- Address commercialization potential
- Assess benefits to California

# 2.0 Methods: Model Construction, Estimation of Survival Rates, and Population Viability Scenarios

## 2.1. Life Table Construction

A demographic population projection model begins with a life table. A life table is a book-keeping tool that compiles the probabilities of transitioning from one life stage to the next for a cohort of individuals. Traditionally these transition probabilities are single estimates, which results in a relatively simple form of matrix population model, a deterministic model. While informative, this approach limits a model's utility for evaluating how fluctuations in transition probabilities (due to natural or anthropogenic causes) influence the population growth rate. In this project, the goals are to estimate distributions, rather than single values, of life-stage transition probabilities that are functions of hydrologic variables as well as estimate background variation not visibly attributable to a mechanistic cause (stochastic modeling). For most life stages, pre-existing data collected by the authors' own surveys and experiments were used and supplemented with data from other researchers. There were no available data on female fecundity, embryo survival, the transition from metamorphosis to first year juvenile, and the transition from juvenile to adult. Thus, new data were collected on female fecundity and embryo survival using field enclosures of egg masses and on metamorphosis to first year juvenile survival using capture-recapture techniques on newly metamorphosed frogs. For the first year juvenile to adult transition, data were too sparse for parameter estimation. In this case, literature estimates for related species of frogs and professional judgment extrapolating from estimates derived for other life stages were used. These baseline transition probabilities are presented here in Section 2 (see subsections titled "Application to Population – Reference Values" for each life stage).

Section 2 also describes model scenarios for each life stage transition. In the scenarios, the transition probabilities and/or their variances are manipulated to represent effects of pulsed fluctuations in discharge and other hydrologic effects on vital rates (see subsections titled "Model Scenarios" for each life stage). Reference transition probabilities and particular scenarios are simulated over multiple generations of frogs. For example, the effects of spring run-off events that cause occasional spills are compared to the effects of annual summer recreational boating flows. The results for the mathematical modeling of *R. boylii* population dynamics are presented in Section 3.

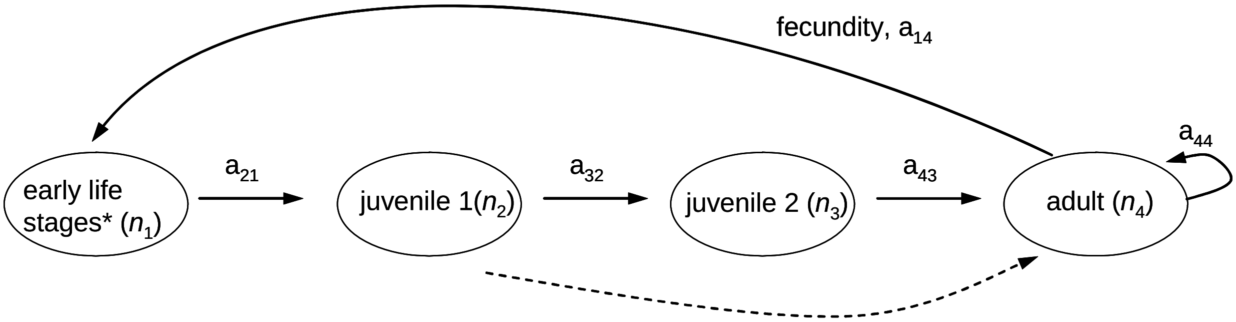
A composite approach, utilizing information from several different watersheds, is employed because different amounts and types of data are available for each individual population. By combining data from several populations, the recommended minimum criteria for conducting *Population Viability Analyses* (PVA's) are met (Table 2.1 and Morris and Doak 2002). Morris et al. (1999) admonish researchers and managers that the value of population viability analysis does not lie in the exact predictions of a single analysis (e.g. that a frog population will have a 50% chance of persisting for 30 years, a typical FERC license term). Rather "a better use of PVA in a world of uncertainty, is to gain insight into the *range* of likely fates of a single population based upon two or more different analyses (if possible), or the *relative* viability of two or more populations to which the same type of analysis has been applied." Despite the limitations of the techniques, PVA applied to 21 different time series from long-term ecological studies has shown a high degree of predictive accuracy. When parameters were estimated from the first half of each data set, and the second half was used to test the predictions of the models, the probability of population decline corresponded well with the observed outcomes (Brook et al. 2000).

**Table 2.1. Guidelines for minimum data requirements to perform population viability analyses (adapted from Morris and Doak 2002). The shaded boxes represent the types of data used here for the *R. boylii* population modeling scenarios.**

| Type of PVA | Data Needed | Applications |
|---|---|---|
| deterministic count-based | >10 years of census/count data | qualitative representation of population status – i.e. declining, growing, relative viability of one population vs. another |
| stochastic demographic | > 4 years of vital rate data (= 3 annual transitions) | provides enough information to develop means, variances, covariances of vital rates for a fully parameterized demographic model |
| sensitivity analyses for deterministic models | < 4 years vital rate data | allows evaluation of management actions and threats |
| multi-site PVA<br>* stochastic with migration among subpopulations | 2 years presence / absence surveys at 20+ sites<br>* 4 years | allows evaluation of population status across a landscape |

## 2.2. Model Statement

A simple 4-stage annual matrix model ($A_t$) of female *R. boylii* life history including three juvenile stages and one adult stage was created (Figures 2.1 and 2.2). Composite annual transition probabilities between stages ($a_{ij}$) often incorporate the survival rates of several distinct life history stages (Table 2.2). For example, the transition from birth to the end of the first year ($a_{21}$) encompasses survival through egg mass stranding and scouring, embryonic and larval development, metamorphosis, and the first winter as a newly transformed juvenile frog. For each component of these composite annual transitions, a distribution of survival rates from the mean and variance of multiple data sources were estimated (Table 2.2), drawing primarily on data collected from populations in hydrologically unregulated California rivers (Appendix A). The distributions of survival values for each component life-stage transition (signified as $s_{stage}$ in Table 2.2) were modeled as beta distributions, except for fecundity, which was modeled as a lognormal distribution (Morris and Doak 2002). This matrix population model was initially



* embryo strand/scour rate x embryo survial to hatching x tadpole survival to metamorphosis x overwintering juvenile

**Figure 2.1. Life stages and transition probabilities included in the matrix model. Annual transition probabilities are designated by $a_{ij}$, where j=initial life stage and i=subsequent life stage. For example, $a_{32}$ = the probability of transitioning (surviving) from juvenile 1 to juvenile 2; $n_i$'s represent starting population vector values. The dotted line represents the 2 year maturity life history hypothesized to occur in some central coast populations.**

Northern California

$$N_{t+1} = \text{TO CLASS (i's)} \overset{\text{FROM CLASS (j's)}}{\underbrace{\begin{bmatrix} 0 & 0 & 0 & a_{14} \\ a_{21} & 0 & 0 & 0 \\ 0 & a_{32} & 0 & 0 \\ 0 & 0 & a_{43} & a_{44} \end{bmatrix}}_{\text{matrix of transition probabilities}}} \times \overset{N_t}{\underbrace{\begin{bmatrix} n_1 \\ n_2 \\ n_3 \\ n_4 \end{bmatrix}}_{\text{population vector}}}$$

Central California

$$N_{t+1} = \begin{bmatrix} 0 & 0 & a_{13} \\ a_{21} & 0 & 0 \\ 0 & a_{32} & a_{33} \end{bmatrix} \times \begin{bmatrix} n_1 \\ n_2 \\ n_3 \end{bmatrix}$$

**Figure 2.2. Matrix model elements and framework for matrix algebra used in calculations for northern California (3 years to maturity) and central coastal California (2 years to maturity) models.**

used to simulate the dynamics of a generic *R. boylii* population in a 10 km reach of an unregulated environment (referred to as the "Reference Model") by drawing transition probabilities at random from the beta or log-normal distribution of each component life-stage, each year for 30 years, following the population size of adult females through time, and calculating the average 30 year population growth rate (lambda, $\lambda_s$). A 10 km reach was chosen to represent a typical *R. boylii* population based on recent genetic (mtDNA, RAPD) evidence demonstrating significant isolation by distance between individuals greater than 10 km apart (Dever 2007). Ten km is also close to typical reach lengths between dams (see Table 2.11). A 30 year simulation window was chosen to represent the typical length of a U.S. Federal Energy Regulatory Commission (FERC) hydroelectric dam license.

As with most amphibians, there are only sparse demographic data for *R. boylii*, primarily from several short-term studies of different populations, and existing studies have not estimated more than one or two demographic rates simultaneously. The choice to pursue stochastic demographic modeling was favored despite this shortcoming for the opportunity to evaluate scenarios of how hydrologic regulation may specifically affect individual life stages and component vital rates. As a result, this modeling effort is constrained to relatively simple stochastic simulations, and is subject to a high level of uncertainty in the estimates of individual vital rates, their distributions, and the resulting population dynamics. A strong cautionary perspective is required when interpreting these modeling results and should be restricted to the relative performance of individual models compared to the reference condition, for which there are the most extensive (but still limited) demographic data. In general, each scenario we explore beyond the reference model is based on quantitative data (when possible) of likely impacts of hydrologic regulation to different life stages (or combinations), but none the less should be considered exploratory and not a representation of any particular 'real' *R. boylii* population.

The Reference Model was initiated (year 1) with a starting population vector ($N_t$) defined as the number of individuals in each life stage, determined from the combination of a starting number of 320 adult females ($n_4$) and the average vital rates (i.e. births and deaths) for each life stage. The starting population vector therefore represents a population beginning at a stable age distribution of individuals across life stages. The starting number of adult females for the reference model is estimated from the average number of egg masses found in unregulated rivers (see compilation of unpublished and published data in Table 2.12; average 32 clutches/km x 10 km hypothetical reach). As such, the starting number of adult females is a parameter with multiple long-term (>5 yrs.) estimates from both un-regulated (reference) and regulated conditions. Because of the range of values that each life stage transition encompasses, the results of any one run of this model (with only 30 random draws of each life-stage transition) are not expected to be broadly representative. To incorporate the uncertainty and variability within and among life-stage transitions, the 30-year model was simulated 10,000 times, and the average stochastic population growth rate ($\lambda_s$) and the probability that the *R. boylii* population drops below a quasi-extinction threshold are reported (Morris and Doak 2002). Quasi-extinction thresholds are often used in population dynamics models to represent a minimum viable population size, below which populations may be exceedingly vulnerable to stochastic genetic and demographic (Allee) effects and also below which accurate forecasting of population dynamics becomes extremely questionable (e.g. that at very low densities populations are likely to be governed by very different demographic rates and processes). Morris and Doak (2002) suggest applying quasi-extinction thresholds of at least 20 breeding individuals, but a more conservative approach for populations of conservation concern would be to set the threshold at the lowest density of a known stable population (based on long-term time series data). For the Reference Model, the quasi-extinction threshold was set to two adult females per river km, or 20 adult females in the simulated population occurring within a hypothetical 10 km reach. This quasi-extinction value generally falls at the low end of the range of observed females (or egg mass proxies) in populations that appear stable or even increasing (SF Eel, 107 females/km, Ten Mile Cr., 13 females/km, Alameda Creek, Camp Ohlone reach 20 females/km), and those that are likely to be more vulnerable demographically (NF Feather, Cresta reach, 2 females/km, Alameda Creek below Calaveras dam, 3 females/km).

Because of the paucity of demographic data for *R. boylii*, neither correlation among vital rates nor density dependent functions were incorporated into the model structure, as is otherwise suggested by many authors. Ignoring the potential for correlation among variables implies that the vital rates for each life-stage (*s*) are independent of one another. For example, such independence implies that a 'good' year for embryonic survival is not necessarily a 'good' year for larval, juvenile, or adult survival. Without more extensive demographic data collected across a number of years for each life stage simultaneously, the consequences of this simplifying assumption cannot be completely evaluated. However, based on first principles, some level of both positive and negative correlation is expected to exist among at least some of the vital rates, though we have not detected any significant auto-correlation in lambda from existing time-series data as might be expected if correlations among vital rates were particularly strong. We tested for auto-correlations among lambda values at lag times of 1-4 years for five *R. boylii* populations with 5 or more continuous years of egg mass censuses (SF Eel, TenMile Ck, Alameda Creek-Camp Ohlone reach, NF Feather-Poe reach, and NF Feather-Cresta reach, Kupferberg et al. *unpublished data*) and none were significant. Similarly, the assumption of density-independent survival for each life stage may also be expected to potentially affect the resulting population dynamics simulated by the reference model. Empirical evidence suggests that most amphibians experience strong density dependent growth and survival primarily during aquatic larval stages (Brockelman 1969, Wilbur 1976, 1977). However, for *R. boylii* in particular, there is very little evidence to suggest the prevalence of a larval density-dependent bottleneck (Kupferberg 1997, Kupferberg *unpublished*). Kupferberg (1997) experimentally manipulated *R. boylii* larvae as part of a competition experiment with Pacific treefrogs (*Pseudacris regilla*) and Bullfrogs (*R. catesbeiana*), and found no change in *R. boylii* survival when reared alone at two densities at the high end of naturally observed densities, 28/m$^2$ and 56/m$^2$ (Figure 2.3). Additionally, empirical evidence also indicates that there can be carry-over effects in Ranid frogs such that larval growth history has a strong influence on survival in subsequent stages (Altwegg 2003, Altwegg and Reyer 2003). However, we find no relationship between the number of clutches laid at individual breeding sites, a potential proxy for larval density, and the size of metamorphic frogs in August at the SF Eel river (Kupferberg *unpublished*, Figure 2.4), suggesting that carry-over effects due to larval density may be uncommon.

The remainder of this section provides the methods for estimating each vital rate included in the Reference Model, along with details of the particular demographic scenarios explored with this model to evaluate the potential consequences of hydrologic modification on the overall dynamics of *R. boylii* populations. The scenarios are grouped into three categories: (1) modifications of starting conditions and evaluation criteria, (2) modifications to vital rates, and (3) combination models (Table 2.3).

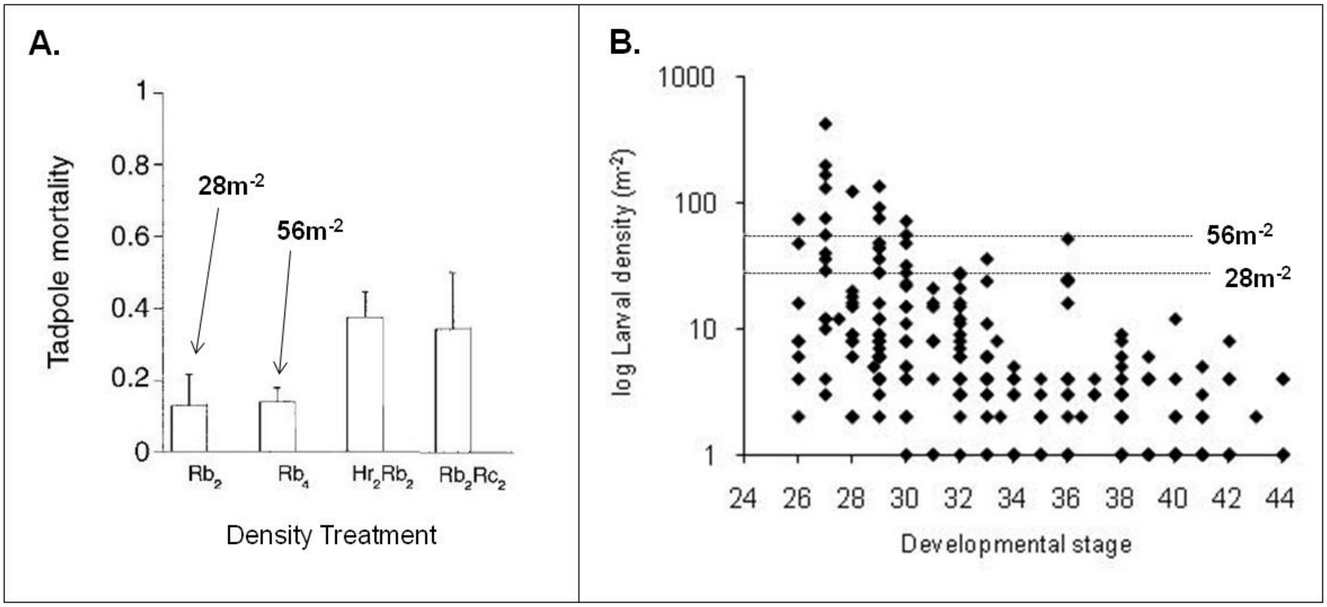


**Figure 2.3. Tadpole mortality (A) in mesocosm experiments conducted at the SF Eel (Kupferberg 1997) indicates that survival is not density dependent for single species groups of *Rana boylii (Rb)* tadpoles (Hr = *Hyla regilla,* Pacific treefrog Rc = *Rana catesbeiana,* Bullfrog). Experimental densities in enclosures (two or four tadpoles) equivalent to 28 and 56 individuals per m$^2$ are higher than the large majority of quadrat samples (B) measuring ambient tadpole density during the summers of 1992-1994. Tadpole densities are only that high early in the rearing season, when tadpoles are young and small, as indicated by Gosner stage.**

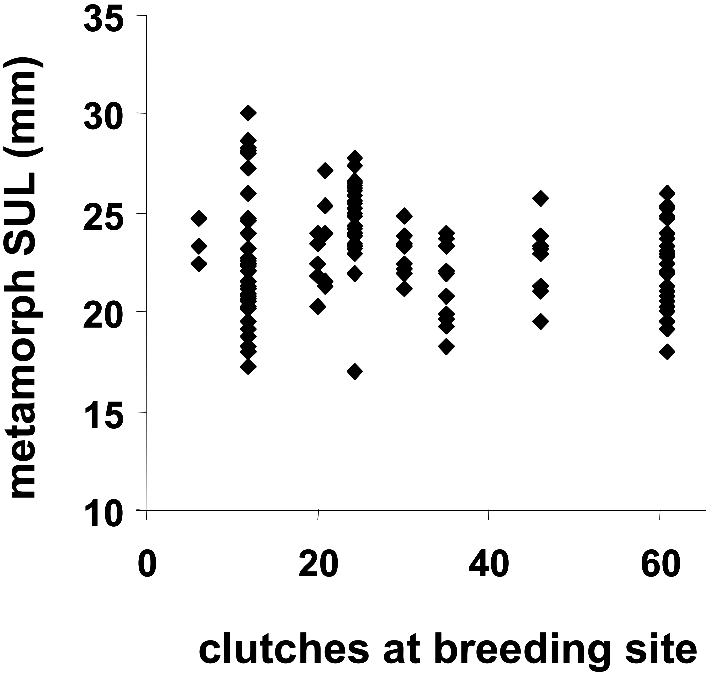


**Figure 2.4. Larval density, as indicated by the number of clutches laid at breeding sites in the South Fork Eel River during spring 2008 was not correlated with the size (Snout Urostyle Length) of recently metamorphosed frogs (n=159) captured at the same sites in late August.**

**Table 2.2. A life table for *Rana boylii* with a description of Reference Model transition probabilities and component vital rates.**

| Annual transition probability (aij) | Parameter estimation equation | Component life stage transitions | Mean (Var) | Data Source |
|---|---|---|---|---|
| early life stage survival, $a_{21}$ | $a_{21} = s_{embryo1}$ x $s_{embryo2}$ x $s_{embryo3}$ x $s_{tadpole}$ x $s_{yoy}$ | $s_{embryo1}$= stranding survival | 0.96 (0.002) | SF Eel 1992-2007 |
| | | $s_{embryo2}$ = scouring survival | 0.80 (0.089) | SF Eel 1992-2007 |
| | | $s_{embryo3}$ = hatching of embryos into tadpoles | 0.83 (0.04) | baskets in SF Eel, Alameda, NFFR |
| | | $s_{tadpole0}$ = background tadpole to metamorphosis | 0.15 (0.03) | SF Eel 1992, 2006, 2008; Alameda 2006 |
| | | $s_{tadpole1}$ = tadpole survival through 1 pulse | 1[1] | |
| | | $s_{tadpole2}$ = tadpole survival through 2 pulses | 1[1] | |
| | | $s_{tadpole3}$ = tadpole survival through 3 pulses | 1[1] | |
| | | $s_{tadpole4}$ = tadpole survival through 4 pulses | 1[1] | |
| | | $s_{yoy}$= metamorphosis and over-wintering of young of the year frogs | 0.37 (0.020) | Funk et al. 2005; Berven 1990; Boone 2005; Altwegg 2003; Altwegg and Reyer 2003; Harper and Semlitsch 2007 |
| juvenile$_1$ survival, $a_{32}$ | $a_{32} = s_{juv1}$ | $s_{juv1}$ = juvenile$_1$ to juvenile$_2$ | 0.26 (0.038) | Scott, Rathburn, and D'Amore (unpublished data: *R. draytonii* in San Simeon, Pico Crks.) |
| juvenile$_2$ survival, $a_{43}$ | $a_{43} = s_{juv2}$ | $s_{juv2}$ = juvenile$_2$ to adult [2] | 0.54 (0.055) | Wheeler, Hurdygurdy Creek 2002-06 |
| adult survival, $a_{44}$ | $a_{44} = s_{adult}$ | $s_{adult}$ = adult to adult | 0.54 (0.055) | Wheeler, Hurdygurdy Creek 2002-06 |
| female embryos, $a_{14}$ | $a_{14} = s_{adult}$ x fecundity | fecundity = egg mass size x sex ratio | 871 (98,412) | counts (SF Eel, Alameda, NFFR) |

1. Tadpole survival with 1,2,3, and 4 pulses is set to 1 (100%) because there are no summer pulses in the Reference Model.

2. This lifestage was eliminated for scenarios modeling a 2 year to maturity life history.

**Table 2.3. Modeled scenarios for *Rana boylii* populations. The scenarios are grouped into five categories: reference models, models addressing starting conditions and evaluation criteria (e.g., starting population size), models where vital rates are modified, combination models for 3 year maturity populations and combination models for the Central Coast, 2 year maturity, populations. Each scenario is named and the specific parameter values used for that scenario are presented.**

| Model Number | Scenario | Components Manipulated |
|---|---|---|
| **Reference Models** | | |
| 1 | Reference Model | None |
| 2 | Central Coast populations reference | None |
| **Modified Starting Conditions and Evaluation Criteria** | | |
| **Starting population vector ($N_t$)** | | **(**$N_0 = [n_1, n_2, n_3,$ **$n_4$**] ) |
| 3 | Regulated starting population | $N_0$ = [1130  297  160  **46**] |
| 4 | Eel River starting population | $N_0$ = [32098  8440  4558  **1050**] |
| 5 | North Fork Feather River (Cresta reach) starting population | $N_0$ = [642  169  91  **21**] |
| **Extinction threshold** | | |
| 6 | Low quasi-extinction threshold | q.e. = 10 (1 adult female / km) |
| 7 | High quasi-extinction threshold | q.e. = 40 (4 adult females / km) |
| **Modified Vital Rates Scenarios** | | |
| **Spring flow** | | |
| 8 | Regulated embryonic strand & scour | $\mathbf{s}_{embryo1}$= 0.90 (0.04), $\mathbf{s}_{embryo2}$= 0.77 (0.14) |
| 9 | Worst case embryonic strand & scour | $\mathbf{s}_{embryo1}$= 0.52 (0.002), $\mathbf{s}_{embryo2}$= 0.43 (0.155) |
| 10 | Reduced fecundity (11%) | f = 778 (59181) |
| 11 | Reduced fecundity (20%) | f= 700 (69462) |
| 12 | Combine 9 & 10 | $\mathbf{s}_{emb1}$= 0.52 (0.002), $\mathbf{s}_{emb2}$= 0.43 (0.155), f = 778 (59181) |
| 13 | Combine 9 & 11 | $\mathbf{s}_{emb1}$= 0.52 (0.002), $\mathbf{s}_{emb2}$= 0.43 (0.155), f= 700 (69462) |
| **Summer flow** | | |
| 14 | Increase base flow, lower temperatures | $\mathbf{s}_{tadpole0}$ = 0.13 (0.03) |
| 15 | High mortality summer pulse (.46) x1 | $\mathbf{s}_{tadpole1}$ = 0.46 (0.03) |
| 16 | High mortality summer pulse (.46) x1, scour algae | $\mathbf{s}_{tadpole0}$ = 0.11 (0.03), $\mathbf{s}_{tadpole1}$ = 0.46 (0.03) |
| 17 | High mortality summer pulse (.46) x2 | $\mathbf{s}_{tadpole1-2}$ = 0.46 (0.03) |
| 18 | High mortality summer pulse (.46) x3 | $\mathbf{s}_{tadpole1-3}$ = 0.46 (0.03) |
| 19 | High mortality summer pulse (.46) x4 | $\mathbf{s}_{tadpole1-4}$ = 0.46 (0.03) |
| 20 | Low mortality summer pulse (.61) x1 | $\mathbf{s}_{tadpole1}$ = 0.61 (0.03) |
| 21 | Low mortality summer pulse (.61) x1, scour algae | $\mathbf{s}_{tadpole0}$ = 0.11 (0.03), $\mathbf{s}_{tadpole1}$ = 0.61 (0.03) |
| 22 | Low mortality summer pulse (.61) x2 | $\mathbf{s}_{tadpole1-2}$ = 0.61 (0.03) |
| 23 | Low mortality summer pulse (.61) x3 | $\mathbf{s}_{tadpole1-3}$ = 0.61 (0.03) |
| 24 | Low mortality summer pulse (.61) x4 | $\mathbf{s}_{tadpole1-4}$ = 0.61 (0.03) |

| Model Number | Scenario | Components Manipulated |
|---|---|---|
| **Combination Models** | | |
| 25 | *R. boylii* decline history (9, 15) | - |
| 26 | *R. boylii* decline history (9, 10, 15) | - |
| 27 | *R. boylii* modern regulated (5,8) | - |
| 28 | *R. boylii* modern regulated (5,8,15) | - |
| 29 | *R. boylii* modern regulated (5,8,17) | - |
| **Central Coast Populations Combination Models** | | |
| 30 | Regulated starting population | $N_0$ = [1406  370 46] |
| 31 | Regulated embryonic strand & scour (30) | $\mathbf{s}_{embryo1}$= 0.90 (0.04), $\mathbf{s}_{embryo2}$= 0.77 (0.14) |
| 32 | Worst case embryonic strand & scour (30) | $\mathbf{s}_{embryo1}$= 0.52 (0.002), $\mathbf{s}_{embryo2}$= 0.43 (0.155) |

## 2.3. Vital Rate Estimation for Each Life Stage

This section provides a detailed description of how vital rates were determined for each life stage including:  adult female fecundity, embryo background hatching rate, embryo (egg mass) scour and stranding rates, tadpole survival to metamorphosis, first over winter survival, juvenile survival, and adult survival. First, several long-term data sets for *R. boylii* that were used in the derivation of several vital rates are described. Following that, each major subsection covers a particular vital rate and includes: (1) information on how data for that rate was obtained (e.g., field study or literature search), (2) the manner in which data were applied to the Reference population model, and (3) a description of any model scenarios that were run by altering the reference value for that vital rate.

### *2.3.1. Long-term censuses of* Rana boylii *egg masses*

*Rana boylii* population monitoring was conducted in three watersheds, in the form of annual egg mass surveys. These egg mass surveys were used in the estimation of several parameters and vital rates including; starting population size, embryonic survival, and adult fecundity. Each of these parameter and rates are detailed in subsequent sections below. In Alameda Creek censuses were supervised by Steve Bobzein, Ecological Services Coordinator, East Bay Regional Parks District, beginning 1997 in the Camp Ohlone Reach and in 2003 for the reach in proximity to the Calaveras Creek confluence (Bobzein and DiDonato 2007). In the NF Feather, censuses began in 2001 for the Poe reach and 2002 for the Cresta reach. Censuses were conducted by Garcia & Associates for PG&E and for the California Energy Commission Pulsed Flow Program. NF Feather data compiled here are from several reports (GANDA 2003; 2004a; 2004b; 2004c; 2004d; 2006; 2007). At the SF Eel, Kupferberg began annual censuses in 1992 and continued through 2007. Similar search techniques were used in all three systems, with multiple visits per season, at intervals ≤ two weeks. View boxes or mask and snorkel were used and egg masses were marked to prevent double counting.

The number of egg masses found each year was used as an index of the number of breeding females. Using the number of egg masses as an estimator of population size is an accepted method for *Ranid* frogs (Crouch and Patton 2000; Loman and Andersson 2007; Petranka et al. 2007), which produce single discrete egg masses and spawn once in a year. Drift fence studies for pond breeding Ranids show very close correspondence between the number of egg masses and the number of female frogs (Couch and Patton 2000). Capture-recapture estimates for adult female population size for *R. boylii* in one small Sierran creek, Clear Ck., are in close correspondence to numbers of egg masses found (Van Wagner 1996).

### 2.3.2. Adult Female Fecundity and Background Embryo Survival

Two vital rate distributions, the proportion of embryos successfully hatching into tadpoles and the number of eggs laid by a female frog, were derived empirically by *in situ* rearing egg masses at the SF Eel, Alameda Creek, and NF Feather. To understand trends of egg mass size in relation to oviposition date and to relate egg mass volume to number of individual eggs, sets of egg masses were placed in flow through enclosures at each successive site visit. So as to disturb a minimum number of egg masses, yet obtain as much information as possible on temporal variation in fecundity, the dimensions of all recently laid egg masses were measured to calculate egg mass volume. The information on temporal variation in fecundity was used to develop model scenarios concerned with the timing of egg mass loss when pulsed flows occur.

The basic method of embryo data collection, conducted during the spring of 2007, involved placing recently laid egg masses in flow through enclosures (one per enclosure), rearing to hatching, counting all tadpoles and unhatched embryos, and then releasing the tadpoles. Enclosures were plastic laundry baskets, or buckets with windows cut out, with 1mm fiberglass mesh glued over the openings. After hatching, individuals were transferred in batches (up to a few hundred at a time) to white plastic trays and enumerated using tally counters and released to their natal environment. Un-hatched embryos were returned to the enclosures to continue developing. If they did not develop after several visits the embryos were considered not viable, and counted as mortality. To quantify the relationship between egg mass volume and egg number, the dimensions (length, width, and depth) of recently laid egg masses were measured to the nearest 0.5 cm using a ruler. Egg mass volume was calculated using the formula for a sphere using the median axis of the egg mass as a radius (volume = $(4/3)*\prod*((0.5*\text{median axis})^3)$). Analysis of covariance was used to assess differences in fecundity among populations.

A total of 56 egg masses were successfully reared to hatching and counted (Table 2.4). Generally, larger volume egg masses have more embryos (Figure 2.5), and analysis of covariance indicates that egg mass size differences among the populations are statistically significant (Table 2.5). Alameda Creek frogs produce more embryos than SF Eel and NF Feather individuals. The significant interaction between site and egg mass volume suggests that there may be variation in individual egg size from different populations, where more small eggs occur in the same volume as fewer large eggs. Further, this site by volume interaction may also be explained if egg masses were systematically found closer to the time of laying in some populations than others, which would result in a different relationship between volume and egg number due to the swelling that occurs after initial deposition (Rombough and Hayes 2005).

### *2.3.2.1. Application to the Population Model – Reference Values*

The Reference Model accounts for the dynamics of only female individuals. Assuming a 50:50 sex ratio, the number of eggs in each egg mass was divided by two, and the mean and variance calculated from the resulting number of embryos in "half egg masses" is 871, var= 98,413 (Table 2.4). Background embryonic survival, not including egg mass stranding or scouring (see 2.3.3 below), was estimated from mean survival to hatching inside the flow-through enclosures across all three populations (0.83, var = 0.04, Table 2.4).

**Table 2.4. Fecundity and survival to hatching of *Rana boylii* in the study watersheds. To represent the number of female embryos, the total number of embryos was divided by two; assuming a 50:50 sex ratio in each egg mass.**

| | Alameda | SF Eel | NF Feather | 3 Site Mean |
|---|---|---|---|---|
| **Mean # of embryos / 2** | 1078 | 763 | 745 | 871 |
| **Variance of embryos / 2** | 76989 | 94596 | 44369 | 98413 |
| **Sample size** | 20 | 23 | 13 | 56 |
| **Mean (proportion) survival to hatching** | 0.83 | 0.82 | 0.84 | 0.83 |
| **Variance of survival to hatching** | 0.05 | 0.04 | 0.03 | 0.04 |

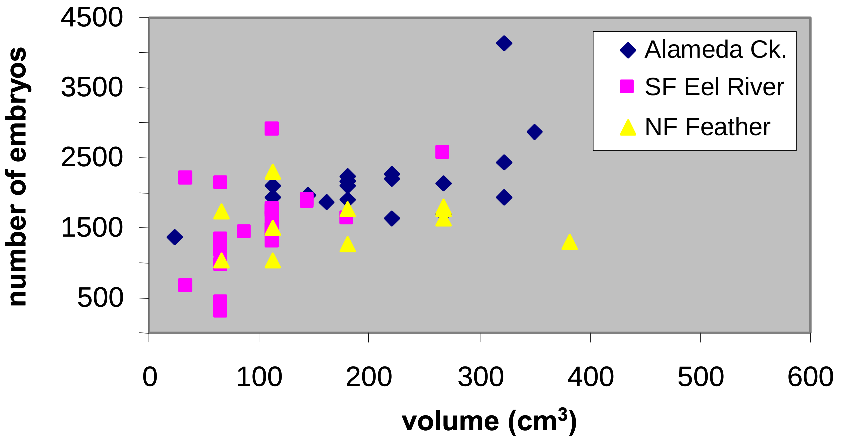


**Figure 2.5. Embryo number as a function of clutch volume, calculated using the median axis of the clutch as the diameter of a sphere.**

**Table 2.5. Analysis of covariance of embryo number, n=55 clutches. One NF Feather clutch was excluded due to its advanced Gosner stage when first measured compared to other clutches. Multiple R = 0.66, multiple $R^2$= 0.44.**

| Source | Sum-of-Squares | df | Mean-Square | *F* ratio | *P* |
|---|---|---|---|---|---|
| Clutch Volume | 2009158.348 | 1 | 2009158.348 | 10.999 | 0.002 |
| Site | 1711676.000 | 2 | 855838.000 | 4.685 | 0.014 |
| Site*Clutch Volume | 3248993.146 | 2 | 1624496.573 | 8.893 | 0.001 |
| Error | 8950728.856 | 49 | 182667.936 | | |

### *2.3.2.2. Model Scenarios*

There is a trend that larger females breed earlier. Decreasing egg mass volume over time as the breeding season progresses was observed at both the SF Eel and Alameda Creek (Figure 2.6). This result is consistent with a previously observed pattern among *R. boylii* from the NF Feather River where larger females appear at breeding sites at the beginning of the breeding season and smaller females subsequently (GANDA 2008). This pattern is relevant for understanding the demographic consequences of pulsed flow timing on *R. boylii* populations. Models (10) and (11) explore scenarios to evaluate the potential population-level consequences of this loss by reducing the distribution of fecundity values by 11% and 20% (Table 2.3).

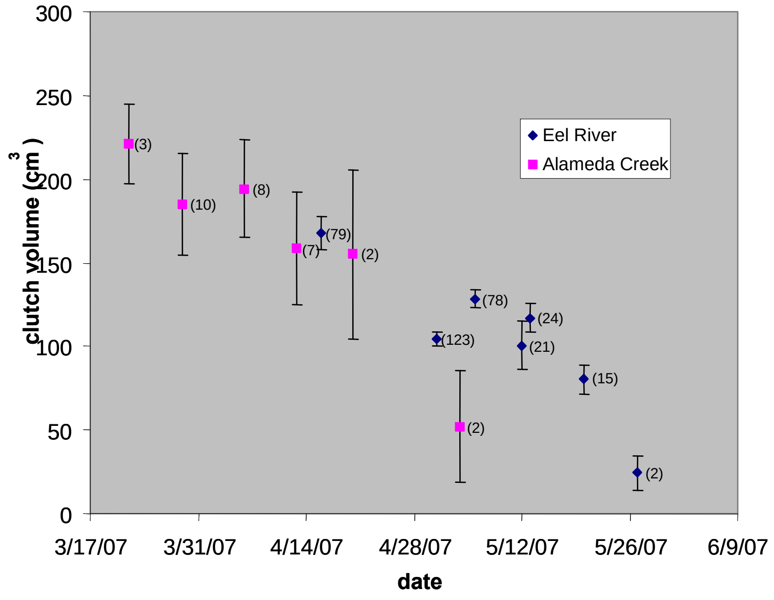


**Figure 2.6. Earliest laid clutches are larger than those laid later in the spring. Sample size of clutches observed at Gosner stage 13 or below on particular dates in parentheses (Gosner 1960).**

### *2.3.3. Survival of Stranding or Scouring events*

In addition to the background rate of survival to hatching, the fate of whole egg masses was modeled to capture a potentially important source of hydrologically-induced mortality. Such mortality in unregulated rivers represents natural variation in hydrologic conditions during embryonic incubation. In regulated rivers, this variation is determined primarily by water release schedules and hydropower management. Based on observations from both the long-term SF Eel data set and more recent egg mass surveys in regulated rivers, distributions of mean annual egg mass scouring rates (due to flow increase) and stranding (due to flow decrease), $s_{emb1}$ and $s_{emb2}$, respectively were developed.

#### *Application to the Population Model – Reference Values*

Reference rates of egg mass scour due to flooding during spring spates and stranding (dessication) due to rapidly falling water stage was quantified for the SF Eel (1992-2007). In some years, direct observations of the fate of each marked egg mass was followed (1992, 1994-1996, 2003, 2005-2007) and the proportion of total egg masses surviving scouring and stranding was calculated. For the other eight years, stranding and scouring survival were estimated by matching the hydrologic conditions (as determined from hydrographs, rainfall records, and lay dates) to the most similar year among those with data on individual egg mass fates and assigning the same survival rates. Across the entire time series from the SF Eel, the 16 year mean (var) annual survival of egg masses through stranding conditions was 0.956 (0.0024), and survival through scouring conditions was 0.802 (0.089). The distribution of annual survival rates (Figure 2.7) emphasizes that most years have little stranding or scouring (survival near 1) punctuated with occasional years of late spring spates (scouring >60% of egg masses) or dry spring conditions leading to rapidly falling stage. Annual survival due to stranding or scouring was modeled as two component vital rates ($s_{emb1}$ $s_{emb2}$) which can then be manipulated in the altered hydrologic scenarios below in section 2.3.3.2.

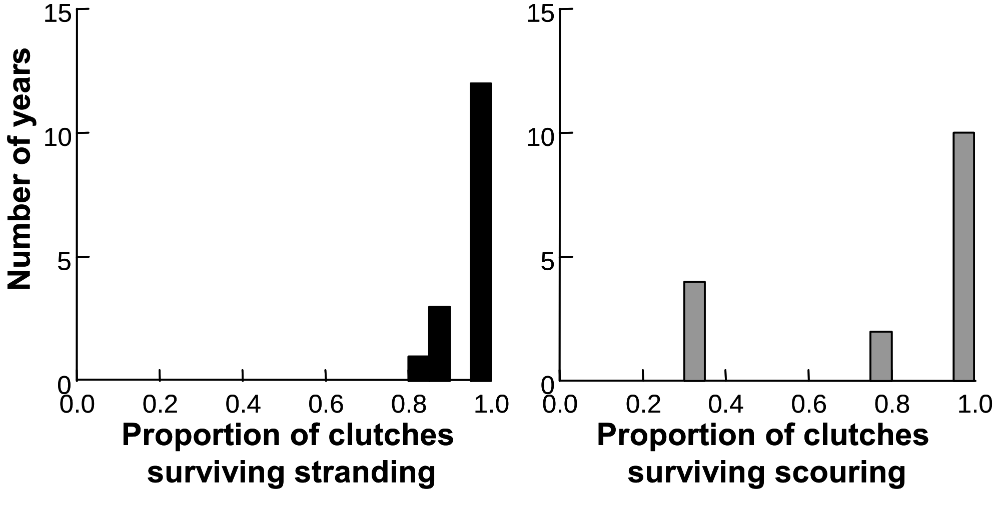


**Figure 2.7. Distribution of survival rates of *R. boylii* egg masses in relation to hydrologic stressors, i.e. stranding or scouring, over 16 years at the SF Eel River.**

### *Model Scenarios*

Distributions of $s_{emb1}$ and $s_{emb2}$ for regulated rivers were estimated using observations of stranding and scouring mortality (due to aseasonal manufactured pulses and flow cessation) in four different rivers (Table 2.6; see Kupferberg et al. 2008, Ch. 2, Table 2.1 and GANDA 2008 for details). Two scenarios represent the conditions present in regulated rivers; model (8) represents the full range of stranding and scouring conditions present in regulated rivers including years in which no pulsed flows or flow cessation occurs, and model (9) represents a worst-case scenario of stranding and scouring assuming that anthropogenic pulsed flows or flow cessation occurs every year during oviposition and incubation (Tables 2.3 and 2.6).

Additional simulations were constructed to explore the combination effects of hydrologically modified spring flow conditions (see above, models 8 & 9) and the possibility that these flow events may disproportionately affect the most fecund females in the population as they tend to breed earlier in the spring (see 2.3.1.2 above). If mortality-inducing spills from dams occur most often early in the spring, then the contributions of most fecund individuals to future generations may be the most in jeopardy. Models (12) and (13) build on and can be compared to models 10 and 11 by incorporating the observation that egg masses laid earlier in the season have more eggs per clutch. Were these early clutches to be scoured, the number of eggs per clutch of remaining breeders would be smaller (by 11% and 20%). For example, based on embryo counts from the SF Eel and Alameda Creek, if the clutches laid during the first week of a seven week breeding season were eliminated (approximately the first 15% of the breeding period), the mean fecundity (eggs per clutch) drops from the reference value of 871 to 778 (value used in model 10). If the clutches laid during the first 30% of the duration of the breeding season are lost, the mean fecundity drops to 700 (value used in model 11; Table 2.3).

**Table 2.6. Hydrologic effects on persistence of egg masses observed in four regulated rivers (5 river reaches).**

| River Reach | Year | Flow Effect | Number of Clutches | Proportion Not Scoured | Proportion Not Stranded |
|---|---|---|---|---|---|
| Pit 4 | 2002 | aseasonal pulsed flow | 25 | 0.32 | 1.00 |
| Trinity | 1991 | aseasonal pulsed flow | 31 | 0.00 | 1.00 |
| Trinity | 1992 | aseasonal pulsed flow | 28 | 0.00 | 1.00 |
| Trinity | 1994 | no pulsed flow | 24 | 1.00 | 1.00 |
| SF American | 2004 | flow cessation | 7 | 1.00 | 0.57 |
| NF Feather (NFF) Cresta | 2002 | aseasonal pulsed flow | 10 | 0.50 | 1.00 |
| NFF Cresta | 2003 | no pulse flow | 28 | 1.00 | 1.00 |
| NFF Cresta | 2004 | no pulse flow | 31 | 1.00 | 1.00 |
| NFF Cresta | 2005 | no pulse flow | 22 | 1.00 | 1.00 |
| NFF Cresta | 2006 | flow cessation | 4 | 1.00 | 0.50 |
| NFF Poe | 2002 | no pulse flow | 28 | 1.00 | 1.00 |
| NFF Poe | 2003 | “natural” high flows | 48 | 0.85 | 1.00 |

| River Reach | Year | Flow Effect | Number of Clutches | Proportion Not Scoured | Proportion Not Stranded |
|---|---|---|---|---|---|
| NFF Poe | 2004 | no pulse flow | 47 | 1.00 | 1.00 |
| NFF Poe | 2005 | “natural” high flows | 63 | 0.89 | 1.00 |
| NFF Poe | 2006 | flow cessation | 88 | 1.00 | 0.48 |
| | **Model (8)**<br>mean (var) all years | | | **0.771 (0.140)** | **0.903 (0.040)** |
| | **Model (9)**<br>mean (var) for pulse / flow cessation years only | | | **0.427 (0.155)** | **0.517 (0.002)** |

### *2.3.4. Survival of Tadpoles to Metamorphosis*

To derive the mean value and distribution of tadpole to metamorphosis survival ($s_{tadpole0}$), two contrasting approaches were employed. The first approach relies on estimating *R. boylii* survival to metamorphosis using data collected from rearing experiments conducted in enclosures (Kupferberg 1997; Kupferberg et al. 2008; Catenazzi and Kupferberg unpublished data). Due to the confined nature of these enclosure experiments (no opportunity for dispersal, reduced vulnerability to predators, etc.), estimates derived from these experiments are likely at the high end of the range of survival rates. The experiments included trials with invertebrate predators present (Kupferberg 1997; Kupferberg et al. 2008, section 4), as well experiments in which predators were excluded (Catenazzi and Kupferberg unpublished data).

The second approach combines mark-recapture data sets from the SF Eel and Alameda Creek to estimate survival to metamorphosis of a cohort of wild individuals laid as eggs in a given river reach. This approach may underestimate survival to metamorphosis because of dispersal away from the natal stream reach. The data sets are: (1) egg mass sampling in spring 2006 (see Section 2.3.1), (2) fecundity and embryo survival estimates from 2007 (see Section 2.3.2), and (3) population size and daily survival rates of newly metamorphosed *R. boylii* collected in fall of 2006 (Appendix B).

Seven steps of calculations were used for the second approach. In step (1), the starting number of eggs was calculated (= total # egg masses observed * average #/mass). For step (2) the initial number of tadpoles was estimated (= total eggs x background survival x stranding/scouring). In step (3) the population size of newly metamorphic (young of the year) *R. boylii* was estimated from the 3-day capture-recapture efforts and was based on the “best” population estimate model from Program CAPTURE (Otis et al. 1978; White et al. 1982; see Appendix B for detailed methods). Because the population sizes of young of the year frogs was conducted several weeks after the bulk of metamorphosis occurred (i.e. only a few tadpoles were remaining in the river), the population estimate needed to be adjusted to account for those individuals that did not survive the first several weeks of life as frogs. For step (4) the median date of metamorphosis was estimated and for step (5) the days elapsed between that date and the first date of capture-recapture work in fall determined. At

Alameda Creek, that date was determined by the median date of metamorphosis observed among individuals in a rearing experiment (see Kupferberg et al. 2008, Section 4). At the SF Eel the median date was determined based on the ratio of tadpoles to young of the year frogs located during field sampling conducted mid-August. In step (6) the population estimate for young of the year frogs (from step 3) was adjusted to the population size at metamorphosis by back-calculation using the highest daily survival rate generated by Program MARK (White and Burnham 1999; Cooch and White 2007) for the capture recapture data (see Appendix B for details). For step (7), to get the final tadpole survival rate to metamorphosis, the adjusted population size generated in the previous step (5) was divided by the starting number of hatchlings derived in step (2). Table 2.7 shows the step by step calculations for each study area.

**Table 2.7. Steps to determine *Rana boylii* tadpole to YOY Survival based on 2006 and 2007 field data.**

| Steps | SF Eel River | Alameda Creek |
|---|---|---|
| 1. number of eggs = # egg masses * average #/mass) | 210546.6 | 109986.600 |
| 2. Background survival to hatching rate | 0.819 | 0.828 |
| 3. Initial # tadpoles | 172437.7 | 91068.9 |
| 4. YOY population size estimate (± S.E.) | 622 ± 24.3 | 1717 ± 889.2 |
| 5. Median date of metamorphosis<br>1st date of cap-recap:<br>Days elapsed | 25 Aug 2006<br>16 Sept 2006<br>22 | 17 Aug 2006<br>4 Oct 2006<br>47 |
| 6. Adjusted YOY population estimate | 2603 | 3664 |
| 7. Tadpole to YOY survival rate | 0.0151 | 0.0402 |

### *Application to the Population Model - Reference Values*

Combining all available *R. boylii* data for the two study areas (Table 2.8), the average survival to metamorphosis was 0.15, with a variance of 0.03 (Table 2.2). The values of tadpole survival rate included in this calculation are comparable to the range of estimates made for other Ranid species (Calef 1973, Licht 1974).

**Table 2.8. *Rana boylii* tadpole survival to metamorphosis values used in overall estimate of this vital rate.**

| Approach | Survival to Metamorphosis | Data Source |
|---|---|---|
| Rearing experiments | 0.045 | SF Eel $2m^2$ enclosures of natural substrate, with competitors and predators (Kupferberg 1997) |
| | 0.33 | Alameda basket enclosures, with predators<br>(Kupferberg et al. 2008) |
| | 0.32 | SF Eel basket enclosures, without predators<br>(Catenazzi and Kupferberg, *unpublished data*) |
| Capture - recapture | 0.0151 | SF Eel 2006 |
| | 0.0402 | Alameda 2006 |

### *Model Scenarios*

To simulate the direct effects of elevated velocity on tadpole survival occurring during summer whitewater boating flows, short-term power generation, or emergency shut-downs, scenarios including 1, 2, 3, and 4 pulsed flows during tadpole rearing were created. Models (15-19) use an average tadpole loss rate of 53.7% (mean $s_{tadpole1-4}$ = 0.463 , var = 0.03) for each pulse, and as such each pulse was modeled as an additional vital rate, e.g. another sub-component of the first year transition probability. The vital rate $s_{tadpole1-4}$ and its variance were calculated based on the mean survival of tadpoles from five different studies of tadpole vulnerability to increased flows including experiments using a Brett chamber (@ 30 cm/sec), a large artificial flume (16-22 cm/sec), an in-stream flume (0-30 cm/sec), and an in-stream drift fence (0-70 cm/sec) (Kupferberg et al. 2008). Velocities used in these laboratory and field experiments were comparable to those seen in actual field pulse flows. For example, at the Pit River in 2002, test flows ranging from 5.25 cubic meters per second (cms; 150 cfs) base flow up to 33.98 cms (1200cfs) produced a range of velocities up to ~50cm/sec (most ~ 30cm/sec) (SpringRivers Ecological Sciences LLC 2002; Kupferberg et al. 2008). At the NF Feather in 2008, test flows from 7.08 to 16.99 cms (250 to 600cfs) produced a range up to ~55cm/sec (most measurements 18-37 cm/s, GANDA 2008). Given the level of uncertainty in estimating the form of the relationship between flow fluctuations and tadpole survival and the possibility that pulsed flows may be more and less severe, the above model scenarios were compared to a parallel set of models using the highest survival rate observed in the tadpole vulnerability studies listed above. Models (20-24) incorporate only the data from the large artificial flume experiments ($s_{tadpole1-4}$ = 0.61, var = 0.03; Table 2.3), where velocities ranged from 16-22 cm/s and on average 61% of tadpoles were able to maintain position.

The direct effects of flow velocity on tadpoles alone fail to consider two potentially important aspects of ecological complexity when discharge is increased in a regulated river; flow effects on algal resources, and flow effects on developmental temperatures. First, increases in current velocities are likely to negatively affect algal food resources as floating mats of algae and detritus are dislodged and transported to downstream reservoirs, and as attached algae can be scoured off of rock surfaces. To model the potential combined effects of both direct tadpole mortality with a single summer pulse and indirect mortality that may result from reduced food availability following the pulse, the background tadpole survival to metamorphosis rate ($s_{tadpole0}$) in models (16, high direct mortality) and (21, low direct mortality) was manipulated. These scenarios were guided by the results of tadpole rearing field experiments with contrasting food levels; either with only epilithic periphyton (i.e. low food quality and quantity) or with a combination of epilithic periphyton and abundant macroalgae and diatoms (Catenazzi and Kupferberg unpublished data). Epiphytic diatoms, especially taxa which contain cyanobacterial endosymbionts, represent a much higher quality diet for tadpoles (higher fat and protein) which is known to enhance survival, growth, and development (Kupferberg et al. 1994). When tadpoles were reared in flow through enclosures under identical conditions other than food level, there was a 27.8% decrease in survival from hatching to metamorphosis when loose algae with epiphytes was not present. Accordingly, the Reference Model value of $s_{tadpole0}$ was decreased by 27.8% to 0.108 in models (16) and (21) (Table 2.3).

A second potential indirect consequence of elevated discharge during the summer is lower instream temperatures which may affect tadpole growth, development, and survival. For example, if discharge/baseflow levels are increased to dampen effects of peaking or recreational boating pulse flows, water temperature is expected to decrease (releases are most often drawn from the hypolimnion of the upstream reservoir). While little data collection on thermal consequences of different base flow scenarios has been collected, the potential population consequences of colder summer water temperatures on tadpole survival were bounded using data from the recent tadpole rearing experiment described above. Tadpole experiments compare the survival of individuals raised at summer mean temperature of 18.8 C to those raised at 16.4 C using a natural gradient of stream water temperatures present in tributaries and the mainstem of the SF Eel R, which results in a 15% decrease in survival at cooler temperatures. Accordingly, model (14) uses a value of $s_{tadpole0}$ of 0.128 (15% lower than that used for the Reference Model, 0.15; Tables 2.2 and 2.3). While the results of this rearing experiment provide some guidance to the potential magnitude of temperature effects of higher base flows, the exact relationship between temperature and survival is likely to be complex and site-specific.

### 2.3.5. First Year Over-Winter Survival

This lifestage covers the time period from metamorphosis in late summer/early fall through winter and ends when frogs are essentially one year old.

#### Application to Population Model – Reference Values

Initial plans were to derive first year over-winter survival rates from field-based capture-recapture of newly metamorphic *R. boylii* marked in the fall and recaptured the following spring. While the capture-recapture field work was successful in fall 2006, capture rates the following spring (2007) were very low, leading to large uncertainties in estimates of over-winter survival. Appendix B describes the capture-recapture field methods and the steps for deriving over-winter estimates with the data collected. However, these estimates were not used in the Reference Model or any subsequent scenarios due to the large uncertainties and low capture-recapture rates in spring 2007. Alternatively, rates derived from a literature search on over-winter survival rates of newly metamorphosed Ranid frog species were used. A variety of studies provided estimates for various time periods starting from immediately post-metamorphosis to a maximum of one year later. Only those studies that covered the entire over-winter time period were used, and an average survival estimate was calculated from the following species and references: *Rana blairi, R. clamitans, R. lessonae, R. luteiventris*, *R. sphenocephala,* and *R. sylvatica* (Altwegg 2003; Altwegg and Reyer 2003; Berven 1990; Boone 2005; Funk et al. 2005; Harper and Semlitsch 2007). This provided a Reference Model estimate of $s_{YOY}$ of 0.3674, with a variance of 0.02 (Table 2.2).

### Model Scenarios

All models draw from the same distribution for first over-winter survival ($s_{YOY}$ = 0.37, var =0.02) because no specific predictions of the possible direct hydrologic effects of river regulation for the first over-winter period of newly metamorphosed frogs were developed. However, the lack of hydrologic simulations for this vital rate does not preclude the possibility that carryover or other higher-order interactions may affect the survival of metamorphic frogs over the first winter, but rather the lack of currently available data to estimate such effects. Previous experiments do show that *R. boylii* tadpoles subjected to pulsed elevations of velocity have reduced growth rates (Kupferberg et al. 2008) and pen studies with other Ranid species show that size at metamorphosis can often be an important determinant of surviving the first winter (Altwegg and Reyer 2003).

## 2.3.6. Survival from Age 1 to Age 2

This is the first year that frogs are defined as juveniles and covers the time period from one year of age to two years of age.

### Application to Population Model – Reference Values

The survival of *R. boylii* during the juvenile terrestrial period (estimated to be from age 1 to 3) has not been studied, and as a result there is a lack of either empirical or published data for *R. boylii* in particular or other Ranid frogs in general. However, unpublished data for a stream-dwelling population of California red-legged frogs (*Rana draytonii*) was available (Scott, Rathbun, and D'Amore pers. comm.). Population studies on *R. draytonii* were conducted at Pico Creek and San Simeon Creeks in the central coast mountains of California (San Luis Obispo County) from 1991 to 1994. Approximately 800 m of Pico Creek and 1km of San Simeon Creek were surveyed on several occasions each year. Frogs were individually marked and juveniles were defined by the field researchers as ranging from 35 to 69mm snout-vent length (Scott, Rathbun, D'Amore pers. comm.). Program MARK was used to estimate juvenile survival rates for each of the two study populations (see analogous methods below in section 2.3.9; D'Amore pers. comm.). For the *R. boylii* Reference Model, a mean and variance of the two juvenile survival estimates (Pico and San Simeon) was calculated to represent survival from age 1 to age 2 ($s_{juv1}$ = 0.26, var =0.04; Table 2.2).

#### Model Scenarios

All model scenarios draw values from the same distribution for survival from age one to two as in the Reference Model.

### 2.3.7. Survival from Age 2 to Age 3

This is the second year that frogs are defined as juveniles and covers the time period from two years of age to three years of age, when female frogs are likely to reproduce for the first time in northern locales (GANDA, unpublished growth data).

#### Application to Population Model – Reference Values

In the absence of any empirical or literature values for juvenile survival from age 2 to age 3, the simplifying assumption was made that this vital rate would be similar to the adult female survival rate estimated from relatively robust empirical data (0.54 with variance 0.055, see Section 2.3.9 below and Table 2.2). The underlying assumptions for using this rate were: (1) the survival rate should improve (i.e., be higher than that for age 1 to age 2) as individuals get older, and (2) juveniles should actually have a relatively high survival rate because they are not yet reproducing or migrating and thus exposure to predators should be reduced and energy reserves would not be devoted to reproduction.

#### Model Scenarios

All model scenarios draw values from the same distribution for survival from age 2 to 3 as in the Reference Model except for models (2) and (30-32) which represent a shortened (2 years to maturity instead of three; Table 2.3). *Rana boylii* growth that has been observed for marked individuals in Central California populations informs this supposition (Gonsolin, unpublished data). In these scenarios, this vital rate was eliminated from the life-history (see Section 2.4 for more details).

### 2.3.8. Adult Survival Estimates

Adult (sexually mature individuals) survival rates were derived from capture-recapture data collected by researchers at two study areas: Hurdygurdy Creek in the South Fork Smith River drainage, and an unnamed tributary in the Poe Reach of the North Fork Feather River.

Frogs were marked and identified in the field using Passive Integrated Transponder (PIT) tags and/or chin pattern recognition (e.g., GANDA 2006; Wheeler et al. 2005; Wheeler 2007), all of which provide individual identification. Data were summarized to represent annual capture-recapture periods (Table 2.9). Multiple captures of a given individual within a capture-recapture period was counted as one capture. Based on information provided by researchers at each study area, data were pared down to adults only. At Hurdygurdy Creek adult males were defined as individuals 40mm and larger (snout-urostyle length, SUL) and adult females were 50mm SUL and larger (Wheeler 2007; C. Wheeler pers. comm.). At the NF Feather, adults (both sexes) had previously been defined as 40mm or larger SUL (J. Drennan, pers. comm.). However, there is no evidence to suggest that individuals mature or ultimately grow to smaller sizes at the NF Feather than at Hurdygurdy Creek, so adults males were defined at 40mm SUL and larger and adult females at 50mm SUL and larger for the purposes of developing survival rate estimates (Table 2.9).

Program MARK (White and Burnham 1999; Cooch and White 2007) was used to derive annual survival rate estimates for adult frogs at each study area. Separate estimates were derived for males and females. Program MARK offers four "pre-defined" models which allow two parameters to vary over time (in this case year): survival (Phi) and capture probability (p). These four models were evaluated for each sex at each study area and the "best" model was chosen based on the lowest Akaike Information Criterion (AIC) value. This information-theoretic criterion provides a balance between model fit (based on likelihood theory) and precision (enforced by a penalty for the number of parameters) (Burnham and Anderson 2002). Survival rate estimates, and associated standard errors and variances, were then selected from that best model and are presented in Table 2.10, below. In all analyses the sin link function and 2nd part variance estimator were used (Cooch and White 2007).

### *Application to Population Model – Reference Values*

For the matrix population model, the adult female survival rate and associated variance from the unregulated Hurdygurdy Creek (0.54, var = 0.055) was used (Table 2.2). The estimate for adult female survival from the regulated NF Feather River was similar, though slightly lower, and was used as corroboration of the estimate from Hurdygurdy Creek (Table 2.10).

**Table 2.9. Location, sampling approach, and researcher contacts for the two study sites where adult *Rana boylii* survival rates were developed.**

| Study area | County, State | Sampling Approach | Years of Surveys | SUL Range By Sex (mm) | Observers / Researcher Contact |
|---|---|---|---|---|---|
| Hurdygurdy Creek | Del Norte, CA | PIT tagging of individuals at a large breeding site | 2002-2006 | Females: 52-76<br>Males: 40-62 | Clara Wheeler, USDA Forest Service, Redwood Sciences Lab, Arcata, CA<br>cawheeler@fs.fed.us<br>(Wheeler 2007) |
| Unnamed tributary to North Fork Feather River | Plumas, CA | Chin pattern recognition of individuals in tributary and at associated river breeding site | 2004-2007 | Females: 50-76<br>Males: 40-59 | Joe Drennan<br>GANDA Environmental Consultants, San Francisco, CA<br>jed@garciaandassociates.com |

**Table 2.10. Annual survival rate and capture probability estimates for adult *Rana boylii* at two study sites.**

| Study Site | Sex (n) | "Best" Model[1] | Survival Rate (Phi) ± s.e. (variance) Overall Or By Year (depending on model) | Capture Probability (p) ± s.e. |
|---|---|---|---|---|
| Hurdygurdy Creek<br>2002-2006 | F (39) | Phi(.), p(t) | 0.54 ± 0.23 (0.055) | 2003: 0.78 ± 0.46<br>2004: na<br>2005: 0.21 ± 0.19<br>2006: 0.30 ± 0.33 |
| | M (144) | Phi(t), p(.) | 2002-03: 0.34 ± 0.09 (0.008)<br>2003-04: 0.51 ± 0.11 (0.01)<br>2004-05: 0.14 ± 0.06 (0.004)<br>2005-06: 0.36 ± 0.10 (0.011) | 0.08 ± 0.12 |
| Unnamed tributary to North Fork Feather River 2004-2007 | F (179) | Phi(.), p(t) | 0.50 ± 0.08 (0.007) | 2005: 0.80 ± 0.14<br>2006: 0.29 ± 0.09<br>2007: 0.66 ± 0.22 |
| | M (95) | Phi(.), p(.) | 0.11 + 0.04 (0.001) | *1.0000 + 0.000 note: this estimate is not reliable* |

1. Notation: (.) = parameter does not vary over time, (t) = parameter varies over time.

### Model Scenarios

All model scenarios draw values from the same distribution of adult survival $a_{44}$=0.54 (0.055).

## 2.4. Central Coastal California Populations Reference Model

There is evidence from Central Coastal California *R. boylii* populations (e.g. Alameda Creek - S. Bobzien unpublished data and Coyote Creek - E. Gonsolin unpublished data) that individual females reach reproductive maturity after two years of age rather than the three years of age assumed by the Reference Model (see Section 2.2). To address whether this shorter life-history predisposes Central Coast populations to be more or less sensitive to anthropogenic changes in hydrology an exploratory Central Coast populations Reference Model (2) was constructed. This model assumes the same mean vital rates and distributions as the Reference Model (1) except for the elimination of second juvenile stage ($s_{juv2}$). Results from this model should be viewed as exploratory, as there are key simplifying assumptions that can not currently be evaluated including: (1) the frequency of 2-year maturity within and among Central Coast populations is dominant, and (2) populations reaching maturity at age 2 are governed by the same demographic parameters (vital rates) as populations reaching maturity at age 3. For the latter assumption, basic life-history theory would suggest that populations reaching maturity earlier would have different demographic rates to achieve the same contribution to the next generation. For example, earlier maturing species would be expected to have higher fecundities per reproductive bout if the number of reproductive opportunities are fewer. Although Alameda Creek clutches were observed to contain more embryos than the other populations, very little other demographic data was available from Central Coast populations (only limited fecundity, embryo and tadpole survival from Alameda Creek), so the generality of these assumptions cannot currently be evaluated.

With this 3-stage matrix model the following scenarios were simulated: model (30) adjusts the starting population size the mean number of egg masses per/km in regulated rivers (4.6/km), model (31) combines regulated river embryonic strand and scour rates ($s_{emb1}$, $s_{emb2}$) with the reduced starting population size in (30), and model (32) which combines the most extreme reductions in embryonic survival due to stranding and scouring (similar to model (9)) with the reduced starting population size in (30).

## 2.5. Typical Study Reach Lengths, Starting Population Size, and Quasi-Extinction Thresholds

To initiate model runs, it was necessary to define a starting population size (a vector of the number of individuals in each life stage) and an extinction threshold. These values were also manipulated to evaluate their affects on viability outcomes in several scenarios.

### *2.5.1. Application to Population Model – Reference Values*

All models (Reference Models and scenarios) define a population as the total number of breeding females occurring in a hypothetical 10km reach, and are intended to represent the way in which *R. boylii* populations are often studied (e.g. river reach bounded by dams/reservoirs up and downstream that are often assumed to represent barriers to dispersal). It was also assumed that this reach length represents a biologically functional local population. However it does exclude the potential influence of long-distance emigrants and immigrants. The starting population vector ($N_0$) was estimated to be the stable age distribution that would result from knowing the average number of breeding adult females multiplied by the average transition probability ($a_{ij}$) for each life-history stage. The average number of breeding females was estimated from the average of the number of breeding females/km observed in a series of unregulated study populations multiplied by the average regulated reach length (Kupferberg unpublished data). The reach length chosen for modeling, 10 km, was based on the mean of a sample of regulated Sierran river reaches where *R. boylii* populations have been studied (Table 2.11) and is generally supported by a recent genetic study of *R. boylii* (Dever 2007). A compilation of egg mass census data from several researchers in California served as the basis for the estimate of the average number of breeding females (32/km x 10 km = 320 adult females, Table 2.12, Figure 2.8).

**Table 2.11. Reach lengths in a sample of Sierra Nevada regulated rivers with known populations of *Rana boylii*.**

| Project | River | Reach length (km) |
|---|---|---|
| Spring Gap Stanislaus | Middle Fk. Stanislaus | 19.8 |
| Poe | North Fk. Feather, Poe | 12.1 |
| Rock Creek - Cresta | North Fk. Feather, Cresta | 10.46 |
| Pit 3,4,5 | Pit 4 | 7.0 |
| DeSabla | Butte Creek | 16.41 |
| DeSabla | West Branch Feather | 23.01 |
| UARP | Silver Creek | 9.65 |
| UARP | South Fork American | 4.5 |
| UARP | Slab Creek Reach, S. Fk. American | 12.9 |
| **mean (± s.e.)** | | **12.87 ± 1.99** |

**Table 2.12. A summary of recent egg mass census data from California populations of *Rana boylii*.**

| River system | Site Name | Location | Reach Length (km) | % Sampled | #/km | se | Years Sampled | Data Source |
|---|---|---|---|---|---|---|---|---|
| Middle Fork Stanislaus | Sand Bar Dam Reach | Central Sierra | 19.8 | 5.2 | 6.2 | 3.6 | 2001-2003 | ECORP Consulting, Inc. for PG&E, 2004 |
| Trinity | Mainstem Trinity | N. Coast | 22.5, 33.3 | 100 | 0.45 | 0.17 | 1991-1994, 2004-2006 | Lind 2005; Ashton, Bettaso, and Welsh unpublished data |
| NF Feather | Poe | N. Sierra | 12.07 | 66.3 | 7.27 | 1.65 | 2001-2008 | Garcia and Associates for PG&E |
| NF Feather | Cresta | N. Sierra | 10.46 | 76.5 | 2.24 | 0.50 | 2002-2008 | Garcia and Associates for PG&E |
| Pit | Pit4 | N.Sierra | 7 | 100 | 8 | 2.7 | 2002-2005 | Maria Ellis, Spring Rivers, PG&E |
| Alameda | Downstream Calaveras Ck | SF Bay Area | 3.2 | 100 | 3.3 | 3.3 | 2003-2008 | Bobzein and DiDonato 2007, Kupferberg unpublished data |
| **Regulated River Mean Egg Mass Density** | | | | | **4.6** | **1.15** | | |
| Stanislaus | Rose Ck. | Central Sierra | 0.65 | 100 | 29 | | 2001 | Lind et al. 2003 |
| Tuolumne | NF Tuolumne | Central Sierra | 0.3 | 100 | 9 | | 2001 | Lind et al. 2003 |
| San Joaquin | Jose Ck | Central Sierra | 1.2 | ? | 4.6 | | 1995, 2002 | Lind et al. 2003 |
| Smith | Hurdygurdy Ck | N. Coast | 4.75, 1.65 | 100 | 34.6 | 4.5 | 1991-1992, 1998-2000, 2002-2007 | Lind 2005, Clara Wheeler pers. comm. |
| Eel | S. Fk. Eel | N. Coast | 5.2 | 100 | 106.9 | 7.5 | 1992-2008 | Kupferberg 1996, and unpublished data |
| Eel | Ten Mile Ck | N. Coast | 4 | 100 | 12.92 | 2.96 | 1993-2003, 2008 | Kupferberg 1996, and unpublished data |
| Trinity | SF Trinity | N. Coast | 15.6 | 100 | | | 1992-1994, 2004-2006? | Lind 2005 |
| Trinity | SF Trinity | N. Coast | 5.9 | 100 | 69.9 | 22.5 | 2004-2006 | Ashton, Bettaso, Welsh unpub. data |
| Yuba | Clear Ck. | N. Sierra | 0.82 | 100 | 29 | 9.5 | 1992-1994 | Van Wagner 1996 |

| River system | Site Name | Location | Reach Length (km) | % Sampled | #/km | se | Years Sampled | Data Source |
|---|---|---|---|---|---|---|---|---|
| Yuba | Shady Creek | N. Sierra | 1.6-4.3 | 100 | 5.4 | | 1998-2003 | Yarnell, pers. comm. |
| Alameda | Camp Ohlone | SF Bay Area | 1.6 | 100 | 20 | 6.6 | 1997-2008 | Bobzein and DiDonato 2007, Kupferberg unpublished data |
| **Un-regulated River Mean Egg Mass Density** | | | | | **32.13** | **10.31** | | |

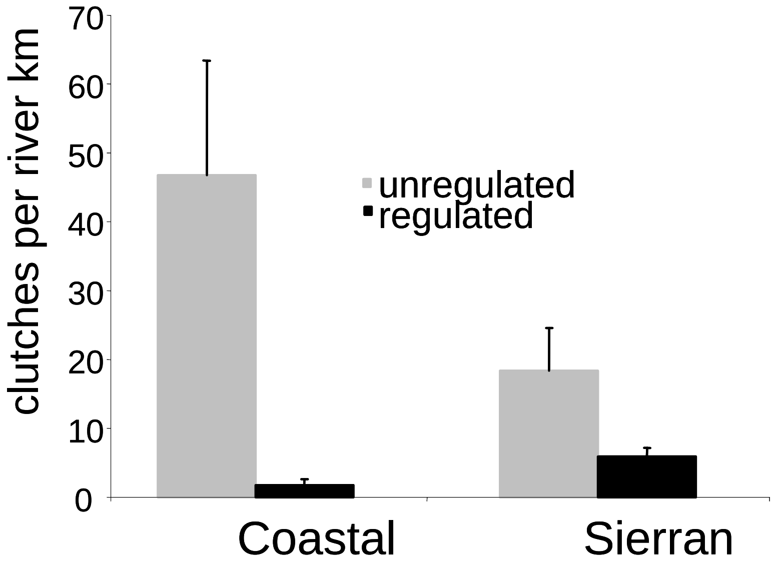


**Figure 2.8. Summary of breeding population sizes of *Rana boylii* compiled from several researchers in California (see Table 2.11).**

### *2.5.2 Model Scenarios*

The outcome of the Reference Model (32 females/km = 320 adult females in the population), was compared to models which begin with more robust (model 4), smaller (model 3), and much smaller (model 5) starting population vectors (Table 2.3). In model (3), the mean regulated average of 46 adult females in a 10km reach was used (Table 2.11). Model (4) begins with a robust population, mirroring the mean for the SF Eel, the system for which there is the longest continuous record of population dynamics. Checking that the extinction probability of this scenario is indeed low, provides an opportunity to validate that the predictions of the Reference Model were within the realm of biological reason for a robust *R. boylii* population, and to give confidence in its general predictions. In model (5) a starting value only slightly above the previously defined quasi-extinction threshold was used, based on the actual population size in the NF Feather Cresta reach of 2.1 females/km. There is substantial uncertainty in defining a quasi-extinction level, so one scenario explores the consequences of setting this level at half the Reference Model value (model 6), 1 female/km, and another sets it at double the Reference Model value (model 7), 4 females/km (Table 2.3).

## 2.6. Combined Effects Scenarios

Several scenarios were developed to examine the interactions and compounding effects of multiple effects. These scenarios were intended to be biologically realistic representations to the extent that populations often experience compounded factors such as small population sizes combined with local stressors that may negatively affect one or more vital rate(s). In particular, these scenarios examine the fate of *R. boylii* during the time period of its observed decline (approx. the last 50 years) and also assess combined effects on current populations.

### 2.6.1. *Simulation of* Rana boylii *decline history*

Model (25) explores the population consequences of beginning with a robust population and subjecting it to the effects of spring spills and rapid flow cessation, and a single high-mortality ($s_{tadpole1}$= 0.46) pulsed flow per summer as might have historically occurred for project maintenance. Model (26) adds the effect of reduced fecundity, assuming that there is less control of dams earlier in the season, and that first 15% of eggs are scoured away, thus eliminating the early large female contribution to the population (Table 2.3).

### *2.6.2. Worst-Case Modern Scenarios – Small Populations and Hydrologic Stressors*

In models (27- 29), the NF Feather Cresta reach starting population size estimate was applied (based on average count of egg masses from 2002-2007, 21 females or ~2/km were estimated Table 2.12), combined with the distribution of strand and scour rates measured for regulated rivers. Model (27) assesses the potential for recovery of a small population in a hydrologically regulated system, assuming there are no summer pulsed flows. Models (28) and (29) include the effects of one (28) or two (29) high-mortality ($s_{tadpole1-2}$=0.46) summer pulsed flows combined with the diminished starting population size and hydrologically regulated spring strand and scour conditions.

### *2.6.3. Central Coast Population Combination Models*

The potential population-level consequences of smaller population size (model 30) and two levels hydrologic stress for the faster maturing Central Coast populations were estimated. Model (31) adds the distribution of both potentially beneficial and detrimental effects of regulation on stranding and scouring, while model (32) incorporates the worst case rates of embryonic stranding and scouring in regulated rivers along with the small starting population. In some instances, regulated river populations might experience less stranding relative to an unregulated river if stage height were maintained at a constant level, rather than declining over time.

## 2.7. Sensitivity Analysis Methods

Sensitivity analyses are traditionally used to evaluate the importance of individual vital rates (or components of composite vital rates) to overall model outcomes (Caswell 2001; Morris and Doak 2002). Sensitivity results can inform decisions about which particular life-history stages to be targeted for future research (to further constrain uncertainties in demographic estimates) or for direct conservation action in the case of recovery programs for declining species or eradication efforts for invasive species (Crouse et al. 1987; Kareiva et al. 2000). For matrix population models in particular, traditional sensitivity and elasticity analyses vary single vital rates over a narrow range of values while holding all other vital rates at their 'best' estimates (Reference Model conditions in this case). By systematically varying individual vital rates over small ranges and comparing the resulting proportional changes in deterministic lambda (λ) values, the relative importance of individual vital rates can be assessed. However, many populations of conservation concern experience wide variation in multiple vital rates simultaneously, and the resulting changes in the population dynamics are often assumed to be synergistic. For example, decreasing both embryonic survival and fecundity due to scouring spring spates may disproportionately affect future reproduction. As a result, these real-world populations violate several of the critical assumptions of traditional sensitivity and elasticity analysis: that changes in vital rates are small and result in only linear changes to lambda, and that changes in multiple rates will be additive combinations of their individual sensitivities or elasticities. To account for these possible non-linearities among vital rates across biologically relevant ranges, while still maintaining the power to infer the relative importance of individual vital rates, we chose to favor a new simulation-based multivariate approach to traditional sensitivity analysis (Morris and Doak 2002, Wisdom and Mills 1997). Briefly, this method requires establishing upper and lower bounds for each vital rate that are driven by the observed variation in each rate (Wisdom et al. 2000, Wisdom and Mills 1997), generating a large number (5000) of matricies by drawing at random from within these ranges for each vital rate (to create a uniform distribution), and then calculating the deterministic lambda for each matrix. The resulting dataset of deterministic lambda values and associated vital rate values can then be evaluated for the strength of correlations between each vital rate, or combinations of vital rates, and variation in lambda (Morris and Doak 2002). We used this multivariate approach to evaluate the importance of individual vital rates for overall *R. boylii* population dynamics for the two different reference (un-regluated) models; three years to maturity (Model 1) and two years to maturity (Model 2). To bound the possible values of each vital rate for this multivariate sensitivity analysis in a biologically comparable way (Wisdom and Mills 1999), we used the output of the 10,000 runs of each reference model (Models 1 & 2) to calculate the 95% confidence interval of vital rate values (Wisdom et al. 2000). These values were then used as the upper and lower bounds of the uniform distributions for each vital rate in the multivariate sensitivity analysis. As suggested by other authors, we report several metrics from these analyses; the maximum potential value of lambda generated by increasing each vital rate to its maximum value (holding all other rates at their best estimates), the percent of variation in lambda explained by each vital rate (squared correlation coefficients), and the total percent of variation in lambda explained by all of the one-way correlations.

# 3.0 Population Modeling Results and Discussion

The results of all model simulations are summarized in Table 3.1. The three main response variables are: (1) the cumulative probability of the *R. boylii* population reaching the quasi-extinction threshold within thirty years, (2) the difference in extinction probability between the Reference Model and each scenario, and (3) the mean stochastic population growth rate ($\lambda_s$). The IUCN has developed threshold criteria for assigning species to its Red List categories (for details, see IUCN 2001) when quantitative predictions of extinction risk are produced by population viability analyses. A 50% or higher risk of extinction in 10 years or three generations is considered "Critically Endangered", ≥ 20% risk in 20 years or five generations is "Endangered", and ≥ 10% risk in 100 years is considered vulnerable. While these thresholds were developed for a species as a whole rather than single populations, they are presented here as potentially useful benchmarks for categorizing the future outlook for *R. boylii* populations in the modeled scenarios.

**Table 3.1. *Rana boylii* population modeling results. The scenarios are grouped into five categories: reference models, models addressing starting conditions and evaluation criteria (e.g., starting population size), models where vital rates are modified, combination models for 3 year maturity populations and combination models for the Central Coast, 2 year maturity, populations.**

| Model | Scenario | 30-yr extinction probability | Multiplicative change in probability of extinction[1] | λs |
|---|---|---|---|---|
| **Reference Models** | | | | |
| 1 | Reference Model | 0.05 | - | 1.21 |
| 2 | Central Coast reference populations | 0.02 | -2.5 | 1.46 |
| **Modified Starting Conditions and Evaluation Criteria** | | | | |
| **Starting population size** | | | | |
| 3 | Regulated starting population | 0.2 | 4.0 | 1.17 |
| 4 | Eel River starting population | 0.01 | -5.0 | 1.21 |
| 5 | North Fork Feather River (Cresta reach) starting population | 0.67 | 13.4 | 1.21 |
| **Extinction threshold** | | | | |
| 6 | Low quasi-extinction threshold | 0.02 | -2.5 | 1.21 |
| 7 | High quasi-extinction threshold | 0.11 | 2.2 | 1.21 |
| **Modified Vital Rate Scenarios** | | | | |
| **Spring flow** | | | | |
| 8 | Regulated embryonic strand & scour | 0.11 | 2.2 | 1.16 |
| 9 | Worst case embryonic strand & scour | 0.23 | 4.6 | 1.09 |
| 10 | Reduced fecundity (1st 15% egg masses removed) | 0.07 | 1.4 | 1.18 |
| 11 | Reduced fecundity (1st 30% egg masses removed) | 0.09 | 1.8 | 1.16 |

| Model | Scenario | 30-yr extinction probability | Multiplicative change in probability of extinction[1] | λs |
|---|---|---|---|---|
| 12 | Combine 9 & 10 | 0.85 | 17.0 | 0.87 |
| 13 | Combine 9 & 11 | 0.88 | 17.6 | 0.86 |
| **Summer flow** | | | | |
| 14 | Increase base flow, lower temperatures | 0.12 | 2.4 | 1.14 |
| 15 | High mortality summer pulse (.46) x1 | 0.27 | 5.4 | 1.03 |
| 16 | High mortality summer pulse (.46)x1, scoured algae | 0.64 | 12.8 | 0.94 |
| 17 | High mortality summer pulse (.46) x2 | 0.73 | 14.6 | 0.90 |
| 18 | High mortality summer pulse (.46) x3 | 0.97 | 19.4 | 0.80 |
| 19 | High mortality summer pulse (.46) x4 | 1 | 20.0 | 0.75 |
| 20 | Low mortality summer pulse (.61) x1 | 0.16 | 3.2 | 1.09 |
| 21 | Low mortality summer pulse (.61) x1, scoured algae | 0.50 | 10 | 0.98 |
| 22 | Low mortality summer pulse (.61) x2 | 0.39 | 7.8 | 1.00 |
| 23 | Low mortality summer pulse (.61) x3 | 0.68 | 13.6 | 0.91 |
| 24 | Low mortality summer pulse (.61) x4 | 0.81 | 16.2 | 0.88 |
| **Combination Models** | | | | |
| 25 | *R. boylii* decline history (9, 15) | 0.91 | 18.2 | 0.84 |
| 26 | *R. boylii* decline history (9, 10, 15) | 0.96 | 19.2 | 0.79 |
| 27 | *R. boylii* modern regulated (5,8) | 0.77 | 15.4 | 1.16 |
| 28 | *R. boylii* modern regulated (5,8,15) | 0.92 | 18.4 | 1.00 |
| 29 | *R. boylii* modern regulated (5,8,17) | 0.99 | 19.8 | 0.87 |
| **Central Coast Populations Combination Models** | | | | |
| 30 | Regulated starting population | 0.25 | 12.5 | 1.45 |
| 31 | Regulated embryonic strand & scour (30) | 0.35 | 17.5 | 1.37 |
| 32 | Worst case embryonic strand & scour (30) | 0.9 | 45.0 | 0.98 |

1. Values in this column represent the multiplicative increase or decrease in the probability of extinction relative to the appropriate reference model. For example, Model (3) represents a population that is four times **more** likely to go extinct than the Model (1) population and Model (6) represents a population that is two and one half times **less** likely to go extinct than the Model (1) population. Model (1) is the appropriate reference model for all models except 30, 31, and 32; for these, Model (2) is the appropriate reference model.

## 3.1. Reference Model

Simulations of Reference Model parameter values (Table 2.2) result in an average 30-year extinction probability of 5% and an average stochastic population growth rate of 1.21, leading on average to robust population sizes within 30 years (Figure 3.1). These key response values, while within the realm of expectations for a population occurring over a 10 km unregulated reach, should not be interpreted strictly as representing the population dynamics of any particular *R. boylii* population, but rather the standard against which each of the various scenarios explored were compared. In this way, the relative impact of each scenario can be compared against a hypothetical unregulated population (Table 3.1) and observed values of λ in populations with more than five years of continuous monitoring (Table 3.2).

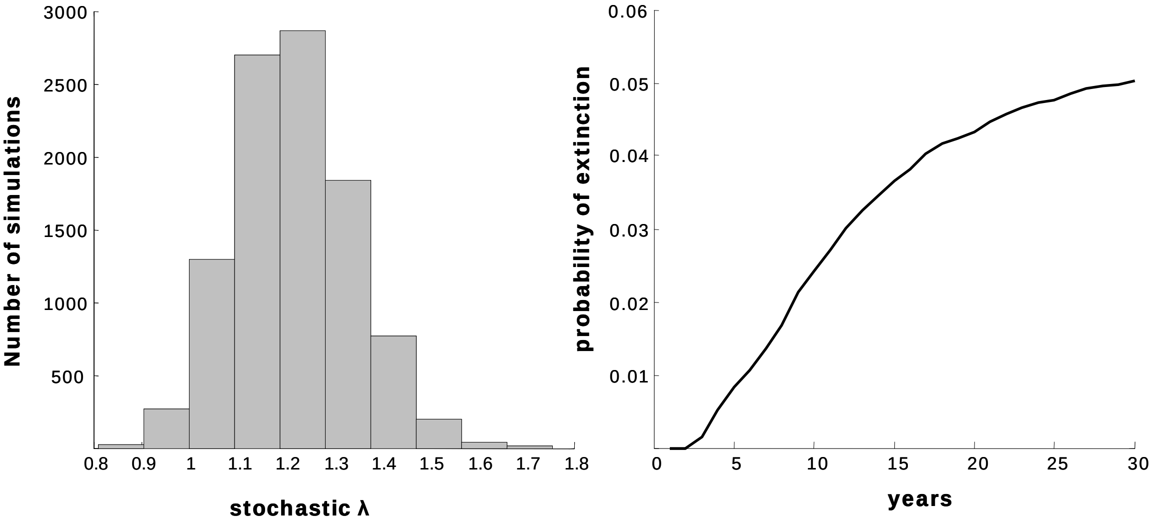


**Figure 3.1. Reference Model (1) distribution of population growth rates (stochastic λ) over 10,000 simulations of 30-year trajectories of *R. boylii* populations (left). Cumulative extinction probability over 30 years (right) generated from 10,000 random simulations drawing from Reference Model values and distributions of vital rates.**

**Table 3.2. Range and variation of λ, the annual proportional rate of change in *Rana boylii* populations from rivers with long term population monitoring programs (>5 years).**

| Location | Flow status | period of continuous record | n | $\lambda_{min}$ | $\lambda_{max}$ | $\lambda_{geo\ mean}$ | Coefficent of variation (%) |
|---|---|---|---|---|---|---|---|
| SF Eel | unregulated | 1992-2008 | 16 | 0.63 | 2.1 | 0.99 | 36.5 |
| Ten Mile Creek | unregulated, bullfrogs | 1993-2003 | 10 | 0.35 | 3.125 | 1.16 | 104.7 |
| Alameda Ck., Camp Ohlone | unregulated | 1997-2008 | 11 | 0.38 | 2. 9 | 1.11 | 67.9 |
| NF Feather, Poe | regulated | 2001-2008 | 7 | 0.98 | 1.61 | 1.25 | 16.1 |
| NF Feather, Cresta | regulated, aseasonal pulsed flows | 2002-2008 | 6 | 0.18 | 2.8 | 1.03 | 89.2 |

## 3.2. Manipulations of Starting Population Size and Quasi-Extinction Threshold

Under natural hydrologic conditions, the size of the population at the beginning of each simulation has a strong effect on the cumulative risk of extinction, where by chance alone, the expectation is that smaller populations will have an elevated risk of dropping below the quasi-extinction threshold. The results of models (3) and (5) illustrate the degree to which *R. boylii* populations in regulated rivers are at greater risk of extirpation by virtue of their low abundance, even before the effects of hydrologic stressors are considered in models (8-24). There is only a 1% chance of extinction when populations start with 105 breeding females/km, compared to a 20% chance of extinction when starting with 4.6 females/km, the regulated river mean (models 3 and 4 in Table 3.1; Figure 3.2). If initial adult population size is close to the extinction threshold, as with model (5) mimicking the NF Feather Cresta population size, the risk of extinction is 67%, more than 13 times the extinction risk of the reference population (Table 3.1).

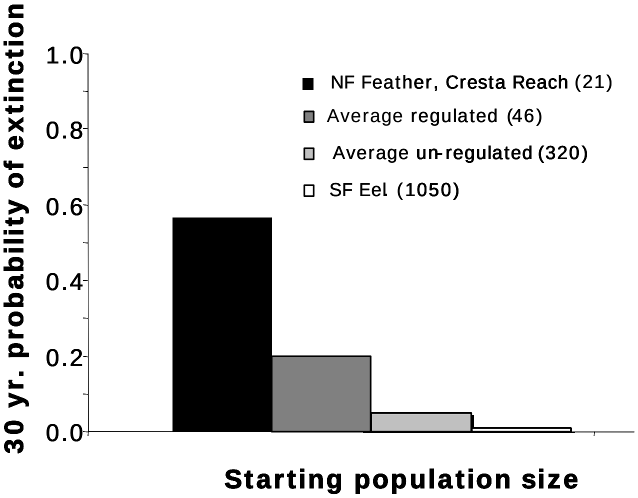


**Figure 3.2. Extinction risk in relation to starting population size. From left to right the models are (5), (3), (1), and (4).**

The quasi-extinction threshold was varied to evaluate its relative contribution to overall population extinction risk (Figure 3.3). When the quasi-extinction threshold is set at 40 adult females (double the Reference Model level), populations persist at a lower rate (extinction risk more than doubles compared to the Reference Model). As expected when the threshold is set lower, to 10 adult females, or just 1/km as in model (6), the extinction risk decreases by more than half relative to the Reference Model (Table 3.1). Closer scrutiny of existing *R. boylii* population trends suggest that the quasi-extinction threshold of 20 individuals in a hypothetical 10 km reach may in fact be too low, as some populations with mean adult female densities above this level (2/km) appear to be in strong demographic decline (see NF Feather River Cresta reach and Alameda Creek below Calaveras Dam data in Table 2.12 in this report and section 3 of Kupferberg et al. 2008). Model (7) raises the quasi-extinction threshold to 40 total adult females, and while the results are more precautionary from a conservation perspective and potentially represent a more biologically realistic estimate of quasi-extinction for *R. boylii*, this may still be too low. An empirically derived quasi-extinction threshold could be developed by examining the least dense, yet stable, populations; such a threshold might lie in a range between 54 and 129 total individuals. For example, among coastal populations, *R. boylii* at Ten Mile Ck. appear stable over 18 years at a mean adult female density of 12.9/km. In the Sierra Nevada, the potentially stable Shady Creek population has a density of 5.4 females/km, based on six years of data (S. Yarnell, pers. comm.). The uncertainty surrounding the estimates of this model feature highlights the need for a long-term monitoring program in an unregulated Sierran River and the importance of the current and future monitoring conducted for FERC hydroelectric license compliance.

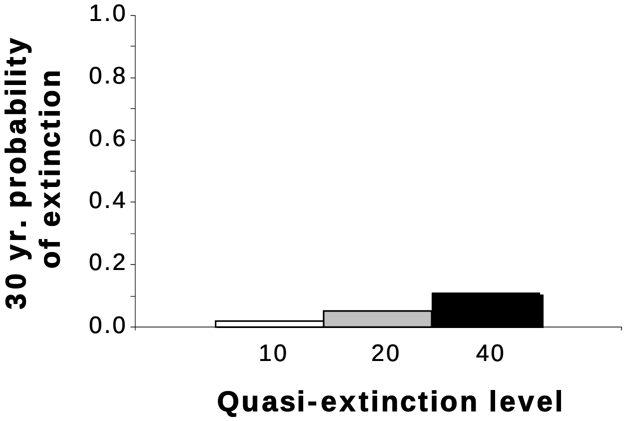


**Figure 3.3. Extinction risk in relation to extinction threshold, models (6), (1), and (7).**

## 3.3. Modified Vital Rate Scenarios

### *3.3.1. Spring Flow Conditions*

A primary hydrologic stressor of interest to be assessed with models (8-13) is rapid flow fluctuation in the spring. Losses of whole (or partial) egg masses have been observed due to fluctuations in spring hydrographs due to a wide range of causes including dams being overtopped during spill events, power houses experiencing emergency shut downs, planned recreational flows, or stage height dropping rapidly after control of the river flow is regained. Two modeled scenarios (‘regulated’ and ‘worst-case regulated’) represent gradations in frequency of spring flow fluctuation. The regulated scenario, model (8), which draws from a broad distribution of conditions including years when there are no spills and years with regulated hydrologic effects, results in a doubling of extinction risk relative to the reference population (Table 3.1). The worst-case scenario, drawing from a distribution in which there are losses due to flow fluctuation occurring every spring, leads to a four-fold increase in extinction risk (Table 3.1, Figure 3.4).

Models (12) and (13) simulate the potential second order effects of flow fluctuation during the spring *R. boylii* breeding season that relate to differences in fecundity between early and late breeding females. The results of these simulations illustrate the important contribution that early breeding large-bodied females make to future generations, though the expectation is that such effects would co-occur with altered spring flow conditions and not alone as was modeled in (10) and (11) but rather combined with increased strand and scour conditions as in models (12) and (13) (Table 3.1, Figure 3.4). Declines in fecundity alone, models (10 & 11), do not cause major changes in population extinction probability, with less than a doubling of extinction risk compared to the Reference Model (Table 3.1). However, when reduced fecundity distributions are combined with the worst-case regulated rates of stranding and scouring (9), the effects are multiplicative. The probability of population extinction increases dramatically to 17 times (12) and nearly 18 times (13) the background extinction risk in the Reference Model (Table 3.1, Figure 3.4).

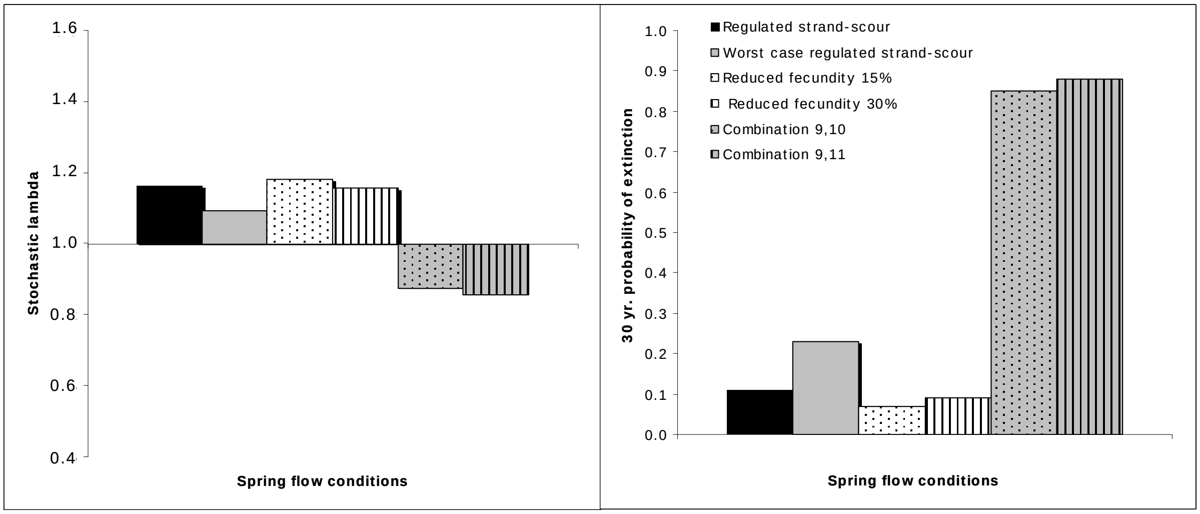


**Figure 3.4. Multiplicative effects of stranding and scouring of egg masses combined with decreased fecundity of females breeding after flow fluctuations cease.**

### *3.3.2. Summer Flow Conditions*

Anthropogenic changes to flow conditions during the summer were simulated by varying the survival of tadpoles to metamorphosis under scenarios of continuously elevated base flow or pulsed increases in discharge. The expectation that cooler water associated with increases in base flow results in decreased tadpole survival (with very large uncertainties around the magnitude of these impacts) was modeled. Results suggest that the probability of extinction for this model (14) would increase 2.4 times above the Reference Model (Table 3.1). For pulsed flows that would elevate velocities sufficient to cause 54% tadpoles to die in each pulse ($S_{tadpole1-4}$

= 0.46), only at a frequency of one pulse per summer (model 15) does the mean stochastic lambda remain above a value of one(Figure 3.5). With four pulsed flows per summer with elevated tadpole mortality (model 19), extinction becomes almost a certainty, with a probability = 0.97 (Figure 3.5). Even if tadpole survival through a pulse is higher ($s_{tadpole1\text{-}4}$ = 0.61), as might be expected if less severe velocity fluctuations occurred, the probability of extinction remains three times higher than the Reference Model (model 20). With multiple pulses the risks fall in the endangered and critically endangered categories with near certainty of population extinction when subject to four pulses per summer (Table 3.1, Figure 3.6).

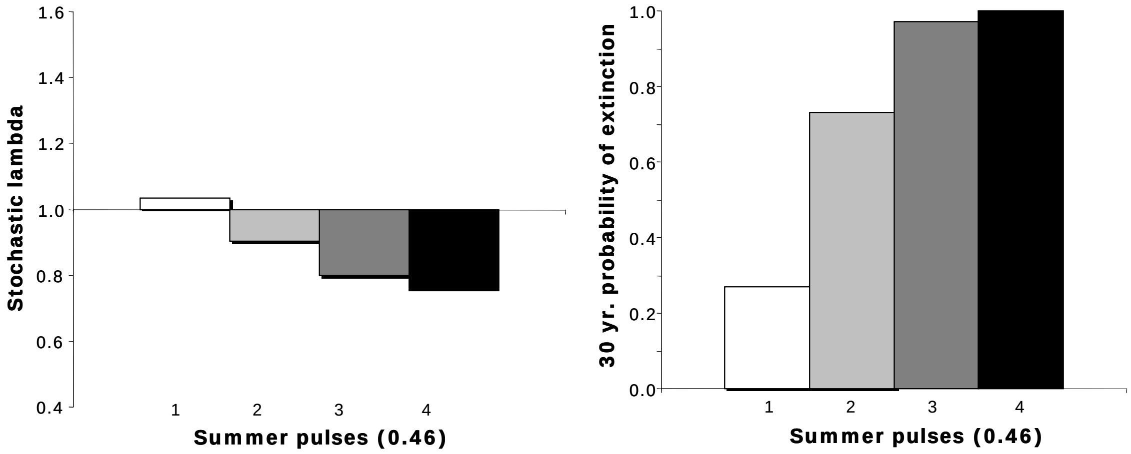


**Figure 3.5. Low tadpole survival (0.46) pulsed flow scenarios, models (15) and (17-19), simulating 1 to 4 pulses per summer.**

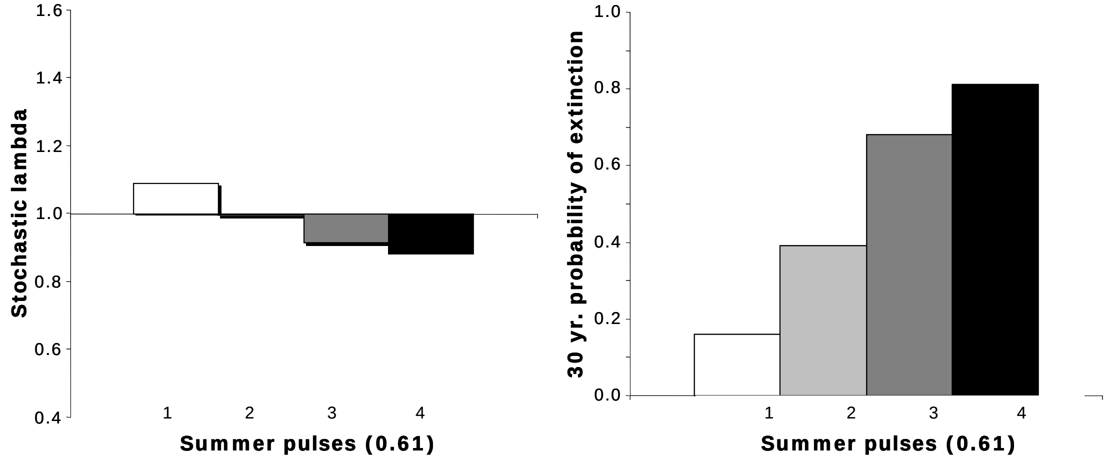


**Figure 3.6. High tadpole survival (0.61) pulsed flow scenarios, models (20) and (22-24), simulating one to four pulses per summer.**

The previous summer flow scenarios take into consideration the direct, short-term effects of tadpoles being swept downstream when current velocity increases during a pulse, and do not incorporate longer-term or indirect effects, which are also expected to be important. When the background rate of tadpole survival is adjusted to account for the export of algal and detrital food resources, even the single summer pulse models (16) and (21) become unsustainable with mean population growth rates below 1, and elevates the risks of extinction to extreme levels at both the high and low estimates of direct mortality (Table 3.1, Figure 3.7). This response illustrates that small changes in background tadpole survival rate (from $s_{tadpole0} = 0.15$ to $s_{tadpole0} = 0.108$) combined with other effects can have dramatic synergistic negative consequences for population persistence.

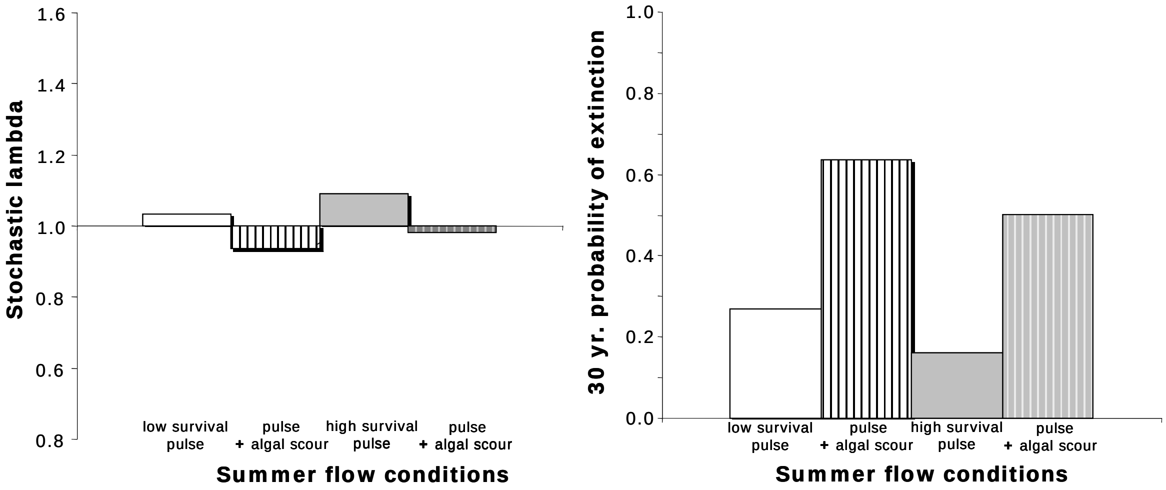


**Figure 3.7. Single summer pulsed flow effects accounting for effects of algal scour, models (16) and (21).**

## 3.4. Combined Scenarios

### *3.4.1. Spring and Summer Hydrologic Stressors*

When the effects of both spring and summer hydrologic alteration are considered to act in concert in *R. boylii* populations, the relative increases in extinction above the Reference Model were very large (Table 3.1). Models (25) and (26) simulate a hypothetical decline history for *R. boylii*, in which a robust average unregulated river population is subjected first to worst case scenario stranding and scouring in the spring and then an annual summer pulsed flow that might have occurred due to scheduled maintenance. The results of model (25) indicate that a population would have very small chances of surviving the joint hydrologic effects relative to the reference condition, and when decreased fecundity is taken into account, as in model (26), the extinction risk increases more than 19 times (Table 3.1, Figure 3.8). Models (27-29) begin with a population equal to the mean abundance of frogs in the NF Feather Cresta reach, with 2.1 adult females/km. Model (27) combines the small starting population size with only the background rate of stranding and scouring typical of regulated rivers as a hydrologic stressor, and thus simulates the potential for recovery of an *R. boylii* population approaching the quasi-extinction threshold, were all other hydrologic stressors eliminated. This potential is relatively low, as indicated by the large increase in extinction risk between model (27) and (1). When the Cresta-specific small starting population size is combined with spring project stranding and scouring effects, and then exposed to white water boating or other pulsed flows once (28) or twice per summer (29), the probability of extinction approaches one (Table 3.1, Figures 3.8 and 3.9).

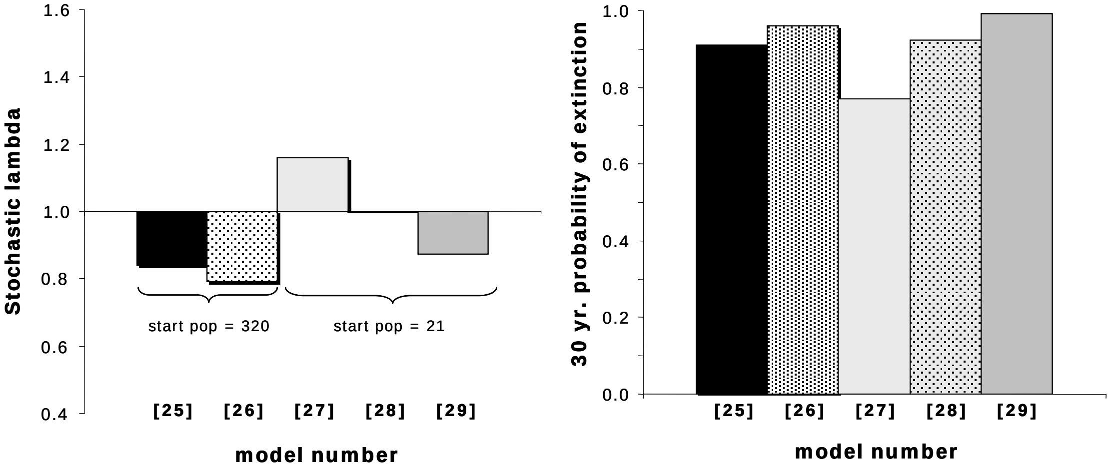


**Figure 3.8. Scenarios combining the effects of spring and summer hydrologic stressors on embryonic survival, fecundity, and tadpole survival.**

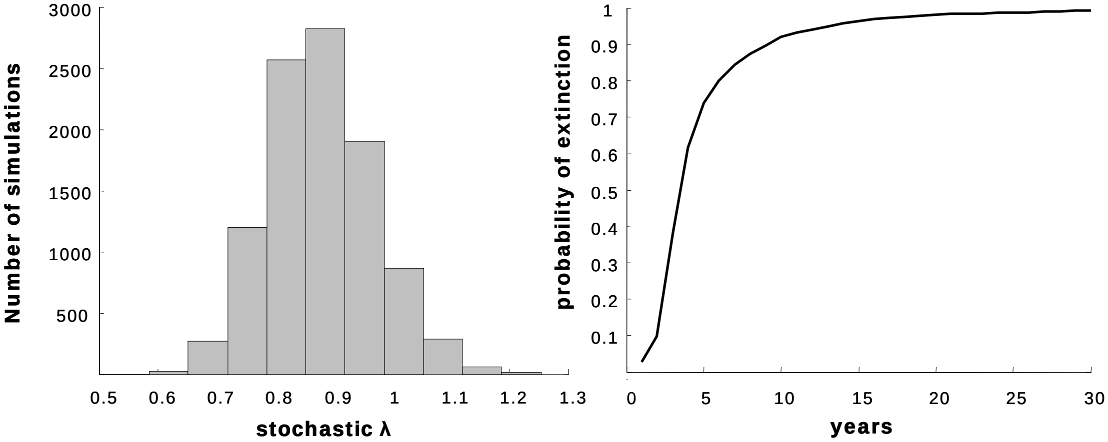


**Figure 3.9. Modern regulated worst-case model (29). Distribution of population growth rates (stochastic λ) over 10,000 simulations of 30-year trajectories of *R. boylii* populations (left), including small starting population size, regulated egg mass stranding and scouring, and two summer pulsed flows. Note that the cumulative probability of extinction plateaus at 10 years (right), rather than 30 in the Reference Model (Figure 3.1).**

### *3.4.2. Central Coast Population Scenarios*

The scenarios in which females reach reproductive maturity at age 2 rather than age 3 must be interpreted with the caveat that no appropriate information is available on the specific survival rates of juveniles and adults in Central Coastal California populations (i.e, 4+ year studies). Life-history theory would predict an adjustment of vital rates in order to maintain replacement level between populations with a one year difference in reproductive maturity, where each individual on average should produce one offspring that survives to reproductive age regardless of strategy. Results of simulations with the Central Coast population model suggest that decreasing the starting population size to the regulated river mean (30) increases extinction risk by more than ten fold compared to the Central Coast Reference Model (2), from 0.02 to 0.25 (Table 3.1, Figure 3.10). When the effects of stranding and scouring are added, models (31) and (32), the probability of extinction increases again for the worst case scenario level of embryonic mortality (Table 3.1). While these two scenarios, to a certain extent, echo the situation for frogs in Alameda Creek, they are not intended to be direct simulations of this population in particular, but rather an exploration of the possible differences in vulnerability of Central Coast *R. boylii* populations to altered spring flow conditions in particular, as most Central Coast populations occur in smaller streams and creeks with predominately drinking water and irrigation reservoirs rather than rivers with large hydroelectric dams.

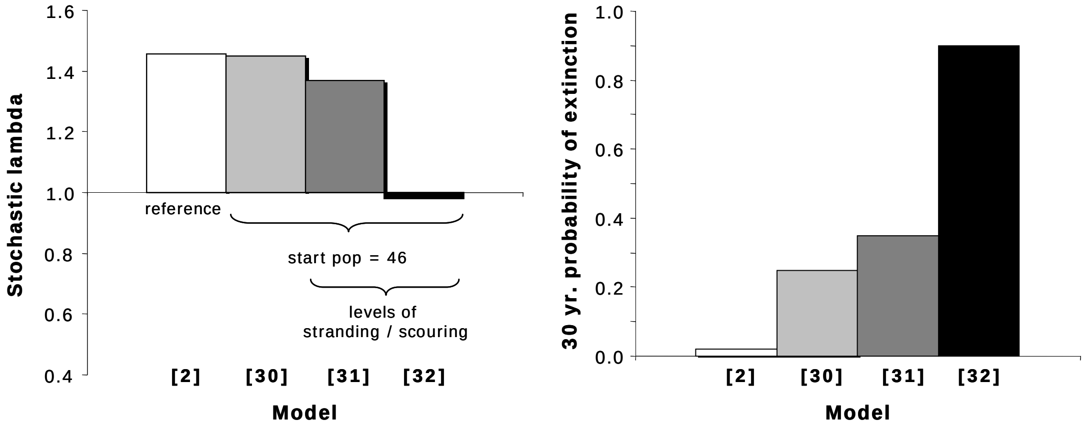


**Figure 3.10. Effects of reduced starting population size combined with two levels of egg mass stranding and scouring in Central Coastal California populations of *R. boylii*.**

## 3.5. Sensitivity Analyses

Sensitivity of individual vital rates (VR) to overall performance of the Reference Model for northern and central California populations of *R. boylii* is reported in Tables 3.3 and 3.4, respectively. Sensitivity is measured as the maximum population growth rate ($\lambda_{max}$) and the maximum proportional change in lambda (P($\lambda$)) when matrices are constructed with individual rates set at $VR_{max}$ and all other VR are held at the best estimates ($VR_{best}$). Multivariate sensitivity, where all VR are varied simultaneously, are reported as squared correlation coefficients between each VR and the population growth rate over 5000 matrix simulations where VR are drawn randomly from uniform distributions between $VR_{min}$ and VR $_{max}$. As described in Section 2, $VR_{min}$ and $VR_{max}$ were directly estimated from the 95% CI observed for each VR in the Reference model outputs (three years to maturity- Model 1, two years to maturity- Model 2). For the Reference Model (Model 1), highest value for the maximum proportional change in lambda (P($\lambda$)) comes from varying the survival of tadpoles to metamorphosis (Table 3.3). The more robust multivariate sensitivity analysis suggests that four life stage transitions have similar importance in driving population dynamics: scouring of egg masses, survival of tadpoles to metamorphosis, first year survival of recently metamorphosed frogs, and adult survival. When combined, these four factors explain the majority of variation in lambda ($r^2$ sum for top 4 VR =0.66), and importantly the sum of $r^2$ for all VR is very high (0.88), suggesting that one-way effects are a sufficient description of the modeled population dynamics (as opposed to multiplicative interactions). Life history theory alone would suggest *a priori* that adult survival should be an important determinate of population dynamics, since individual females reproduce multiple times and body size/age is linked to fecundity. These results suggest that variation in the survival of some early aquatic life stages (egg masses and tadpole survival) can also directly affect the overall population dynamics. These findings emphasize the need to consider hydrologic and other environmental conditions that may reduce early life stage survival in the overall conservation and management of this species. We also find very similar patterns in the multivariate sensitivity analysis for the two years to maturity Reference model (Model 2), with the same four life stages explaining 79% of the variation in lambda (compared to 0.91 for all VR's).

While this multivariate sensitivity analysis is among the most appropriate and informative methods for evaluating the relative importance of different life stages of this particular species, it is not without caveats and limitations. Foremost is the need to define the maximum and minimum values for each VR in a way that accurately reflects the biological differences among VR values (e.g. annual tadpole survival may be inherently lower and more variable than adult survival), because the ranges over which VR values are varied can substantially alter the outcome of the sensitivity analysis. While the best available data for *R. boylii* were used to calculate VR values and distributions (from which the 95% CI were estimated), there remains a high degree of uncertainty in all of the estimates. In particular, due to the varied data sources and populations from which the VR estimates were derived, in most cases corrections for observation error were not possible. Lack of correction may artificially inflate the variance estimates and parameter distributions. Thus, as more data are collected and the estimates of individual vital rates become more precise, the conclusions about which life stages are key drivers of population dynamics are also expected to be more accurate.

**Table 3.3. Reference model sensitivity analysis.**

| Vital Rate (VR) | VRmin | VRmax | VRbest | λmax | P(λmax) | r2 |
|---|---|---|---|---|---|---|
| $S_{emb1}$ | 0.84 | 1.00 | 0.96 | 1.41 | 0.01 | 0.00 |
| $S_{emb2}$ | 0.03 | 1.00 | 0.80 | 1.47 | 0.05 | 0.18 |
| $S_{emb3}$ | 0.29 | 1.00 | 0.83 | 1.46 | 0.04 | 0.02 |
| $S_{tadpole}$ | 0.00 | 0.62 | 0.15 | 1.92 | 0.37 | 0.15 |
| $S_{meta}$ | 0.12 | 0.66 | 0.37 | 1.59 | 0.14 | 0.06 |
| $S_{juv1}$ | 0.01 | 0.71 | 0.26 | 1.74 | 0.24 | 0.17 |
| $S_{juv2}$ | 0.10 | 0.94 | 0.54 | 1.58 | 0.13 | 0.11 |
| $_{adult}$ | 0.10 | 0.94 | 0.54 | 1.73 | 0.24 | 0.16 |
| F | 413 | 1627 | 871 | 1.60 | 0.15 | 0.03 |

**Table 3.4. Central Coast populations reference model sensitivity analysis.**

| Vital Rate (VR) | $VR_{min}$ | $VR_{max}$ | $VR_{best}$ | $\lambda_{max}$ | $P(\lambda_{max})$ | $r^2$ |
|---|---|---|---|---|---|---|
| $S_{emb1}$ | 0.84 | 1.00 | 0.96 | 1.86 | 0.01 | 0.00 |
| $S_{emb2}$ | 0.03 | 1.00 | 0.80 | 1.95 | 0.07 | 0.15 |
| $S_{emb3}$ | 0.29 | 1.00 | 0.83 | 1.93 | 0.06 | 0.01 |
| $S_{tadpole}$ | 0 | 0.62 | 0.15 | 2.81 | 0.53 | 0.21 |
| $S_{meta}$ | 0.12 | 0.66 | 0.37 | 2.18 | 0.19 | 0.06 |
| $S_{juv1}$ | 0.01 | 0.71 | 0.26 | 2.47 | 0.35 | 0.17 |
| $S_{adult}$ | 0.10 | 0.94 | 0.54 | 2.33 | 0.27 | 0.26 |
| F | 413 | 1625 | 871 | 2.20 | 0.20 | 0.05 |

# 4.0 Conclusions and Recommendations

## 4.1. Conclusions

Overall, the conclusions from this modeling exercise are well supported by first principles arising from the seasonally synchronized life cycle of *R. boylii*, where the most vulnerable life stages are present in rivers during the lowest and most consistent flows of the year in Mediterranean climates. Spawning occurs in spring or early summer as flood waters recede, and larvae metamorphose in late summer or early fall prior to the onset of rain-driven floods. Artificial flow regimes deviating from this natural pattern of flow fluctuation are expected to threaten locally-adapted communities of organisms, including *R. boylii*. Although summer and fall pulsed flows in regulated rivers may not be of greater magnitude than historic base flow discharges, the model illustrates that when the timing and frequency of pulses are de-coupled from the timing of *R. boylii*'s natural life cycle, the effects can be projected forward from stage to stage, and ultimately influence population persistence. Empirically, negative effects of altered hydrology for *R. boylii* such as egg mass scouring, have long been documented (Lind et al. 1996). Population viability analysis provides a tool with which such impacts can be evaluated in a long-term population context, and also provides a quantitative framework to define priorities for future data collection.

**The conservation of *R. boylii* in regulated rivers depends on management that minimizes atypical flow fluctuations during the breeding and tadpole rearing seasons.** The results indicate that the direct effects of anthropogenic hydrologic stressors on individual vital rates, such as embryonic and larval survival, can result in a several fold higher risk of population extinction above populations in hydrologically natural environments. Model simulations mimicking spring flow fluctuations and common hydroelectric project effects on egg masses, such as spring spills and rapid flow cessation, double the risk of extinction, from 5% in the Reference Model to 11% in Model (8). Similarly, these recommendations extend beyond spring flows to include summer flows, since multivariate sensitivity analysis also indicates that tadpole survival to metamorphosis is among the most important vital rates for overall population dynamics. For example, even single extreme flow events (with an annual recurrence interval), such as a summer recreational boating flow or discharge manipulation to conduct studies of fish habitat for a FERC license application, are predicted to result in a three to five fold increase in the 30-year extinction risk, from 5% to 16% (Models 1 & 20), or from 5% to 27% (Models 1 & 15), depending on the level of tadpole mortality. Because one of the major differences between *R. boylii* populations in regulated and unregulated rivers is the increased frequency of hydrologic mass mortality events (e.g. stranding and/or scouring), our model results support the hypothesis that conditions for *R. boylii* populations downstream of dams could be much improved by reducing these events with alternative dam management (e.g. reducing atypical flows and mimicking natural hydrographs).

**Combinations of hydrologic effects often result in disproportionate (e.g. non-additive) changes to *R. boylii* population dynamics.** Such effects are likely to occur in natural *R. boylii* populations, but are often overlooked when single factors are studied or modeled in isolation of one another. For example, the synergy between egg mass scouring and decreased fecundity simulated in Model (12) produced disproportionate increases in the 30-year risk of extinction compared to each effect alone (Models 8 & 10). The 30-year extinction risk is 85% for Model (12), which is 17 times higher than the Reference model, and almost 5 times greater than the sum of the first order effects (11% and 7%, Models 8 & 10). Similarly, when tadpole mortality during a single pulsed flow is combined with high rates of egg mass stranding and scouring (Model 25), the resulting increase in extinction risk is also multiplicative (Model 25 = 91%, Model 9 + 15 = 50%). These results emphasize that attempts to estimate the effect of any one anthropogenic hydrologic impact (e.g. summer recreational flows, extended spring spills, reduced available breeding habitat) without consideration for the myriad other impacts occurring simultaneously will likely underestimate the potential population-level consequences. By extension, we recommend that studies of hydrologic impacts consider the suite of stressors potentially affecting *R. boylii* populations as a whole rather than focusing on any one in isolation.

**There is good congruence between observed *R. boylii* breeding trends in three focal watersheds; SF Eel, Alameda Creek, and NF Feather, and the results of model scenarios combining similar differences in starting population sizes and the frequency of spring and summer hydrologic stressors** (see Section 3 Kupferberg et al. 2008). The results of this modeling exercise are not intended to mimic the dynamics of any one population, but rather explore the potential for different hydrologic stressors to affect population dynamics. That being said, the rough similarity between some of the most well-studied *R. boylii* populations (both regulated and un-regulated) and model results provides support that the model structure generally captures *R. boylii* population dynamics. For example, SF Eel and Alameda Creek (Camp Ohlone reach) populations are stable or increasing in the presence of naturally-occurring low frequency spring pulsed flows that cause scouring mortality and low levels of stranding mortality (analog to Models 1 & 2). Alameda Creek populations below the Calaveras Creek confluence, where water releases from Calaveras Reservoir decrease stream temperatures and elevate velocities during the breeding season, are exhibiting declines in breeding (analog to Models 30, 31, & 32). In the case of the NF Feather, the decline of the Cresta reach *R. boylii* population began three years after pulsed flows for whitewater boating were instituted during the egg (2002) and tadpole (2002-2005) rearing seasons (analog to Models 28 & 29). By comparison, *R. boylii* populations in the NF Feather (Poe reach) exhibited increases in breeding over the same time period (analog to Models 3, 8, & 27). While we are reassured by this general congruence, we emphasize that this model framework is not intended to be predictive of any one *R. boylii* population. Given the large uncertainties surrounding estimates of individual vital rates and their distributions (uncorrected for observation and other errors), the utility of this modeling exercise lies in the comparison of hypothetical model scenarios relative to our best estimate of population dynamics in hydrologically un-regluated environments. Individual scenarios should be viewed as hypotheses awaiting confrontation with future data collection. As such, this modeling effort highlights an urgent need to gather field data targeting key *R. boylii* vital rates (tadpole, 1st juvenile year, and adult survival), and impacts to them. In the absence of such data, the results from the Reference Models as compared to the set of hydrologic scenarios provide an additional tool for water resource managers to assess potential risks of various flow regimes for *R. boylii* populations.

## 4.2. Recommendations

This section is divided into two parts with the intent to clarify and emphasize particular sets of recommendations. High priority recommendations that derive directly from the modeling work and comparative hydrologic scenarios are outlined. The next section identifies critical information gaps and priorities for future research.

### *4.3.1. Management Recommendations Indicated by Model Outputs and Sensitivity Analyses*

A central tenet of the natural flow regime paradigm is that regulated flows should mimic natural patterns of temporal variation in hydrology to sustain fluvial geomorphic processes, functional food webs (Power et al. 1996; Poff et al. 1997; Richter et al. 2003), and match the adaptations of organisms to the conditions in which they evolved (Lytle and Poff 2004). The management recommendations stemming from this modeling exercise support the general ecological principles of this approach. Under natural (un-regulated) levels of hydrologic variation, *R. boylii* populations are expected to be self-sustaining over a thirty year time period with a low probability of extinction. Simulations mimicking different hypotheses about life stage impacts (and combinations) due to hydrologic regulation all suggest higher extinction risk and more vulnerable population demography (lambda near or below 1). While large uncertainties exist in the estimation of many of the vital rate parameters (Section 2, Appendix B), in every instance where decisions were made during model development the goal was to incorporate the most rigorous, un-biased quantitative data available. Only when no rigorous data were available for *R. boylii* did we resort to the inclusion of quantitative data from sister taxa (in the case of $S_{tadpole}$ and $S_{juv1}$). As a result, the outcome of this modeling exercise should be interpreted as preliminary, and results are expected to be refined with the inclusion of additional demographic data. With these caveats, the following recommendations are made:

- Eliminate manufactured pulsed flows once frog breeding begins in the spring through the early fall when metamorphosis occurs.
- Adopt water management strategies that anticipate the potential for synergistic and indirect effects among multiple hydrologic and environmental changes. Some changes to flow regimes may be positive for one species but have unintended negative consequences for another. For example, tradeoffs are likely to exist between increasing base flows to buffer the effects of pulsed flows or to aid out-migrating anadromous fish pass potential barriers, resulting decreases in stream temperature. Because decreases in water temperature can affect growth and survival rates of tadpoles, such tradeoffs need to be evaluated and anticipated. Similarly loss of algal food resources from summer pulse flows can have negative effects on tadpole survival. Additionally, the importance of the most fecund, early breeding females for overall population dynamics needs to be

evaluated, as the contributions of these individuals to recruitment may be the most vulnerable to early season hydrologic impacts.

- Gather data simultaneously on key demographic parameters during FERC relicensing studies (egg mass, tadpole, adult survival at a minimum), and incorporate new demographic estimates to future PVA's for *R. boylii* populations.
- Improve long-term monitoring programs for *R. boylii* in both regulated and unregulated (reference) river systems. In particular, a reference (un-regulated) Sierra Nevada population urgently needs to be identified and studied. Ideally, this site will be the focus of both monitoring and research on demographic parameters. For science-based management to be a viable option, attempts to link flow changes to population responses need to coincide with long-term biological monitoring of an appropriate sentinel species (Souchon et al. 2008). In order to apply this modeling approach of comparing scenarios, reliable data on population trends are needed for populations spanning the broad range of environments where *R. boylii* occurs.
- Appropriate State and/or Federal agencies should elevate the protection status of *R. boylii* (e.g., listing under the California or Federal Endangered Species Act). Evidence has accumulated over the last five years documenting the range-wide decline of *R. boylii* and has identified genetically unique populations in the Southern Sierra Nevada and Central Coast Ranges of California (Lind 2005) where declines are more pronounced. Likely mechanisms for *R. boylii* population declines are well documented and populations that are extant in regulated streams continue to show evidence of declines (Kupferberg et al. 2008, this report).

Mitigation and adaptive management of the flow regime effects on *R. boylii* populations identified Table 1.1 may be achieved by applying the above recommendations. These approaches for improving early life stage survival are summarized in Table 4.1. A key element to the success of applying the natural flow regime paradigm is knowledge of the highly site specific relationship between discharge, water surface elevation, and current velocity in the edgewater habitats used by *R. boylii*. This report has focused on *R. boylii*, however, it should be noted that a number of species, more commonly thought of as pond breeders, also breed along the margins of California's rivers. The species whose egg masses and larvae may be similarly susceptible to the direct and indirect effects of flow fluctuation include California Red-legged frogs (*Rana aurora draytonii*), Pacific Chorus frogs (*Pseudacris regilla*), Western toads (*Bufo boreas*), and newts (*Taricha torosa, T. granulosa, T. rivularis, T. sierrae*). It is thus imperative that conservation actions and river restoration efforts intended to improve conditions in the main part of the channel for a target organism be implemented in concert with an appropriate monitoring program of the species whose early life stages inhabit edgewaters.

**Table 4.1. Overview of potential mitigation and restoration options for *Rana boylii* in regulated rivers.**

| Project Operations | Short-term impacts | Long-term impacts | Mitigation/Restoration |
|---|---|---|---|
| Intentional aseasonal flows (power generation, recreation, out-migration of salmonid smolts); Unintentional spill of water over dam | - scouring or desiccation of egg masses[1,2] / tadpoles[3]<br>- export spring and summer algal productivity[4,5], reduced resources for tadpoles, reduced insect abundance[5], food web repercussions | - discharge decoupled from environmental cues (e.g. rainfall, air temperature) triggering inappropriate behavioral responses by adults, juveniles, delayed onset of breeding[1,6]<br>- smaller population sizes[1,2] | - mimic natural hydrograph to degree possible<br>- flow regimes and ramping rates to minimize impacts during breeding and rearing periods<br>- change management of water elevation in upstream reservoir |
| Intentional de-watering of stream channels for rescue operations | - desiccation of egg masses / tadpoles | Unknown | - observe minimum instream flow requirements<br>- post-event ramping rates that minimize disturbance |
| Unintentional powerhouse outages resulting in rapid increase in flows in bypass reaches, followed by rapid decrease in flows | - changes to margin water temperature, depth, and velocity,<br>- scouring/desiccation of eggs/tadpoles, depending on ramping rate, magnitude of change, channel shape | Unknown | - change timing of planned outages (for repairs, etc.) to outside of breeding and rearing season |
| Reduced winter/spring flows | - absence of scouring/depositional flows that prevent riparian encroachment<br>- reduced breeding habitat, greater distances between breeding sites[3] | - vegetation encroachment, altered channel morphology, reduced breeding habitat<br>- population loss/fragmentation[3], reduced gene flow, altered metapopulation dynamics | - mimic natural hydrograph to degree possible<br>- restore some components of spring snow-melt hydrograph[7] |
| Altered summer baseflows | - lower water temperatures<br>- change in available habitat (channel shape) | - promotes habitats that support non-native predatory fish, amphibians, and invertebrates, increased predation on eggs, tadpoles | - adjust water release temperatures (mix of depths)<br>- develop basin-scale plans for fish stocking relative to frog needs |

| **Project Operations** | **Short-term impacts** | **Long-term impacts** | **Mitigation/Restoration** |
|---|---|---|---|
| Movement of water among river basins | - potential for increased disease and parasite transmission | Unknown | - reassess water redistribution to eliminate, or shift timing to decrease disease (fall, winter) |

*References*: 1. GANDA 2008; 2. Kupferberg et al. 2008; 3. Lind et al. 1996; 4. Spring Rivers 2002; 5. GANDA 2006; 6. Borque 2008; McBain and Trush, Inc. 2009.

### 4.3.2. Research Priorities Indicated By Information Gaps

The best available data and newly collected field data were used to define vital rates for each *R. boylii* lifestage in this model. However, several of the vital rate values used in this exercise were based on related species or incorporated several, currently untested, assumptions. The main demographic parameters that require immediate follow-up investigation are tadpole, first year overwinter, and juvenile survival (Table 2.2). Additionally, the demographic impact of different hydrologic scenarios is only well-described for egg mass survival (stranding and scouring patterns). For example, predicting the actual survival consequences for tadpoles reared under different hydrologic conditions is prevented by substantial data gaps. While there are data from field enclosure and laboratory studies estimating survival and critical swimming velocities (section 4, Kupferberg et al. 2008) and anecdotal observations from the field of tadpole mortality after pulsed summer flows (Section 2 of Kupferberg et al. 2008), the critical challenge is to develop a functional understanding of how particular changes in flow management directly affect annual tadpole (or other life stage) survival. Such data are critically needed to improve our ability to accurately forecast the consequences of altered hydrologies for *R. boylii* populations, and could be collected as part of the FERC relicenscing process.

The result that *R. boylii* populations are very sensitive to early life stage survival is consistent with findings for trout in which the timing of floods which scour redds are known to be limiting factors (Strange et al 1993), but contrasts with other amphibian population projection models (Biek et al. 2002; Vonesh and De la Cruz 2002; Govindarajulu et al. 2005). Those models suggest that the most sensitive vital rates are post-metamorphic juvenile survival, the life stage for which there are no direct observations in *R. boylii*.

There are other anthropogenic stressors on *R. boylii* in regulated rivers that were not explored in this model, but which deserve further study. For example, predation pressure likely increases when invasive species (e.g. bullfrogs *Rana catesbeiana,* crayfish, and non-native fish) flourish in waterways subject to flow diversion and regulation (Hayes and Jennings 1988; Moyle and Light 1996; Marchetti et al. 2004). There may also be stressors originating outside a population’s watershed, such as downwind drift of organophosphate pesticides (Davidson 2004; Sparling and Fellers 2007), that influence early life stage vital rates and could act in synergy with the hydrologic stressors. Thermal regime effects both directly related to hydrologic regulation and indirectly due to watershed-scale land-use change (e.g., logging) also require further investigation.

## 4.4. Benefits to California

This research will be valuable to the adaptive management of regulated rivers in terms of evaluating the relative merits of competing flow proposals. By assessing whether early stages of the *R. boylii* life cycle are likely to be affected by the flow regime attribute under consideration, managers can determine if their actions may put populations further at risk or aid in their restoration. During FERC relicensing of hydropower projects, there are often discussions of the effects of proposed base flows, pulsed flows, and other conditions on a native aquatic species. The hydrologic scenarios modeled in this study cover a range of potential flow regimes and their influences on different life stages of *R. boylii*. These models can aid in the assessment of risk for this particular sensitive species and others with similar ecological niches, ultimately providing an additional tool for both hydropower licensees and regulatory agencies to evaluate and compare relative risks among species.

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# 6.0 Glossary

| | |
|---|---|
| Allee Effect | The point when the spatial distribution and density of a population inhibit the ability of individuals to find mates and reproductive rates decline rapidly. |
| Analysis of Covariance | A statistical method for analyzing the differences in the means of two or more groups of data, while accounting for variation in one interval-ratio variable. |
| Epilithic Periphyton/Diatoms | Algae that grows on the surface of rocks in a waterbody. |
| Fecundity | The number, rate, or capacity of production of offspring. |
| FERC | Federal Energy Regulatory Commission; the government body that licenses hydroelectric projects |
| *F* Ratio | A statistical ratio in analysis of variance (ANOVA) ; the variation explained by a set of treatments or factors in relation to the unexplained (error) variation |
| Lambda ($\lambda$) and Population Growth Rate | Annual proportional change in population, such that $\lambda = 1$ indicates stability, values $> 1$ indicate growth, and values $< 1$ indicate decline |
| Matrix Population Model | A type of population model that uses matrix algebra and pre-defined parameter values for different age classes or life stages to project population growth rate ($\lambda$) and extinction probabilities into the future. |
| Oviposition | Egg laying |
| Population Viability Analysis | The process of defining vital rates and potential threats for a species or population and incorporating these into an analysis of the likelihood of persistence of that species/population over a given time period into the future. |

| | |
|---|---|
| PIT (tag) | Abbreviation for "Passive Integrated Transponder" tags, which are injectable, internal, radio-type tags that when scanned with the appropriate reader, provide a unique identification number for individual animals. |
| Ranid Frog | Any frog species that is a member of the amphibian genus *Rana* and family Ranidae. |
| Recruitment | The amount by which a population changes in size during one stage or over one interval in time, such as recently metamorphosed young of the year frogs growing to become adults of reproductive size. |
| Scouring | Removal of frog egg masses from stream substrates, usually by high water flows. |
| Stable Age Distribution | The proportion and/or number of individuals in age class or life stage under the assumption that the population is at equilibrium. |
| Stochastic | Processes and variables that are random, non-constant, and unpredictable. |
| Stranding | Dessication of frog egg masses due to rapidly dropping water flow levels. |
| Vector (of starting population sizes) | A definition of the number of individual in each life stage to be used in subsequent matrix algebra computations of a population model. The entire vector is determined based on defining the number of individuals in one lifestage and carrying that through mathematically to define all the others based on the concept of a *stable age distribution* (see above). In matrix algebra terms, a vector is a matrix which has one of its dimensions equal to one. |

# APPENDIX A. Detailed Descriptions of Study Areas

## South Fork Eel River

The SF Eel has relatively pristine habitat. It has moderate bank slopes, moderately confined valleys with bedrock outcrops, small but continuous riparian zones, coarse substrates, and moderately steep gradient features including steps, riffles, and pools. The study reach encompasses confluences with five perennial tributaries and other ephemeral drainages inhabited by *R. boylii* but not used for breeding. Substrates are sandstone and mudstone-shale bedrock and boulders. The river has riffle pool morphology with cobble, pebble, and gravel point bars. One riffle pool sequence is ≈ 5-7 times the bank full channel width (≈35 m). The river runs through mixed coniferous forest and the common riparian species are similar to the NF Feather, alder (*Alnus latifolia*) and sedge (*Carex nudata*). Detailed geomorphic descriptions are in Seidl and Dietrich (1992). The algal based food web has been extensively studied by Power (1990) and Power et al. (2008). *R. boylii* breeding behavior in relation to channel morphology at the site is described in Kupferberg (1996).

## Hurdygurdy Creek

The Hurdygurdy Creek study area was located in the lower section of the creek within 2km of the confluence with the South Fork of the Smith River, Del Norte County, California (Figure A.1). Hurdygurdy is a fifth order tributary (to the Smith River) with cool wet winters and warm dry summers. General vegetation type is mixed hardwood/Douglas-fir (*Pseudotsuga menziesii*) forest in the uplands with alder (*Alnus* sp.) and willow (*Salix* sp.) in the riparian zone. Average annual rainfall is 280 cm (range 152-330 cm) (Gasquet Ranger Station, Smith River National Recreation Area, eleven air miles north). During the study, ambient water and air temperatures ranged from 6 to 18° C and 6 to 30° C, respectively. Hydrologic and geomorphologic events in Hurdygurdy Creek are reflective of high winter/spring run-off events and include debris flows, flooding, and braided channel migration. Even with this relatively active geomorpohology, stream mesohabitats (e.g. low gradient riffles, main channel pools) have maintained sizes and positions over many years. Discharge averages 100 $m^3sec^{-1}$ in winter with 10-year flood events reaching as high as 140 $m^3sec^{-1}$ (D. Fuller, Bureau of Land Management, personal communication). Summer discharge can be as low as 1 $m^3sec^{-1}$ (M. McCain, USFS Gasquet Ranger District, personal communication). Capture-recapture surveys of adult frogs was conducted at a large breeding area approximately 877m upstream from the river confluence; at this site, the stream is braided and approximately 40m wide (Wheeler 2007).

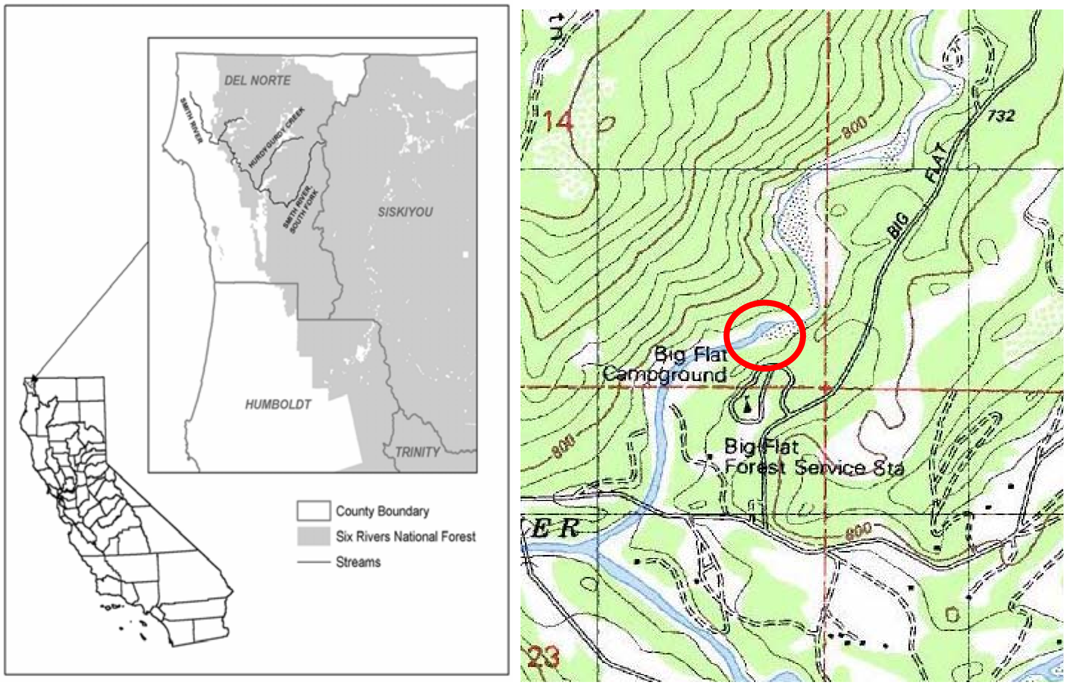

**Figure A.1 Location of Hurdygurdy Creek study area (from Wheeler 2007)**

### North Fork Feather River

The NF Feather, on the western slope of the Sierra Nevada, has numerous geologic formations and volcanic features, incised canyons, and steep forested slopes. The canyon shape provides conditions for a series of dams along the river, each capturing flow for hydropower generation before sending it downstream to the next in-stream reservoir. Typical of *R. boylii* breeding habitat in the Sierra Nevada, the breeding sites throughout the Poe and Cresta reaches of the NF Feather, are in close proximity to creek confluences, contain shallow coarse cobble bars, and are vegetated by sedges and willows (*Salix* spp). The shallow rocky margins provide appropriate depth and velocity conditions for oviposition and larval rearing, while the rocks and sedges provide cover for newly metamorphosed frogs. Tributaries provide adult habitat.

### Alameda Creek

Similar in area to the SF Eel watershed but receiving less precipitation, the Alameda Ck watershed provides a portion of San Francisco's drinking water. The unregulated study reach is hereafter referred to as the Camp Ohlone reach and is upstream of the dam and tunnel which divert water to Calaveras Reservoir (Figure A.2). Calaveras Reservoir captures runoff from Calaveras Ck. and Arroyo Hondo, and then flows back into Alameda Ck. The downstream regulated egg survey reaches, are a section in the steep gradient bedrock "Little Yosemite" canyon, which experiences water diversion, and an alluvial section below the confluence with Calaveras Ck, referred to as the Sunol reach. The topography and vegetation of the Alameda Ck reaches are typical of Central Coast Range oak woodlands and grasslands. Riparian vegetation includes Sycamore (*Platanus racemosa*), mulefat (*Baccharis salicifolia*), alder, willow, sedge (*Carex* sp.), and cattail (*Typha* sp.). The watershed has heterogeneous (i.e., steep, moderate and shallow) hill slopes. Alameda Ck flows through a series of alluvial valleys with small to moderately developed flood plains linked by narrow bedrock-channel corridors. The creek can become intermittent in the upper parts of the watershed. In years with low precipitation, scour pools created by fallen trees become important refugia for amphibians. Alameda Ck is unique among the study sites because California Red Legged Frogs, (*Rana draytonii*) also occur there. *R. draytonii* use slightly different habitats within the creek, usually ovipositing at the upstream margins of pools where conditions are more sheltered from flows, in deeper water on vegetation instead of rocks like *R. boylii*.

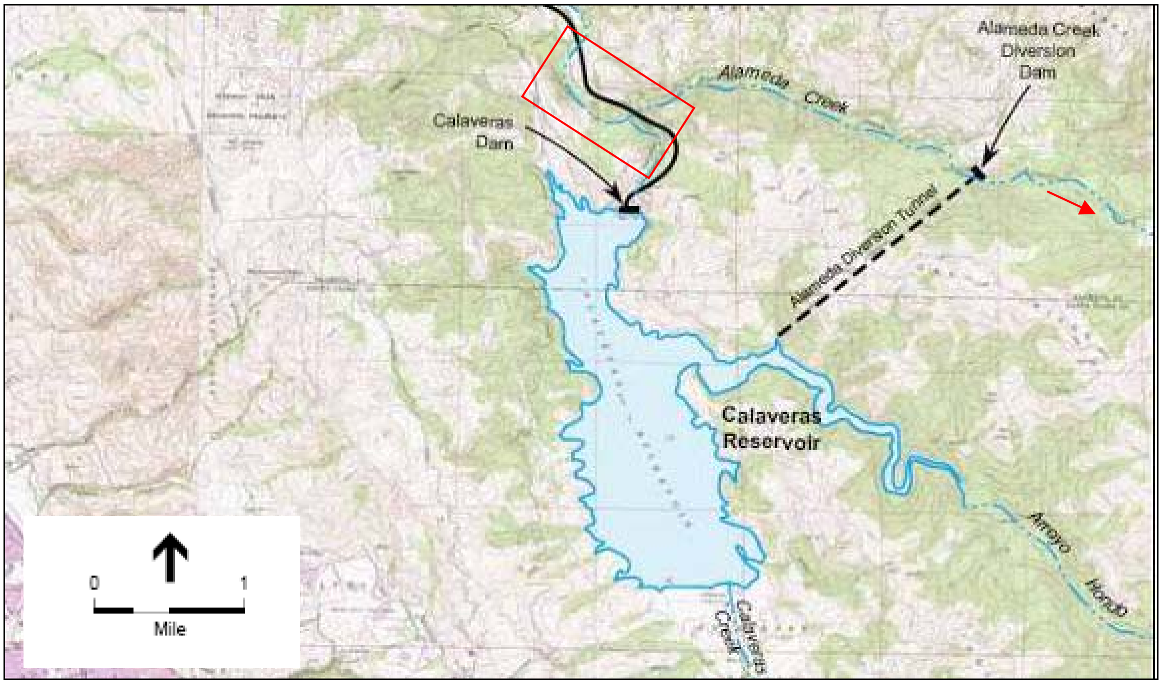

**Figure A.2 Alameda Ck study systems. Down stream regulated reaches include sections upstream and downstream of the confluence with Calaveras Ck (red box). The unregulated Camp Ohlone reach is upstream of the Alameda Diversion Tunnel, in the direction of the red arrow but is off this map. Source of map SFPUC 2007, available online http://www.sfgov.org/site/uploadedfiles/planning/vol3_sec5-4_wsip-dpeir.pdf accessed July 28, 2007.**

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# APPENDIX B. Detailed Young of the Year Data Collection and Population and Survival Rate Estimates

### Capture-Recapture Field Methods

Over the course of three days in the fall of 2006 at each of two study areas, young of the year foothill yellow-legged frogs were marked. Surveys on the South Fork Eel River (SF Eel) occurred on September 16, 17, and 21, 2006 along a 650m length of river. Surveys on Alameda Creek occurred on October 4, 5, and 6, 2006 along a 379 m length of stream (see Kupferberg et al. 2008 for details on each study area). Additional visits to these sites were made in spring of 2007 in an attempt to develop overwinter survival estimates. The SF Eel was visited on June 27-29, 2007. Alameda Creek was visited on March 29 and 30, and due to low capture numbers, again on June 13-15, 2007. On all visits, frogs were marked subdermally with Visible Implant Elastomer (VIE; from Northwest Marine Technology™) which is a silicone-based biocompatible compound that cures to a pliable state. Though initially visible with the naked eye (a few days), the elastomer eventually fades, thus, marks are not likely to affect the vulnerability of frogs to predators. Most of the available elastomer colors will fluoresce under a deep violet (405 nm) light. Research on a variety amphibian and other aquatic species has found that, if used properly, this marking technique does not typically cause injury or mortality to the study species (e.g. Anholt et al. 1998, Vasconcelos and Calhoun 2004).

Frogs were marked using an insulin syringe and 29-gauge needle to inject a small amount (2-3 mm) of elastomer subdermally on the ventral side of their rear legs. Each day a different color and alternate rear leg was used. For Fall 2006, on the first day at each location, frogs were marked with orange elastomer on their right rear leg, on the second day frogs were marked with pink elastomer on the left rear leg, and on the third day, frogs were marked with blue elastomer on their right rear leg next to the orange mark if a recapture from Day 1. For Spring 2007 visits, the following color/leg combinations were used: first day – yellow on left rear, second day - green on right rear, and third day - red on left rear.

To increase detection of marked individuals, each captured frog was scanned with a deep violet light flashlight while the observer was sitting partially covered in a large, thick, black plastic garbage bag. For each individual captured, the following information was recorded: date, life stage (though all marked individuals were young of the year), capture/recapture status, colors on capture, colors on release, snout-urostyle length (mm), weight (g), and location along the study reach.

### Population Estimates and Daily Survival Rates

Individual capture histories were generated from batch mark data using a SAS program developed by the authors and a USDA Forest Service statistician (J. Baldwin, pers. com.). For population estimates, Program CAPTURE was used; this program was developed by J. Hines of the U.S. Geological Survey available at http://www.mbr-pwrc.usgs.gov/software/ and downloaded on 10 January 2007. Previous versions of this software were developed by G. White, D. Anderson, K. Burnham, and D. Otis (Otis et al. 1978 and White et al. 1982). The appropriate population estimation model was chosen using the testing options available in this software. If a particular model was selected as the best fit to the data, but no estimator was available for that model, estimates from the next most appropriate model(s) were used.

For daily survival rate estimates, Program MARK (White and Burnham 1999, Cooch and White 2007) was used to derive estimates for young of the year frogs at each study area. Program MARK offers four "pre-defined" models which allow two parameters to vary over time (in this case day): survival (Phi) and capture probability (p). These four models were evaluated for each study area. Survival rates from Day 1 to Day 2, Day 2 to Day 3, and overall were evaluated. In all analyses the sin link function and 2nd part variance estimator were used.

At the SF Eel, 337 individuals were captured over the course of the three days. Six individuals died during capture and holding or were found dead under stream-side rocks and were not used in the population estimates. The most appropriate model was one in which capture probabilities varied by time, behavioral response (e.g., "trap-shy" response), and by individual characteristics (e.g., due to gender or home range, etc.). However, no estimator existed for this model, so estimates are presented for the next two best-fitting models: (1) the heterogeneity model – capture probabilities vary by individual and (2) the null model – constant capture probabilities. Population estimates from these two models were quite different (Table B.1).

At Alameda Ck, 447 individuals were captured over the course of three days. Ten of these died during capture and holding or were found dead under stream-side rocks and were not used in the population estimates. The most appropriate model was one in which capture probabilities varied by behavioral response (e.g., "trap-shy" response). The estimator for this model yielded an estimate with an extremely high standard error, so the estimate based on the null model is also presented (Table B.1).

The highest estimated daily survival rate for each study area was used in subsequent analyses. For the SF Eel the highest daily survival rate was 0.937 and for Alameda Creek it was 0.984. The rationale for using these high values was that these estimates were based on very short recapture intervals (i.e. days) for which survival rates are expected to be high. Also these values were only used to aid in the derivation of other transition probabilities; they are not presented on their own as a true survival rate for this life stage (e.g., see Section 2.3.4 Survival of Tadpoles to Metamorphosis).

**Table B.1. Fall 2006 population estimates for young of the year *Rana boylii* at the South Fork Eel River and Alameda Creek study sites. Estimates were generated by Program CAPTURE.**

| Site | Model Type | Model Selection Criterion[1] | Population Estimate | Standard Error | 95% Confidence Interval |
|---|---|---|---|---|---|
| SF Eel | Heterogeneity | 0.82 | 622 | 24.28 | 579-673 |
| | Null | 0.75 | 1199 | 172.83 | 922-1608 |
| Alameda Ck | Behavior | 1.00 | 1717 | 889.23 | 812-4816 |
| | Null | 0.20 | 834 | 56.82 | 738-961 |

1. Values closest to 1 are most appropriate model(s).

Though initially the plan was to generate over-winter survival estimates by recapturing frogs marked in Fall 2006 in Spring 2007, VIE marks were not reliable over this extended period of time. Because the marks were reliable over the short term, is was possible to derive new population estimates for Spring 2007, for the approximately one year old frogs using the least biased Chapman (1951) version of the Lincoln-Peterson estimator. From those estimates, overwinter survival rates were extrapolated based on the logic that the difference between the fall and spring population size estimates roughly equated to overwinter losses.

Captures and recaptures were low during spring visits at both study sites. At the SF Eel site, a total of 23 individual frogs were captured and marked over the three day period in June. Using Day 2 and Day 3 captures and one recapture, the population was estimated to be 47 (± 21.91) with 95% confidence intervals of 4 to 90. Only one individual was found with a mark from the previous fall (Table B.2). The difference between the fall population estimate of 622 (Table B.1) and the spring population estimate of 47 gives a loss rate of 92.4 %, and thus a survival rate of 7.6%, or as a proportion, 0.076.

At the Alameda Creek site, two capture-recapture surveys were done; a two-day visit in March and a three-day visit in June. The population estimate for the March visit was 19 (± 3.98) with 95% confidence intervals of 11-27. In June, only four individuals were captured and four others escaped so no estimates were done. For all spring Alameda Creek visits, a total of four individuals were found with marks from the previous fall (Table B.2). The difference between the fall population estimate of 1717 (Table B.1) and the spring estimate of 19 gives a loss rate of 98.9%, and thus a survival rate of 1.1% or as a proportion, 0.011.

**Table B.2. Spring 2007 capture-recapture results and Lincoln-Peterson population estimates for one year old *Rana boylii* at the South Fork Eel River and Alameda Creek study sites. For Days 1-3, individuals were given day-appropriate color marks as described in the methods. For Days 4 and 5 at Alameda Creek, individuals were not marked.**

| Site | Day 1 | Day 2 | Day 3 | Day 4 | Day 5 | Population Estimate Approach | Population Estimate | Standard Error, and 95% C.I. |
|---|---|---|---|---|---|---|---|---|
| SF Eel | 7 total, all unmarked; 4 escapes | 11 total, 1 fall06 recap; 9 escapes | 7 total, 1 recap from previous day; 4 escapes | *na* | *na* | L-P estimate from Day 2 and Day 3 captures only | 47 | 21.91,<br>4 - 90 |
| Alameda Creek | 8 total, 1 recap from fall06 | 10 total, 4 recaps from previous day, 2 from fall 06, 1 from both | 1 unmarked, 1 recap with marks from fall06 and spring 07 (day 1) | 1 escape | 1 unmarked, 1 recap with marks from spring 07 (day 1); 3 escapes | L-P estimate from Day 1 and Day 2 captures only | 19 | 3.98,<br>11 - 27 |

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