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Arnold Schwarzenegger
Governor

PULSED-FLOW EFFECTS ON FOOTHILL YELLOW-LEGGED FROG (*RANA BOYLII*):

INTEGRATION OF EMPIRICAL, EXPERIMENTAL, AND HYDRODYNAMIC MODELING APPROACHES

FIRST-YEAR PROGRESS REPORT

PIER INTERIM PROJECT REPORT

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"Research Powers the Future"

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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), conducts public interest research, development, and demonstration (RD&D) projects to benefit California.

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Pulsed-Flow Effects on the Foothill Yellow-Legged Frog (Rana boylii)*: Integration of Empirical, Experimental, and Hydrodynamic Modeling Approaches—First-Year Interim Report* is the first-year progress report detailing preliminary results for the hydropower pulsed-flow program (contract number PFP-03) conducted by the University of California, Davis, and its affiliates. The information from this project contributes to PIER's Energy-Related Environmental Research Program.

For more information about the PIER Program, please visit the Energy Commission's website at www.energy.ca.gov/pier or contact the Energy Commission at 916-654-5164.

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Abstract

This report synthesizes data obtained through 2005 on how flow variation from the management of hydroelectric dams, natural storm events, and experimental manipulations of current velocity, influences the foothill yellow-legged frog (*Rana boylii*). Egg and tadpole survival, population dynamics, tadpole behavior and growth, and habitat responses to flow fluctuation are examined.

A review of literature and Federal Energy Regulatory Commission related reports indicates that egg masses are negatively affected by pulsed flows via scouring, if flows occur during or after oviposition, and via desiccation, if oviposition occurs during high flows that subsequently drop. Multiple studies document tadpole stranding and potential negative effects on metamorphs. South Fork Eel River population monitoring shows that the magnitude and timing of spring pulse flows are key factors in survival of eggs and tadpoles. While large-magnitude spring pulses decrease egg survival, smaller pulses later in the spring cause even higher mortality. Fluctuations in population growth are associated with spring pulse events three years prior.

Experiments undertaken by this project suggest that during pulse flows, tadpoles seek refuge from higher velocities in the substrate, but many are swept downstream. Tadpoles confined to refugia face energetic costs in terms of growth and development.

Results will be verified in follow-up experiments and analyses during 2006 and 2007. Questions about habitat availability during pulsed flows will be addressed through hydrodynamic modeling.

Keywords: Foothill yellow-legged frog, *Rana boylii*, pulse flow effects, tadpole swimming, amphibian populations, FERC relicensing, river regulation, 2D hydraulic modeling

Executive Summary

Introduction

The foothill yellow-legged frog (*Rana boylii*) is one of a few California amphibians whose complete life cycle is associated with fluvial environments. The life stages of *R. boylii* occur along a mobility continuum from immobile (eggs) to highly mobile (adults), such that adaptations that improve survival rate vary in relation to ontogeny. To avoid disturbance, the timing of this complex life history and set of habitat preferences is synchronized with the seasonality of runoff during the predictable cycle of wet winters and dry summers occurring across *R. boylii*'s range.

Over the last half century, *R. boylii* has declined dramatically, especially in Southern California and the southern Sierra Nevada mountains. Dams and reservoirs have been cited as likely factors in this decline because they drastically alter the disturbance regime and sediment budget of rivers in which native species have evolved, resulting in permanent alteration to in-stream habitats. The ensuing impact on *R. boylii* survival has been a focus of study over the last decade, but many knowledge gaps remain. Perhaps one of the largest gaps is in understanding the effects of large aseasonal fluctuations in water discharge, referred to as pulsed flows, on *R. boylii* and their habitat. Those life stages that are confined entirely to the aquatic environment, eggs and tadpoles, are particularly vulnerable to changes in flow.

This report synthesizes findings obtained before December 31, 2005, on how the magnitude and frequency of flow variation influences (1) egg and tadpole survival; (2) population dynamics; (3) tadpole behavior, growth, and development; and (4) availability and stability of habitat conditions for eggs and tadpoles.

Purpose

This three-year project encompasses a multifaceted study approach to address the direct effects of pulsed flows on vulnerable life stages of *R. boylii* and the indirect effects of pulsed flows on *R. boylii* habitat. During year one, 2005, existing empirical data from the scientific literature and FERC hydropower relicensing reports were catalogued, reviewed, and summarized. Specific knowledge gaps were identified, and experiments were conducted to begin filling knowledge gaps specific to tadpole response to flow change. The goal for 2006 is to develop hydrodynamic modeling tools for assessing how flow regime–induced changes in habitat availability and heterogeneity affect variables related to *R. boylii* physical tolerances. The integrated results of this work should provide a mechanistic understanding of the processes that take place when pulsed flows occur during the biologically active season for *R. boylii*. This model-based method may be used in future pulsed-flow planning to reduce environmental impacts. To produce generalizable results, this integrated research approach is designed to elucidate mechanisms, not to mimic site-specific pulsed-flow scenarios related to a particular hydropower project. In 2007, the goal is to collect further demographic data and develop a population projection model for *R. boylii* under different hypothetical flow scenarios.

Project Objectives

Phase I objectives met during 2005 were to:

- Gather and review available literature and reports that provide information on the effects of pulsed flows on *R. boylii*.
- Comprehensively describe and summarize the report data. A meta-analysis approach was deemed to be inappropriate due to data quality issues.
- Identify specific knowledge gaps regarding effects of pulsed flows on *R. boylii* habitat, behavior, survival and/or response variables correlated with overall fitness, and population dynamics.

Phase II objectives, begun in 2005 and to be completed in 2006 and 2007, are to:

- Address specific knowledge gaps identified in Phase I with a series of small-scale laboratory and field experiments.
- Develop a model-based method to evaluate changes in habitat-scale hydrodynamics.
- Use results from lab and field manipulations to assess how modeled changes in habitat availability and heterogeneity will influence *R. boylii* survival.

Results and Preliminary Conclusions from 2005

Phase I: Statewide Report and Literature Review

The following patterns were consistent across most of the statewide studies and FERC-related reports that were reviewed:

1. Egg masses are negatively affected by pulsed flows via scouring if flows occur during or after oviposition. Negative effects associated with desiccation occur if oviposition (egg laying) takes place during high flows followed by rapid flow recession. Thus the timing, magnitude, and duration of pulsed flows are the critical characteristics that can be changed to reduce impacts to egg masses.
2. Stranding of tadpoles following pulsed-flow releases has been observed. There is also an indication that pulsed flows may lead to a lower abundance of tadpoles at particular locations.
3. Effects of pulsed flows on post-metamorphic life stages are not clear. Preliminary evidence for short-term behavioral responses to these flows needs further research.
4. Methods to quantify habitat vary among studies. Stationary polygon and transect methods are most relevant to the requirements of immobile stages (eggs and early tadpoles). Shifting transect methods provide information on the overall area of suitable habitat. Polygon methods also provide information on the number of suitable habitat patches as well as overall area.
5. A quantitative graphical analysis of data culled from reports showed that variation in suitable habitat area due to changes in discharge is site specific. Some sites show

increasing area while others show decreasing area as discharge increases, indicating the importance of channel morphology and local features.

Phase II: Population Monitoring, Experiments, and Hydrodynamic Modeling

Three study sites in Northern California were selected to explore the relationship between existing hydrologic and frog population data and to conduct the hydrodynamic modeling. Two sites are in regulated systems (North Fork Feather River and Alameda Creek), and one site is in an unregulated system (South Fork Eel River) for comparison. Population records date back to 2001 for the NF Feather River, 1997 for Alameda Creek, and 1992 for the SF Eel River. Initial analyses are focused on the longest data set (SF Eel River) to maximize power for pattern detection and are presented in Section 3 of this report. Field and flume experiments on larval response to increased velocity are presented in Section 4. These analyses are ongoing and will be completed for all three sites by the end of Phase II.

The following preliminary conclusions were drawn from the SF Eel River long-term population monitoring:

1. Annual fluctuations in population growth on the unregulated SF Eel River are not associated with the magnitude of winter peak discharge, but rather are associated with spring pulse-flow events three years prior. This indicated that spring pulsed flows affecting the survival of eggs and larvae can change population dynamics.
2. Timing of breeding in the spring is not associated with stage height on the SF Eel River; there is only a very weak trend for frogs to breed later in years with higher water levels. It is likely that increasing water and air temperature cue the initiation of breeding as some previous studies suggest.
3. The magnitude and timing of spring pulse flows on the SF Eel River have an important influence on whether embryos survive to hatching. While large-magnitude pulses decrease egg survival, smaller-magnitude pulses later in the season can cause higher mortality.

Preliminary results from the pilot larval experiments are as follows:

1. Tadpoles become significantly less active as stream velocity increases and stay in micro-refugia in the substrate. In the flume experiment, embeddedness of the substrate did not change the short-term behavioral response of tadpoles to increasing velocity. The critical velocity at which tadpoles were flushed out of a microhabitat and swept downstream could not be determined in the pilot experiment, but likely lies between 20 and 40 cm/s.
2. During the experiments, less than 50 percent of tadpoles that were relocated to higher-velocity microhabitats (10–15 cm/s) were able to either find refuge in the substrate or swim cross-current to a lower-velocity patch. Two methods of relocation (group vs. individual) were assessed. Among individual trials, no tadpoles returned to near-shore patches.
3. Tadpoles reared at elevated velocities (6–12 cm/s) over the course of several weeks were significantly smaller and less developed than tadpoles reared at low velocities

(0–3 cm/s). This key result from the rearing experiment suggests the cumulative effects of confinement to substrate refugia within high-velocity environments might have implications for future population trends.

4. The role of predation in determining survival inside refugia and when swept downstream could not be addressed during flume experiments, but may play an important role in survivorship.

The preliminary findings of these pilot experiments suggest that when a pulsed flow occurs, a portion of tadpoles seeks refuge from higher velocities in the substrate while most are swept downstream. A small percentage successfully moved cross-current back to near-shore microhabitats. Those tadpoles confined to substrate refugia face energetic costs in terms of growth and development that may influence future reproductive output and population dynamics.

Directions for 2006–2007 (Year 2)

Year two of this study will address the following questions:

- What is the critical (threshold) velocity at which tadpoles are swept downstream? Does it vary with developmental stage?
- Is the magnitude of flow change that creates velocity and depth conditions "unsuitable" to both eggs and tadpoles site specific? "Unsuitable" is defined as too high for proper growth and development or beyond the velocity threshold for tadpole swimming ability.
- What traits of the channel morphology (cross-section shape, bank steepness, or longitudinal gradient) contribute to the pattern—observed in the statewide review data—of changes in habitat area as discharge increases?
- How do the diversity and connectivity of suitable microhabitats change during a pulse?
- What conditions lead to stranding of tadpoles in unconnected microhabitats?
- How does the availability of refugia change during a pulse event? Refugia are defined as microhabitats where velocity and depth are such that tadpoles can access the interstitial substrate before being swept downstream.

Directions for Year 3

Begin a demographic study of *R. boylii* and initiate development of matrix models that could predict population trajectories under varying scenarios of pulsed-flow frequency.

Recommendations for Future Studies

1. Exploratory research is needed on short-term behavioral responses to pulsed flows by post-metamorphic life stages.
2. Future FERC relicensing or other studies on *R. boylii* would be improved by:
    a. Including comparisons of impaired and unimpaired hydrographs, data on spill and pulse frequency, channel cross-sections, and other relevant hydrologic and

geomorphic information for the study area in order to facilitate comparisons among watersheds and provide context for the observed results.

b. Including bankfull width or upstream drainage area in evaluations of habitat area to facilitate direct comparisons among rivers/watersheds.

c. Presenting the sampling effort (for example, number sites, search time, or area) clearly in text and figures.

d. Using consistent life stages that are clearly defined.

e. Improving abundance/population estimates through more rigorous field techniques such as mark-recapture or multiple visits over short periods.

Benefits to California

The primary benefits of this research are fundamental to the conservation of *R. boylii*, a California Species of Special Concern. Detailed results fill key knowledge gaps on the direct negative effects of aseasonal pulse flows on vulnerable life stages of *R. boylii*. The study conclusions allow for more informed resource management decisions and ultimately the possibility for improved in-stream habitat conditions, particularly if the findings are incorporated into future hydropower relicensing projects.

The methods used in this research have applicability beyond the conservation of *R. boylii*. In particular, the use of 2-D hydrodynamic modeling to evaluate changes in aquatic habitat conditions would be beneficial to determining flow recommendations for multiple riverine species.

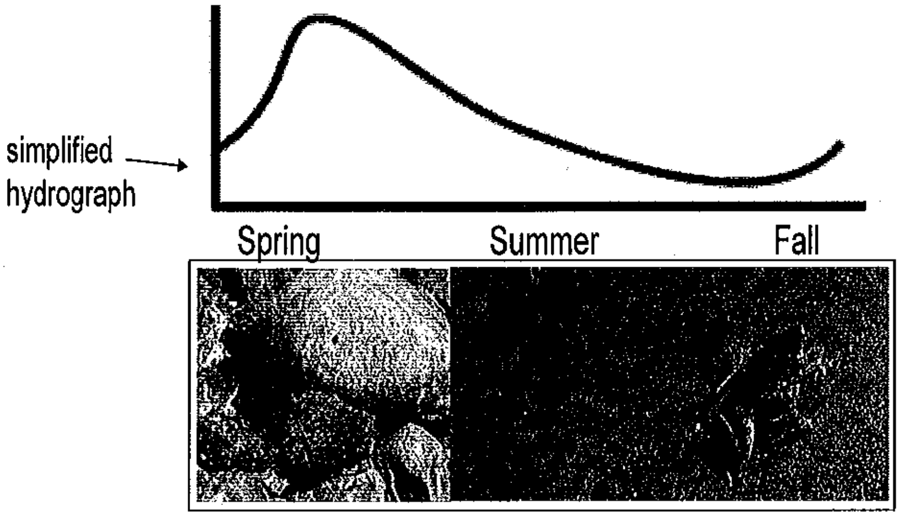
1.0 Introduction

Over the last half century, *Rana boylii*, the foothill yellow-legged frog, has declined dramatically, especially in southern California and the southern Sierra Nevada mountains. It has disappeared from 54% of known historic sites (Davidson et al. 2002) and has been listed as a California Species of Special Concern (Jennings and Hayes 1994; Jennings 1996; California Department of Fish and Game 2004). Potential causes are many, but those related to dams and flow regulation are especially ubiquitous. Habitats have been destroyed and fragmented as river channels were converted to reservoirs. Alterations to the disturbance regime and sediment budget of dammed rivers have drastically modified the remaining river channel environment. Predation by non-native predators such as bullfrogs (*Rana catesbeiana*), fish, and crayfish has increased as these invasive species flourished in California waterways subject to flow diversion and regulation (Moyle and Light 1996; Marchetti et al. 2004). As a result, *R. boylii* have either disappeared or declined to small population sizes relative to nearby populations in unregulated rivers within the same watershed (S. Kupferberg, personal observation, and unpublished USFS data). This project focuses on the effects of one aspect of flow regulation, the extreme aseasonal fluctuation in water discharge volume during the *R. boylii* larval rearing season.

1.1. Background and Overview

The ability to avoid, withstand, and recover from disturbance is crucial for organisms living in the highly variable environment of a river. *R. boylii* is such an organism, whose entire life cycle is associated with fluvial environments. Adult frogs are almost always found close to water, from small creeks to large rivers, and often use cover within the stream as a primary refuge. Clutches of eggs are laid on channel substrates in spring or early summer, and larvae metamorphose in late summer or early fall prior to the onset of the next rainy season's floods. Overwintering occurs in refugia in tributaries and springs (Nussbaum et al. 1983; Rombough 2006. To avoid disturbance, the timing of this complex life history is synchronized with the seasonality of runoff during the predictable cycle of wet winters and dry summers occurring across *R. boylii's* range (Kupferberg 1996; Lind and Welsh in revision)

R. boylii avoidance of disturbance is disrupted in regulated rivers when pulsed-flow discharges are decoupled from the physical and biological factors that normally vary with runoff, such as air temperature, precipitation, and the abundance of algae (Power 1992; Power et al. 1996; Wootton et al. 1996). These factors are important determinants of when the transitions from one amphibian life stage to the next occur. Warming temperatures cue breeding (Zweifel 1955; Kupferberg 1996, NFF9), precipitation inhibits breeding (Fukuyama and Kusano 1992), and algal assemblage determines growth rates and time to metamorphosis (Kupferberg et al. 1994; Kupferberg 1997). Even when the timing of a flow pulse may be during a season of natural runoff fluctuation, such as during breeding, the magnitude and frequency of pulses above an artificially low base flow can exceed natural discharge fluctuation by orders of magnitude. Combined, these factors pose serious threats to amphibian conservation in rivers in general and to *R. boylii* specifically.



Immobile → **Mobile**

Life stage	**Eggs and Embryos**	**Larvae**	**YOY/Juveniles**	**Adults**
Adaptations to Flow Fluctuation	❖ low velocity microsites ❖ channel sections w/ stable stage and velocity ❖ egg adhesion / clutch cohesion ❖clutch shape deforms to be hydrodynamic	❖ swimming ability ❖ seek refuge in interstices ❖ mouthparts used to hold on to substrate	❖ swimming ability ❖ refuge in interstices	❖ strong swimmers ❖ move to over-wintering refugia (e.g. tribs.)
Potential Mitigation Measures	❖ timing/duration pulses to avoid breeding season ❖ flow regime maintains channel morphology ❖ maintain Q_{min} to prevent egg dessication / stranding ❖ limit Q_{max} to prevent egg scour	❖ timing / duration of pulse flows relative to swimming ability ❖ maintain interstices ❖ ramping rates ❖ Q_{min} for habitat heterogeneity	❖ timing / duration of pulse flows relative to swimming ability ❖ maintain interstices ❖ ramping rates ❖ Q_{min} for habitat heterogeneity	❖ time pulses relative to seasonal movements ❖ maintain connectivity between regulated river and tributary population centers

Figure 1. Life stages of *R. boylii* and the corresponding adaptations which have evolved in the predictable flow regime of California's Mediterranean climate. Potential measures to mitigate the impacts of artificial flow fluctuation are also indicated.

The life stages of *R. boylii* (as well as other aquatic taxa) occur along a mobility continuum from immobile (eggs) to highly mobile (adults) such that adaptations which improve survival rate vary in relation to life stage (Figure 1). Current knowledge of *R. boylii's* adaptations to surviving fluctuating flows is limited to the egg and adult life stages, the stages that experience flow variation naturally. For example, *R. boylii* has evolved breeding site preferences, such that dispersed adults move and congregate at the margins of relatively wide and shallow river reaches (VanWagner 1996). These channel shapes provide suitable habitat depth and velocity conditions for oviposition across a range of discharge volumes, resulting in a decreased susceptibility to rapid changes in flow (Kupferberg 1996, Yarnell 2000; Lind and Welsh in revision). Under a natural flow regime, discharge gradually declines in early summer and larvae hatch to occupy slow, shallow channel margins. Larvae, juveniles, and the different size classes of adults selectively occupy the margins of diverse river habitats (Van Wagner 1996; Yarnell 2000). However, little is known about how *R. boylii* larvae respond to changes in water velocity and current direction or about the limits of larval and adult swimming ability.

This project sought to examine the effects of pulsed flows on *R. boylii* through a combination of (1) analyses of existing empirical data; (2) laboratory and field experiments to quantify the physical tolerances of vulnerable life stages and observe behavioral responses to changes in flow conditions; and (3) development of a hydrodynamic modeling approach that evaluates short-term direct and indirect effects of pulsed flows on all life stages of this frog. The integrated results of this work provide a better understanding of the current impacts of pulsed flows, along with a model-based methodology that can be used to mitigate impacts in future pulsed-flow planning.

1.2. Project Objectives

This study employed a two-phased approach designed to occur over two years, with each phase completed at the end of each year. Phase I involved a review of published and unpublished literature, collation and analysis of data from recent studies, and identification of knowledge gaps. Phase II is using that information to design and conduct experiments on larval behavior and initiate development of a hydrodynamic model-based assessment of *R. boylii* habitat. The complementary efforts of data review, modeling, and experiments were essential to the primary objective to translate model predictions regarding habitat parameters into actual effects on *R. boylii*.

Phase I objectives to be completed by the end of year one were to:

- Gather and review available published literature, unpublished reports, and other sources on the effects of pulsed flow on *R. boylii* habitat, reproductive success, and survival.
- Analyze and/or descriptively summarize these data from recent studies in a comprehensive way. Determine whether statistical meta-analysis is appropriate.
- Identify knowledge gaps regarding which aspects of fluctuating flows (e.g., frequency, timing, magnitude) may have important impacts on *R. boylii* populations and habitat.

Phase II objectives to be completed by the end of year one were to:

- Conduct pilot larval field and flume experiments to quantify larval swimming abilities and assess behavioral responses to changes in shear stress created by varying depth, velocity, and substrate. This included developing a study design and methodology for year two field and flume experiments.

- Select study sites for hydrodynamic modeling efforts and conduct base topographic surveys of each site.
- Begin calibrating the model to each study site, including initial measurements of low-flow conditions.

Phase II objectives to be completed by the end of year two are to:

- Conduct repeated larval field and flume experiments based on methodologies and findings determined in year one.
- Develop a model-based methodology to evaluate changes in habitat-scale hydrodynamics from a series of low and high pulse-flow scenarios and subsequent changes in habitat availability and heterogeneity.
- Use results from lab and field experiments to assess how modeled changes in habitat availability and heterogeneity influence *R. boylii* individuals. For example, use observed tadpole swimming ability and modeled velocity vector output to determine the functional connectivity of neighboring habitat patches.

1.3. Report Organization

Previous proposals and progress reports were divided into separate discussions of Phase I and Phase II work. In this annual report, the sections are reorganized. The results and methods of Phase I, the review of previously published data, are in Section 2. Rather than addressing Phase II as a discrete heading, new primary results are presented under two new headings. Empirical analyses focused on unpublished and newly gathered data specific to three study watersheds ("case studies") are in Section 3. Hydrodynamic modeling is included with the case studies in Section 3.3. Field and laboratory experiments investigating the effects of velocity on tadpole growth and movement are presented in Section 4. Instead of separate sections for methods and result, the methods for each analysis are presented immediately before the pertinent results. Conclusions and recommendations are presented in Section 5.

2.0 Review of Statewide Published Data and FERC Study Reports

Due to its declining status, *R. boylii* has increasingly become a focal species in water management planning, especially in FERC relicensing programs for hydroelectric dams. However, the geographically dispersed nature of these hydropower facilities along with the fact that multiple power companies, environmental consultants, and state and federal agencies are engaged in different licensing efforts, has limited the potential for a comprehensive assessment of pulsed-flow effects on *R. boylii*. The following discussion and analyses provide a summary of pulsed-flow effects on *R. boylii* based on a review of existing unpublished reports and published literature. The review documents and analyzes, to the degree possible, the direct effects of pulsed flows on each life stage as well as the effects of changing flows on habitat condition and availability. The review and analyses identify where specific information is lacking and provide guidance for the latter phases of this research (i.e., experiments and hydrodynamic modeling).

A total of 27 recent (1999–2005) study reports and one published article were obtained from a variety of sources including utility company staff, utility company and FERC relicensing websites, environmental consultants, and a literature search (Appendix A). All but one (TRI1) of the 27 reports were prepared for FERC relicensing efforts. The reports represented seven major river basins in California, six of which drain the western slope of the Sierra Nevada/Cascade mountain range. Most (23) of the studies contained specific information on *R. boylii* distribution, abundance, habitat, and/or effects of pulsed flows. Pulsed flows in these studies were conducted for several purposes: hydroelectric power generation, recreation, and to provide varying conditions for habitat modeling and assessing effects on biota at different discharges (i.e., test flows). Five reports contained no specific information on *R. boylii* and focused on other information collected during FERC relicensing studies, such as historic and predicted hydrologic regimes, geomorphology, and fish habitat. The 23 studies with information on *R. boylii* were thoroughly reviewed, while the others were peripherally reviewed. In order to simplify formatting throughout the text and tables, each study report was assigned a code (e.g., NFF1) that is referenced in both Appendix A and the References section of this report.

Section 2 is divided into three parts. In Section 2.1, the qualitative narrative reviews of the statewide reports and published literature are divided into three sub-sections by *R. boylii* life stage—egg masses, tadpoles, and post-metamorphic life stages (including young of the year [metamorphs], juveniles, and adults). This organization conceptually parallels the mobility continuum described in Figure 1 and differentiates the effects of pulsed flows on aquatic vs. "terrestrial" (post-metamorphic) life stages. Section 2.2 provides a quantitative analysis of habitat suitability among river basins at different discharges, as well as an assessment of the methodologies and assumptions used. Section 2.3 summarizes the review of study reports and identifies how these results will be applied to the experimental and modeling components of this study. Some organizational and substantive changes for future relicensing studies are recommended. The results contained in Section 2 are primarily descriptive and qualitative. The one exception is the analysis of habitat suitability at different flows (Section 2.2), which employed a graphical approach to examine multiple discharges among several different rivers.

2.1. Qualitative Summary of Pulsed-Flow Studies/Reports

The objectives of this statewide report review were to summarize effects of pulsed flows on each *R. boylii* life stage across all studies, document the level of evidence, and identify information gaps. Ten of the 23 study reports contained some information on the effects of pulsed flows on at least one life stage of *R. boylii* (Appendix A). The other 13 reports provided information on relative abundance and microhabitat associations (see Section 2.3.2), qualitative assessments of pulsed-flow effects on habitat suitability, or quantitative assessments of habitat suitability at different flow levels (see Section 2.2).

2.1.1. Egg Survival Associated with Pulsed Flows

Direct negative effects of pulsed flows on *R. boylii* egg masses were evident in all five studies where pulsed flows were assessed in the field. Direct effects fell into two categories—scouring and desiccation. Egg masses were damaged or scoured by high flows that occurred after oviposition. Eggs laid during higher flows were at risk of desiccation when flows were subsequently reduced. In the North Fork Feather River, studies in two different reaches, Cresta and Poe, documented 50% and 14.6% lost or damaged egg masses, respectively (NFF3; NFF7; Table 1). In the Pit River, 14 of 27 egg masses were scoured or at risk of scouring during test flows. Of these, seven were actually scoured and the remainder were moved to protected areas prior to flows (PIT2). In the Trinity River, 100% of egg masses were scoured in each of two years when test flows occurred subsequent to oviposition (TRI1; Table 1). Risk of desiccation was documented in one study on the South Fork American River. In this study, three of seven egg masses were found to be at risk as flows dropped from 3.7 to 2.5 cubic meters per second (cms); see UAR6 and Table 1.

Based on these studies, the timing of a pulsed flow has a larger apparent effect than its magnitude. Pulsed-flow releases during or after oviposition caused egg mass scouring, while flow increases that occurred prior to oviposition did not appear to have negative effects (TRI1; Table 1). However, relatively large increases above base flow had differing effects on survival in different rivers. All egg masses were lost with 500%–1000% increases in flows on the Trinity River, but half (or less) of all egg masses were lost (or damaged) with similar increases on the North Fork Feather and Pit Rivers (Table 1). These incongruities were likely due to differences in geomorphology and channel shape at individual breeding sites and among river basins. The analyses of habitat suitability in Section 2.2 provided more insights on that front.

Even though the degree of pulsed-flow effects varied among river basins, the majority of studies demonstrated that the egg mass loss rate was near the extreme of the known natural range of variability, representing what would be rare events. Natural high flows occur in unimpaired streams as a result of rainfall and snowmelt events. While these events typically occur prior to *R. boylii* oviposition, they have also occurred during and following oviposition. Kupferberg (1996) documented egg mass desiccation during a dry year and scouring during a wet year on the South Fork Eel River (SF Eel River) in northwestern California. However, egg

Table 1. Pulsed-flow effects on *R. boylii* egg masses in California (from recent FERC relicensing study reports and scientific publications)

River	Flow Events Date — Reach	Maximum % Change from Base Flow	Observed Effects	Reference
North Fork Feather	June 2002 — Cresta	540% (7.1–45.3 cms)	3 of 6 (50%) egg masses scoured or displaced	NFF7
	May 2003 — Poe	(discharge info not provided in report)	7 of 48 (14.6%) egg masses were scoured or damaged from fluctuating flows and spill events	NFF3
Pit	May 2002	636% (4.2–31.3 cms)	14 of 27 (52%) egg masses scoured or likely to be scoured during test flows	PIT2
South Fork American	June 2004	- 24% (3.7–2.5 cms)	3 of 7 egg masses (43%) at one site were at risk for desiccation by dropping flows; they were moved or otherwise protected by surveyors	UAR6
Trinity	May–June 1991 and 1992	1991: 475% (15.0–86.3 cms) 1992: 1043% (16.0–183.0 cms)	Oviposition was pre-pulsed flow releases from dam; 31 (100%) egg masses scoured in 1991 and 28 (100%) were scoured in 1992	TRI1 (Lind et al. 1996)
	April–June 1993	309% (27.5–112.5 cms)	Extended natural and artificial releases due to wet year so survey data incomplete.	
	April–May 1994	272% (13.9–51.9 cms)	Oviposition (24 egg masses) was post-pulsed flow; all appeared to survive	

mass losses were relatively low in each year (10.3% and 20.2%). Further research on the SF Eel River population of frogs over a longer time period showed that losses due to natural high flows were as high as 71% in 2005 (details in Section 3.2). In a four-year study of another northern California coast range stream, Hurdygurdy Creek, eggs were laid post–high flows in two years and prior to storm events/high flows in two years. For the two years in which eggs were laid post–high flows, there was no egg loss, and for the two years that eggs were laid prior to storms, egg loss or damage was 10.3% in one year and 42.1% in the other year (C.A. Wheeler, pers. comm.). Thus, egg mass losses have occurred under natural conditions; however, the frequency of such late spring floods was low in natural systems. The 2005 SF Eel River flood was a rare event and was either the largest or the second largest pulse (depending on how magnitude is calculated) over 42 years of hydrologic record.

In contrast, the frequency of this kind of springtime extreme flow fluctuation has been dramatically higher in regulated rivers that have in-line reservoirs managed to "fill and spill" or to provide white water boating recreational flows or short-term power generation. A frequency analysis of precipitation events, spills, and emergency shutdowns of dam operations in the Pit River showed that there were large-magnitude pulses in 15 out of 29 years (PIT4). Roughly half of those pulses could be mitigated by increases in base flow. Within-year frequency of pulses was also higher than what would be observed in an unregulated river, with as many as nine peaks per breeding season (PIT4). A frequency analysis of spills and pulses in the Mokelumne River Project stated that "except for critically dry (CD) and dry (D) years, almost every year since 1970 has had a sudden, relatively large increase in flows (>2000 cfs (56.6 cms)) over several days out of Salt Springs Reservoir" during the breeding season (MOK6 p. 4). For the twelve CD and D years since 1970, 67% of the years had unfavorable hydrologic conditions in the form of abrupt increases and decreases associated with spills (MOK6 pp. .4-5).

Increased frequency of unfavorable hydrologic conditions that cause recruitment loss has been shown to be correlated with population declines in both fish and amphibians. For small-bodied fish that use shallow slow habitats, populations from a diversity of regulated rivers were unable to recover when large changes in discharge occurred frequently, every breeding season, or repeatedly within one breeding season (Bain et al. 1988; Kingsolving and Bain 1993; Freeman et al. 2001). Four amphibian species experienced declines during a long-term (26-year) monitoring study at the Savannah River site due to a shortened hydroperiod (Daszak et al. 2005). The hydroperiod concept is useful and analogous to the length of the pulse-free period utilized by *R. boylii* for successful recruitment.

Another key difference between unregulated and regulated rivers is the relatively low overall abundance of egg masses in the study reports reviewed. From 30 to 112 egg masses/km have been documented in unimpaired streams (Kupferberg 1996; Lind et al. 2006; Lind 2005; and Figure 11 below). The apparently low densities of egg masses in the studies reviewed here (Table 1) may be a result of long-term effects of aseasonal pulsed flows from dams. However, information from reference (unregulated) rivers in the same geographic area was not included in the reports; i.e., the natural systems that have been studied in detail are in the northern California Coast Ranges, and the reports reviewed here were almost exclusively from Sierra Nevada drainages. Even so, with such low abundances, the losses due to pulsed flows observed in these systems give reason for concern. Individual egg masses can contain between 400 and 1500 eggs, and though each mass represents only one adult female (Jones et al. 2005), it is nevertheless a substantial reproductive output. In populations at risk, reducing negative effects on this life stage could be the difference between local extinction and recovery.

Several of the pulsed flows in the studies were manufactured for recreational boating (e.g., NFF7 and NFF8). To assess the effects of these flows on *R. boylii* population dynamics, one must take into consideration the findings presented in Section 3.1 of this report. Those results indicate a multi-year lag time between recruitment (egg masses or larvae) losses and a numerical response in the breeding population size. After a lag time reflecting sufficient time for young of the year to reach reproductive maturity, egg counts can indicate the cumulative effects of boating flows on eggs and tadpoles. In the Cresta Reach of the North Fork Feather River, monthly boating flows were initiated in 2002. The 2005 egg numbers reflect the effect of 2002 boating flows which included pulses during the spring breeding season, which is known to be a vulnerable life stage (Figure 2; NFF7; NFF8; NFF9; J. Drennan, lead author of these reports, pers. comm.). For the subsequent years in which the flows were restricted to the tadpole and young-of-the-year life stage, there are, as yet, no population response data. Only the 2006 and beyond egg censuses will show whether there is a numerical response in the population to pulse flows experienced by tadpoles and young of the year.

One of the most powerful sampling tools for detecting environmental disturbance effects on a population is the Before-After-Control-Impact (BACI) approach (Green 1979; Underwood 1994). In this experimental design, a series of samples are taken over time before and after a possible impact of an environmental change in both the potentially affected region, called the "impact," as well as an unchanged "control" location. Underwood (1994) states, "If there is an environmental disturbance that affects the population, it would appear as a statistical interaction between the difference in mean abundance of the sampled populations in the control and potentially impacted locations before the disturbance, and that difference after the disturbance." This pattern can be seen graphically in a plot comparing abundance through time between the control and impact sites. Before the perturbation, the control and impact lines would be roughly parallel. After the perturbation, the lines would no longer be parallel.

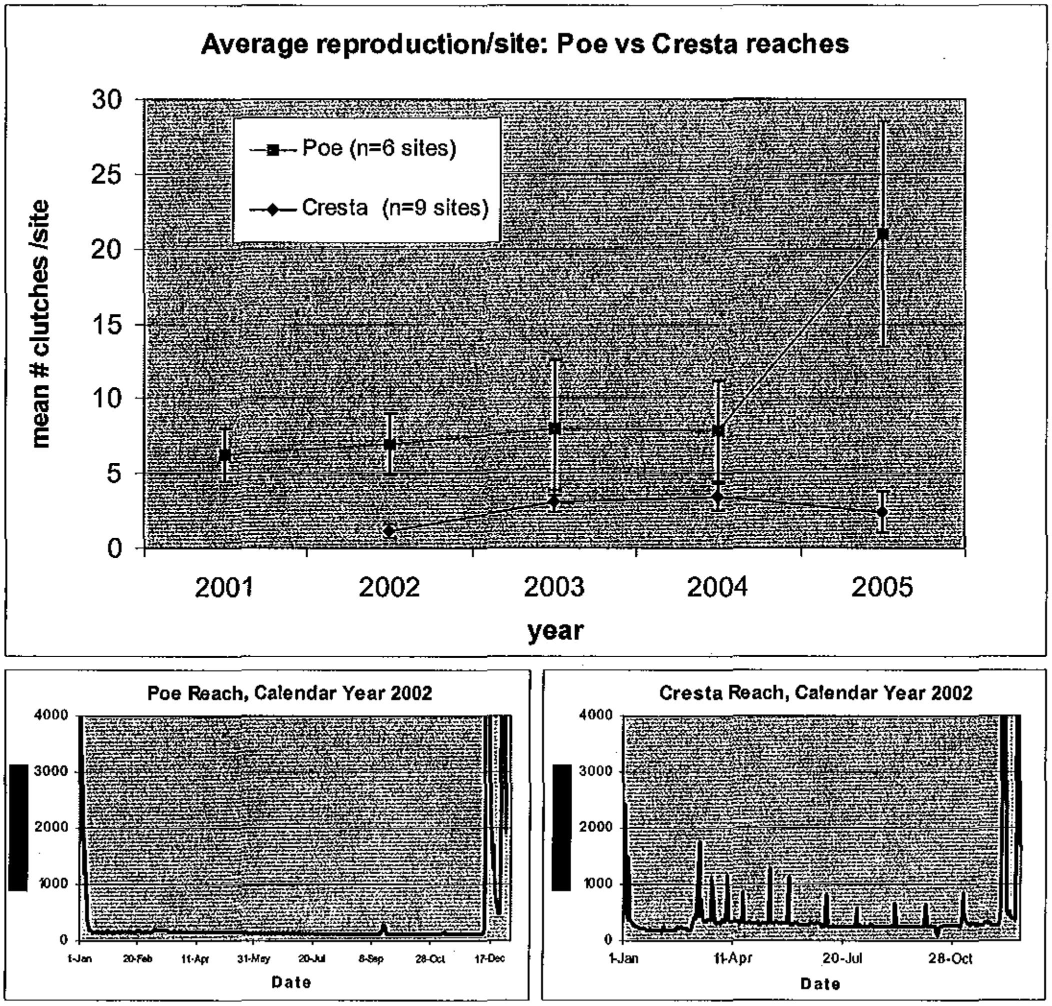


Figure 2. Relative abundance of *R. boylii* egg masses on Poe and Cresta reaches of North Fork Feather River from 2001 to 2005. Data were compiled from reports NFF7, NFF8, and NFF9, and from J. Drennan (pers. comm.). The 2002 Cresta data are corrected for likely undercount of eggs. Because 39% of clutches were found by snorkeling in 2003, the 2002 count was adjusted up by a factor of 0.39. Discharge plots at bottom of figure show 2002 flows for Poe and Cresta reaches.

Comparing the population trajectories of *R. boylii* in the Cresta and Poe reaches (Figure 2) it appears that such a pattern is beginning to emerge. Ultimately, to apply a true BACI analysis to the Cresta and Poe egg data, there need to be multiple samples in time after the initiation of recreational boating flows—i.e., appropriate *F* ratios cannot be calculated without estimates of both the "before" and "after" variances in egg number through replicate years (Hurlbert 1984; Stewart-Oaten et al. 1986). An *F* ratio is a ratio of the variances of two samples. If the current pattern remains robust after the needed data are collected, it is likely that an annual frequency of multiple boating flows on the Cresta Reach would eliminate the occasional high recruitment years that are a characteristic of amphibian population dynamics in general and that sustain populations over the long term (Semlitsch et al. 1996; Meyer et al. 1998; Daszak et al. 2005).

2.1.2. Effects of Pulsed Flows on Larvae

Only three of ten studies that evaluated direct effects of pulsed flows, assessed effects on the larval (tadpole) life stage (Table 2). Even in these three studies, the evidence was based on either anecdotal accounts of stranding or variation in tadpole abundance before and after pulsed flows. This life stage is challenging to work with in the field due to its cryptic coloration, behavior, and mobility which lead to difficulties in obtaining reliable counts. Nevertheless, stranding of tadpoles was observed in all three studies (NFF7; NFF8; MOK1; Table 2) and a significant decrease in tadpole abundance was observed immediately following a pulsed-flow event in one study (NFF7). This decrease in abundance was presumably related to tadpole displacement out of the survey area. However, in another study, tadpole abundance varied depending on the location in the study reach and didn't show a consistent decreasing or increasing trend relative to pulsed flows (NFF8).

An assessment completed in the North Fork Mokelumne River (MOK1) provided the most quantitative evidence of actual and potential negative effects of pulsed flow on tadpoles (Table 2). That study quantified newly wetted area and potential area of isolated pools during a 1000+% increase pulsed-flow event and measured the actual number and area of isolated pools following the event. Fifty-seven isolated pools and five stranded tadpoles were found following the pulsed-flow event, indicating a significant risk for tadpoles (MOK1).

Table 2. Pulsed-flow effects on *R. boylii* larvae (tadpoles) from recent FERC relicensing study reports in California

River	Flow Event Dates — Reach	Maximum % Change from Base Flow	Observed Effects	Reference
North Fork Feather	Jun 2002 — Cresta	540% (7.1-45.3 cms)	Tadpole counts declined substantially from pre to post pulsed-flow surveys. 1 tadpole found stranded after ramping down of flows.	NFF7
	Jul 2002 — Cresta	300% (7.1-28.3 cms)	Tadpole counts varied before and after pulsed flows, increasing at some sites and decreasing at others.	
	Jul–Aug 2003 — Cresta	380% (7.1-33.9 cms)	2 tadpoles were observed stranded after a 1200-cfs pulsed flow in July.	NFF8
North Fork Mokelumne	Sept 2003	1014% (0.62-6.9 cms)	5 tadpoles found stranded in isolated pools following after pulsed flow. Tadpole abundance declined substantially following pulsed flow.	MOK1

2.1.3. Effects of Pulsed Flows on Post-Metamorphic Life Stages

Six studies assessed the effects of pulsed flows on the post-metamorphic life stages of *R. boylii*—young of the year, juvenile and adult frogs—using mainly qualitative approaches. Of these, one study in the North Fork Feather River documented similar abundances of young of the year and juveniles prior to and immediately following pulsed flows, but lower numbers during pulsed flows (NFF1; Table 3). Three of the studies monitored abundances over several months within a year and found no patterns that could be attributed to the pulsed flows throughout the study (NFF7; NFF8; MOK1; Table 3). One study in the North Fork Mokelumne River that monitored abundances over several years suggested that the reduced juvenile abundances observed during the course of the study might be due to higher and later spring flow releases over the same time period. These increases were due to a combination of implementation of a new license agreement and natural flows from wet water years (MOK4; Table 3).

Table 3. Pulsed-flow effects on post-metamorphic life stages of the *R. boylii* (young of the year, juveniles, and adults) from recent FERC relicensing study reports in California

River	Flow Event Dates — Reach	Maximum % Change from Base Flow	Observed Effects	Reference
North Fork Feather	Sept 2000 — Poe	355% (3.1–14.2 cms)	Abundance of young of the year and juveniles was similar before and after pulse flows but reduced during pulsed flows.	NFF1
	May-Oct 2002 — Cresta	540% (7.1–45.3 cms)	Abundance of juveniles and adults varied throughout the summer with no apparent pattern relative to pulsed-flow releases.	NFF7
	May-Oct 2003 — Cresta	540% (7.1–45.3 cms)	Abundance of juveniles and adults varied throughout the summer with no apparent pattern relative to pulsed-flow releases.	NFF8
North Fork Mokelumne	Sept 2003	1014% (0.62–6.9 cms)	Abundance of young of the year and adults varied before and after flows with no apparent trend.	MOK1
	2001–2003	Higher and later peak flows	Reduced abundance of juveniles over time.	MOK4

Prior to this review, researchers assumed that post-metamorphic frogs were at lower risk from high flows than other life stages due to their higher mobility (Figure 1). However, there is an indication (via a finding of reduced abundance during pulsed flows) that there may be a short-term behavioral response to these flows. Determining whether or not reduced abundance is the result of detectability (e.g., poor visibility conditions in turbid water, observer bias) or a real behavioral response to flows requires further investigation. Further research is also needed on the cumulative effects of multiple pulsed flows at monthly or biweekly intervals throughout the biologically active season and over years.

2.2. Analysis of Habitat Area and Discharge

Ten of the 23 reports reviewed in detail contained some level of analysis of flow effects on *R. boylii* habitat (Appendix A). Of these ten, five included quantitative data on suitable habitat area at different flow levels. In order to assess the effects of pulsed flows on *R. boylii* habitat condition and availability, data from these five reports were normalized and graphically evaluated. The objective of this analysis was to determine whether a consistent relationship between discharge and suitable habitat area occurred during a pulsed flow. In addition, the methods used to define and quantify *R. boylii* habitat in each of the reports were evaluated.

2.2.1. Methods

The five quantitative studies represented five different rivers, with two studies in the North Fork Feather River, and one each covering Silver Creek (a South Fork American tributary), the Stanislaus River (Middle Fork and South Fork in the same study), and the Pit River. Information on habitat area from each report was summarized to achieve consistent metrics that allowed graphing of habitat change versus discharge change. The following formulas were used to calculate percent change in discharge (Q) and percent change in habitat (H), respectively:

$$\%\Delta Q = ((Q\textit{test} - Q\textit{base})/Q\textit{base})\text{-}*100 \qquad \%\Delta H = ((H\textit{test} - H\textit{base})/H\textit{base})*100$$

where *test* indicates a pulsed-flow discharge and *base* indicates the base flow discharge.

For these analyses, the goal was to analyze "site"-level data from each study. Most studies defined a site as a discreet geomorphic feature encompassing only one side of the river (with the exception of the North Fork Mokelumne River studies where both sides were surveyed). However, data were not always presented at the "site" level. For example, in the NFF4 report, data were presented only at the subsite level and had to be summarized up to the site level. Across all studies, "sites" ranged from approximately 50 to 500 m in length. In addition, only sites that the study report indicated to be occupied by *R. boylii* were included. Some studies included additional "random" or non-occupied but potentially suitable reference sites.

Table 4. Suitability (oviposition and larvae) criteria and field methods used to quantify suitable habitat area for *R. boylii* in pulsed-flow studies

	Suitability Criteria		
Report	**Water Depth (cm)**	**Velocity (cm/sec)**	**Field Methods**
NFF4	< 50	< 20	-- "Shifting transects": perpendicular transects from shoreline to 5 m out into river; could shift based on change in shoreline with increasing flows -- Riparian vegetation not considered in suitability
NFF5	< 50	< 20	-- Shifting transects -- Riparian vegetation not considered in suitability
UAR3	< 48.8	< 10	--Stationary polygons, measured at every discharge with new polygons added at higher discharges as needed --Riparian vegetation not considered in suitability
STA1	< 40	< 20	-- Combination of shifting and stationary transects -- Riparian vegetation not considered in suitability
PIT2	< 43	<15	-- Suitable habitat area delineated in polygons at each flow -- Riparian vegetation was considered in suitability*

* For quantitative analysis, all habitat polygons, vegetated or not, were combined in order to be consistent with other studies.

The studies used various methods to define and identify suitable habitat (Table 4), and then quantified the area of suitable habitat as discharge changed. In general, suitable habitat was based on needs for oviposition and tadpole rearing. Because of the different definitions and methods used, the combined data from multiple studies could not be subjected to a comprehensive meta-analysis. Despite these differences, data are presented using consistent metrics to allow the reader to qualitatively compare results among studies. Though not a formal statistical approach, the null hypothesis tested was that there would be little or no directional change (i.e., a systematic increase or decrease) in habitat area with increasing discharge.

2.2.2. Results and Discussion

Assessment of Habitat Methods and Assumptions

As mentioned above, several different approaches were used in the studies to quantify habitat suitability (Table 4). A brief discussion of these methods is needed to identify the appropriate application, advantages, and disadvantages of each. The methods can be divided into two broad categories—stationary and shifting measurements. In the stationary approach, suitable habitat area was delineated at one flow (usually base flow) and then remeasured at the same locations at progressively higher flows. With the shifting method, suitable habitat areas were delineated at each flow level—they might be the same area or a newly suitable area resulting from the flow change. For both methods, either transects or polygons were used in the field to delineate areas of suitability based primarily on water depth and water velocity. For polygons, standard shapes (e.g., circles, squares, rectangles) were delineated in the field, appropriate dimensions were measured, and then area geometric formulas were used to calculate total suitable area. For transect methods, perpendicular transects were extended from the stream shoreline into the thalweg (the deepest part of the stream channel) and the combination of the shoreline distance and perpendicular transect length were used to calculate the area of the resulting rectangle. Two studies used a combination of these approaches (UAR3; STA1; Table 4).

Each method or combination of methods offers advantages and disadvantages. Stationary methods measure changes in a particular location through a range of flows. The resulting data from this approach could be used to assess whether a particular *R. boylii* breeding area, eggs, and tadpoles would be affected by an increase in base flows or longer-term pulsed flows. Breeding site fidelity or at least multi-year use of the same breeding areas (by different individuals) has been documented in *R. boylii* (Kupferberg 1996; Lind 2005; C. Wheeler, pers. comm.). Stationary polygon data recorded at several breeding areas in the same stream would provide some gauge of the immediate effects on frog populations.

Methods that use either shifting transects or shifting polygons provide information on suitability of habitat in the same general area but also typically include new suitable habitat that emerges at higher flows as shoreline areas are inundated. These methods are useful for assessing changes in total habitat availability at different flow levels. The assumption of these methods is that more habitat means more frogs—i.e., habitat is limiting. However, there is conflicting evidence that oviposition habitat is limiting for *R. boylii*, though this may be due to the scale of these analyses. For example, one of the reports reviewed (PIT4) indicated that in one breeding area of the Pit River, there was a significant amount of suitable habitat not currently used, which led to the conclusion that habitat was not necessarily limiting. A study on the Trinity River demonstrated that over a 63-km reach, the area of suitable habitat declined by 94% over a 30-year period following construction of a dam. When habitats were restored, they were quickly colonized by *R. boylii* (Lind et al. 1996 [TRI1). This result seems to point to the potential for habitat being limiting or at least having an influence on potential population size at a more extensive spatial scale.

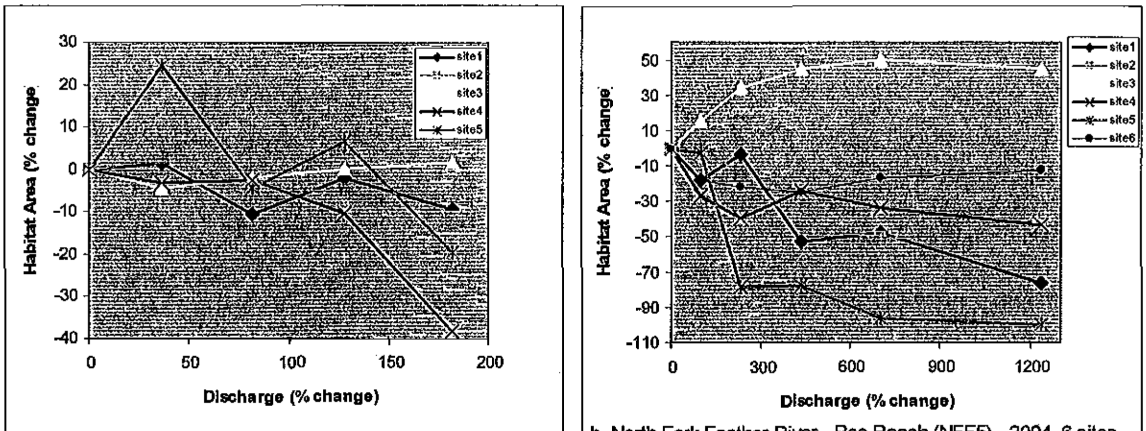
In general, the transect method would be more objective and repeatable than the polygon method because a variety of polygon shapes could be drawn to delineate habitat. However with the polygon approach, it is possible to derive information on number of suitable habitat patches as well as overall area. The transect methods only allow calculation of overall area.

Using suitability criteria that are appropriate for the study stream/reach (e.g., Table 4) is a sound approach, though it requires good habitat association information for each life stage of *R. boylii* for a particular stream/reach. Suitability criteria in the studies reviewed here focused exclusively on oviposition and tadpole-rearing requirements. Data available in the reviewed studies were used to develop additional descriptive information for other life stages to guide the modeling efforts (see Section 2.3.2).

The utility of these habitat assessment methods depends on which response variable is most relevant; i.e., the amount of area (habitat availability) or the stability of conditions within a particular patch (habitat persistence). Determining which response variable is more important may depend on the *R. boylii* life stage of interest and where it falls on the developmental mobility continuum (Figure 1). For less-mobile life stages, stationary polygon methods will provide the most relevant information, while shifting transect methods would be useful for examining suitability at more extensive spatial scales and for more-mobile life stages. For young-of-the-year fish, an Instream Flow Incremental Methodology (IFIM) study comparing a regulated and unregulated reach of the same river found that in the reach with pulsed flows, young-of-the-year abundances were more frequently correlated with persistence of slow, shallow-water habitats than with habitat availability or magnitude of flow extremes (Freeman et al. 2001).

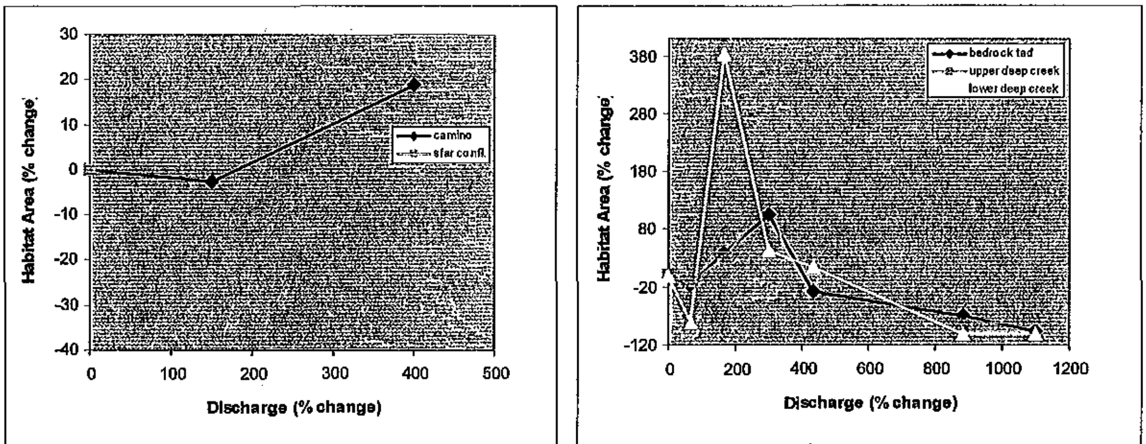
Graphical Analysis of Quantitative Data

Quantitative data on suitable habitat area relative to flow/discharge were available for five rivers, including one reach which had data for two different years (Figure 3). Graphs of the North Fork Feather River from 2002 and 2004 demonstrated that in general, habitat area decreased as discharge increased, but there were a few sites where the area-discharge relationship was positive or fluctuated among different flows (Figures 3 a & b). In 2004 there was also an indication of a threshold above which habitat area leveled off (Figure 3b). Similarly for Silver Creek, there was a negative relationship with one site and a positive relationship with the other site (Figure 3c). On the Pit River, all three sites showed an initial increase in habitat area with increasing discharge followed by subsequent decreases and then leveling off (Figure 3d). Sites on the Middle and South Fork Stanislaus Rivers demonstrated decreasing area with increasing discharge (Figure 3 e & f).



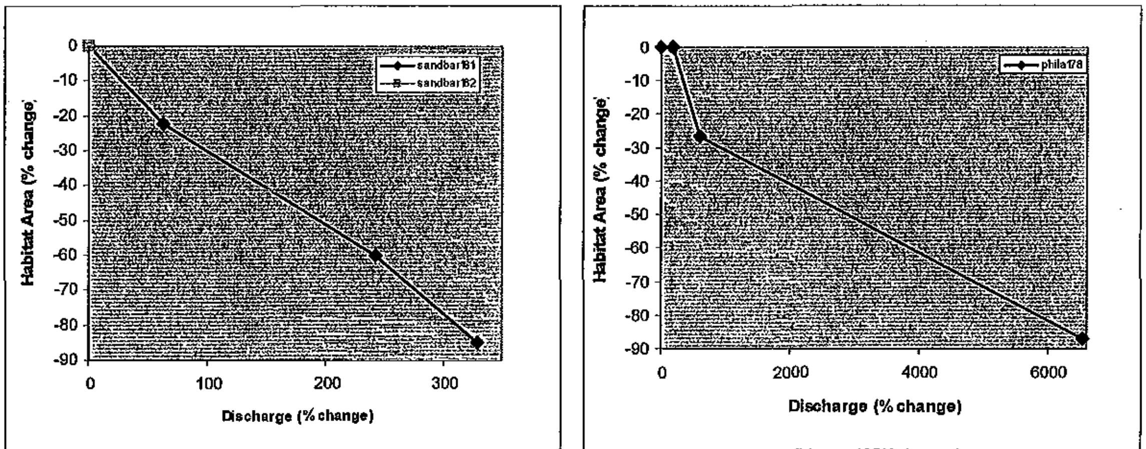
a. North Fork Feather River - Poe Reach (NFF4) - 2002, 5 sites

b. North Fork Feather River - Poe Reach (NFF5) - 2004, 6 sites



c. Silver Creek - (UAR3) - 2 sites

d. Pit River - Pit 4 reach (PIT2) - 3 sites



e. Middle Fork Stanisluas River - (STA1) - 2 sites

f. South Fork Stanisluas River - (STA1) - 1 site

Figure 3. Change in *R. boylii* suitable habitat area relative to change in discharge for five river reaches (including two years from one reach) in the Sierra-Cascade mountain ranges of California. Data were collated to the "site" level (see Section 2.2.1) for each reach.

Overall, the qualitative finding for the five regulated rivers reviewed is to reject the null hypothesis that there is little or no directional change in habitat area with increasing discharge. Rather, there appears to be a trend of decreasing habitat area with increasing discharge. In some cases there appears to be a threshold above which relatively flat lines are observed (i.e., slopes close to zero) when plotting percent change in habitat relative to change in flow. For NFF5 (Figure 3b), below about a 400% increase (~23 cms), slopes were heterogeneous and there was substantial variability among the six sites. Above a 400% discharge increase, all lines were parallel and close to zero slope. In this area of the curves, the null hypothesis would be accepted. This pattern also occurred at the Pit River, though in both cases, habitat area at these threshold points was still lower than at regulated base flows.

The expectation that the null hypothesis is true for unregulated rivers was based on *R. boylii's* preferential use of wide channels with shallowly sloped banks at the SF Eel River. One-dimensional modeling (using Hydrologic Engineering Centers River Analysis System, (HEC-RAS, U. S. Army Corps of Engineers) in that river showed that depth and velocity were relatively insensitive to changes in discharge at *R. boylii* sites relative to random sites (Kupferberg 1996). The two-dimensional models under development for this study (see Section 3.3) can explicitly test whether habitat area is similarly stable when discharge increases and also whether the pattern observed is a function of cross-sectional shape, longitudinal gradient, or both (see Section 2.3.2).

The pattern of decreasing habitat with increasing discharge could also be a result of vegetation encroachment. Riparian vegetation information was included as part of suitability criteria in the Pit River study only, though that component was ignored to make all of the studies comparable (Table 4). Riparian vegetation characteristics, which can make habitat unsuitable due to excessive shading of potential breeding areas, should probably be included in suitability criteria in future studies and analyses, unless an assumption can be made that extended high flows (or increased base flows) will eventually result in loss of this vegetation. However, the degree to which riparian vegetation can be removed through increases in base flow and/or the addition of large winter and early spring pulses will depend on how large the flows are, how established the vegetation is, and local channel morphology (e.g., McBain and Trush 1997).

A significant caveat to these overall results is that even though all results were converted to the same units, the range of discharge change (30% to over 6000 %; i.e., <1–2 orders of magnitude) was not consistent among studies. This means that only portions of the full habitat-discharge curve were available for each river and that flow increases occurred over different increments. Depending on which portion of the curve was examined and how flow increased, different conclusions could be reached.

Comparability of results among streams/rivers could be improved if bankfull width was measured at each "site" where habitat measurements were made. That metric, along with information on upstream watershed size or another index representing the unimpaired discharge of the river, would allow sites to be classified and categorized such that more appropriate comparisons could be made. Analogous data from geologically similar unregulated rivers would also provide context for understanding whether the observed patterns in the regulated rivers have resulted from changes in channel morphology due to long-term reduced flows resulting from upstream dams/diversions.

2.3. Conclusions and Recommendations from Statewide Report Review

2.3.1. Summary of Results

The following patterns were consistent across the majority of studies reviewed:

1. Egg masses were negatively affected by pulsed flows via scouring, if flows occurred during or after oviposition, and desiccation, if oviposition occurred during high flows and then water levels dropped. Thus the timing of pulsed flows is the critical characteristic that can be changed to reduce impacts to egg masses. The inter-annual and intra-annual frequency of flooding was also a key component in the difference between pulsed flows in regulated and storm-generated flows in unregulated rivers.
2. There was evidence for both the potential and actual stranding of tadpoles following pulsed-flow releases. In addition, there was some indication that pulsed flows may lead to lower abundances at particular locations.
3. Pulsed-flow effects on post-metamorphic life stages were not clear. Preliminary evidence for short-term behavioral responses to these flows needs further research.
4. Methods used for quantifying suitable habitat varied among studies. Stationary polygon/transect methods were most relevant to evaluating habitat persistence, a factor important to immobile life stages (eggs and early tadpoles). Shifting transect methods provided information on overall availability of suitable habitat area. Shifting polygon methods also provided information on the number of suitable habitat patches as well as the overall area.
5. General trends in habitat suitability across all studies suggested that change in habitat area varied depending on site features/channel morphology.

2.3.2. Application of Results to Experimental and Modeling Components of This Study

Egg Masses

The review of study reports confirmed the initial assumption that this first, immobile life stage is very vulnerable to direct effects of pulsed flows (Figure 1). All studies that assessed pulsed-flow effects on egg masses found substantial loss or damage. The timing and frequency of pulsed flows appeared to be more important than magnitude, but that conclusion was confounded by different site level conditions and microhabitat selection by breeding frogs. Microhabitat data garnered from the reviewed studies will be used to guide suitability criteria during the hydrodynamic modeling component of this project (see discussion on Quantifying Habitat Area, below, as well as Section 3.3). To further explore effects of lag time in population response, additional information for the modeling effort will be compiled from the study reports.

Tadpoles

Prior to initiating this research, the authors speculated that quantitative data on pulsed-flow effects on the larval life stage would be sparse. This was confirmed by review of the study reports. Only three studies (NFF7; NFF8; MOK1) attempted to assess pulsed-flow effects on tadpoles, and the approaches used were mainly anecdotal (e.g., a few observations of stranding) or indirect (estimates of potential stranding area), as summarized in Table 2. Documentation of the extent of stranding in the field is an important information need, though it was beyond the scope of this study.

The tadpole life stage is the most challenging to study in the field because of small size, cryptic coloration, and the general lack of information on behavior and ecology. Thus, when abundance appears to decrease or is variable after a pulsed flow, as in the NFF7 and MOK1 studies, the fate of the "missing" tadpoles is unknown. Observations made under controlled experimental conditions (presented in Section 4) will help fill a key information gap about tadpole response to changes in water depth and velocity.

Understanding "lateral or longitudinal movement or entrainment as well as the refuge value of certain hydraulic conditions" has been shown to be key in the application of habitat modeling for riverine littoral species (Gore et al. 1989 p. 35). Initial results point to the importance of interstices as a flow refuge. Experiments slated for the summer of 2006 will address whether the use of this flow refuge represents a tradeoff (increased predation risk), such that "missing" tadpoles represent loss to predators. Hydrodynamic modeling will be applied to the problem of quantifying potential areas of stranding, as was done in the MOK1 study (Section 3.3). As with egg masses, tadpole microhabitat data garnered from the reviewed studies will be used to guide suitability criteria during the hydrodynamic modeling process (see discussion on Quantifying Habitat Area, below, and Section 3.3).

Post-Metamorphic Life Stages

Two types of information from the study reports are applicable to experiments and modeling for the young of the year, juvenile, and adult life stages. First, as with both egg masses and tadpoles, microhabitat data could be gleaned from the study reports that will be used to refine the hydrodynamic modeling work (see following paragraph and Section 3.3). Second, the unexpected result that young-of-the-year and juvenile life stages may be showing a temporary behavioral response to pulsed flows could be tested with experiments. For example, water temperature and flow could be manipulated independently in an artificial stream environment to determine whether young of the year behaviors are a response to increasing velocity and depth, or to decreasing temperatures, or both. However, such research is currently beyond the scope of this study.

Quantifying Habitat Area

Graphical analysis of the study report data indicated that the amount of suitable habitat at different discharges was variable and likely depended on the site morphology characteristics. The use of two dimensional (2-D) hydrodynamic modeling to evaluate changes in habitat (see Section 3.3) can explicitly test whether habitat area is stable when discharge increases. The systematic surveying methods required for 2-D modeling will aid in determining whether this pattern is consistent or simply an artifact of the more subjective transect and polygon sampling methods used in the studies reviewed.

The 2-D modeling will also be used to test if the pattern of decreasing habitat area with increasing discharge observed in the graphical analysis is a function of cross-sectional shape, longitudinal gradient, or both. For example, an asymmetric channel cross-section may be suitable for oviposition, but have unnaturally steep banks because the low-flow channel is positioned within the historic thalweg and not adjacent to the historic floodplain. The pattern of decreasing habitat with increased discharge could also result from a situation in which the newly inundated areas are places where vegetation has encroached, due to a low regulated base discharge relative to historic unimpaired base flows, and thus unsuitable.

Information beyond the immediate topic of examining pulsed-flow effects on *R. boylii* was noted during the review process. In particular, life stage–specific microhabitat association data were available in many of the reports. While there is published information on microhabitat associations for egg masses (e.g., Fuller and Lind 1992; Kupferberg 1996; Lind 2005), much of it concerns northern California Coast Range streams, whereas the FERC study reports focused on Sierra-Nevada rivers. For other life stages, very few quantitative data have been published regarding their microhabitat associations (but see Hayes and Jennings 1988; VanWagner 1996; Yarnell 2005), so the study reports were especially helpful. Data in the study reports included characteristics such as water depth and velocity, habitat type, and vegetation, which were recorded for each individual observation of a particular life stage (i.e., egg mass, tadpole group, individual frog). These data were sometimes summarized in the body of the reports and were usually available on copies of field data sheets in report appendices. These data are being used by a team (including two of the authors, A.L., and S.Y.) that is developing a habitat suitability model for the DeSabla-Centerville Project relicensing. Through that effort, electronic data are currently being compiled in a more complete fashion with direct involvement of many of the consultants who originally collected it. The authors will be analyzing that data for the DeSabla team. The resulting information should also be useful for fine-tuning the hydrodynamic models developed for the present PIER project, but will be presented in venues other than reports to the California Energy Commission.

2.3.3. Suggestions for Format and Content of Future FERC Studies and Reports

This section details some consistent weaknesses of study reports and suggests ways to improve future studies and reports.

Review of 23 reports with different emphases and by a variety of authors (see literature cited and Appendix A) revealed the following information to be missing, difficult to find, or in need of improved methodologies:

1. Historical vs. impaired hydrographs and frequency analyses were not included in amphibian reports (with a notable exception being the MOK6 report), nor were cross-sections included in amphibian reports. The stated rationale for choosing a range of test flows was usually based on other demands (i.e., whitewater recreation, fisheries, etc.) but was not defined in terms of historical reference discharge, which would encompass

the range of unimpaired spring flows. Illustrations of channel cross-sections showing the stage to discharge relationship for the test flows would simplify and expand the interpretation of the results.

2. Sampling effort, in terms of linear distance surveyed or time, was often difficult to derive. Also, when abundance data were presented, they were usually not converted to a relative abundance or density. Therefore, comparing sites, rivers, and years was either challenging or not possible.
3. Quantification and comparison of suitable habitat area could be improved with measurements of bankfull width at each "site" where habitat data were recorded. In addition, information on upstream watershed size or another index representing unimpaired drainage area would be useful. Clear definitions of what constitutes a "site" (from both the perspective of *R. boylii* and geomorphologic conditions) would facilitate appropriate among-site and among-river comparisons. Analogous data from geologically similar unregulated rivers would also provide context for understanding whether the patterns observed in regulated rivers have resulted from changes in channel morphology due to long-term reduced flows.
4. Life stage definitions were not always clear and were not consistently defined among study reports. For example, some studies identified three post-metamorphic life stages (metamorph, juvenile or sub-adult, and adult) and some only used two (juvenile, adult). In addition, young of the year (or metamorphs) were often lumped in with one- and two-year-old frogs and called "juveniles." The authors propose that future studies use three post-metamorphic life stages—young of the year (i.e., metamorph), juvenile, and adult—with the following definitions:
    - Young of the year—seen only in the late summer and fall (approximately August–October); easily distinguished due to small size at that time of year.
    - Juvenile—small individuals seen in the spring and early summer that do not exhibit secondary sex characteristics (e.g., males with enlarged thumbs, gravid females)
    - Adult—large individuals (2–3+ years old) that exhibit secondary sexual characteristics.
5. The review of reports that contained only primarily survey results (8 of 23) indicated that improved methods are needed for estimating abundance of tadpoles and young of the year. This problem is not unique to *R. boylii* and is a challenge in nearly all amphibian population studies. However, none of the studies reviewed used marking techniques or other methods that increase precision (e.g., double counts, repeated visits over short periods of time such as a day) to quantify population sizes. Rather, they relied on simple counts that are notoriously imprecise due to problems with detectability (Nichols 1992). Studies of other amphibians have shown that using some sort of marking technique provides the most repeatable and precise abundance estimates (e.g., Jung et al. 2002). Having precise estimates of abundance, while challenging when overall counts are low, is critical for documenting responses to pulsed flows or other influences. In

addition, the timing of capture-recapture surveys needs to closely coincide with pulsed flows so that observed effects can be linked to flows rather than being confounded by issues such as natural attrition or metamorphosis. In addition to revisiting the pre-flow site, the area searched post-flow should be expanded downstream, since it is likely that pulsed flows cause downstream dispersal.

6. Expand the scope of sampling to include longer tributary reaches during the breeding season. Studies typically included short surveys of tributaries (100–500 m; a few included longer reaches, up to 1.5 km) starting from the confluence with the river and extending upstream. These surveys were often conducted later in the summer, when evidence of breeding would be difficult to find. Based on these surveys, adult frogs were generally believed to spend the majority of the year in tributaries and move to the river for the breeding season only. To understand the population dynamics of a given section of mainstem river, it is critical to understand the role of adjacent tributary streams. R. boylii are known to breed in very small (2–3 m wide) tributary streams (Yarnell 2005; A. Lind, pers. obs.). Surveying longer sections of tributaries during the breeding season would provide data on the contribution of tributaries to annual recruitment in situ and in the river. Such data would help determine whether local populations of *R. boylii* are acting as sources, sinks, or are simply in equilibrium, and therefore aid in risk assessments for pulsed-flow planning.

3.0 Case Studies of Three Watersheds: Pulse Effects in Regulated and Unregulated Rivers

3.1. Study Areas

Three study reaches were selected in areas of known *R. boylii* breeding and rearing habitat across a diversity of managed river and unregulated stream types. Preference was given to reaches with established populations of breeding and rearing individuals, where previous flow and/or *R. boylii* studies had been completed, and with a diversity of habitat types similar in character to other known breeding and rearing areas. Study reaches were selected in watersheds of different sizes, each varying by approximately an order of magnitude in discharge, in order to assess the effectiveness of the modeling techniques on rivers of different stream order. Two regulated reaches, the Poe Reach of the North Fork Feather River, and Alameda Creek downstream of the confluence with Calaveras Creek, were selected because they are subject to periodic late spring and summer pulsed flows. There are many factors that *R. boylii* may use to link the timing of the breeding season to the natural decline of spring flows, including water temperature, air temperature, day length, and discharge in overwintering tributaries. Aseasonal pulsed releases from dams have the potential to drastically alter the local hydraulic conditions at breeding and nursery sites in a manner decoupled from other environmental cues. For comparison, a third study reach was selected on an unregulated river, the South Fork Eel, where pulse magnitude and duration are directly coupled to rain events.

Each site has extensive records including hydrologic data and multiple-year frog population surveys. These data will be used in combination with data collected during this study to determine relationships between discharge, physical habitat, and biological response variables.

Study reaches are located on the North Fork Feather River (NF Feather River) near Pulga, Calif., the South Fork Eel River (SF Eel River) within the University of California Angelo Reserve, and Alameda Creek within the Sunol-Ohlone Regional Wilderness Area (Figure 4). Ranging in size of drainage area upstream from 146 km^2 to 2395 km^2, each watershed provides riverine habitat representative of typical *R. boylii* habitat in that region. Table 5 summarizes the hydrologic and geomorphic characteristics of each study reach.

Table 5. Geomorphic characteristics of each study reach

River	Regulation	Drainage Area Upstream (km^2)	Elevation (m)	Reach Length (m)	Reach Morphology	Dominant Riparian Vegetation	Dominant Substrates	Mean Annual Discharge (cms)*
NF Feather	Poe Dam	2395	415	150	Riffle-pool	Willow, blackberry, sedge	Boulder, cobble	25.36
SF Eel	none	146	395	110	Riffle-pool	Alder, sedge	Bedrock, cobble	4.30
Alameda	Calaveras Dam	360	135	50	Riffle-run	Alder, sedge	Cobble, gravel	0.15**

*Based on the following years of record, respectively: 1980–2003, 1989–2002, 1995–2004.

**Alameda Creek discharge does NOT include flows over 5.6 cms (low-flow gage only).

shallow coarse cobble bar covered with patches of sedges at the water's edge just downstream of the creek confluence. The shallow rocky margin provides the appropriate depth and velocity conditions for oviposition and tadpole rearing, while the coarse bar and sedges provide good cover for newly metamorphosed individuals. Annual flows in the Poe Reach reflect the highly managed nature of the NF Feather River system (Figure 6).

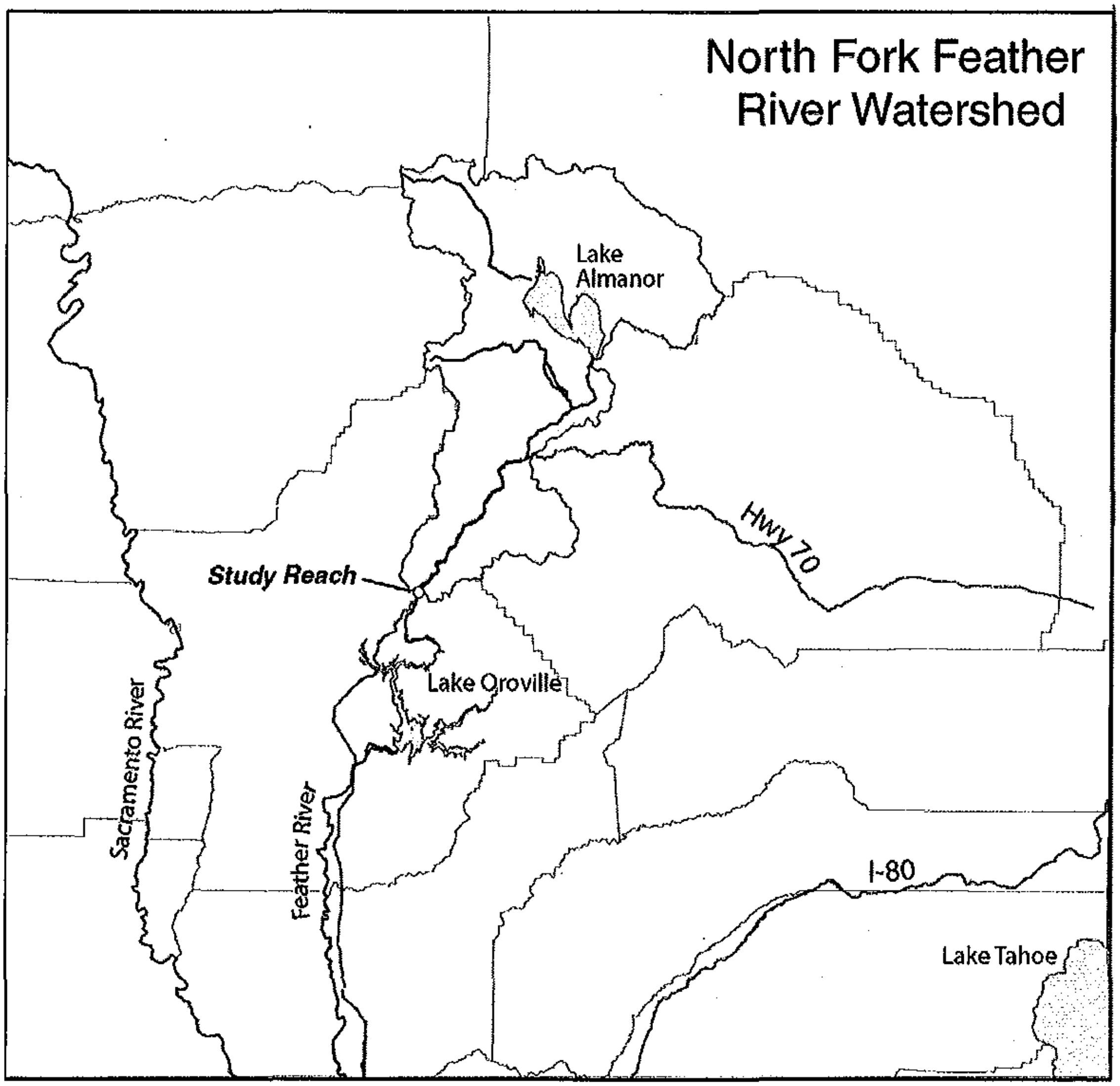


Figure 5. Location of NF Feather River study reach

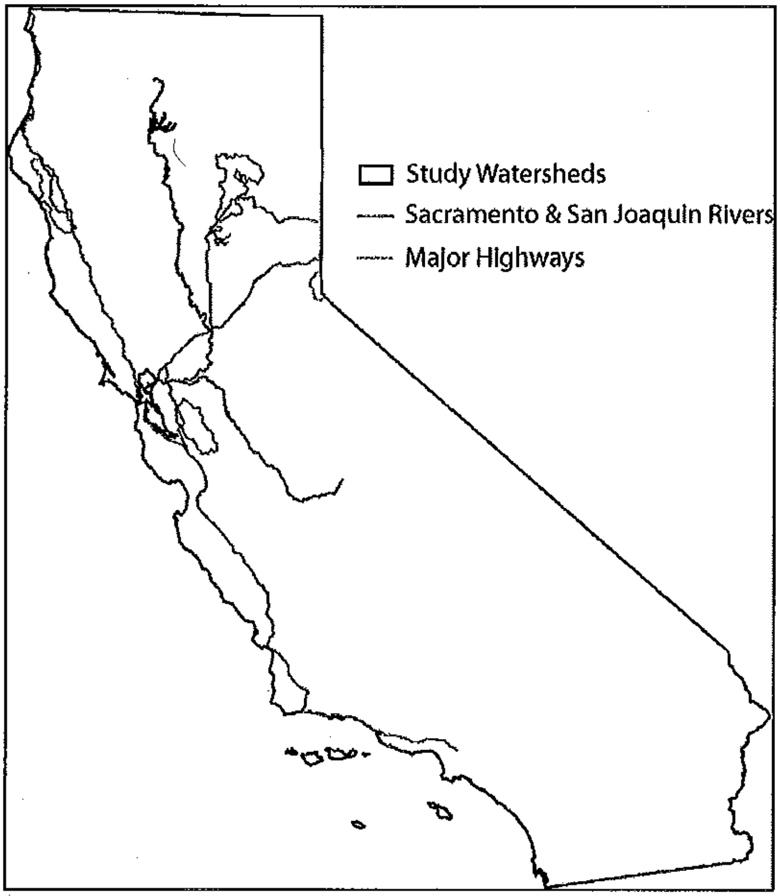


Figure 4. Location of study watersheds in Northern California

The NF Feather River drains the western slope of the Sierra Nevada mountains from 2200 m in elevation near the base of Mt. Lassen into Lake Oroville at an elevation of 300 m. With a total watershed area of 2395 km^2, the basin contains 18 dams that provide water to irrigation districts downstream. The NF Feather River is typical of most mid-elevation Sierran rivers in having moderate to steep slopes; steep, confined valleys with regular bedrock outcrops; narrow, disconnected riparian zones; coarse substrates; and steep channel morphologies including cascades, steps, riffles, and pools. These geomorphic characteristics provide ideal conditions for a series of dams along the river corridor, each capturing the river's flow for hydropower generation before sending it downstream to the next in-stream reservoir. The result is a river that contains short, free-flowing reaches between each dam and an annual hydrograph that is generally flat during the low-flow season, except when pulsed flows are released, and spiked throughout the high-flow season as natural spill events occur.

The NF Feather River study reach is located adjacent to the town of Pulga, Calif., at the confluence with Flea Valley Creek, 1500 km downstream from the Poe Dam (Figure 5). The study reach encompasses a *R. boylii* breeding and rearing site that has had documented use for the last several years (NFF9). Typical of many breeding sites in the Sierras, the reach contains a

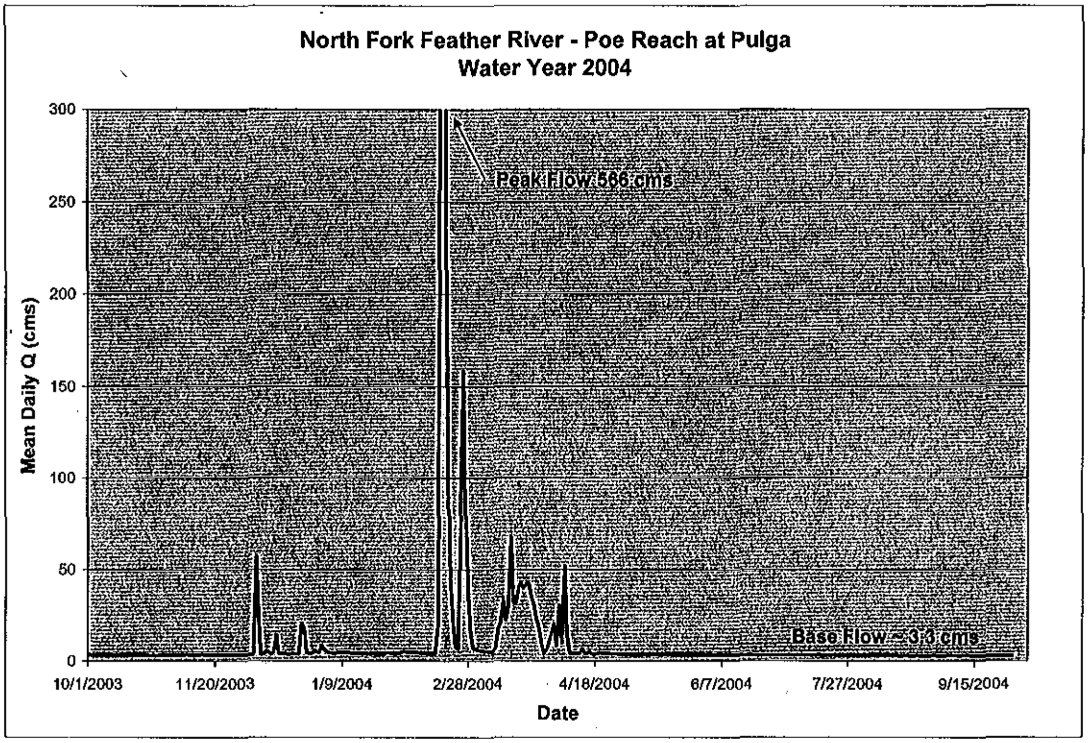


Figure 6. 2004 Hydrograph at the Pulga gage in the Poe Reach of the NF Feather River

The SF Eel River study reach is located in the heart of the University of California Angelo Reserve, approximately 1.5 km downstream from the small town of Branscomb (Figure 7). The study reach encompasses a well-documented breeding and rearing site that is located on the shallow upstream end of a cobble bar (Kupferberg 1996). Sedges line the water's edge and adults have been observed at the head of a large pool in the downstream end of the study reach (Kupferberg, pers. obs.). Annual flows on the SF Eel River reflect the natural spring runoff hydrograph typical of unmanaged Cascadian rivers (Figure 8).

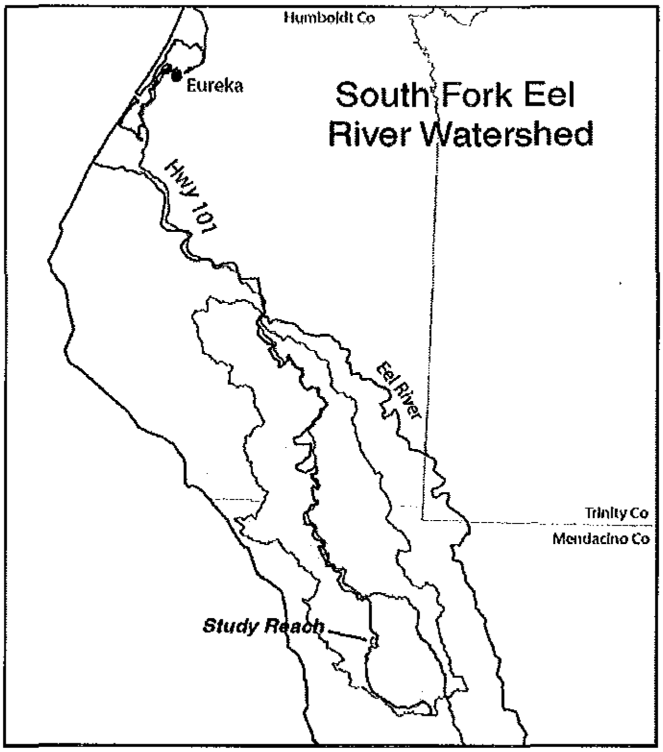


Figure 7. Location of the SF Eel River study reach

In contrast to the NF Feather River, the SF Eel River watershed lies at an elevational range of 90 to 720 m and drains 1785 km^2 of the eastern slope of the Cascade range in Mendocino County into the mainstem Eel River, which ultimately enters the Pacific Ocean. Considered to be the most productive sub-basin in the Eel River system for anadromous fish, the SF Eel River provides unregulated flows and relatively pristine habitat conditions, although portions of the river have historically had large sediment inputs due to logging and road maintenance (pers. comm. P. Steel, manager of Angelo Reserve). The SF Eel River is typical of most north coast rivers in having moderate slopes, moderately confined valleys with few bedrock outcrops, small but continuous riparian zones, coarse substrates, and moderately steep channel morphologies including steps, riffles, and pools. Although the SF Eel River runs through second-growth redwood forest, the riparian species are similar to those found along the NF Feather River, including sedges, alders, and willows.

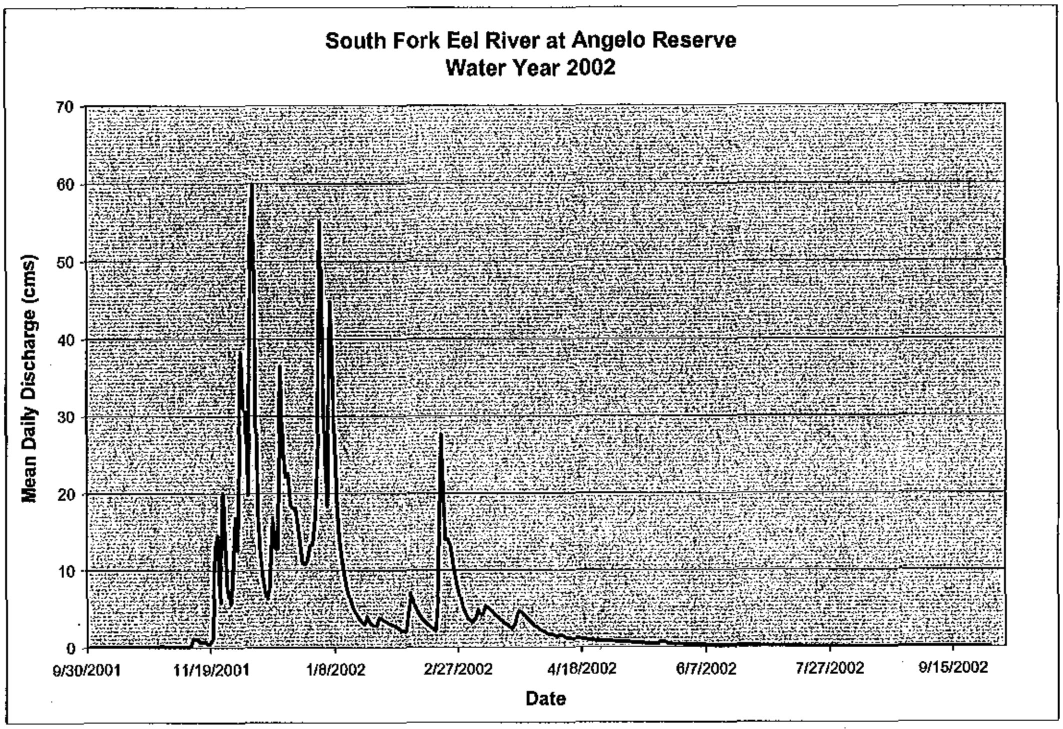


Figure 8. 2002 hydrograph at the SF Eel River gage located in the Angelo Reserve

Similar in area to the SF Eel River watershed but receiving less precipitation, the Alameda Creek watershed lies at an elevational range of 50 to 750 m and drains 1638 km^2 of the Coast Range directly into San Francisco Bay. Development within the watershed ranges from remote wildlands in the upper reaches within the Sunol-Ohlone Regional Wilderness area to urban cities in the Livermore Valley and along San Francisco Bay. An integral piece of the San Francisco Bay area water supply system, the Alameda Creek watershed contains three large reservoirs and multiple diversion dams and tunnels that join the main pipeline carrying water from the Hetch-Hetchy Dam on the Tuolumne River in the Sierras. With topography and vegetation more typical of central coast watersheds, the wildlands section of upper Alameda Creek runs through oak woodland and grassland with riparian species dominated by grasses, willows, and alders. This portion of the watershed has moderate to shallow slopes, open valleys with few bedrock outcrops, continuous riparian zones with small to moderate developed floodplains, coarse and fine substrates and shallow channel morphologies such as riffles, runs, and pools.

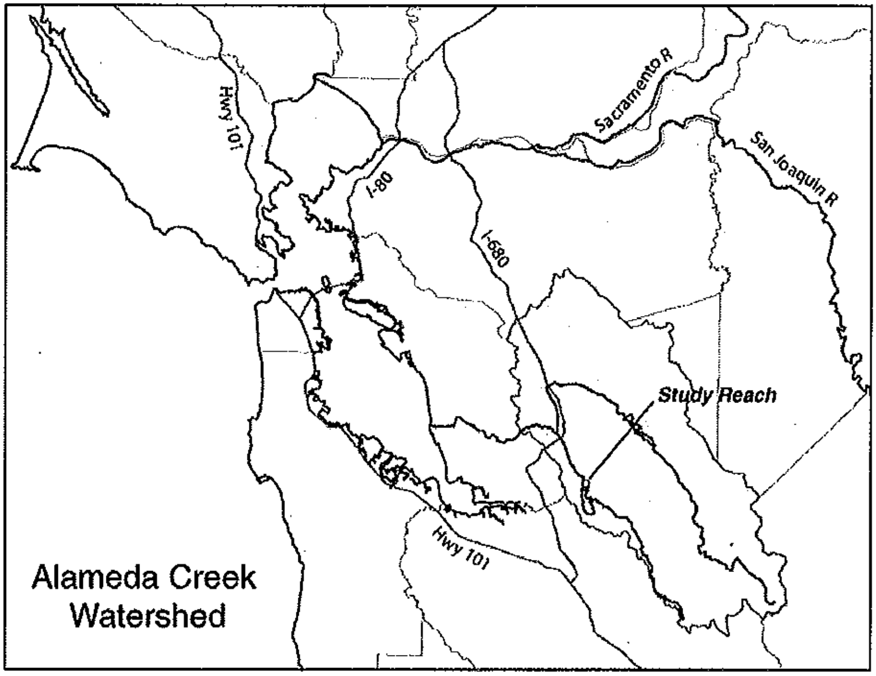


Figure 9. Location of the Alameda Creek study reach

The Alameda Creek study reach is located within the Sunol-Ohlone Regional Park in the upper reaches of the watershed approximately 2 km downstream of the Calaveras Dam adjacent to USGS gaging station 11173510 (Figure 9). The study reach encompasses a small, recently documented breeding site at the tailout of the gaging pool. A mid-channel cobble bar is located just downstream of the pool and several patches of tall cattails and sedges line the water's edge. This site is unique among the study reaches in that California red-legged frogs (*Rana aurora*) have also been observed breeding in the pool. Annual flows on Alameda Creek currently reflect a dewatered flow regime with occasional flood-related spill events. Due to seismic instabilities in the Calaveras Dam, the reservoir is only kept at 1/3 capacity and high storm flows are allowed to spill. The result is a hydrograph that, while somewhat natural in shape, is drastically reduced in magnitude, with occasional disproportionately high-magnitude peaks associated with spills (Figure 10).

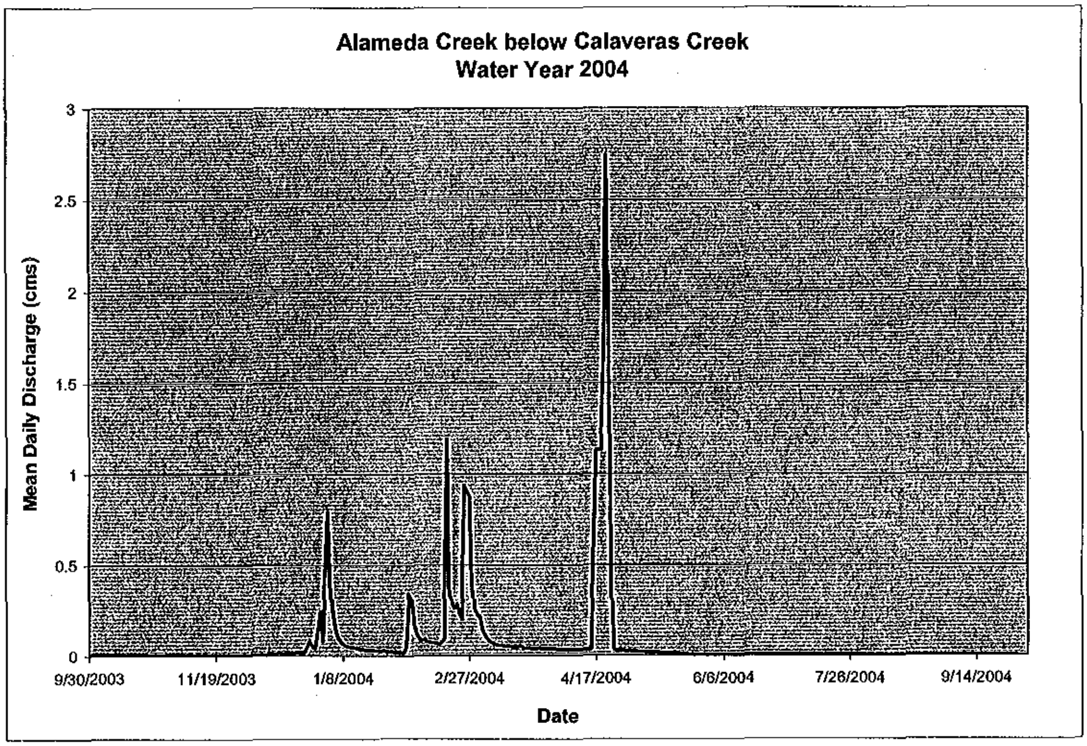


Figure 10. 2004 hydrograph at the USGS gage downstream of Calaveras Creek, including a spill-related spring pulsed flow

3.2. Analysis of Existing Hydrologic and Frog Population Data

At each of the three case study locations, frog population monitoring in the form of annual egg mass surveys have been conducted. At Alameda Creek, censuses began in 1997, supervised by Steve Bobzein, Ecological Services Coordinator, East Bay Regional Parks District. In the Poe Reach of the North Fork Feather River, censuses began in 2001 and were conducted by Garcia & Associates for PG&E and for research funded by the Energy Commission's Pulsed Flow Program. At the SF Eel River, annual censuses began in 1992, conducted by Kupferberg. These data were analyzed during year one, and similar analyses will be applied to the other two data sets pending permission from the respective authors. The goal during year two will be to test whether the patterns described below in Section 3.2.2 are robust across river systems.

3.2.1. Relating Pulse Flows to Population Dynamics and Egg Mass Survivability on the SF Eel River: Methods

At the SF Eel River, egg mass surveys were conducted along 5.2 km of the river within the Angelo Reserve. Over 14 years of monitoring, a total of 35 discrete breeding sites were identified. Visual search efforts were concentrated at breeding locations, but river sections between sites were also examined. An average of 3.9 ± 0.3 (1 s.e.) surveys were made each year. When an egg mass was found, a wooden craft stick was placed in the riverbed adjacent to the clutch, and the fate of each clutch recorded in subsequent surveys.

For each monitoring year, the maximum winter discharge, the incidence of pulsed flows, and the discharge when oviposition began were determined from the compiled hydrologic record in unpublished data from Power and Dietrich (see Appendix B for detailed methodology) and from the Angelo Reserve website (http://angelo.berkeley.edu/index.htm). In addition, the length of the breeding season and the population growth rate, lambda (λ), were calculated. Relationships between hydrologic variables and frog variables were assessed using Pearson's correlation coefficients and Mann-Whitney U-tests comparing population growth rate after pulse versus non-pulse breeding seasons.

Additional analyses focused on spring 2005 data. The season was unusually rainy with four storms occurring after breeding began. These discharge events varied in magnitude and duration and were considered "natural experiments" to determine the effect of pulsed flows on survival.

3.2.2. Relating Pulse Flows to Population Dynamics and Egg Mass Survival

Several key results emerged from the long-term monitoring data on *R. boylii* breeding population size and the hydrologic record at the SF Eel River. While the population size was stable and the number of reproductive females in 2005 was similar to when the census began in 1992, the annual change in the population, lambda (λ), varied greatly (Figure 11). If adults over-winter in or near the main channel or if over-wintering survival of adults were driving population dynamics, one would expect a negative correlation between maximum winter discharge and the number of adults breeding the following spring. This was not observed. Lambda was not related to the magnitude of the preceding winter's peak flow (r^2=-0.09).

However, population variation (λ) was associated with spring pulse-flow events in prior years. Large-magnitude late-spring pulses (>20 m^3/s) occurred in 4 of 17 years on record; however, in 8 of 17 years, the maximum spring discharge occurred after egg laying began. "Non-pulse years," defined as those in which the maximum spring discharge was prior to or at initial egg laying, occurred in the remaining 9 years. As seen in Figure 12, three years after pulse years, lambda was significantly less ($\lambda = 0.86 \pm 0.09$) than three years after non-pulse years ($\lambda = 1.16 \pm 0.09$) (Mann-Whitney U=39, p=0.01) (Figure 12). This lag time between poor recruitment years and the dip in the number of adult females laying eggs likely represents the time it takes for tadpoles to become full-size breeding adults. Although males can reach reproductive size at age two, females need to attain a larger body size to be reproductive (VanWagner 1996). This result that flow regimes affecting embryonic and larval survival can change population dynamics is a new finding for *R. boylii*.

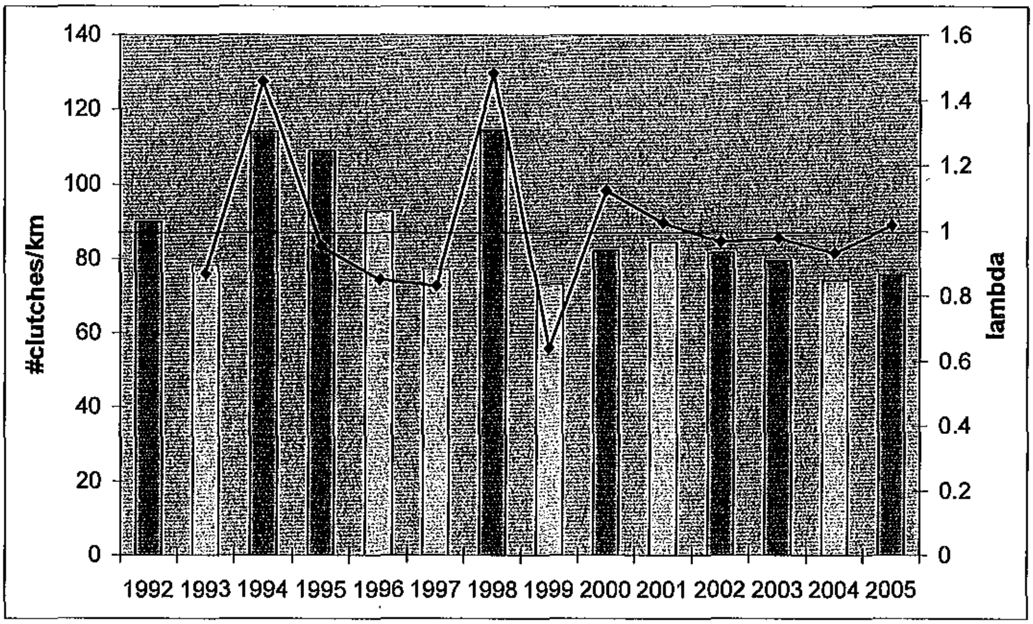


Figure 11. Clutch density along 5.2 km of the SF Eel River. Lambda represents the yearly rate of population growth. Light shaded bars indicate clutch number three years after a spring with pulsed flows.

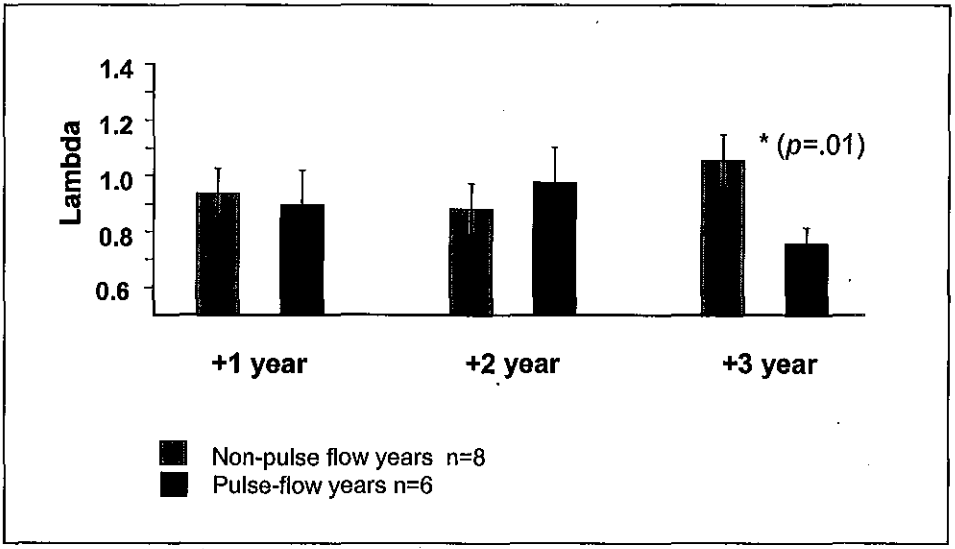


Figure 12. Population growth rate (lambda) is significantly less 3 years after pulse years (0.86 ± 0.09) than after non-pulse years (1.16 ± 0.09) (Mann-Whitney U=39, p=0.01). The effects of spring pulse flows were not detectable after 1 or 2 years.

Analyses of the long-term flow and frog population datasets also revealed that the onset of breeding in the spring was not determined by stage height. Frogs initiated breeding across more than an order of magnitude of variation in spring discharge, from 0.66 to 13.02 cms (Figure 13). There was only a very weak trend for frogs to breed later in years with higher water levels (r^2=0.27) (Figure 14). Increasing water and air temperatures are most likely the primary cues for initiation of breeding (Kupferberg 1996; NFF9).

Detailed analysis of the hydrologic and frog population data specific to spring 2005 revealed that both pulse magnitude and timing affect whether embryos survive to hatching. Of the four pulse events that occurred during the spring of 2005 (Figure 15), pulse #2 with the largest magnitude caused the greatest mortality (Figure 16). When comparing the effects of pulse #1 and pulse #3, however, it is evident that a smaller-magnitude pulse can cause higher mortality if it comes later in the season. Fifty-nine percent of the clutches laid prior to pulse #1 (a flow increase from 2 to 18 cms), survived intact. Only 19% of the clutches laid after pulse #2 survived pulse #3 intact, despite a pulse-flow magnitude of less than half (a flow increase from 2.5 to 8.7 cms). As eggs age, the jelly loses cohesion and adhesion to the rock. In the Pit River test flow study (PIT2), eggs that became dislodged as velocities increased were on average 4–5 days older than eggs that remained attached to the rocks.s

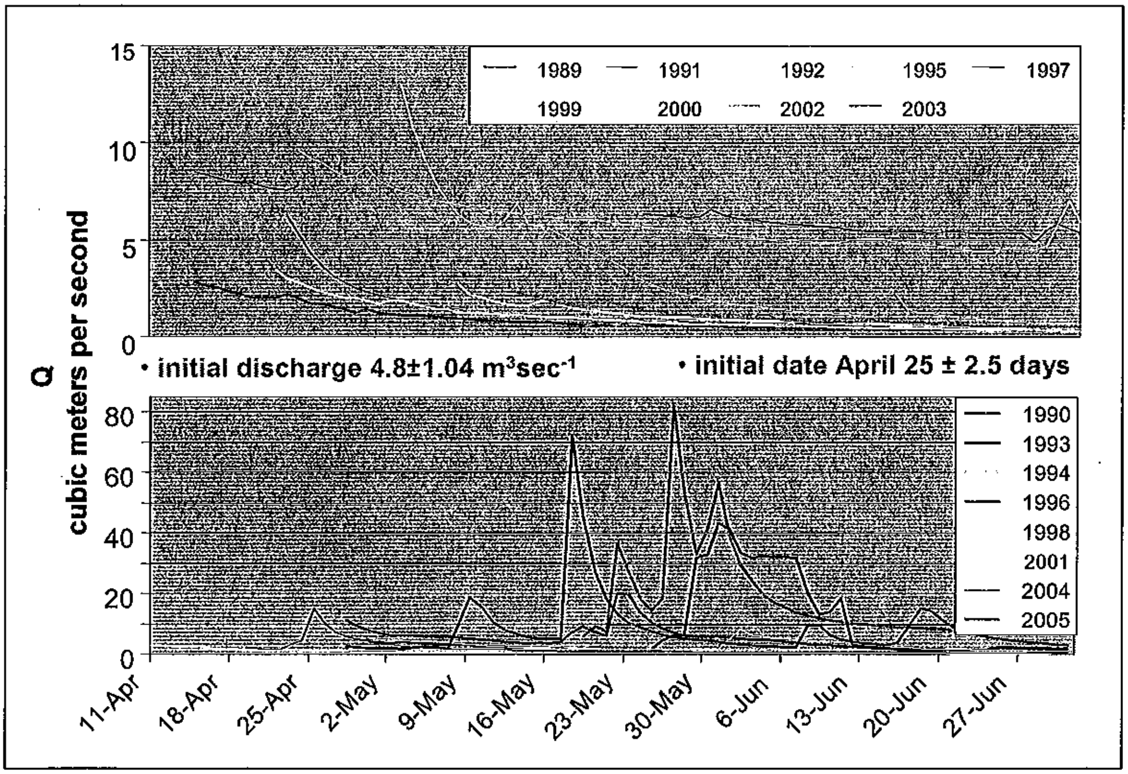


Figure 13. Spring hydrographs for years with egg censuses. Each discharge (Q) curve begins on the date when eggs were first observed that year, $Q_{initial}$. Non-pulse years are shown in the top graph; pulse years are shown in the bottom graph. Pulse years are years in which the ratio of $Q_{initial}$:Q_{max} > 1.

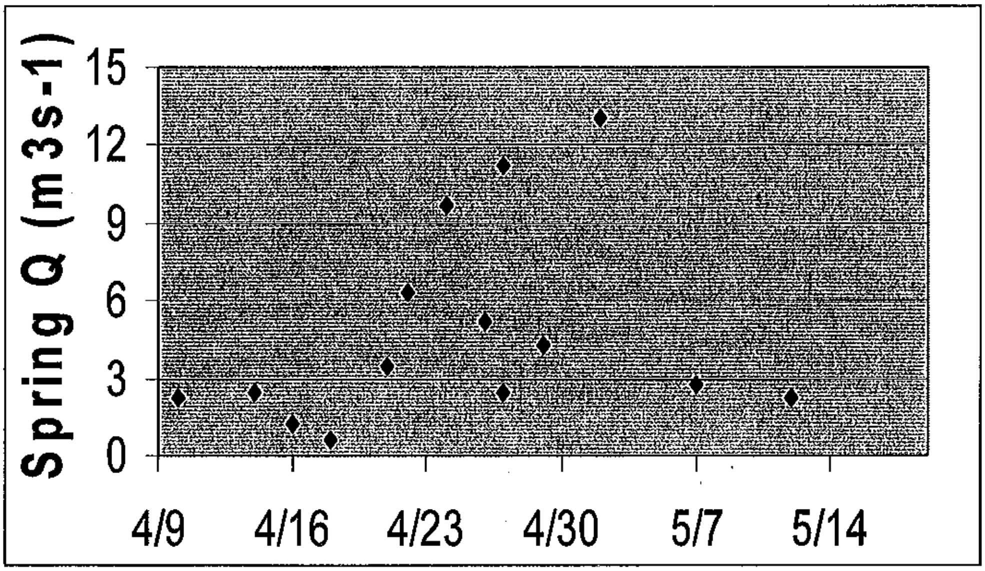


Figure 14. Discharge (Q) versus date when eggs were first observed from 1992–2005

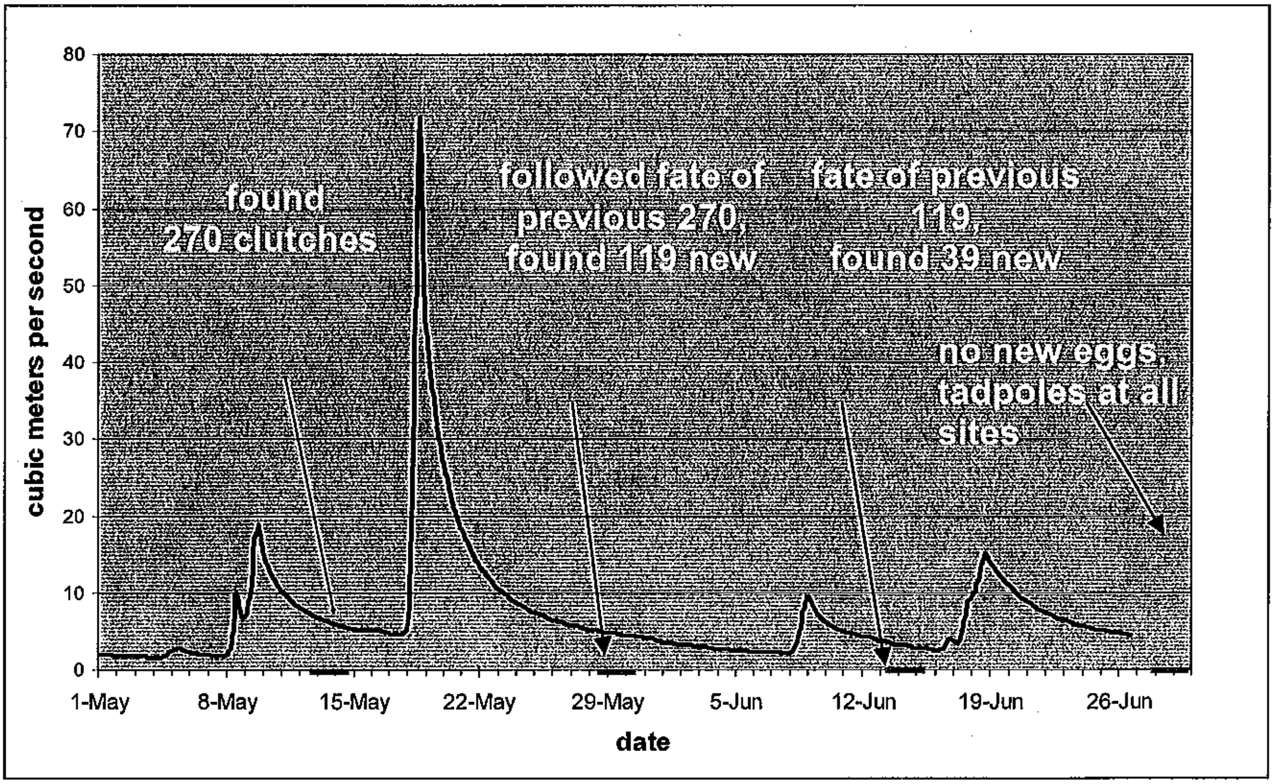


Figure 15. Spring 2005 hydrograph of the SF Eel River (Branscomb gage). Arrows indicate egg mass census dates; text indicates numbers of clutches found along the 5.2-km reach.

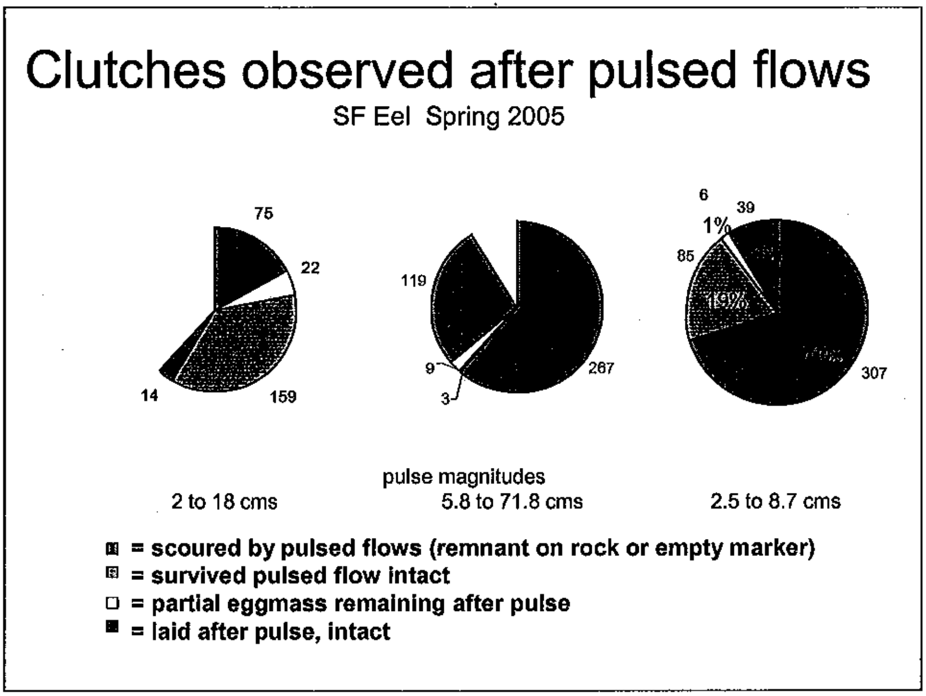


Figure 16. Embryo survival after natural pulse-flow events. The missing sections in the first two pie diagrams indicate the portion of the season's total number of eggs not yet laid when the pulse-flow event occurred.

3.3. Hydrodynamic Modeling

3.3.1. Methods and Data Analysis

The hydrodynamic modeling will be completed using River 2D, a two-dimensional, depth-averaged finite element model used by California Fish and Game and others in fish habitat evaluation studies (Steffler and Blackburn 2002). The model is designed specifically for use with natural streams and rivers in that it incorporates local roughness values, variations in wetted areas as flows fluctuate, and supercritical/subcritical flow transitions. The inputs to the model include comprehensive reach-scale topographic surveys, detailed roughness parameters, and at least two sets of low-flow and high-flow depth and velocity measurements for calibration and validation purposes. Detailed surveys of topography, hydraulic conditions, and substrate at each of the three study reaches during the low-flow and high-flow seasons provide the data necessary to calibrate the model.

Topographic surveys were completed using a robotic total station (Topcon model GTS-802A) and a GPS-RTK (Global Positioning System–Real Time Kinematic) survey system (Topcon model Hyper Lite Plus). Due to the varied conditions among the study sites including heavy vegetation, steep canyon walls and deep water, both types of total stations were needed to fully survey each site. Surveys were completed at a resolution of approximately 1 m by 1 m in order to capture the detail of the near-shore environment adequately for the modeling. Velocity measurements were taken throughout each study reach with emphasis on the near-shore environment using a Marsh-McBirney flow meter attached to a wading rod. Monumented cross-sections were established at each study site to measure discharge and a wetted perimeter at various flows. The edge of water was also surveyed using the total stations at various discharges to determine the spatial extent of flow for calibration and validation purposes.

To determine the persistence of local hydraulic conditions and the availability of suitable habitat as discharge changes in each study reach, a series of flow regime scenarios will be run through the model. This will likely entail a stepped procedure that mimics up-ramping rates so that changes in habitat availability over time can be compared with the mobility rates of various life stages. A range of low to high flows specific to the types of pulse flows typical to the study system will be evaluated.

The output from the modeling scenarios will be analyzed in a variety of ways to determine how velocities (magnitude and direction), depths, and habitat types change as flow fluctuates. Changes in velocity magnitude and direction at each modeled discharge will provide information on whether mobility thresholds of vulnerable life stages are exceeded. Questions of habitat availability and persistence will be addressed by importing resulting depth and velocity distributions for each discharge into a geographic information system (GIS) for spatial analysis. Froude number, calculated from depth and velocity, has been shown to be a good indicator of habitat type when calibrated to the range of depth variability inherent to the study stream (Panfil and Jacobsen 1999). Using ArcGIS software (ESRI 2002), the planform distribution of habitat types, based on Froude number, can be evaluated to answer specific questions, such as whether habitat types shifted from one patch to a neighboring patch or were lost, or whether connectivity between suitable habitats was maintained during the pulse, an especially important question for life stages with limited mobility. In addition, quantitative measures of diversity and habitat heterogeneity will be calculated using techniques recently developed in studies in the Yuba River watershed (Yarnell 2005) and compared across flow scenarios to determine relative changes. Changes in velocity magnitude and direction, habitat availability, and habitat heterogeneity for each flow scenario will then be evaluated in relation to the behavioral response and habitat requirements of *R. boylii* to determine any potential direct or indirect effects.

3.3.2. Preliminary Data

Topographic surveys of each study reach were completed in fall 2005 and winter 2006. The topography of the SF Eel River study reach and the spatial extent of a late-summer low flow (dated 10-22-05) are shown in Figure 17. These data will be input into River2D and a discretized mesh will be generated for the hydrodynamic modeling. Subsequent surveys of flow extent, depth, and velocities will be used to calibrate and validate the model results.

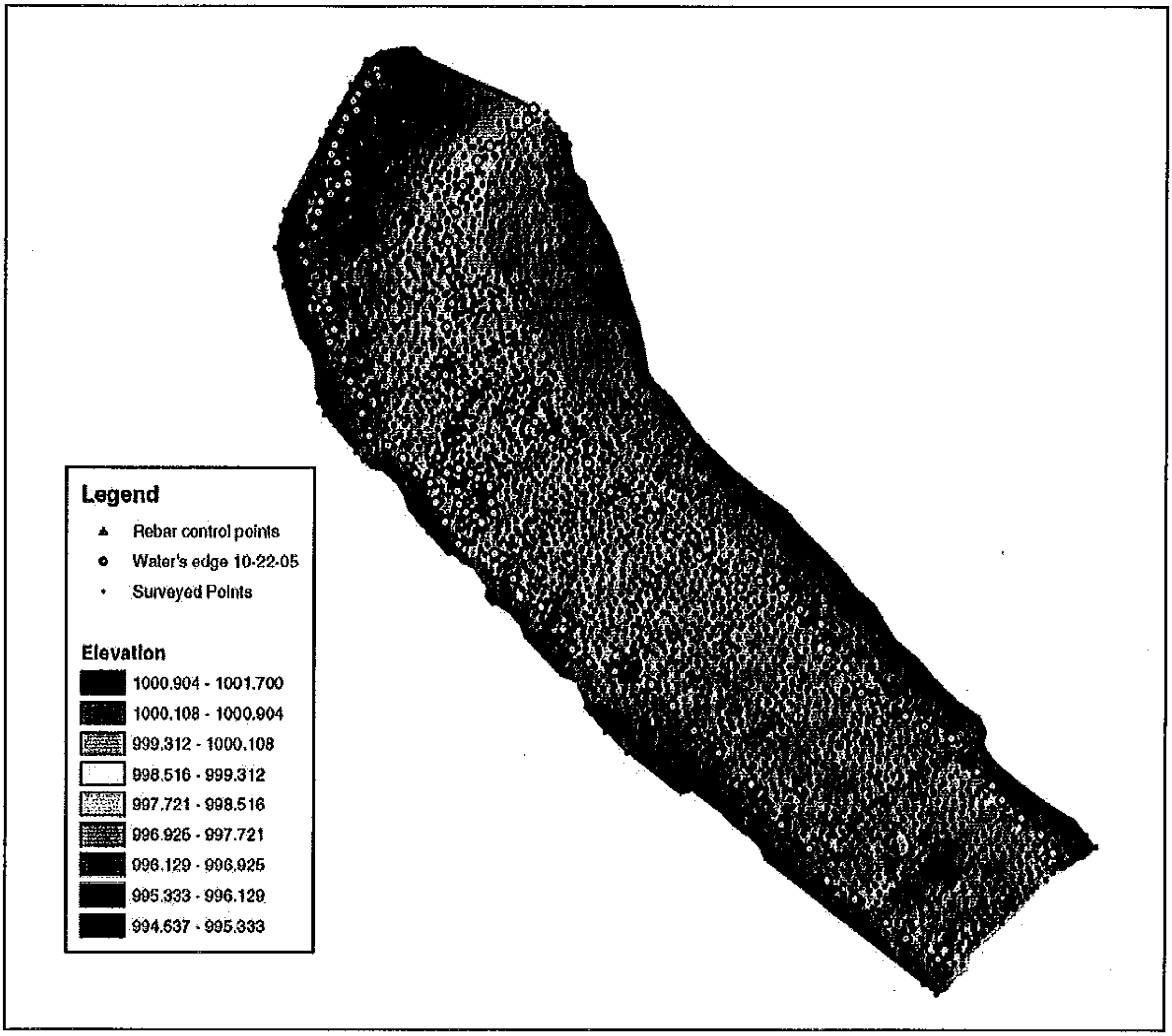


Figure 17. Topographic survey data for the SF Eel River study reach. Low-flow water's edge surveyed on October 22, 2005.

4.0 Larval Experiments

Larval experiments were conducted to address three questions:

1. On a short time scale, what is the behavioral response to increasing velocity?
2. Can tadpoles swim back to patches of preferred depth and velocity?
3. What is the cumulative impact of the observed behavior patterns on growth and development?

4.1. Behavioral Response to Velocity Manipulation

Velocity and substrate were manipulated in an artificial stream channel to determine the hydrologic conditions which cause larvae to alter normal movement and to be entrained into the current.

4.1.1. Artificial Stream Channel Methods

The artificial stream facility is located at the Redwood Sciences Lab, Arcata, Calif. It is a rectangular doughnut-shaped tank with pumps that recirculate water (Figure 18). Two shallow cobble bars were constructed in the long sections of the tank using a false bottom, and the short sections of the tank were deep pools. Two groups of larvae were tested in each trial; one group had an embedded substrate and the other did not. Each trial lasted one hour, consisting of three 20-minute velocity levels. Response variables were tadpole activity level and the rate of movement out of the test patches. Two observers monitored emigration continuously and assessed the number of tadpoles active at five-minute intervals. For each velocity time period in a replicate, the rate of emigration was calculated using least-square regression and the mean percent active was calculated. Incidental observations of swimming behavior, e.g., distance moved upstream in one burst, were also recorded. One pilot and five other replicate trials were completed. Treatment effects were assessed by repeated measures Analysis of Variance using Systat 11 (Wilkinson 2005).

R. boylii larvae from the SF Eel River were transported to the artificial stream. Larvae were also collected from the Mad River, near Arcata, Calif., for a pilot trial. Although the original intention was to test groups of tadpoles that had been reared in high- and low-velocity conditions separately, there was inadvertent mixing of individuals in the holding tanks such that each test group had a mixture of tadpoles. SF Eel River tadpole groups were drawn from a pool of 167 individuals, with Gosner stages ranging from 29–37, mean ± s.d. = 34.4 ± 1.8. Groups were randomly assigned to treatments. Mad River tadpoles were more developed, at Gosner stages 40–41 (Gosner 1960).

Because interstitial refugia appeared to be important from preliminary observations, two substrate conditions were created. In one treatment, 55 cobbles/small boulders were placed on top of a foam bed. In the other treatment, a similar number of rocks was embedded within the foam by carving out an indentation for each rock to mimic the filling of interstitial spaces which can sometimes occur in regulated rivers. Foam was used because natural fine sediments would damage the pumps. For similar reasons, clean rocks, rather than rocks covered with periphyton, had to be used. Each rock was measured along its intermediate axis to the nearest 0.5 cm. Rock

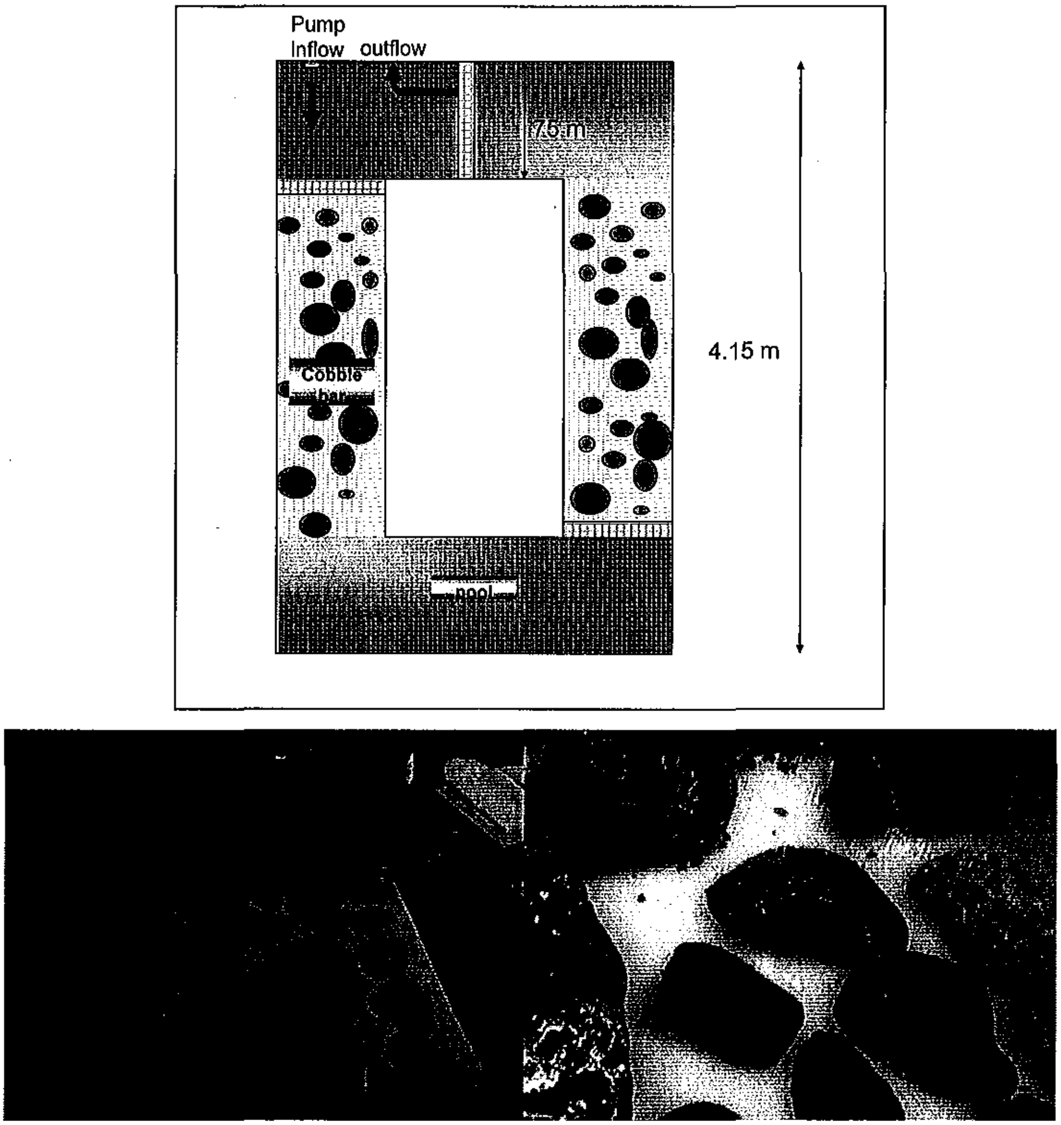


Figure 18. Schematic of artificial channel (top). Light blue rectangles represent rock patches either embedded within or placed on top of foam (bottom left and right). Fiberglass mesh (1 mm) screens were placed at the upstream end of each patch and in front of the outflow. Shallow areas are indicated by lighter shading.

height on a solid surface vs. rock height placed in, or on, the foam was also measured to the nearest 0.5 cm. The median grain size in each treatment was 110 mm. Embeddedness was 53.3 ± 1.4% in the "embedded" treatment and 12.3 ± 1% in the "unembedded" treatment ($p<0.001$). Some gravel was used in each simulated bar to fill gaps and cracks where the foam abutted channel walls. Mean depth (± 1 s.d.) was the same on the embedded and the un-embedded sides, 19.2 ± 2.0 cm and 19.7 ± 4.4 cm, respectively.

Velocity conditions were created by engaging different arrays of pumps: v1 = filter pump only; v2 = filter + chiller pump with valve 2/3 open; v3 = filter + chiller pump with valve fully open and small pump on; v4 = all previous pumps on + large pump. V4 was only used during the pilot trial. To assess the spatial variation at v2 and v3, measurements arranged in a uniform grid were taken at each flow (three mid-column measurements at each of 12 points). Basic descriptive statistics were calculated. To assess temporal variation in velocity across trials, the probe was mounted at a fixed station on the unembedded side and readings taken every five minutes during trials. Water temperatures ranged from 20° to 21 °C.

4.1.2. Behavioral Response Results and Discussion

Velocity conditions in the two patches were not identical spatially due to the positions of the pumps just upstream of the embedded test patch. This side was more turbulent, as shown by the larger standard errors and ranges of measurements taken pre-trial across a grid encompassing the whole patch (Table 6). The difficulty of moving all the rocks and the wet foam from one side of the flume to the other and re-gravelling to seal off the false bottom precluded switching the positions of the embedded and un-embedded test patches. The mean velocities measured through time during the trials were similar to the mean velocities observed pre-trial. Although the two substrate treatments did not experience exactly the same velocity conditions, the authors believe that the differences do not change the interpretation of the outcome of the experiment. Specifically, there were no significant differences in tadpole performance between the two sides of the flume. Nor were there any significant interactions between embeddedness treatment (side of flume) and velocity.

Table 6. Variation in mid-column velocity (cm/sec) through space and time as created by four different pump arrays in the artificial stream channel. The "at-a-station" measurements taken during the trials were in the un-embedded side.

Substrate	Pump configuration	Pre-trial mean ±s.e. (cm/s) (n=12 pts in space)	Pre-trial range (cm/s)	Trial mean ± s.e. (cm/s) (n=20 pts in time)	Trial range (cm/s)
Unembedded (away from pumps)	V1 = filter only	approx. 1	0–2	0.95 ± 0.15	0–2
	V2 = filter + chiller, valve 2/3 open	4.8 ± 0.27	4–6	6.20 ± 0.50	3–10
	V3 = filter +chiller, valve fully open + small pump	19.0 ± 0.92	13–23	17.00 ± 0.70	16–22
Embedded (near pumps)	V1 = filter only	approx. 1	0–2		
	V2 = filter + chiller, valve 2/3 open	4.4 ± 0.6	0–8		
	V3 = filter +chiller, valve fully open + small pump	17.0 ± 1.7	0–26		

Tadpoles became significantly less active as velocity increased (Figure 19). There was no significant effect of the embeddedness level on the proportion of tadpoles active, and there was no statistical interaction between the velocity and embeddedness factors (Table 7). Proportionally fewer tadpoles left the artificial cobble bars when velocities were increased as shown by the decreasing slopes of the emigration vs. timelines shown for each of the ten replicates in Figure 20. The mean slope was significantly lower at the two elevated velocities compared to the base flow conditions (Figure 21). There was not a significant effect of substrate embeddedness on rates of emigration from bar to pool, and there was not a significant interaction between substrate and velocity (Table 8).

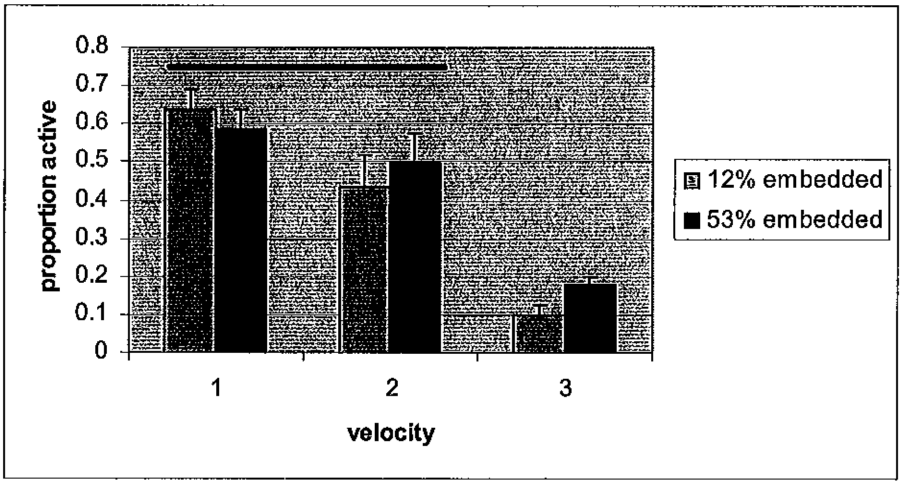


Figure 19. Mean tadpole activity level (measured every 5 minutes) during five paired hour-long trials. Activity at v1 (0–2 cm/s) was not significantly different from activity at v2 (5–8 cm/s) (Bonferroni-adjusted *p* =0.15). Activity at v3 (16–22 cm/s) was significantly different from activity at v1 (p<0.001) and v2 (p=0.001).

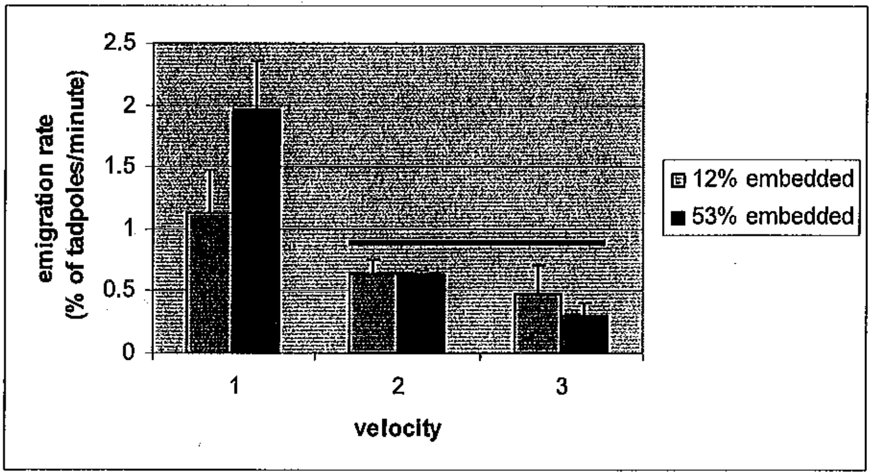


Figure 20. Tadpole movement out of the test patches was significantly lower when velocity was elevated above base flow conditions, but did not differ significantly between the two higher velocities (Bonferroni-adjusted p-values for emigration at v1 vs. v2=0.017, v1 vs. v3=0.008, v2 vs. v3=0.66). For depiction of the full data set, see Figure 22.

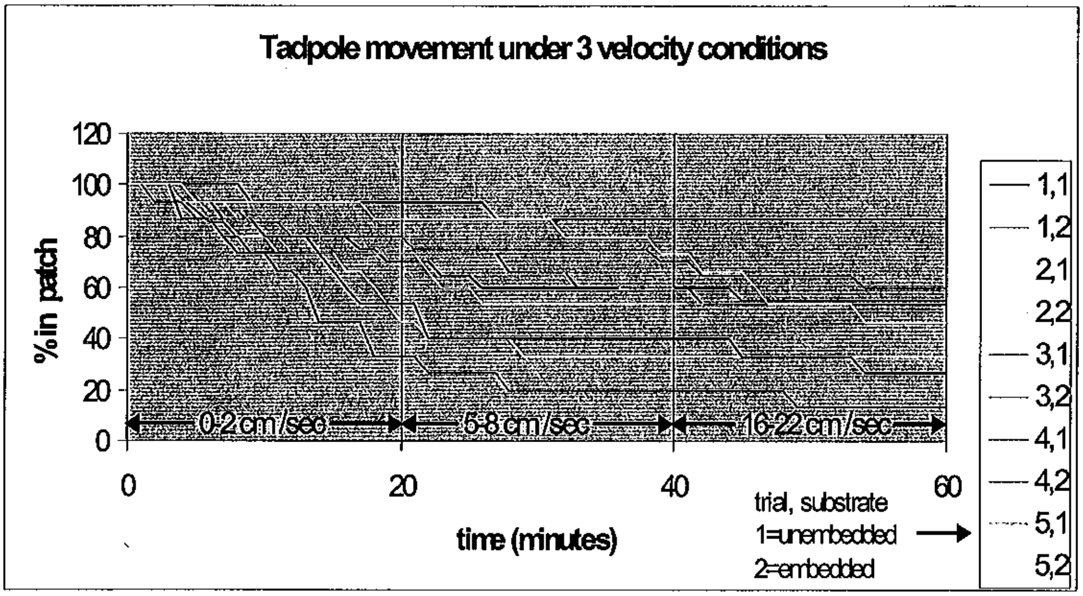


Figure 21. Tadpole emigration from the simulated "cobble bars" to a downstream "pool." Mean slope of the lines in each time period were calculated from least-squares regression (v1=1.754, v2=-0.6, and v3=-0.383). Comparisons of these slopes are depicted above and are equivalent to the percent of tadpoles leaving per minute.

Table 7. Repeated-measures analysis of tadpole activity in simulated cobble bars during the artificial stream channel experiment.

Source	**Mean Square**	**Wilks' Lambda**	***df***	***F***	***p***
Analysis of Differences (MANOVA, Multivariate Analysis of Variance)					
Velocity		0.066	2,7	49.5	<0.001
Velocity x Substrate		0.802	2,7	0.87	0.46
Analysis of Totals (ANOVA, Analysis of Variance)					
Substrate Embeddedness	0.008		1	0.42	0.53
Error	0.018		8		

Note: The univariate test of substrate treatment is on the percent of tadpoles active totaled across velocity time periods 1, 2, and 3.

Table 8. Repeated-measures analysis of rates of tadpole emigration from simulated cobble bar to pool in artificial stream channel experiment.

Source	**Mean Square**	**Wilks' Lambda**	***df***	***F***	***p***
Analysis of differences (MANOVA)					
Velocity		0.301	2,7	8.13	.015
Velocity x Substrate		1.39	2,7	1.76	.24
Analysis of Totals (ANOVA)					
Substrate Embeddedness	0.452		1	1.286	.29
Error	0.352		8		

Note: The univariate test of substrate treatment is on tadpole emigration rate totaled across velocities 1,2, and 3.

Among the incidental swimming observations at v2 and v3, a common sequence of events occurred when a tadpole left or lost its position in a micro-refuge: first the tadpole would swim upstream against the current, then if caught in turbulence or at the end of a burst, it would stop tail movements, drift downstream (rest), then dive and swim for the bottom, finally hold onto a rock with mouthparts or rest if a crevice was found. There were fewer bursts of upstream swimming at v3, and the differences in mean distances swum using repeated measures ANOVA were not significant (Figure 22). Median burst distance was 0.5 m. If however, bursts are characterized as short (< 0.5 m) versus long (≥ 0.5 m), then there is an increase in the proportion of long bursts at v2, but it was not significant (*p*=0.1, chi-square=4.5, df=2) (Table 9).

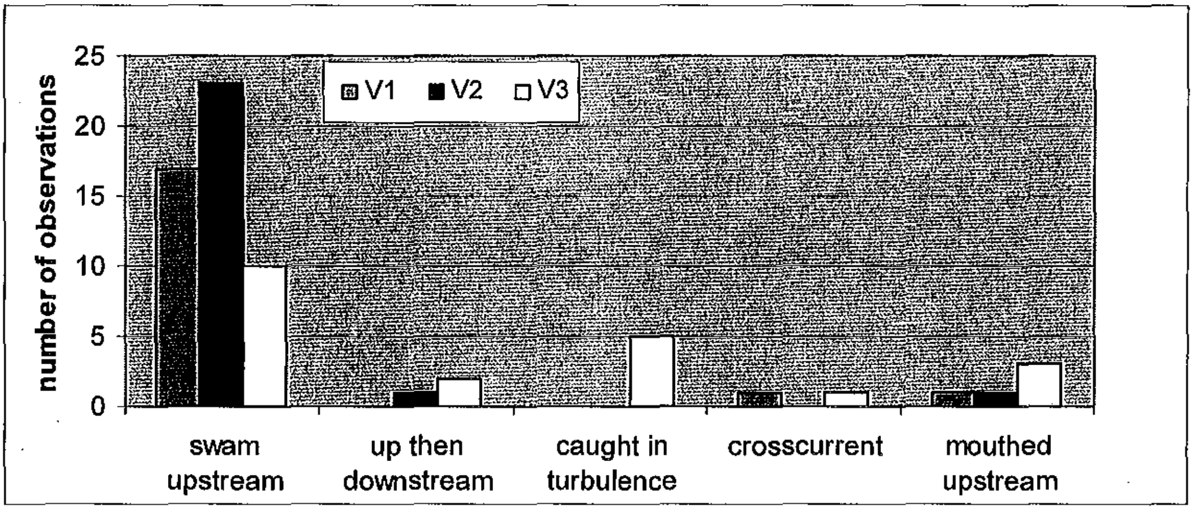


Figure 22. Incidental observations of upstream movement by tadpoles at three velocities

Table 9. Chi-square analysis of the proportion of long and short swimming bursts at the three experimental velocities during the artificial stream channel experiment (chi-square=4.5, df=2, *p*=0.1)

Velocity	Long bursts # observed (expected)	Short bursts # observed (expected)	N
1	5 (8.6)	14 (10.4)	19
2	14 (10.9)	10 (13.1)	24
3	5 (4.5)	5 (5.5)	10
N	24	29	53

The results of the flume experiment illustrate the short-term behavioral response to increased velocity. At low velocity, counter to expectation, tadpoles entered the pool, which was much deeper than the preferred depths observed in the field. Possibly they swam into the downstream pool at the lowest velocity because they did not sense the patch boundary. In a real river tadpoles might perceive a boundary when encountering an increase in velocity or turbulence at the patch edge where the transition to riffle or downstream pool would be, and then change movements accordingly. Two observations support this explanation. First, at the moment the pumps were switched up to the next velocity level and tadpoles experienced increased velocity, they would briefly swim against the current, drift, and then seek refuge. Second, although tadpole activity at v2 was not significantly different from v1, there was a significant decrease in emigration from the patch. Moreover, the significant differences in activity level between v2 and v3 were not accompanied by significant differences in emigration rate. As velocity increased from v2 to v3, tadpoles sought refuge behind rocks and wiggled down into very small crevices in order to not be swept away. Some individuals found more-protected spots than others, and those that left the patch at v3 did so because they could no longer maintain their position. Thus the emigration at v3 and v1 are qualitatively different.

To determine what the critical velocity is for displacement and how response to velocity varies across life stages, this experiment will be repeated during 2006 using a range of larval developmental stages and recent metamorphs if possible. A different flume facility/artificial stream channel will be sought out because the exact threshold velocity causing entrainment could not be produced by the pump configurations available. During the pilot experiment with Mad River tadpoles at v4 (40–50 cm/s), all tadpoles were immediately flushed out of the experimental patches. Therefore the critical velocity likely lies between 20 and 40 cm/s, a range which could not be achieved with the permutations of pump arrays available at the Redwood Sciences Laboratory facility.

4.2. Transplant and Relocation Experiments

To determine whether larvae can return to shore and to assess the most feasible method for studying the return to preferred depths and velocities in the field, two types of pilot manipulations were conducted. In one set of manipulations, individual tadpoles were moved and observed continuously. In the other type of manipulation, a group of tadpoles was relocated within a gridded area enclosed by a downstream drift fence. Location was determined after a set period of time. Based on the results of these pilot experiments, a method for the 2006 field season will be chosen.

4.2.1. Relocation Methods

During July 2005, 10 movement trials of individual tadpoles were conducted in which tadpoles were displaced 1–3 m away from shore. Tadpoles were observed with mask and snorkel for as long as possible. A control treatment (n=5) in which a tadpole was caught and then released at its point of origin was also included. Tadpoles were approximately 4–6 weeks post-hatching between Gosner stages 27–31, 15 mm snout vent length. Tadpole response was determined to fall in one of the following categories: returns to near-shore environment, is swept away/disappears, or finds interstitial refuge. Time and distance to one of these endpoints was noted.

Because this first method was very time intensive to produce a small number of replicates, a second type of trial involving a larger sample of tadpoles was utilized. Drift fences were constructed perpendicular to shore extending from an existing tadpole site toward the thalweg. The "L" shaped fence enclosed the downstream and mid-stream edge of a 12.5 m^2 patch. In each

0.5 m^2 grid square, velocity magnitude and direction were measured. A group of 50 larvae collected locally were relocated 2 m upstream from the drift fence and 2 m away from the shore to a location with a flow refuge behind a boulder. The release square represented a transition between the low-flow near-shore environment and swifter current away from shore (Figure 24). Tadpoles in this trial were larger, with a total length of 16 ± 0.48 mm (mean ± 1 s.e., n=50). After allowing 15 minutes for acclimatization, larvae were released. Two hours later, the trial area was searched and tadpole locations noted. Distance moved was calculated based on the mid-points of each 0.5 m^2 grid square.

For the drift fence experiment, the Froude number of each grid square was calculated. Froude number is defined as the ratio of inertial to gravitational forces:

$$Fr = \frac{v}{\sqrt{gd}}$$

where v is velocity, g is gravity, and d is depth. Non-parametric Mann-Whitney U Tests were used to compare the Froude numbers of tadpoles present vs. absent grid squares.

During 2006, trials will be conducted at the same three field sites surveyed for 2-D modeling so that the trajectories of tadpole movement can be evaluated in the context of planform velocity vector maps produced by the model.

4.2.2. Results and Discussion of Relocation Experiments

In the group release experiment, almost half of the tadpoles, 24, were relocated at the end of the trial. The whereabouts of the other half could not be determined. None were observed caught against the drift fence, although fish were observed near the fence and predation is a possibility. The number of tadpoles maintaining their position in the release square, moving to shore by cross-current swimming, and number moving to higher-velocity cells are shown in Figures 23 and 24. The mean Froude number of cells where tadpoles were found was 0.060 ± 0.01 (n=13) compared to tadpole absent cells 0.160 ± 0.036 (n=24). This difference is statistically significant (chi-square approximation of Mann-Whitney U=34.54, df=1, p<0.001).

Figure 23. Drift fence experiment with flags marking the corners of the 0.5-m^2 grid squares

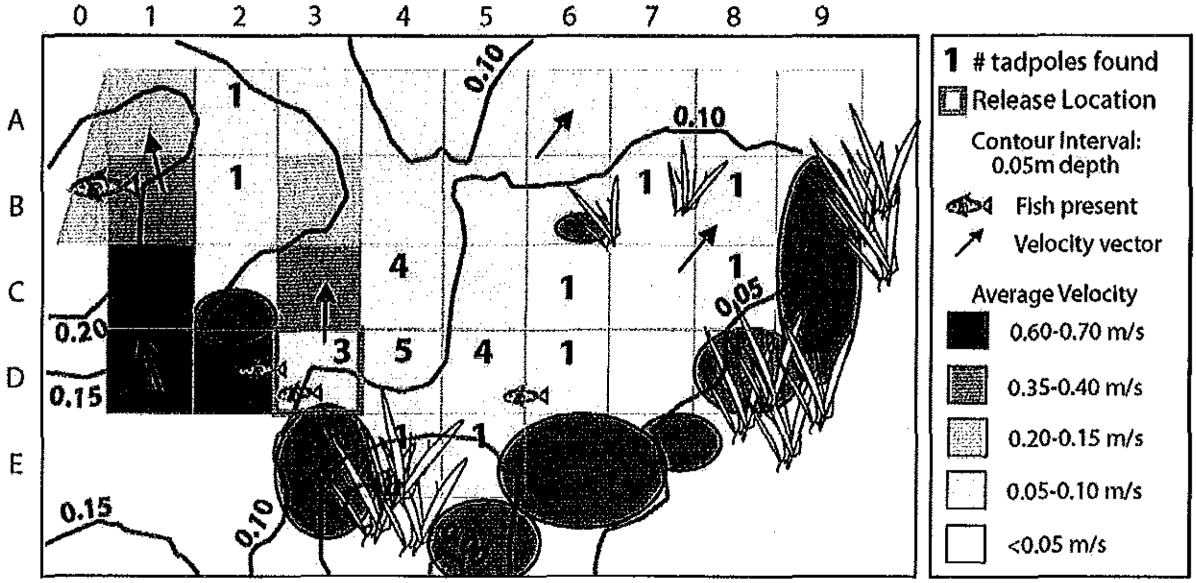


Figure 24. Schematic diagram of drift fence area indicating numbers and locations of tadpoles found at the end of the trial. Fifty tadpoles were released in the square D-3.

In the open relocation trials and the closed drift-fence trials, the percentage of tadpoles able to return to the near-shore microhabitat was low, 18% and 0% respectively (Table 10). The mean net distance moved downstream in the drift fence trial was 1.44 ± 0.24 m and 0.95 ± 0.2 m in the open trial. Unlike the swimming in the artificial stream channel, no bursts of upstream swimming greater than 0.5 m were observed. Most upstream swimming occurred within the low-flow boundary layer next to the rocks, and individuals were swept into the current when they came up into the water column.

Table 10. Results of relocation trials in which tadpoles were moved 1–2 m away from shore to areas with mid-column velocities in the 5–10 cm/s range

	Drift Fence Trial	**Open Relocation Trials**		
Final Location or Fate	**% of Tadpoles (n=50)**	**% of Tadpoles (n=10)**	**Distance (m) (mean ± 1s.e.)**	**Time (min) (mean ± 1s.e.)**
Returns to a cell near shore	18%	0%	n/a	n/a
Swept away / disappears	52%	80%	0.94 ± 1.0	8.8 ± 2.4
Finds refuge	30%	20%	1 ± 0.0	7.7 ± 2.4
Total	100%	100%	0.95 ± 0.2 range=0.0–1.9	8.6 ± 2.2 range=0.1–19.3

4.3. Cumulative Effects of Velocity Manipulation

To evaluate the cumulative impact of the behavioral responses observed in the flume and field relocation trials—that tadpoles seek refuge in the interstices and only a small proportion successfully appear to be able to return to their original microhabitat—longer-term manipulations focused on growth and development were conducted.

4.3.1. Methods of In-situ Tadpole Rearing

Tadpoles were reared in high- and low-velocity environments in the SF Eel River (Figure 25). On June 15, 2005, a clutch of eggs was divided in half, with one half left attached to its rock in the river. The other half was placed in a flow-through enclosure made of a plastic laundry basket with 1 mm fiberglass mesh glued over the openings. Post-hatching on July 3, tadpoles were divided among 12 replicates, 25 per enclosure. Midway during the experiment, density was decreased to 15 per enclosure to mimic the naturally occurring declining density caused by dispersal and predation. Enclosures were randomly assigned to treatments and then placed either near the original location, or where the current was faster.

Figure 25. Flow through rearing enclosures; left shows the interior of a high-velocity treatment

As the stage height declined, velocity differences between the treatments narrowed. At approximately 7–10 day intervals, enclosures were moved further from shore to reestablish the velocity differences between the two treatments, and thus mimicking a "pulse." Depth was maintained between 15–20 cm, within the natural range of tadpoles observed at the site. At each movement of enclosures, surface velocity was measured visually using the float method. On two occasions the visual estimations were verified using a Marsh Courtney flow meter when surface, mid-column, and bottom velocity measurements were made. This regime of moving the enclosures roughly mimics a weekly pulse flow.

Tadpoles were fed ad libitum. Enclosures were stocked with rocks covered with algae along with copious loose algae and dried aquarium fish-food algae tablets. Temperature data loggers were placed in each enclosure. Water temperature was recorded hourly for the duration of the experiment. Tadpole snout-vent length, tail length (mm), weight (mg), and developmental stage were measured on August 8, 2005. The total duration of the treatment was five weeks.

Treatment effects on tadpole size and development were compared using t-tests. Data from all the individuals within each replicate enclosure were pooled by calculating a mean size, weight, and Gosner stage. Mean temperatures were also compared with a t-test. Bonferroni adjustments for multiple comparisons were made to maintain an experiment-wide error rate of α=0.05.

4.3.2. Results and Discussion of Larval Rearing Experiment

Tadpoles raised at elevated current velocities were significantly smaller and less developed than tadpoles reared at low velocity (Table 11). On average, pulsed-flow tadpoles weighed half as much as low-velocity tadpoles.

Low-velocity tadpoles experienced a range of 0–3 cm/s, with mean mid-column velocity = 1.65 ± 0.26 cm/s. Tadpoles in the pulsed-flow treatment experienced a range of 6–12 cm/s, with mean mid-column velocity = 8.8 ± 0.6.

Table 11. ***Rana boylii*** **tadpoles exposed to simulated weekly pulse flows were significantly smaller and less developed than tadpoles reared continuously in a low-velocity environment (*p*-values adjusted for multiple comparisons)**

Response Variable	Low Velocity n=6 enclosures, 15 larvae/enclosure	Elevated Velocity n=6 enclosures, 15 larvae/enclosure	*t*	*df*	*p*
Body length (mm)	12.66 ± 0.43	10.98 ± 0.29	-3.2	10	0.003
Total length (mm)	35.3 ± 1.5	29.50 ± 1.9	-4.4	10	0.003
Gosner stage	34.50 ± 0.3	32.37± 0.24	-5.9	10	<0.001
Weight (g)	0.62 ± 0.05	0.33 ± 0.04	-4.8	10	0.003

It is unlikely that the growth and developmental differences could have been caused by differences in food availability or temperature. Thermal regime in the two treatments was nearly identical (mean temperature high velocity = 18.459 ± 0.258 °C vs. mean temperature low velocity = 18.464 ± 0.212 °C, t=-0.40, p=0.97), and tadpoles were fed ad libitum. There was always a visual surfeit of algae in the enclosures and rocks were changed weekly. Food was also supplemented with dried algae tablets, formulated for aquarium fish.

4.4. Conclusions from Tadpole Experiments

A composite explanation emerges from these preliminary experiments of what happens when an aseasonal pulse occurs. A portion of the tadpoles will seek flow refugia in the substrate, and another portion will be swept downstream. Few will successfully move cross-current back to shore. Those tadpoles in the substrate face energetic costs that slow growth and development. Previous studies have shown that larval growth and development rates are correlated with components of adult fitness (Smith 1987; Semlitsch et al. 1988; Berven 1990) and are important demographic factors in influencing overall population growth rate (Govindarajulu et al. 2005). For other ranid frogs, the larval growth environment has been shown to influence post-metamorphic chance of survival and time to sexual maturity (Altwegg and Reyer 2003). Such a trend of smaller size and later time to metamorphosis has been observed at the Mokelumne River (2001–2004) as pulsed flows occurred later into the spring (MOK6). For those tadpoles able to find refuge from high velocities, the effects of pulsed flows on growth and development are important sub-lethal consequences with implications for population trends.

5.0 Conclusions and Recommendations

5.1. Preliminary Conclusions from Year One (2005) and Direction for Years Two (2006) and Three (2007)

The statewide report review (Section 2) revealed several consistent patterns in the effects of aseasonal pulsed flows on *R. boylii* and their habitat. The mechanisms of these effects are best understood for the immobile life stages and habitats and less well understood for the mobile stages.

Egg scour and dessication: Egg masses were negatively affected by pulsed flows via scouring if flows occurred during or after oviposition and via desiccation if oviposition occurred during high flows/spill events and then water levels dropped. Thus the timing of pulsed flows is critical. The higher inter-annual and intra-annual frequency of spring and summer pulsed flows is a key difference between pulsed flows in regulated rivers and storm-generated flows in unregulated rivers. The greater interval (i.e., longer recovery time) between recurrences of pulses which cause heavy recruitment losses may explain why populations in unregulated rivers are persisting at much higher densities.

Tadpole stranding: Evidence exists for the potential and actual stranding of tadpoles following pulsed flows. Pulsed flows may lead to lower tadpole abundances at particular locations.

Habitat quantification: Although methods used for quantifying suitable habitat varied among studies, the general trends in habitat suitability indicated a large degree of site specificity depending on channel morphology. Habitat surveys using stationary polygon/transect methods are most relevant to the requirements of immobile life stages (eggs and early tadpoles); while shifting transect methods provide information on overall area of suitable habitat. Polygon methods also provide information on the number of suitable habitat patches as well as the overall area.

Three-year lag time: An important pattern emerging from the analysis of existing hydrologic and frog population data from the SF Eel River (Section 3.2) is a three-year lag in *R. boylii* population response to the presence or absence of pulsed flows. In particular, late-spring pulse flows which affect eggs and small tadpoles were associated with inter-annual declines in the breeding population size. Preliminary analyses of data from the NF Feather River indicate similar trends may be occurring in regulated systems.

Although the magnitude and timing of peaks are important in determining the impact of a pulse within a given year, the overall impact on long-term population viability depends largely on the recurrence interval of the pulses capable of causing recruitment loss. The effects of high-magnitude late-spring and summer pulses may be more pronounced in regulated systems due to the increased incidence of such disturbances. The issue of pulse frequency was explicitly addressed in two of the reports reviewed in Section 2 (MOK6 and PIT4). Frequency analyses of pulsed flows were absent from the other FERC relicensing documents specific to amphibians. Although this information may be available, it is scattered in the hydrology studies, reservoir elevation models, or recreational white water boating flow reports.

The authors recommend that frequency/recurrence interval analyses become a central part of the amphibian studies. Year two of this project will further test the hypothesis relating pulse frequency to population change by completing hydrologic frequency analyses on the NF Feather River and Alameda Creek study reaches.

Tadpole use of substrate refugia: Results from the preliminary tadpole experiments (Section 4) have indicated some of the processes by which pulsed flows create the patterns observed in the statewide report review. However, no single experiment can address all components. In designing each experiment, tradeoffs had to be made between controlling the variables of interest and maintaining realism. By conducting a suite of experiments, each focused on one aspect. The artificial channel experiment answered the question, "How do tadpoles behave when velocity increases?" Velocity and substrate were manipulated, but depth was unrealistically constant. There was no "shore" for tadpoles to swim to. Because tadpoles did not have food, foraging issues could not be addressed. In the relocation experiment, the question whether tadpoles can swim back to shore could be addressed, but velocity and substrate were variable. In both of these experiments only short-term behavioral responses were studied. Long-term energetic consequences had to be addressed separately. By considering the results *in toto*, a coherent picture begins to emerge.

Energetic consequences of refuge use: The flume experiments showed that the short-term behavioral response of tadpoles to increases in velocity above base flow conditions is to seek refuge behind rocks or in crevices. If flows are sufficiently short in duration or small in magnitude, a fraction of tadpoles will be able to maintain their position. The threshold velocity at which tadpole swimming ability is inadequate to maintain position may lie between 20 and 40 cm/s, but this requires further experimentation

The relocation trials illustrated that when tadpoles are displaced, only a portion are able to find refugia or return to shallow, low-velocity microhabitats. The size of the fraction returning varied between the two methods tested, and these trials require further replication.

Results from the rearing experiment indicate the long-term energetic effects when tadpoles spend more time under rocks in flow refugia. Growth and development are significantly lower than in low-velocity controls, and these traits are linked to adult fitness. The survival rates of tadpoles that find interstitial refugia or are swept downstream remain unclear. Year two of the project will address this question of interactions between predators and velocity.

Hydrodynamic modeling: These preliminary results have refined the objectives of hydrodynamic modeling effort. Using the model output at each of the three study sites, the following questions will be asked:

- What magnitude of flow change creates velocity and depth conditions "unsuitable" to both eggs and tadpoles, where unsuitable is defined as too high for proper growth and development or beyond the velocity threshold for tadpole swimming ability?
- What traits of the channel morphology (cross-section shape, bank steepness, or longitudinal gradient) contribute to the pattern observed in the statewide review data of changes in habitat area as discharge increases?

- How do the diversity and connectivity of suitable microhabitats change during a pulse?
- What conditions lead to stranding of tadpoles in unconnected microhabitats?
- How does the availability of refugia change during a pulse event—are there microhabitats where velocity and depth are such that tadpoles could access the interstitial substrate before they are swept downstream?

5.2. Recommendations for Future Research and FERC Studies

1. Exploratory research is needed on short-term behavioral responses to pulsed flows by post-metamorphic life stages. The reports reviewed indicated that these life stages may be less active or may leave the immediate shoreline area during high flows. However, it is currently unclear whether the low abundances seen during flows are a result of lower detectability (i.e., observer bias) or a real behavioral response.
2. Future FERC relicensing or other studies on *R. boylii* would be improved by:
    a. Including comparisons of impaired and unimpaired hydrographs, data on spill and pulse frequency, channel cross-sections, and other relevant hydrologic and geomorphic information for the study area.
    b. Presenting sampling effort (e.g., number sites, search time, or area) clearly in text and figures.
    c. Including bankfull width or upstream drainage area in evaluations of habitat area.
    d. Using consistent life stages that are clearly defined.
    e. Improving abundance/population estimates through the use of more rigorous field techniques such as mark-recapture or multiple visits over short time periods.
3. There is a real need for demographic study of *R. boylii* and the development of matrix models that can predict population trajectories under varying scenarios of pulsed-flow frequency. This demographic research will be pursued during 2007.

5.3. Benefits to California

The benefits of this research are multi-faceted in their scale and scope; however, they are fundamental to the conservation of *R. boylii*, a California Species of Special Concern. Preliminary results obtained from this first year of study fill key knowledge gaps regarding the patterns of negative effects of aseasonal pulse flows on *R. boylii* detected in the statewide review. These results include the discovery of a three-year lag in the observed population effects of late-spring pulsed flows and the importance of pulse frequency in determining overall effects on population.

The methodologies developed in this research that apply frequency analysis to frog population dynamics have specific applicability to debates about the impacts of monthly or biweekly recreational whitewater boating flows. Beyond the conservation of *R. boylii*, the use of 2-D hydrodynamic modeling may be used to evaluate changes in aquatic habitat conditions which would be beneficial to determining flow recommendations for multiple riverine species.

In general, comprehensive data based on sound research allow for more-informed management decisions and ultimately the possibility for improved in-stream habitat conditions, particularly if the findings are incorporated into future hydropower relicensing projects.

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