# PULSED FLOW EFFECTS ON THE FOOTHILL YELLOW-LEGGED FROG (RANA BOYLII): INTEGRATION OF EMPIRICAL, EXPERIMENTAL AND HYDRODYNAMIC MODELING

**PIER FINAL PROJECT REPORT**

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# Acknowledgments

The authors would like to thank Wendy Palen, Collin Bode, Mary Power, Betty Sousa, Camille Mac Neally, and Tanya Blacic for their contributions and help with the experimental aspects of this research. Garth Hodgson, Rod Nakamoto, Clara Wheeler, and Bret Harvey provided essential support for the flume experiment completed at the USFS Redwood Sciences Lab. Dennis Cocherel was similarly essential in providing field and laboratory support at UC Davis. We thank Joe Cech for graciously providing laboratory space and use of the Brett Chamber. Luke Fraser assisted in field work at Alameda Ck. Evan Buckland provided assistance with the topographic surveying of each study reach. We would also like to thank Steve Bobzien, Joe Drennan, Maria Ellis, Earl Gonsolin, and Clara Wheeler for their knowledge and help in providing previously published and unpublished data specific to our study sites. We greatly appreciate the assistance from Dan Corcoran, John Gangemi, Sue Orloff, and Alicia Pool in providing copies of the reports and data analyzed in section 2. Critical reviews from Sharon Lawler, N. Leroy Poff, Richard Wassersug, Joe Wheaton and two anonymous reviewers greatly improved this report. This research was supported and funded through the Pulsed Flow Program of the Center of Aquatic Biology and Aquaculture of the University of California, Davis. This research was conducted with the approval of the University of California, Davis Animal Care and Use Committee (Protocol # 06-12357) and the California Department of Fish and Game (Permit #'s SC-8820, SC-001608).

Please cite this report as follows:

Kupferberg, S., Lind, A., Mount, J., and Yarnell, S. 2009. *Pulsed flow effects on the Foothill Yellow-Legged Frog (Rana boylii): Integration of empirical, experimental, and hydrodynamic modeling approaches.* California Energy Commission, PIER. CEC-500-2009-002.

# Preface

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*Pulsed flow effects on the Foothill Yellow-Legged Frog (Rana boylii): Integration of empirical, experimental and hydrodynamic modeling approaches* is a report for contract number 500-01-044, conducted by the Center for Aquatic Biology at the University of California, Davis and the United States Forest Service. The information from this project contributes to PIER's Energy-Related Environmental Research Program.

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# Table of Contents

# List of Figures

# List of Tables

# Abstract

Four analytical approaches support the hypothesis that altered flow regimes, particularly spring and summer pulsed discharges, contribute to the decline of foothill yellow-legged frogs (*Rana boylii*) in regulated rivers. (1) A review of literature and FERC re-licensing reports indicates that egg masses are negatively affected by pulsed flows via scouring, or desiccation, if spawning occurs during spills that abruptly cease. Tadpole stranding was documented in several studies. Effects on young of the year and older life stages were equivocal.  (2) Long-term population monitoring in three watersheds shows that frequency and magnitude of pulsed flows that harm embryos and tadpoles are factors in determining adult population status. These effects are offset by 2-3 years, representing the time to reproductive maturity in central and northern California. (3) Experiments illustrate that tadpoles seek refuge in the substrate as velocity increases, are not adapted for sustained swimming, and are swept downstream. Tadpoles confined to refugia face predation and energetic costs in terms of growth and development. (4) Simulations using River2D, a 2-dimensional hydrodynamic model, show that velocity and depth conditions exceed tolerances of *R. boylii* egg masses and tadpoles during a range of pulsed flows.  While meso-scale suitability of near shore habitat was accurately predicted, error in modeled point velocities at egg locations arose from limitations in fine scale surveying of the large, poorly sorted, rock substrate.  Management that avoids aseasonal flow fluctuations would benefit *R. boylii*, and other taxa, whose lifecycles are synchronous with the natural timing of runoff in California's rivers.


**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 entire life cycle is completed in flowing water. Over the last half century, it has declined dramatically. Dams and reservoirs have been cited as likely factors in this decline as they drastically alter stream flow regimes and sediment budgets. In a managed river, the timing, duration, and magnitude of large-scale discharge events can disrupt frog reproduction. Under a natural flow regime, discharge gradually declines throughout the summer such that eggs and tadpoles rarely experience large magnitude flows. Due to the absence of natural selection for traits to withstand flooding, these early life stages are thus particularly vulnerable to rapid flow fluctuations in late spring and summer, referred to here as aseasonal pulsed flows.

**Project Objectives**

In this study, aseasonal pulsed flow effects were examined by integrating four approaches: 1) analyses of existing empirical data; 2) long term population monitoring; 3) laboratory and field experiments to quantify the physical tolerances and behavioral responses of tadpoles to changes in velocity; and 4) development of a 2-dimensional (2D) hydrodynamic model that evaluates the relationship between discharge and habitat. As *R. boylii* has increasingly become a focal species in water management planning, especially in Federal Energy Regulatory Commission (FERC) re-licensing of hydroelectric dams, data has been collected in numerous watersheds. Because re-licensing is conducted on a project by project basis, the first objective was to produce a comprehensive compilation of empirical data regarding flow regime effects on *R. boylii.* Such a synthesis did not exist prior to this report. To meet objectives two through four, three watersheds were selected for focused study: the South Fork Eel River (SF Eel), Mendocino Co, the North Fork Feather River (NF Feather), Butte and Lassen Cos., and Alameda Creek (Alameda Ck), Alameda Co. These systems range from free-flowing to highly managed for drinking water, power generation, and white water boating.

**Project Outcomes**

The results of this investigation support the conclusion that hydrologic conditions during the breeding and larval rearing season are central to the conservation of *R. boylii*. This report is comprised of an introductory problem statement followed by chapters authored by individual collaborators, and a joint conclusion statement. The primary findings are as follows:

> **Chapter 2: Review of Statewide Data – A. Lind**
> A review of FERC reports revealed several patterns with respect to early life stages. Egg masses were negatively affected by scouring during flow increases or stranding following rapid flow recession. Tadpole stranding was observed during pulsed flows, and in some instances, tadpole abundance decreased. Methods to measure effects of pulsed flows on *R. boylii* habitat varied. Stationary polygon and transect methods were most relevant to the

requirements of eggs and early tadpoles. Shifting transect methods provided information on total area of suitable habitat, while polygon methods yielded data on the number of habitat patches. Graphical analyses of data culled from reports showed that changes in suitable habitat area as discharge increased were highly site specific, either increasing or decreasing depending on local channel shape, form, and river bed features.

**Chapter 3: Early Life Stage Conditions and Frog Populations — S. Kupferberg**
Egg mass censuses on the unregulated SF Eel over 17 years indicated that annual population fluctuations were not associated with the magnitude of winter peak discharge, but rather with spring and summer conditions for recruitment three years prior. While large magnitude pulses decreased egg survival, smaller magnitude pulses later in the season also caused mortality. Spring flows that caused egg and larval mortality influenced adult numbers. Comparisons between two regulated reaches in the NF Feather—"Cresta", which experienced four years of monthly spring and summer whitewater boating flows, and "Poe" that did not—corroborates the lag time hypothesis. The Cresta reach population declined significantly relative to Poe. Divergent population trajectories were also observed when comparing an unregulated and a regulated reach in Alameda Ck.

**Chapter 4: Velocity Manipulation Effects on Tadpoles — S. Kupferberg**
To assess the effects of pulsed flows on tadpoles, a life stage that does not typically experience floods, velocity was manipulated in laboratory flumes and field enclosures. Across all experimental venues, tadpoles sought refuge in substrate as soon as velocity increased. Average critical velocity, defined as the current speed when tadpoles could no longer swim or maintain position, was 20.9 ± 1.6 cm/s. Critical velocity varied negatively with tadpole size and developmental stage. The most easily displaced individuals were those close to metamorphosis. Velocities as low as 10 cm/s caused one quarter of individuals to be displaced. In the absence of flow refugia, swimming against a 5 cm/s current, tadpoles reached exhaustion at 7.4 ± 2.6 min. For recently hatched tadpoles in the field, there were direct lethal effects of velocities as low as 10 cm/s. While in flow refugia, there were also lethal effects of predation, with mortality risk doubled at elevated, yet sub-critical velocities. The velocities that caused negative effects were less than the typical increases in velocity near shore when aseasonal pulsed flows occur.

**Chapter 5: Hydrodynamic Modeling of Habitat – S. M. Yarnell**
A computer model, River2D, was used to predict habitat quality and availability at representative breeding sites under different flow scenarios. First, the precision and accuracy of the model in predicting local hydraulic conditions (i.e. velocity and depth) in the near-shore environment was determined. Changes in local hydraulics were then related to data on *R. boylii* tolerances and habitat use. Simulated depths and velocities generally agreed with measured field values, with similar error in mid-channel areas and the near-shore environment. Modeled velocities at exact egg locations, however, were over-estimated, with a mean error (observed-predicted) of -0.04 ± 0.04 m/s. This was due to a lack of micro-scale resolution in the surveyed bed topography. However, when

coupled with a definition of breeding habitat suitability that encompassed the variability of field-measured values and the range of error within the model output, the model accurately predicted suitable breeding locations.

At the regulated and unregulated site, modeled increases in discharge above typical late spring levels led to decreased habitat availability, with lower discharges providing the greatest usable area. However, during a spring pulse scenario higher initial discharges provided greater buffering capacity against lethal increases in velocity because large proportions of breeding habitat were located in shallow overbank areas. Subsequent increases in discharge thus resulted in relatively smaller increases in velocity. In an aseasonal pulse scenario, due to the low tolerance of tadpoles to small increases in velocity, only 20-30 % of the unregulated site's habitat, and <5 % of the regulated site's habitat remained suitable. In both scenarios, the shallow, wide channel of the unregulated river provided 2-3 times the buffering capacity of the entrenched channel of the regulated river. Steep banks at the regulated site limited the availability of flow refugia.

## Conclusions and Recommendations

The life cycle of *R. boylii* has evolved in synchrony with California's wet winters and dry summers. A fundamental conclusion of this report is that prudent management of flows, mimicking natural timing, can reduce the impact of dams on *R. boylii*.

- Population dynamics appear to be driven by successful egg laying and tadpole rearing, which in turn are determined by spring and summer hydraulic conditions. Careful timing of releases from dams can reduce the losses of *R. boylii* egg masses caused by scouring and stranding, and thus reduce negative effects on populations.
- Tadpoles respond to increases in velocity by seeking refuge in the river bottom. This response, while potentially protective, may result in losses to predation by fish if tadpoles are displaced to the water column or forced under rocks where invertebrate predators dwell. Displacement can occur at low velocities (10-20 cm/s) over short periods of time (< 2 hours). Tadpoles are also stranded by receding pulse flows and recommendations for benign ramping rates would have to be site specific, accounting for factors such as bank slope and particle size.
- Juvenile and adult frogs may face less risk from pulsed flows, due to their mobility, but may still be susceptible if manufactured flows are decoupled from fall rain events that cue migration to off-channel over-wintering sites.
- Areas of suitable habitat can be modeled for eggs and tadpoles, but error in precision of point water velocities in shallow microhabitats with coarse substrate may lead to higher than desired risk to these life stages if model results are applied inappropriately.
- FERC related studies would be improved by: integrating data on hydrology and geomorphology, quantifying the sampling effort (e.g., number sites, search time), and improving abundance estimates through the use of mark-recapture techniques.

**Benefits to California**

The findings of this research are fundamental to conserving amphibians in California's regulated rivers. This overall assessment of the impacts of pulsed flows from hydroelectric projects focuses on one species in particular, but the findings are applicable to many organisms whose complex lifecycles depend on timing for reproductive success. Shortfalls of FERC related studies were identified and recommendations made for improvements. Key knowledge gaps were filled regarding the mechanisms of negative effects of aseasonal pulse flows on *R. boylii*. The 2D hydrodynamic modeling provides a potential tool to improve decision making that balances resource protection with the demands of hydroelectric power generation.

# 1.0  Hydrologic Alteration and *Rana boylii* Conservation

Hydrologic alteration has reduced the abundance and imperiled the status of a wide array of riverine species (Richter et al. 1997; Rosenberg et al. 2000; Bunn and Arthington 2002). *Rana boylii*, the foothill yellow-legged frog, exemplifies this phenomenon, having declined dramatically over the last half century, especially in Southern California and the Southern Sierra Nevada mountains. It has disappeared from 54% of known historic sites (Davidson et al. 2002) and is 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 absences from historic localities are more common the closer the proximity to large dams (Lind 2005). During California's era of hydroelectric dam construction 30-40 years ago, habitats were destroyed and fragmented as river channels were converted to reservoirs. The river channels and biotic communities that remain continue to be affected by altered disturbance regimes and sediment budgets (Power et al. 1996).

In the last decade, there has been a shift in river management research from prescribing minimum flows adequate to inundate habitats to an understanding that the regulated flow regime should mimic patterns of temporal variation in the unimpaired regime in order to sustain fluvial geomorphic processes, biodiversity, and functional food webs (Power et al. 1996; Poff et al. 1997; Richter et al. 2003). Although this "natural flow-regime paradigm" has grown in acceptance among scientists and makes intuitive sense as a part of a precautionary approach to conserving living resources (Cooney 2004), implementation faces many hurdles. Without evidence of clear cause and effect relationships between site-specific flow regime attributes and a desired conservation outcome, such as preventing the extirpation of a threatened species, it is challenging for scientists to persuade stakeholders of the wisdom of mimicking a natural flow regime when hydroelectric dams are being re-licensed. Scientific uncertainty undermines stakeholders' willingness to make ecologically wise choices about flow regime, especially when they are facing the economic and political costs of sacrificing power generation, constraining time-stable delivery of water for irrigation and drinking, and eliminating aseasonal pulses created for recreational whitewater boating.

For *R. boylii*, the general problem in regulated rivers is that the altered timing, duration, and magnitude of discharge do not match its most important adaptation to evade mortality from flow fluctuation—the synchrony of its life cycle with the seasonality of runoff in a Mediterranean climate (Figure 1.1). The entire life cycle takes place in fluvial environments. Foothill yellow legged frogs are almost always found close to flowing water, with different size classes selectively occupying the margins of diverse habitats (e. g. pools, riffles, runs etc.) (Van Wagner 1996; Yarnell 2000, 2005). Spawning occurs in spring or early summer, as flood waters recede, and larvae metamorphose in late summer or early fall prior to the onset of the next rainy season's floods. Although summer and fall pulsed flows in regulated rivers may not be of greater magnitude than historic discharge, the timing and frequency of such pulses can be de-coupled from the timing of *R. boylii*'s life cycle. For example, one risk factor is the scouring of egg masses by large magnitude dam releases (Lind et al. 1996). Additionally, predation pressure increases when invasive species (e.g. bullfrogs (*Rana catesbeiana*), crayfish, and non-native fish)

flourish in waterways subject to flow diversion and regulation (Hayes and Jennings 1988, Moyle and Light 1996, Marchetti et al. 2004). While there may be stressors originating outside a population's watershed, such as downwind drift of organophosphate pesticides (Davidson et al. 2004; Sparling and Fellers 2007), the within watershed patterns of decline, where one would expect similar pesticide exposure, implicate local flow alteration as a proximal cause. Populations in regulated reaches are smaller or disappearing relative to populations in unregulated reaches within the same watershed (Hayes et al. in prep; Bobzein and Didonato 2007; GANDA 2007).

The purpose of this project was to investigate the processes contributing to patterns of frog decline associated with river regulation. In particular, the focus was on providing several lines of convergent evidence to illustrate the links between flow regulation and the physical conditions key to *R. boylii* fitness. The ecological consequences of extreme fluctuation in water discharge volume during atypical times of the year are evaluated using observational and empirical data. An additional goal was to evaluate the usefulness of the experimental and modeling tools available to managers and scientists as they develop new license conditions for hydropower projects.

## 1.1. *R. boylii* Life Cycle and Flow Regime Adaptations

Prior to this project, knowledge of *R. boylii*'s flow regime adaptations has focused on reproductive timing and habitat selection by mobile life stages rather than the physical tolerances of the less mobile stages. The stages occur along a continuum from immobile eggs to highly mobile adults (Figure 1.1). Breeding adults time their spawning to avoid scour and select habitats that confer protection to their immobile progeny (Kupferberg 1996). They congregate in leks (see glossary) at historic breeding sites at the margins of relatively wide and shallow shaped channel sections. Females attach their single clutch of eggs in low velocity locations behind, and sometimes under, rocks. These behavioral adaptations in adults provide relatively stable depth and velocity conditions for eggs across a range of discharge volumes, decreasing susceptibility to moderate changes in flow magnitude (Kupferberg 1996; Yarnell 2005; Lind 2005). Under a natural flow regime, there are low recurrence-interval wet springs with spates, in which only the latest spawning individuals would have reproductive success (Kupferberg 1996, fig. 9), but generally spawning occurs in synchrony with the receding limb of the spring hydrograph.

It is not surprising that *R. boylii* larvae do not have specialized morphological flow adaptations given an evolutionary history in a Mediterranean climate, where discharge would gradually decline throughout the spawning and rearing seasons. *R. boylii* tadpoles lack a ventral suctorial disc used for adhesion, as occurs in anurans whose larvae inhabit turbulent habitats or endure unpredictable flooding (Altig and Johnston 1989; Richards 2002). Recently metamorphosed young of the year frogs have behavioral adaptations to avoid flood mortality by leaving mainstem channels in the fall (Twitty et al. 1967). The timing and frequency of summer and fall pulsed flows in regulated rivers do not match the most prominent of *R. boylii*'s flow regime

adaptations, the timing of the transitions from one life stage to the next and the seasonality of movement through a watershed.



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

**Figure 1.1. Life stages of _R. boylii_ and the corresponding adaptations which have evolved in the historically predictable flow regime (blue line in hydrograph) of California's Mediterranean climate. Red line represents a series of hypothetical aseasonal pulsed flows. Potential measures to mitigate the impacts of artificial flow fluctuation are also indicated. YOY stands for young of the year.**

## 1.3. Project Objectives and Report Organization

Pulsed flow effects on _R. boylii_ were examined by combining: (1) analyses of existing empirical data; (2) laboratory and field experiments that quantify the physical tolerances of vulnerable life stages and observe behavioral responses to changes in velocity; and (3) investigation of a hydrodynamic modeling approach that evaluates the effects of pulsed flows on breeding and rearing habitat.

Objectives specific to the areas of examination are grouped and presented by chapter:

Chapter 2:

- Gather, review, and compile a catalogue of available published literature, unpublished reports, and other sources on the effects of pulsed flow on *R. boylii* habitat, reproductive success, and survival.

- Summarize and analyze the data from recent studies in a comprehensive way. Determine whether a formal statistical meta-analysis is appropriate and conduct one if possible.

- Identify knowledge gaps regarding the aspects of fluctuating flows (e.g., frequency, timing, magnitude) that may have important impacts on *R. boylii* populations and habitat. Provide a summary of the knowledge gaps that the current study (i.e. Chapters 3, 4, and 5 of this document) addresses.

- Evaluate sampling designs, field data collection methods, and analytical methods based on descriptions in the reviewed reports and studies. Make recommendation for improvements to future studies of *R. boylii* and pulsed flow effects.

Chapter 3:

- Select and describe study reaches that span a gradient of hydrologic alteration with respect to pulsed flows.

- Analyze historic hydrologic data and long term egg mass censuses conducted in regulated and unregulated rivers to detect patterns linking frog population abundance to pulsed flow magnitude and frequency.

- Observe egg mass scouring during natural spring pulsed flow events.

Chapter 4:

- Conduct field and flume experiments to quantify larval swimming abilities. Evaluate which methods are most useful.

- Assess behavioral and growth responses of larvae to changes in velocity and substrate.

- Evaluate risk of predation for larvae under elevated flow velocity conditions.

Chapter 5:

- Investigate a 2-dimensional hydrodynamic model-based methodology, using River2D, to evaluate changes in habitat hydraulics for *R. boylii* at two study sites, one regulated and one unregulated. Determine the resolution to which the model can describe egg and larval habitat in comparison to observed oviposition habitat characteristics and larval flow tolerances.

- Determine suitable habitat availability and connectivity as flows fluctuate at each study site. Compare modeled results with empirical flow manipulations done in previous FERC re-licensing studies (in chapter 2).

- Evaluate changes in depth and velocity conditions for eggs in a natural spring pulsed-flow scenario and for tadpoles in an aseasonal (summer) pulsed flow scenario at each study site. Assess results for potential losses due to scour.

Chapter 6:

- Summarize conclusions and management implications
- Recommend future research and direction for FERC studies
- Address commercialization potential
- Assess benefits to California

## 2.0   Review of Statewide Published Data and FERC Study Reports

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**Abstract**

Because of its declining status, the foothill yellow-legged frog (*Rana boylii*) has increasingly become a focal species in water management planning, especially in FERC re-licensing programs for hydroelectric dams. However, due to the dispersed nature of re-licensing efforts, conducted on a project by project basis, and the multiple agencies involved in re-licensing efforts, a comprehensive assessment of pulsed flow effects on *R. boylii* has been challenging. The objective of Chapter 2 was to develop such an assessment and identify remaining information gaps for the experimental (Chapter 4) and modeling (Chapter 5) components of this study. Chapter 2 provides a compilation, review, and summary of empirical data from the scientific literature and FERC hydropower re-licensing reports. During the course of the review, ways in which future FERC re-licensing studies, and other studies of water flow effects, could be improved were also identified

The literature/FERC report review revealed several patterns for different life stages of *R. boylii*. Egg masses were negatively affected by pulsed flows via scouring if flows occur during or after oviposition. Negative effects associated with desiccation occurred if oviposition took 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 managed to reduce impacts to egg masses. Stranding of tadpoles following pulsed-flow releases was observed in some studies. There was also an indication that pulsed flows lead to a lower abundance of tadpoles, though this result was not consistent across all study locations. Effects of pulsed flows on post-metamorphic life stages were not clear and preliminary evidence for short-term behavioral responses of juvenile frogs to these flows needs further research.

Methods to quantify suitable *R. boylii* habitat varied among studies. Stationary polygon and transect methods were most relevant to the requirements of immobile stages (eggs and early tadpoles). Shifting transect methods provided information on the overall area of suitable habitat. Polygon methods provided information on the number of suitable habitat patches as well as overall area. A quantitative graphical analysis of data culled from reports showed that variation in suitable habitat area due to changes in discharge was very site specific. Some sites showed increasing areas while others showed decreasing areas, as discharge increased, indicating the influence of channel morphology and local geomorphic features.

The review of studies identified key information gaps relating to effects of pulsed flows on the tadpole life stage. Effects on activity level, behavior, growth, and survival responses to variation in water velocity and depth were addressed by the experimental component of this study (Chapter 4). The assessment of transect and polygon methods previously used to quantify

suitable habitat at a few discharge levels, identified several weaknesses in these methods and led to development of 2D hydrodynamic models (Chapter 5).

## 2.1. Introduction and Approach

Due to its declining status, *R. boylii* has increasingly become a focal species in water management planning, especially in FERC re-licensing 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 re-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. This review 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. A meta-analysis approach was evaluated and deemed to be inappropriate due to data quality issues, so the majority of the analyses are qualitative in nature. This review also identifies where specific information is lacking and provides guidance for the later phases of this research (i.e., experiments and hydrodynamic modeling in Chapters 4 and 5).

A total of 34 recent (1999–2007) study reports and one published article (1996) were obtained from a variety of sources including utility company staff, utility company and FERC re-licensing websites, environmental consultants, and a literature search (Appendix A). All but three (ALC1, GANDA 2004e, Linda et. al. 1996) of the 35 reports were prepared for FERC re-licensing efforts. The studies and reports represented seven major river basins in California, six of which drain the western slope of the Sierra Nevada/Cascade mountain range. In addition, two smaller streams (one Sierran and one Coastal) were also represented. Most (n=30) 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 re-licensing studies, such as historic and predicted hydrologic regimes, geomorphology, and fish habitat. The 30 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., PG&E and EA Engineering Science 2001) that is referenced in both Appendix A and the References section (2.6) of this chapter.

The remainder of Chapter 2 is divided into three parts. In Section 2.3, the qualitative narrative reviews of the statewide reports and published literature, is 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 1.1 and differentiates the effects of pulsed flows on aquatic vs. "terrestrial" (post-metamorphic) life stages. Section 2.4 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 2.5 summarizes the review of study reports and identifies how these results are being applied in the experimental and modeling components of this study. Some organizational and substantive changes for future re-licensing studies are recommended. The results contained in Chapter 2 are primarily descriptive and qualitative. The one exception is the analysis of habitat suitability at different flows (Section 2.4), which employed a graphical approach to examine multiple discharges among several different rivers.

## 2.2. 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. Fourteen of the 30 study reports contained some information on the effects of pulsed flows on at least one life stage of *R. boylii* (Appendix A). The other 16 reports provided information on relative abundance and microhabitat associations, qualitative assessments of pulsed-flow effects on habitat suitability, or quantitative assessments of habitat suitability at different flow levels (see Section 2.4).

### 2.2.1. Egg Survival Associated with Pulsed Flows

Direct negative effects of pulsed flows on *R. boylii* egg masses were evident in six of eight studies (n = river x year) where pulsed flows were quantitatively 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 NF Feather, studies in two different reaches, Cresta and Poe, documented 50% and 14.6% lost or damaged egg masses, respectively (GANDA 2004a,c; Table 2.1). In the Trinity River, 100% of egg masses were scoured in each of two years when test flows occurred subsequent to oviposition (Linda et. al. 1996; Table 2.1). 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 ECORP Consulting, Inc. 2004b and Table 2.1).

In 2002 in the Pit River, 15 of 27 egg masses were at risk of scouring during test flows. Of these, seven were actually scoured and eight survived. Of the other 12 egg masses, 2 disappeared prior to test flows and 10 were moved to protected areas (Spring Rivers 2002) (Table 2.1). The Pit River data included measurements of mid-column water velocities and total water depths at each egg mass before, during, and after test flows (Spring Rivers 2002 and associated data and field notes). Graphs of cumulative percent scoured were developed to provide preliminary information on critical scouring water velocities and depths. Values for water velocity and depth on the day prior to documented scouring were used as the "scouring" velocity or depth. Discharges during test flows ranged from 4.2 cms (base flow) to 34 cms over the course of seven days in early May as follows: 4.2, 7.1, 11.3, 17, 22.7, 34, 4.2 cms (Spring Rivers 2002). Seven egg masses were scoured by high flows between the 7th and 10th of May when discharge ranged from 11.3 to 34 cms. Mean column velocities for these seven scoured egg masses the day prior to scouring were approximately: 9, 11, 18, 21, 23, 30, and 41 cm/s (Figure 2.1a). Total water depths

for these egg masses the day prior to scouring were approximately: 18, 34, 55, 60, 61, 61, and 69 cm (Spring Rivers 2002) (Figure 2.1b). The scoured egg masses, which were laid between 14 April and 3 May, included some of the earliest egg masses laid that year. Eight egg masses survived the high flows (one was estimated to have been laid during the 11.3 cms flows on 7 May, but was not discovered until after discharge returned to base flow). Although one of the surviving egg masses was estimated to have been laid on 14 April, most of the surviving egg masses were laid between 29 April and 7 May. These egg masses experienced all discharge levels (4.2-34 cms) and maximum mean column velocities from 30-52 cm/s and maximum total water depths of 70-103 cm.

As is often the case in ecological analyses, it is not possible to identify one specific threshold discharge or water velocity for egg scouring from this data. Changes in flow direction as well as increased velocities resulted in scouring (Spring Rivers 2002). It also appeared that the duration of the flow event may have had a potentially larger impact than overall magnitude. The ability of an egg mass to survive high water velocities was likely due to factors such as substrate roughness/relief and associated microscale velocities. For the eggs that were scoured in this study, the age of the eggs also played a role, with older masses more likely to be scoured. At these Pit River frog breeding sites, discharges over 17 cms put a high proportion of egg masses at risk and mean column water velocities as low as 9 cm/s and up to 41 cm/s were detrimental to some egg masses (Figure 2.1).

Two studies provided qualitative assessments of flow effects on eggs. In 2005 in the South Fork Feather River, water depths decreased in the range of 5-10cm at *R. boylii* oviposition sites and no stranding/desiccation was observed (South Feather Water and Power Agency and Stillwater Sciences. 2006). The egg masses in this study were apparently laid after flow releases had declined to near base flow levels. The channel morphology of the site also appeared to buffer the observed changes in water depth (South Feather Water and Power Agency and Stillwater Sciences. 2006). Another study provided a comparison of two reaches of Alameda Ck (ALC1, see also Chapter 3, section 3.3.3). One reach was above the confluence of a tributary that contained a dam and it had natural flow conditions. The other reach was below the tributary with a dam and it experienced both diversion and pulse releases. *R. boylii* egg masses had been documented in both reaches prior to 2005. In 2005, counts were high in the reach above the dam inflow, however, none were found in the reach below the inflow (ALC1). Discharge on both reaches was substantially higher in 2005 than during the previous four years. However, due to concerns about dam safety, high flows extended over a much longer period in the reach below the dam (ALC1).
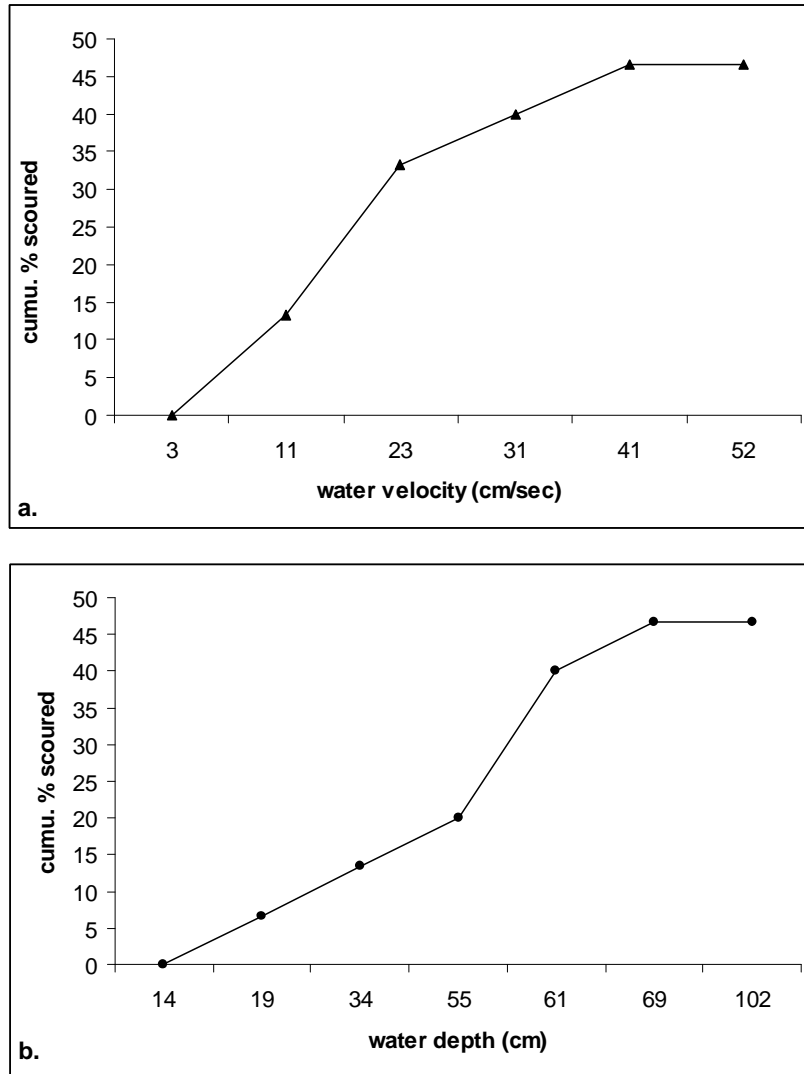
**Figure 2.1. Cumulative percent of egg masses scoured relative to mid-column water velocities (a) and total water depths (b). Measurements were recorded during test flows spanning a range from baseflow (4.2 cms) up to 34 cms.**

Based on all of the studies with data on egg masses, 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 (Linda et. al. 1996; Table 2.1). Research on the factors that trigger the onset of breeding and oviposition for a riverine population of *R. boylii* indicated that a combination of day length and local environmental conditions (water temperature and hydrology) are at work (GANDA 2004e). Information derived from additional research on these factors in the same and other watersheds could contribute to the development of environmental thresholds for this species. Such thresholds would allow water managers to make faster decisions and potentially reduce the level of on-the-ground monitoring needed.

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 NF Feather and Pit Rivers (Table 2.1). 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 2.4 provided more insights on that front.

**Table 2.1. Pulsed-flow effects on *R. boylii* egg masses in California (from recent FERC re-licensing study reports and scientific publications)**

| River | Flow Events Date — Reach | Maximum % Change from Base Flow | Observed Effects | Reference |
|---|---|---|---|---|
| NF Feather | June 2002 — Cresta | 540% (7.1–45.3 cms) | 3 of 6 (50%) egg masses scoured or displaced | (GANDA 2004c) |
| | 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 | (GANDA 2004a) |
| Pit | May 2002 | 710% (4.2–34 cms) | 7 of 15 (47%) egg masses scoured during test flows | Spring Rivers 2002 |
| 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 | ECORP Consulting, Inc. 2004b |
| 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 | (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 | |

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 SF Eel in Northwestern California. However, egg mass losses were relatively low in each year (10.3% and 20.2%). Further research on the SF Eel 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 Chapter 3, Figure 3.8). 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 after natural pulses ceased, 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.). Although egg mass losses have occurred under natural conditions, the frequency of such late spring floods was low in natural systems. The 2005 SF Eel 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 (Kupferberg, S.J. 2003). 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 (Kupferberg, S.J. 2003). 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 (Ibis 2004b 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 (Ibis 2004b 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 178 egg masses/km have been documented in unimpaired streams (Kupferberg 1996; Lind et al. 1996; Lind 2005; and Chapter 3, Figure 3.5). The apparently low densities of egg masses in the studies reviewed here (Table 2.1) 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.

### 2.2.2. Effects of Pulsed Flows on Larvae

Five studies evaluated direct effects of pulsed flows on the larval (tadpole) life stage (Table 2.2). Even in these five 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 three of the five studies (GANDA 2004c,d; Jones and Stokes 2004; Ibis 2004b; Table 2.2) and a decrease in tadpole abundance was observed immediately following a pulsed-flow event in two studies (GANDA 2004c, GANDA 2005). This decrease in abundance was presumably related to tadpole displacement out of the survey area. However, in the second study, a search and rescue operation conducted during the recreational flow release may have confounded the results. Ecologically acceptable ramping rates were exceeded during this operation potentially resulting in stranding or injury of tadpoles (GANDA 2005). 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 (GANDA 2004d).

An assessment completed in the North Fork Mokelumne River (Jones and Stokes 2004) provided the most quantitative evidence of actual and potential negative effects of pulsed flow on tadpoles (Table 2.2). 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. Following the pulsed-flow event, 57 isolated pools and five stranded tadpoles were found, indicating a significant risk for tadpoles (Jones and Stokes 2004).

Water depths and surface water velocities were monitored at larval rearing sites during the July 2002, 2003, and 2004 recreational pulse flows on the NF Feather. Water depths were measured via staff gauges that were installed at the edge of the wetted channel prior to generated recreational flows. Surface water velocity was measured by estimating the distance that floating debris moved in the vicinity of the staff gauge over a two second period (and dividing by two) (GANDA 2005). With the approximate increase from base flow (7.1 cms) to peak recreational flow (33.9 cms) water depths increased from zero to an average of 62, 54, and 65 cm in 2002, 2003, 2004 respectively. Surface water velocities increased from zero to an average of 25, 39, and 31 cm/s in 2002, 2003, and 2004 respectively (GANDA 2005). Differences in averages are due to different sets of sampled sites/subsites in each year. Surface velocity was taken to be a surrogate for mid-column velocity since mid-column velocities were not readily measurable under high flow conditions. The sustained duration (approx. 6 hours) and magnitude of the current velocities observed in the NF Feather are well above those determined by field and laboratory experiments to result in ultimately detrimental behavioral changes and displacement of tadpoles (see Chapter 4).

**Table 2.2. Pulsed-flow effects on *R. boylii* larvae (tadpoles) from recent FERC re-licensing study reports in California**

| River | Flow Event Dates — Reach | Maximum % Change from Base Flow | Observed Effects | Reference |
|---|---|---|---|---|
| NF 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. | (GANDA 2004c) |
| | 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. | (GANDA 2004d) |
| | Jul-Aug 2004 – Cresta | 380 % (7.1-33.9 cms) | Tadpole counts declined from pre to post pulse-flow surveys for July and were too low to assess in August. | (GANDA 2005) |
| 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. | (Jones and Stokes 2004/ Ibis 2004b) |

## 2.2.3. 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 NF Feather documented similar abundances of young of the year and juveniles prior to and immediately following pulsed flows, but lower numbers during pulsed flows (PG&E and EA Engineering Science 2001; Table 2.3). 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 (GANDA 2004c,d; Jones and Stokes 2004; Table 2.3). 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 (Ibis Environmental Services 2004a,b; Table 2.3). A study in the NF Feather also found low numbers of young of the year frogs after several years of manufactured summer pulsed flows. Young of the year were not abundant despite relatively high egg mass counts earlier that year. It appeared that losses of tadpoles during the summer, and not egg loss during spring, may have accounted for the apparently poor recruitment. A primary factor may have been stranding associated with rapid draw down of the water surface elevation during a search and rescue effort that year (GANDA 2005).

**Table 2.3. Pulsed-flow effects on post-metamorphic life stages of the *R. boylii* (young of the year, juveniles, and adults) from recent FERC re-licensing study reports in California**

| River | Flow Event Dates — Reach | Maximum % Change from Base Flow | Observed Effects | Reference |
|---|---|---|---|---|
| NF 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. | PG&E and EA Engineering Science 2001 |
| | 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. | GANDA 2004c |
| | 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. | GANDA 2004d |
| | Jul – Oct 2004 – Cresta | 380 % (7.1-33.9 cms) | Low abundance of juveniles compared to previous years even though higher counts of egg masses; loss of tadpoles in July/Aug recreational flows may be a factor (see Table 2.2). | GANDA 2005 |
| 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. | Jones and Stokes 2004 |
| | 2001–2003 | Higher and later peak flows | Reduced abundance of juveniles over time. | Ibis Environmental Services 2004a,b |

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 (Chapter 1, Figure 1.1). 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.

## 2.3.   Analysis of Habitat Area and Discharge

Eleven of the 30 reports reviewed in detail contained some level of analysis of flow effects on *R. boylii* habitat (Appendix A). Of these 11, 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 (Appendix A). 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. The other reports with data on flow effects on habitat did not include direct measurements of habitat characteristics; rather they included narrative descriptions of habitat conditions under different flow levels (Appendix A).

### 2.3.1. Methods

The five quantitative studies represented five different rivers, with two studies in the NF Feather, 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:

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

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 GANDA 2003 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.

The studies used various methods to define and identify suitable habitat (Table 2.4), 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.

**Table 2.4. 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/s) | Field Methods |
| GANDA 2003 | < 50 | < 20 | —"Shifting transects": perpendicular transects from shoreline to 5 m out into river; could shift based on change in shoreline with increasing flows<br>—Riparian vegetation not considered in suitability |
| GANDA 2004b | < 50 | < 20 | —Shifting transects<br>—Riparian vegetation not considered in suitability |
| Tarbell et. al. 2004 | < 48.8 | < 10 | —Stationary polygons, measured at every discharge with new polygons added at higher discharges as needed<br>—Riparian vegetation not considered in suitability |
| ECORP 2004a | < 40 | < 20 | —Combination of shifting and stationary transects<br>—Riparian vegetation not considered in suitability |
| Spring Rivers 2002 | < 43 | <15 | —Suitable habitat area delineated in polygons at each flow<br>—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.

## 2.3.2. 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 2.4). 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 re-measured 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 (Devine Tarbell et. al. 2004; ECORP 2004a; Table 2.4).

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 produces 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 (Kupferberg, S.J. 2003) indicated that in one already occupied 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). 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 2.4) 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.

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 1.1). 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 2.2). Graphs of the NF Feather 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 2.2 a & b). In 2004 there was also an indication of a threshold above which habitat area leveled off (Figure 2.2b). Similarly for Silver Creek, there was a negative relationship with one site and a positive relationship with the other site (Figure 2.2c). 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 2.2d). Sites on the Middle and South Fork Stanislaus Rivers demonstrated decreasing area with increasing discharge (Figure 2.2 e & f).

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 GANDA 2004b (Figure 2.2b), 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. 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 2D models developed for this study (Chapter 5) are being used to evaluate whether planform habitat area is similarly stable when discharge increases (see Section 2.5.2).

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 2.4). 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).
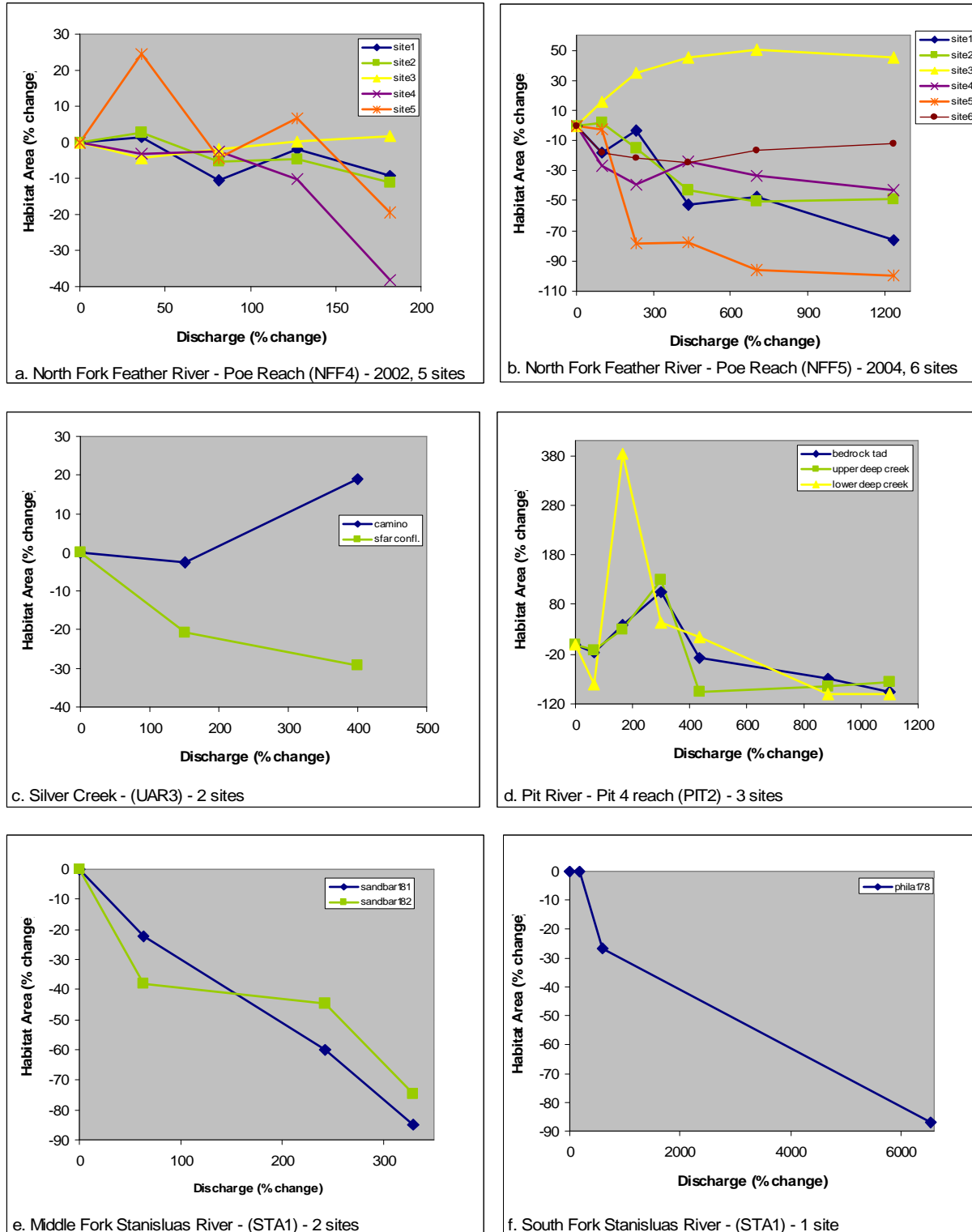
**Figure 2.2. Change in *R. boylii* suitable habitat area relative to change in discharge for five river reaches (including two years from one reach) in the Sierra-Cascade mountain ranges of California. Data were collated to the "site" level (see Section 2.4.1) for each reach.**

26

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.

## 2.4. Conclusions and Recommendations from Statewide Report Review

### 2.4.1. Summary of Results

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

- 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.

- 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.

- Pulsed-flow effects on post-metamorphic life stages were not clear. Preliminary evidence for short-term behavioral responses to these flows needs further research.

- 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.

- General trends in habitat suitability across all studies suggested that change in habitat area varied depending on site features/channel morphology.

### 2.4.2. Application 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 1.1). 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. Egg mass habitat suitability (water depth and velocity) was evaluated at a variety of flows using a 2D model (see Chapter 5).

#### 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 (GANDA 2004c,d; Jones and Stokes 2004) 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 2.2. 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 GANDA 2004c and Jones and Stokes 2004 studies, the fate of the "missing" tadpoles is unknown. Observations made under controlled experimental conditions (presented in Chapter 4) 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 essential for 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. However, the use of this flow refuge represents a tradeoff (increased predation risk) as is explored in Chapter 4 (see Figure 4.16 and associated text), such that "missing" tadpoles may represent loss to predators. Hydrodynamic modeling was applied to the problem of habitat connectivity which relates to stranding concerns (Chapter 5).

#### Post-Metamorphic Life Stages

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 artificial stream environments 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 was 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 2D hydrodynamic modeling employed in this study (Chapter 5) provided spatially explicit quantification of changes in planform habitat area which allowed assessment of the spatial connectivity between suitable habitat patches. It also provided the preliminary data for evaluating whether habitat area was stable over a selected range of discharges.

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 of this report, A.L., and S.Y.) that is developing a habitat suitability model for the DeSabla-Centerville Project re-licensing (e.g., PG&E and Stillwater Sciences 2007). 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 those 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.

## 2.4.3. 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 30 reports with data on *R. boylii*, with different emphases and by a variety of authors, (see references section 2.6 below and Appendix A) revealed the following information to be missing, difficult to find, or in need of improved methodologies:

- Historical vs. impaired hydrographs and frequency analyses were not included in amphibian reports (with a notable exception being the Ibis 2004b 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.

- 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.

- 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.

- 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:

    o 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.

    o 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)

    o Adult—large individuals (2–3+ years old) that exhibit secondary sexual characteristics.

- The review of reports that contained only primarily survey results (16 of 30) 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, with the exception of one research study (GANDA 2004e), the studies reviewed did not use 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.

- 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.

- Most reports in this review focused on single species or sometimes on a set of related species (e.g., amphibians). These reports often made no mention of other studies going on as part of the re-licensing efforts (e.g., studies on fish, temperature, hydrology, geomorphology, etc.). While it would be unwieldy to incorporate all study results into a single report, it is recommended that future re-licensing study reports specifically reference relevant results from other studies in the project area. This will also require doing a better job of integrating studies in the field (e.g., via shared sampling locations). The consequences of decisions made during the re-licensing process will be more clear if relationships between focal species and current (and predicted) variation in other biotic (e.g. predators/prey) and abiotic (e.g., temperature, hydrology) elements can be stated explicitly based on integrated studies.

- Older reports rarely provided clear statements of past and likely future project effects. "Project Nexus" sections have been added to more recent study plans and project reports; however these sections are typically quite general in nature. Identifying key issues relative to the target species or physical process would help to focus studies and increase field work efficiency. As in (7), clarifying these links at the beginning of the re-licensing process and as study results come in, should help with decision-making and setting new license conditions. For example, different river reaches within a project often receive different flow conditions (e.g., peaking versus non-peaking reaches). The intensity and timing of field sampling/survey efforts could be adjusted to specifically assess how the different flow regimes influence focal species or physical processes. The resulting information could then be used to set protection, mitigation, and enhancement measures.

# 3.0   Case Studies in Three Watersheds: Pulse Effects on *R. boylii* Populations in Regulated and Unregulated Rivers

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**Abstract**

Three river systems in Northern California with pre-existing hydrologic and frog population monitoring programs were selected to examine the relationship between pulsed flows and changes in *Rana boylii* abundance over time. The sites are the SF Eel, Mendocino Co, the NF Feather, Butte and Lassen Cos., and Alameda Ck, Alameda Co. Three conclusions are drawn from seventeen years of egg mass censuses on the unregulated SF Eel. First, annual fluctuation in population growth is not associated with the magnitude of winter peak discharge, but rather is associated with spring and summer conditions for recruitment 3 years prior. Second, timing of breeding in the spring is not associated with stage height; 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. The amount of shallow slow habitat area inundated at the channel margin does not cue breeding. Third, magnitude and timing of spring pulse flows 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 because a greater proportion of the population has completed breeding and egg jelly adhesion and cohesion have diminished. Comparisons between frog populations in two reaches in the NF Feather corroborate the three year lag time hypothesis. The reaches are regulated by the Poe Dam (hereafter referred to as the Poe reach) and the Cresta Dam (Cresta reach). The Cresta reach experienced four years of monthly spring and summer whitewater boating pulse flows, while the Poe reach did not. The Cresta reach *R. boylii* population has declined significantly relative to the frogs in the Poe reach. Divergent population trajectories were also observed when comparing an unregulated and a regulated reach in Alameda Ck. In this more southern population, a 2-year time lag between recruitment conditions and adult population size may occur. This evidence, linking a-seasonal flow fluctuations to decline, highlights the pressing need for better protection of *R. boylii* in regulated rivers and the importance of recruitment conditions to population persistence.

## 3.1.   Introduction

Alteration of hydrologic regime poses serious threats to biodiversity in rivers generally, (Bunn and Arthington 2002) and to *R. boylii* specifically. The timing of *R. boylii*'s complex life history is synchronized with the seasonality of runoff during the predictable cycle of wet winters and dry summers occurring across its range in California and Oregon (Kupferberg 1996; Lind and Welsh in revision). The success of this strategy to avoid flood mortality and maximize opportunities for larval growth is disrupted in regulated rivers when pulsed flow discharges are de-coupled 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 spawning (Zweifel 1955; Kupferberg 1996; GANDA 2006), 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 spring breeding, the magnitudes of pulses in regulated rivers are superimposed above artificially low minimum discharges and thus can exceed natural fluctuation by orders of magnitude..

The goal of this section is to examine an array of regulated and unregulated systems with diverse degrees of hydrologic alteration, and thus "provide insight into the range of flow regime variability that a species can tolerate" (Lytle and Poff 2004). *R. boylii* population fluctuations are contrasted across a gradient in frequency and cause of aseasonal pulsed flows, and across a broad scale of mean annual discharge. Recruitment of new individuals to frog populations is assessed by comparing years with and without large spring spates within the unregulated reaches, and by comparing population change between reaches with and without manufactured pulsed flows. Collectively the data are used to illustrate and hypothesize about the relationships between discharge, conditions for eggs and tadpoles, and population status.

## 3.2. Study Areas

Research was conducted at 5 reaches within three different California rivers (Figure 3.1): the unregulated SF Eel in the University of California Angelo Reserve (Mendocino Co.); two regulated reaches of the NF Feather in Lassen National Forest (Butte Co.); one regulated and one un-regulated reach of Alameda Ck in the Sunol-Ohlone Regional Wilderness of the East Bay Regional Park District (Alameda Co.). Each watershed has hydrologic, geomorphic and habitat characteristics typical of *R. boylii* localities in its respective region, the north coast, the Sierra Nevada, and the central coast (Table 3.1). These bioregions correspond with three genetically distinct clades, or branches, in the evolutionary tree developed for *R. boylii* (Lind 2005). These reaches were chosen because they have ongoing monitoring of both frogs and good hydrologic records.

The character of the pulse flows in each reach is distinct (Figure 3.2). Annual hydrographs for the SF Eel illustrate natural seasonal runoff, with peak discharges in winter and occasional spring spates caused by rainfall. The regulated reaches have periodic late spring and summer pulsed flows that are aseasonal. The NF Feather reaches have large magnitude peak flows during winter and spring in wet years when the dams spill at the peak of snowmelt and when rain on snow events occur. The hydrograph is flat during the summer and fall, unless pulsed flows are manufactured as they were in the Cresta reach for whitewater boating (2002-2005, 1x/month June-Oct). The Alameda Ck regulated reach has a hydrograph that, while somewhat natural in shape, has reduced magnitude base flows, with occasional disproportionately high-magnitude peaks associated with flood spills and plateaus associated with continued releases. Since 2001, due to seismic safety concerns about Calaveras Dam, the maximum allowable

reservoir height is 40% of capacity. Water is released to maintain that level (SFPUC 2007). (Figure 3.2). By comparison, the unregulated Camp Ohlone reach on Alameda Ck has pulse magnitudes and durations directly coupled to rainfall. The magnitude of peak flows there is expected to decline under climate change scenarios (Klausmeyer 2005).
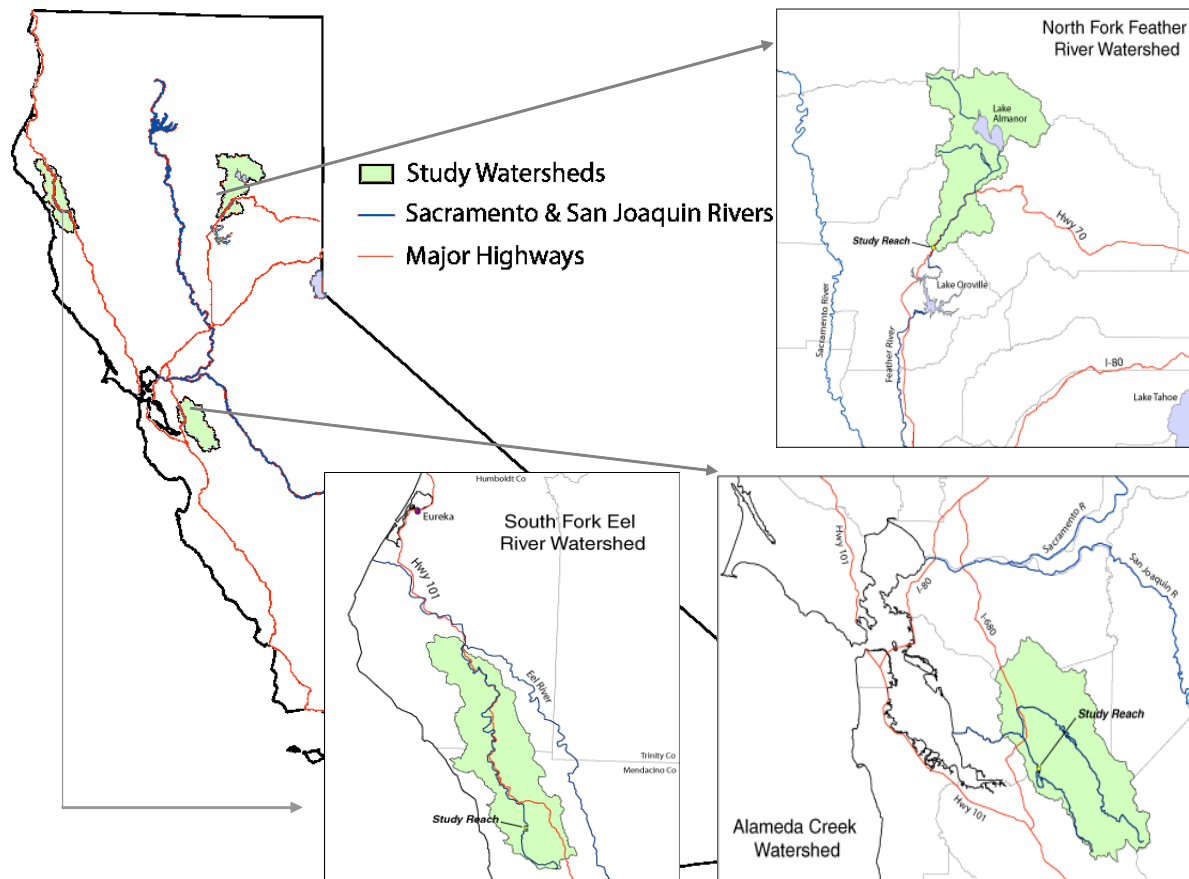


**Figure 3.1. Location of the study watersheds in northern and central California (Teale Data Center 1999)**

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

al. (in press). *R. boylii* breeding behavior in relation to channel morphology at the site is described in Kupferberg (1996).

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

**Table 3.1. General characteristics of the focal river systems' topography, hydrology, geomorphology, and vegetation.**

| River | Reach and nearest USGS gage number | Regulation | Egg census reach length (km) | Drainage Area[1] (km²) | Mean±1 s.d. Annual Discharge[2] (cms) | Elevation (m) | Dominant Channel Morphology | Upland Vegetation | Riparian Vegetation | Dominant Substrate |
|---|---|---|---|---|---|---|---|---|---|---|
| NF Feather | Cresta 11404330 | Cresta Dam | 10.4 (≈8km discontinuous) | 4976 | 22.5±25.6 | 488-424 | Riffle-pool | Chaparral and Mixed Coniferous Forest | Willow, Alder, blackberry, sedge | Bedrock overlain by boulders and cobbles |
| | Poe 11404500 | Poe Dam | 12 (≈8km discontinuous) | 5078 | 25.9±27.4 | 424-287 | Riffle-pool | | | |
| SF Eel | Branscomb[3] 11475500 | none | 5.2 (continuous search length) | 114 | 4.88±1.70 | 427-365 | Riffle-pool | Douglas Fir Forest | Alder, sedge | Bedrock overlain by boulders and cobbles |
| Alameda | Camp Ohlone 11172945 | none | 1.6 (continuous) | 88 | 0.77±0.42 | 380-365 | Riffle-run | Oak Woodland, Grassland | Sycamore, Mulefat, Alder, sedge | Bedrock, Cobble, gravel |
| | Sunol[4] 11173510 11173575 | Calaveras Dam | 1.2 (continuous) | 273 | 1.17±1.07 | 134-122 | Riffle-run | | | |

[1] Area upstream of the gaging station, data from USGS

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

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

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

Similar in area to the SF Eel watershed but receiving less precipitation, the Alameda Ck study reaches' watersheds provide a portion of San Francisco's drinking water. The unregulated study reach is hereafter referred to as the Camp Ohlone reach and is upstream of the dam and tunnel which divert water to Calaveras Reservoir (Figure 3.3). Calaveras Reservoir captures the runoff from Calaveras Ck. and Arroyo Hondo, and then flows back into Alameda Ck. The downstream regulated egg survey reaches, are a section in the steep gradient bedrock "Little Yosemite" canyon, which experiences water diversion, and a second alluvial section below the confluence with Calaveras Ck., hereafter referred to as the Sunol reach. The topography and vegetation of the Alameda Ck. study reaches are typical of Central Coast Range oak woodlands and grasslands. Riparian vegetation includes Sycamore (*Platanus racemosa*), mulefat (*Baccharis salicifolia*), alder, willow, sedge (*Carex* sp.), and cattail (*Typha* sp.). The watershed has heterogeneous, (i.e., steep, moderate and shallow) hill slopes. Alameda Ck. flows through a series of alluvial valleys with small to moderately developed flood plains. Such reaches are linked by narrow bedrock-channel corridors. The creek can become intermittent in the upper parts of the watershed, in years with low precipitation. Scour pools created by fallen trees become important refugia for amphibians in dry years. Alameda Ck. is unique among the study sites because California Red Legged Frogs, (*Rana draytonii*) also occur there. *R. draytonii* use slightly different habitats within the creek, usually ovipositing at the upstream margins of pools where conditions are more sheltered from flows, usually in deeper water and on vegetation instead of rocky substrates like *R. boylii*.
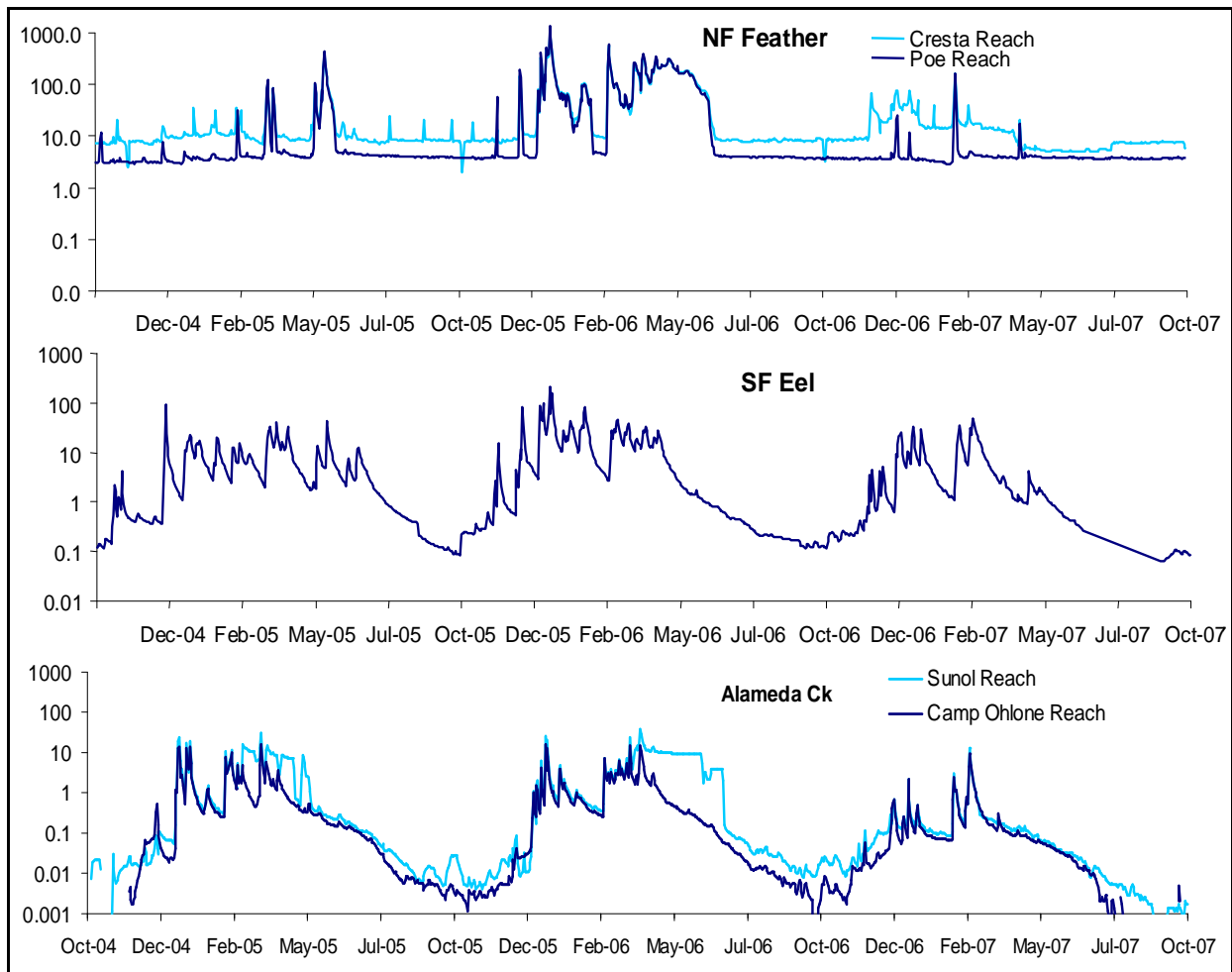
**Figure 3.2. Mean daily discharge (cms) for water years 2005-2007 in Alameda Ck (bottom), the SF Eel (middle) and NF Feather (top).**
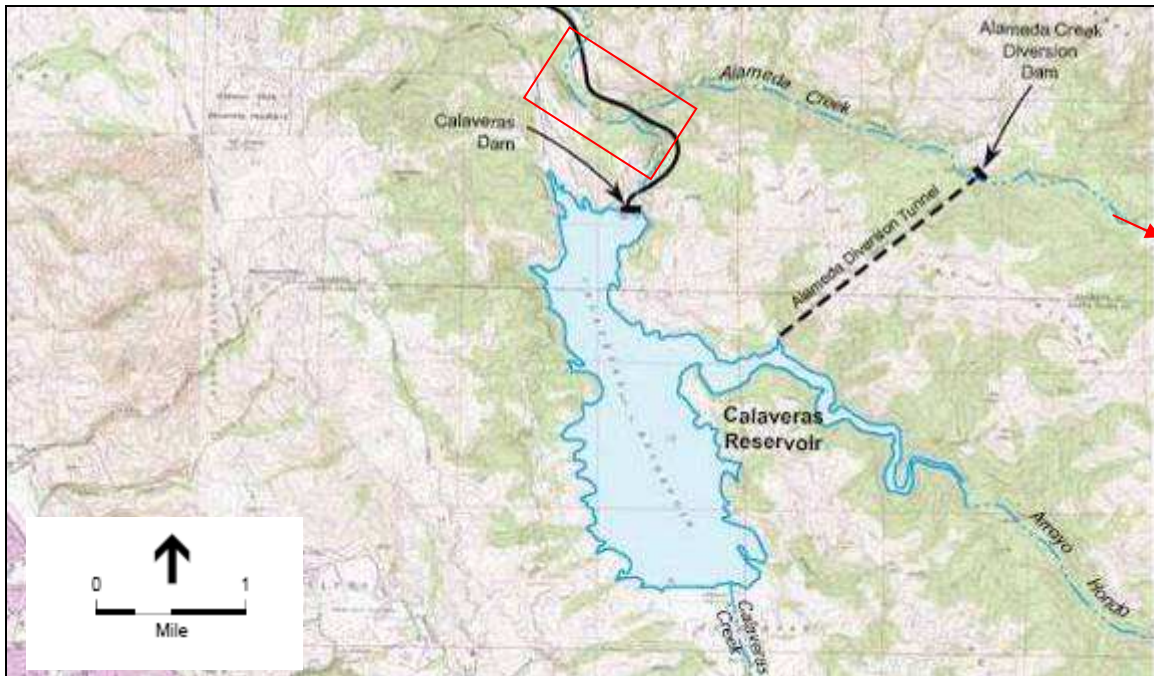
**Figure 3.3 Alameda Ck. study systems. Down stream regulated reaches include sections upstream and downstream of the confluence with Calaveras Ck (red box). The unregulated Camp Ohlone reach is upstream of the Alameda Diversion Tunnel, in the direction of the red arrow but is off this map. Source of map SFPUC 2007, available online http://www.sfgov.org/site/uploadedfiles/planning/vol3_sec5-4_wsip-dpeir.pdf (accessed July 28, 2007).**

## 3.3. Methods for Analysis of Hydrologic and Frog Population Data

Frog population monitoring, in the form of annual egg mass surveys, has been conducted in all five study reaches. Alameda Ck censuses, supervised by Steve Bobzien, Ecological Services Coordinator, East Bay Regional Parks District, began in 1997 in the Camp Ohlone Reach and in 2003 for the reach in proximity to the Calaveras Ck confluence (Bobzien and DiDonato 2007). In the NF Feather, censuses began in 2001 for the Poe reach and 2002 for the Cresta reach. Censuses were conducted by Garcia & Associates for PG&E and for the California Energy Commission Pulsed Flow Program. NF Feather data compiled here are from several reports (GANDA 2003, 2004a,b,c,d, 2006, 2007). At the SF Eel, Kupferberg began annual censuses in 1992 and continued them through 2007. Similar search techniques were used in all three systems, with multiple visits per season, use of a view box or mask and snorkel, and marking of clutches to prevent double counting.

The number of clutches was used as an index of the number of breeding females. Using the number of spawn clumps as an estimator of population size is an accepted method for ranid frogs (Crouch and Patton 2000, Loman 2007, Petranka et al. 2007), which produce discrete clutches and spawn once in a year. Drift fence studies for pond breeding ranids show very close correspondence between number of spawn clumps and number of female frogs (Couch and Patton 2000). Mark-recapture estimates for adult female population size for *R. boylii* in one

small Sierran creek are in close correspondence to numbers of clutches found (Van Wagner 1996).

### 3.3.1 Among river system analyses

Spearman's rank order coefficient of correlation between degree of hydrologic alteration and breeding female population density was calculated for the 5 reaches.   For this purpose of relating the frequency of aseasonal pulsed flow to frog abundance the five reaches are considered independent.  Although all the reaches are subject to similarly timed precipitation events (note concordance of peak discharges in Fig. 3.2), the effects on the frogs in each reach vary independently due to distinct dam management regimes among the three regulated reaches and distinct dates of breeding initiation among all five reaches. With respect to hydrologic alteration during the frog spawning and rearing seasons, the two unregulated reaches, SF Eel and Camp Ohlone reach of Alameda Ck. were assigned tied ranks of 1.5 each. For the three regulated reaches, the Poe reach of the NF Feather was assigned rank 3, because it lacks aseasonal pulsed flows, and the two reaches with aseasonal pulsed flows, the Cresta reach of the NF Feather and the Sunol Reach of Alameda Ck. were assigned tied ranks of 4.5 each. The mean annual density of clutches was calculated for each of the five reaches and assigned ranks, with the lowest density assigned a rank of one and the reach with the highest density ranked 5.

### 3.3.2  Within river system analyses.

At the SF Eel, $3.9 \pm 0.3$ visits were made each year and the average $\pm 1$ s.e. egg masses / year = $546 \pm 40.2$. Visual search efforts concentrated at breeding locations, but river sections between sites were also examined. Wooden craft sticks were placed in the riverbed adjacent to each clutch, to prevent double counting on subsequent visits. In 2005, the fate of each clutch was recorded in subsequent surveys. 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 egg scouring rates.

For each monitoring year at the SF Eel, the maximum winter discharge, the incidence of pulsed flows, and the discharge when oviposition began were determined from the compiled hydrologic record (Power and Dietrich, unpublished data, see Appendix B) and from the Angelo Reserve website (http://angelo.berkeley.edu/index.html). Frequency of post-April 15 pulses, defined as spates >20 cms, was calculated using the USGS historic flow records from 1946-1970 in conjunction with the Power and Dietrich data 1990-2007.

For the SF Eel population, flow regime effects were assessed by relating changes in adult population size to prior hydrologic conditions for recruitment.  The annual proportional rate of change, lambda ($\lambda$) was calculated as  the number of clutches observed in a year divided by the number seen in the previous year, such that $\lambda > 1$ indicates an increase in the number of breeding females, and $\lambda < 1$ indicates a decrease. Relationships between hydrologic variables and frog variables were assessed using Pearson's correlation coefficients and Mann-Whitney U-tests compared population growth rate after springs in which the slope of the recession limb was smooth vs. springs when the recession limb  was disrupted when rainfall occurred.

Specifically, springs were categorized as having a disrupted recession limb if the discharge at any point after breeding was higher than discharge when breeding started ($Q_{post-breeding} > Q_{init}$).

For the NF Feather frog populations, flow regime effects were assessed using a Before-After-Control-Impact analysis of variance (BACI) (Green 1979; Underwood 1994). In this powerful design for detecting environmental disturbance effects, 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." Given a three-year lag between conditions for embryos and tadpoles and recruitment to the adult egg-laying population, egg mass counts from 2002-2004 are considered the "before" data and the counts from 2005-2007 are the "after" data. Although flows manufactured for white water boating began in 2002, the impact on the number of adult females would not be detectable until 2005. Poe is the "control" reach and Cresta is the "impact" reach.

For the Alameda Ck populations, the density of breeding females in the Camp Ohlone Reach was compared to the Sunol Reach using a paired t-test (n= 5 years, 2003-2007).

## 3.4.   Results - Linking Hydrologic Conditions to Frog Populations

The egg mass time series data which serve for both among and within river comparisons are in Figure 3.4

### 3.4.1. Results of among river comparisons.

The mean annual density of breeding females in the five study reaches is negatively correlated with the frequency of pulsed flows during the sensitive spawning and rearing seasons (Spearman's r=-.949). Population densities are higher in the two  unregulated reaches compared to the regulated rivers (Figure 3.4). Abundance is higher in the perennial SF Eel than in the Camp Ohlone reach of Alameda Ck which becomes intermittent in dry years. This is consistent with the range-wide patterns for *R. boylii* with respect to precipitation (Davidson et al 2002). Of the regulated reaches, the abundance is highest in the Poe reach of the NF Feather, and lowest in the Cresta Reach of NF Feather and Sunol Reach of Alameda Ck. This pattern supports the hypothesis that pulsed flows are a contributing factor in *R. boylii* decline.   The hypothesis is further validated by inferences from the within river comparisons (section 3.4.2).
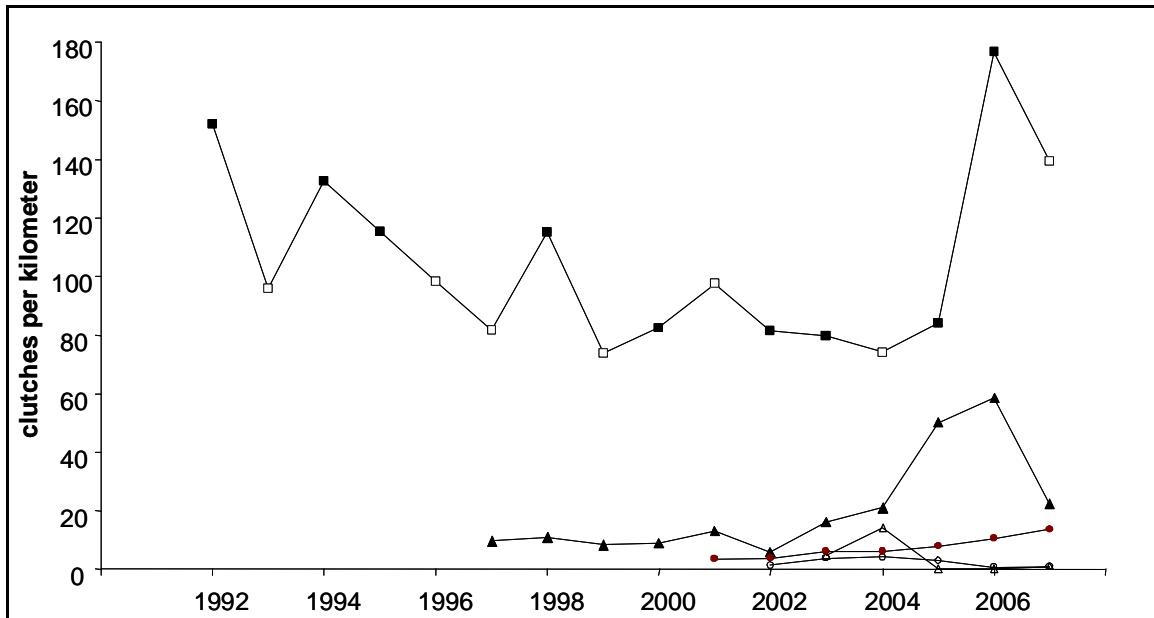
**Figure 3.4. Clutch densities in the five study reaches. For the NF Feather and Alameda Ck, open symbols indicate the density of egg masses in reaches subject to manufactured aseasonal pulsed flows. For the SF Eel, open symbols indicate the density of egg masses three years after natural spawning season pulsed flows.**

## 3.4.2.  Results of within river comparisons.

### 3.4.2.1.  SF Eel: Quantitative Relationships of Pulse Flows to Egg Mass Survival and Population Dynamics

Several key results emerged from close inspection of the long-term monitoring data on *R. boylii* breeding population size and the hydrologic record at the SF Eel (Table 3.2). The annual proportional rate of change in the egg mass index of population size ranged from 0.63 -2.1, but over the long term the population is stable with mean lambda slightly greater than 1.  Variation appeared to be a product of past rather than present disturbance conditions. For example, if disturbance in the form of winter peak discharge effects on adult survival were driving population dynamics, one would expect a significant negative correlation between maximum winter discharge and the change in number of adults breeding the subsequent spring. This was not observed, r = -0.09.

Lambda was negatively correlated with the amount of post-spawning rain three years prior (r = -0.53, n=15). From 1990-2004 large magnitude late-spring pulses (>20 cms) occurred in 3 yrs; however, in a total of 6 of those 15 years, the maximum spring discharge occurred after egg laying began (Table 3.2).  Three years after these springs with post-spawning spates, population size decreased, i.e., $\lambda < 1$ ($\lambda = 0.82 \pm 0.08$).  In the remaining 9 cases, the maximum spring discharge was prior to, or at, initial egg laying and population size increased three years later, i.e. $\lambda > 1$ ($\lambda = 1.2 \pm 0.13$). The 1 and 2 year lag results appear not significantly different from 1, while the differences in lambda are significant for a three year lag (Figure 3.5). This lag time between poor recruitment years and the dip in the number of adult females laying eggs

42

represents the time it takes for larvae to become full-size breeding adults. Although males may reach reproductive size at age two, females in northern populations need to attain a larger body size to be reproductive (VanWagner 1996). Growth curves fit to mark-recapture data from the NF Feather are also consistent with 3 years to maturity for females (Kupferberg and Palen analysis of GANDA unpublished data). For a central California population in Coyote Ck (Santa Clara Co.) time to maturity based on capture-mark-recapture data indicates 2 years to maturity for females (Earl Gonsolin, unpublished data). This result, that flow regimes affecting embryonic and larval survival changes population size, is a new finding for *R. boylii*.
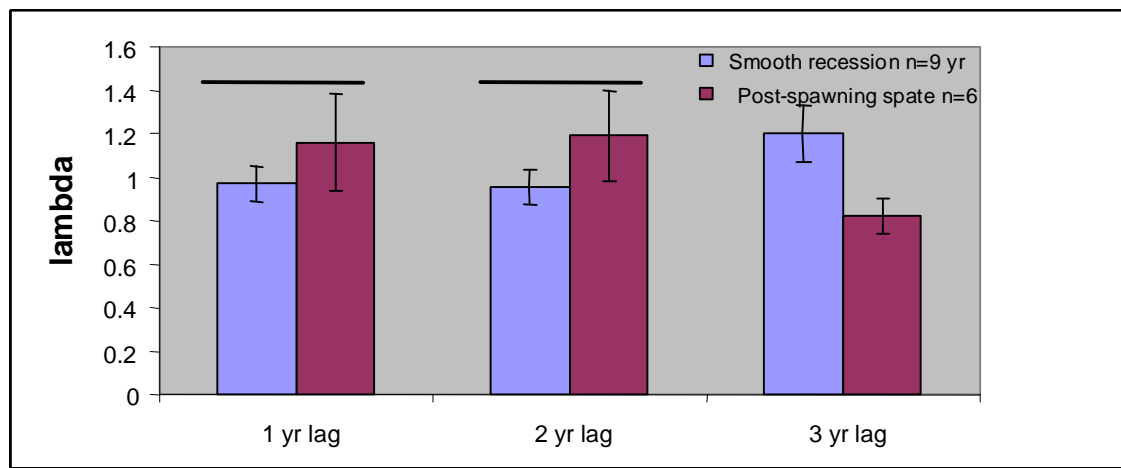


**Figure 3.5. Population growth rate, λ , following springs with post-spawning spates or smooth recession of flow. Only the three year lag time comparison is significant, Mann-Whitney U=47, p=0.05, Bonferroni corrected for 3 comparisons).**

The onset of spawning 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 11.7 cms (Table 3.2). This range of stage height represents a wide range in the quantity of shallow slow velocity habitat as predicted by the hydrodynamic modeling of one particular breeding site at the SF Eel (see chapter 5). There was only a weak trend for frogs to breed later in years with higher water levels (r=0.27). Thus, it appears that availability of oviposition sites and habitat area *per se* are not limiting factors for these frogs. Increasing water and air temperatures are more likely the primary cues for initiation of breeding (Kupferberg 1996; GANDA 2006). The latitudinal gradient in timing also indicates that temperature is an important cue. During the course of this study, 2005-2007, the more southern Alameda Ck frogs began breeding about 3 weeks before SF Eel and NF Feather frogs.

Analysis of the spring 2005 hydrologic and egg mass data revealed that both pulse magnitude and timing affect whether embryos survive to hatching (Figures 3.6 and 3.7). When clutches were detached from substrate and swept downstream, embryos and tadpoles were not found along the margins of the channel during subsequent surveys. Therefore scour of egg masses is likely synonymous with mortality. Of the four storms that occurred, pulse #2 with the largest magnitude scoured the largest total number of egg masses. All of those surviving the first storm

and a portion of the small cohort laid between the two storms were scoured. When comparing the effects of pulse #1 and pulse #3, it is evident that a smaller magnitude pulse can cause high loss if it comes later in the season. Of the clutches deposited prior to pulse #1 (a flow increase from 2 to 18 cms), 59% survived intact. Of the 119 clutches laid after storm #2 , only 6% more survived intact (65%), 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 (Spring Rivers 2002), eggs that became dislodged as velocities increased were on average 4–5 days older than eggs that remained attached to the rocks.

Table 3.2. Hydrologic events and *Rana boylii* population fluctuations at the SF Eel, 1990-2007.

| Year | λ | Preceding winter peak discharge (cms) | Spawning initiation date | Initial spawning daily mean discharge (cms) | Post-spawning spate date | Post-spawning spate peak discharge (cms) | Post-spawning rainfall total (cm) |
|------|------|------|------|------|------|------|------|
| 1990 |      | 102.3 | Apr 24* | 6.7 | May 27 | 82.0 | 37.03 |
| 1991 |      | 89.6 | Apr 24* | 7.78 | -- | -- | 5.79 |
| 1992 |      | 45.3 | Apr 25 | 9.66 | -- | -- | 9.17 |
| 1993 | 0.63 | 240.4 | Apr 30 | 4.33 | June 1 | 67.0 | 27.97 |
| 1994 | 1.38 | 43.07 | Apr 11 | 2.25 | Apr 26 | 8.77 | 14.30 |
| 1995 | 0.87 | 320.9 | May 3 | 13.02 | -- | -- | 8.76 |
| 1996 | 0.85 | 129.2 | Apr 28 | 11.22 | May 22 | 24.3 | 17.40 |
| 1997 | 0.83 | 418.3 | Apr 24 | 5.38 | -- | -- | 8.48 |
| 1998 | 1.41 | 175.9 | Apr 27 | 5.22 | May 29 | 10.8 | 11.73 |
| 1999 | 0.64 | 136.2 | Apr 22 | 3.48 | -- | -- | 3.10 |
| 2000 | 1.12 | 83.0 | May 8 | 2.71 | -- | -- | 4.93 |
| 2001 | 1.18 | 52.9 | Apr 19 | 0.66 | Apr 21 | .96 | 1.47 |
| 2002 | 0.84 | 189.5 | Apr 17 | 1.21 | -- | -- | 7.67 |
| 2003 | 0.97 | 132.5 | May 13 | 2.27 | -- | -- | 0.00 |
| 2004 | 0.93 | 136.2 | Apr 15 | 2.41 | Apr 21 | 15.2 | 8.38 |
| 2005 | 1.13 | 186.5 | Apr 28 | 2.50 | May 18 | 77.8 | 39.04 |
| 2006 | 2.11 | 377.9 | Apr 29 | 4.62 | -- | -- | 4.1 |
| 2007 | 0.78 | 65.5 | Apr 4 | 1.63 | Apr 22 | 4.22 | 14.1 |
| 2008 | .97 | 149.0 | Apr 13 | 1.27 | Apr 22 | 3.36 | 5.5 |
| Mean | 1.04 | 161.8 | Apr 24 | 4.6 | 19.1 days | 29.4 | 12.0 |
| ± s.e. | 0.01 | 2.9 | 0.3 days | 0.1 | 0.6 | 1.6 | 0.3 |

*Spawning initiation date estimated as mean of other years.
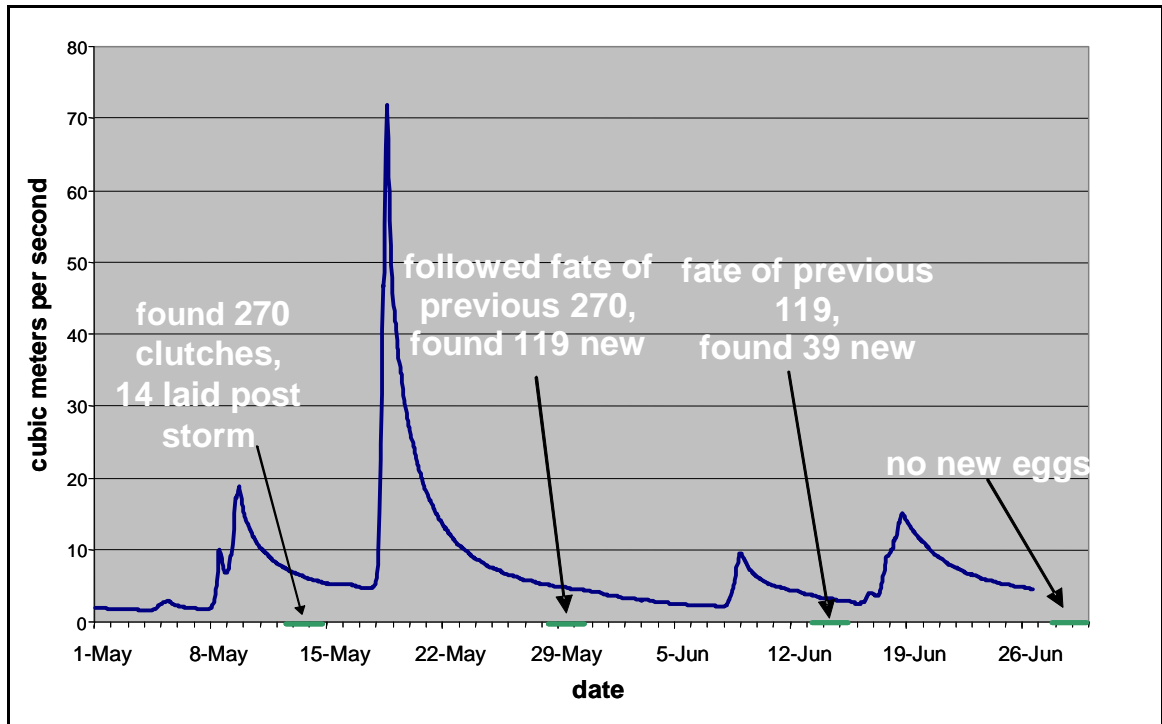
**Figure 3.6. Egg mass censuses in relation to four spates during Spring 2005 at SF Eel.**
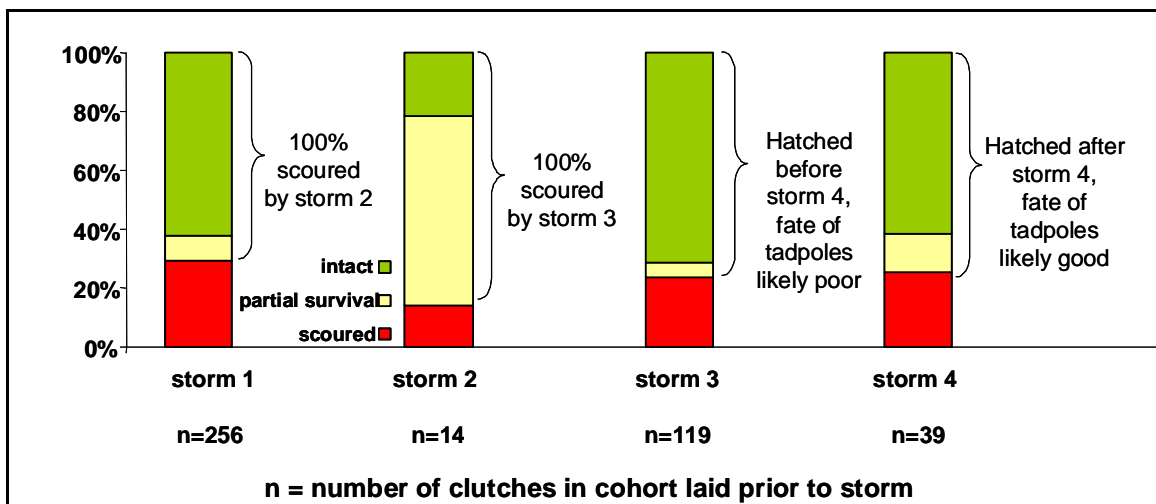


**Figure 3.7. Egg mass status after 4 natural pulse-flow events in 2005 at the SF Eel. Bracketed information indicates the fate of clutches, which survived one spate, in the subsequent spate.**

### *3.4.2.2 NF Feather: Summer white-water boating and frog population trends*

After a lag time reflecting sufficient time for young of the year to reach reproductive maturity, egg mass counts can indicate the cumulative effects of boating flows on eggs and larvae. In the Cresta Reach of the NF Feather, monthly boating flows were initiated in 2002. The Poe Reach did not have boating flows during this same period. In 2005 egg numbers reflect the effect of

45

2002 boating flows which included pulses during the spring breeding season (Figure 3.9). For the subsequent years, 2003-2005, pulsed flows were restricted to months when tadpoles and young-of-the-year life stages were present. Very few eggs were laid in 2006 (4) and 2007 (7) at the index sites in the Cresta reach indicating that tadpole mortality may have been very high in 2003 and 2004. In stark contrast, the Poe reach population has been increasing.

The divergence in population trends can be seen graphically in a plot comparing abundance through time between the Poe (control) and Cresta (impact) reaches (Figure 3.9). Before the perturbation, the trajectories of the Poe and Cresta populations are roughly parallel. After the perturbation, the lines diverge. The divergent trends were significant as seen in the significant ($p$=0.038) interaction between reach and time in a BACI Analysis of Variance (Table 3.3).

**Table 3.3 Analysis of Variance of ln(sum of egg masses found at index sites) within the Poe (control) and Cresta (impact) reaches of the NF Feather, before and after the institution of recreational whitewater boating. Multiple $r^2$=0.765.**

| Factor | Mean Square | F | df | p |
|---|---|---|---|---|
| Reach (control, Poe vs. impact, Cresta) | 6.60 | 19.95 | 1 | 0.002 |
| Time (before vs. after white water boating) | 0.01 | 0.03 | 1 | 0.861 |
| Reach x Time | 2.03 | 6.12 | 1 | 0.038 |
| Error | 0.33 | | 8 | |

Alternative explanations for the divergence between Poe and Cresta trends lack supporting evidence. Seasonal spill-related pulses scoured some egg masses in 2 of 5 years, but occurred early in the breeding season, so mortality was limited to 11-15% of total reproductive output. Size distribution differences of adult frogs between Cresta and Poe populations independently corroborate the egg mass count differences. Missing cohorts of smaller size classes in the Cresta reach is consistent with a lack of production of new recruits to the population since changes to the flow regime in 2002 (GANDA 2007). Similar to the SF Eel, there appears to be no correspondence between adult numbers and winter flow regime. For example, in the Poe reach, the second highest egg mass numbers occurred in 2006, following a wet winter and spring (see full year hydrographs in Figure 3.2).

In 2006, another source of egg mortality related to spills occurred. Eggs that were laid during the prolonged spill (see hydrographs in Figure 3.2) were stranded and totally desiccated after the rapid cessation of spill. Half of the reproductive output for both Poe and Cresta was lost that year. The consequences of these mortality events may not be apparent in the population until the 2009 breeding censuses.
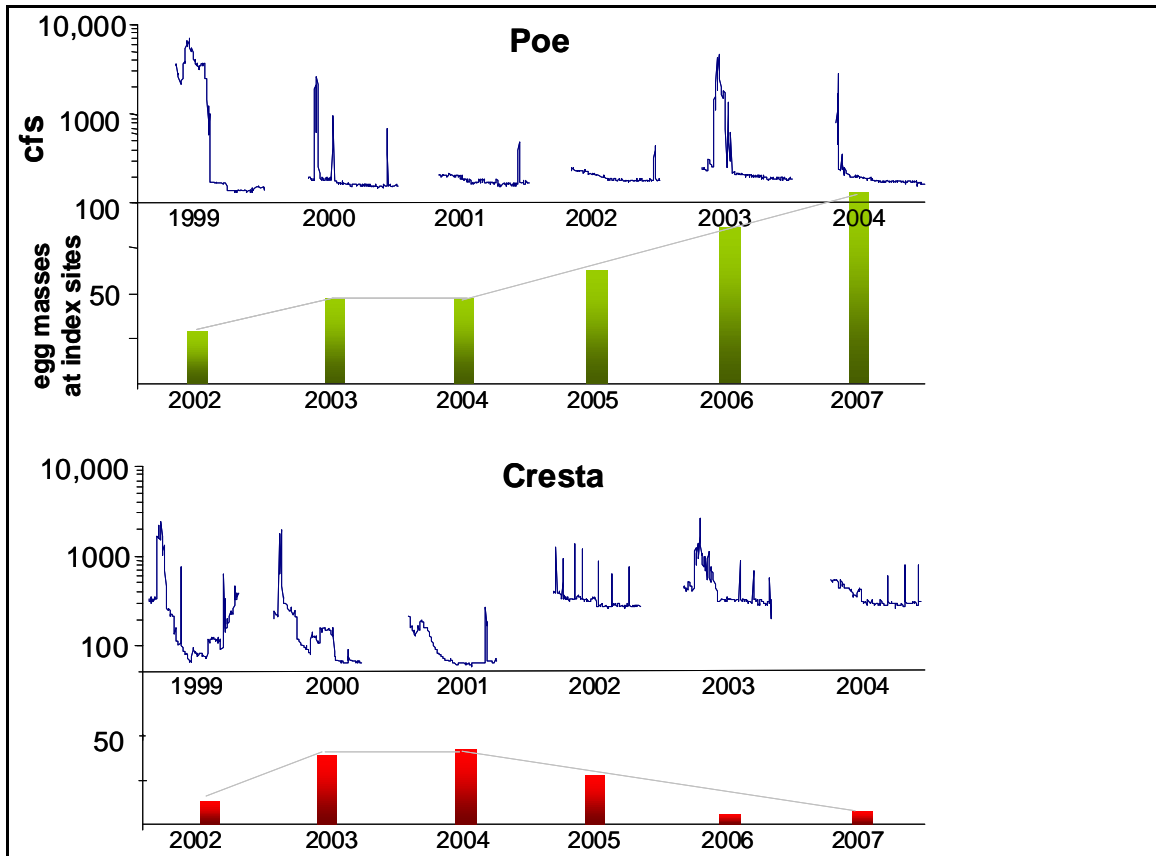
**Figure 3.8. NF Feather breeding female populations (histograms) are higher 3 years after favorable years with no spills (Poe reach) and significantly lower beginning 3 years after recreational pulsed flows (Cresta reach) were instituted in 2002. Hydrographs span six months, April 1– Oct 1.**

### 3.4.2.3. Alameda Creek:  Pulsed flows and divergence of populations

In Alameda Ck, comparisons in population trends between the unregulated Camp Ohlone reach and the regulated Sunol reach reveal a scenario similar to that observed between the Poe and Cresta reaches in the NF Feather. The *R. boylii* population is disappearing in the Sunol reach that experienced higher magnitude and longer duration pulses for three consecutive years ). (Figure 3.9). The differences with the Camp Ohlone reach are significant  (paired t=-2.86, df=4, *p*=0.046. For Alameda Ck flow records are not as extensive, and start dates for oviposition are not as well known, however, for Camp Ohlone, large magnitude (5-10x increase in flow) pulse events after April 1st, occurred 4 times in 13 years (1995-2007) of record or 30.8% of the years. For the declining population below Calaveras Ck. confluence, inter-annual pulse frequency is 50%, 6 out of 12 springs on record (1996-2007).

No breeding (neither *R. boylii* nor *R. draytonii*) was detected below the confluence of Calaveras Ck. during 2005 and 2006 when there were spills from Calaveras Reservoir (Figure 3.2). Conditions at all previously used breeding sites were too swift and deep for egg laying. Detectability and visibility were poor, but if any eggs were laid, there was likely little survival.

Repeated surveys during the subsequent summers for larvae showed no evidence of successful *R. boylii* breeding. In 2007, although conditions returned to a suitable state for breeding, only one *R. boylii* egg mass was found. This was at the most upstream breeding location (30 m downstream from the confluence with Calaveras Ck.) and may represent re-colonization from the upstream diversion reach (Little Yosemite) where breeding female density has been low but consistent 1.21±0.54 (n=5 yrs 2003-2007). Other previously used locations remained unoccupied in 2007, except for one site where two clutches of *R. draytonii* eggs were found.

Within the unregulated Camp Ohlone reach (Figure 3.9), the relationship between egg conditions and population size in subsequent years does not reveal as convincing a pattern as was observed in the NF Feather and SF Eel. The correspondence between years with breeding/rearing season pulsed flows and a decrease in the number of breeding females two years later does not hold for 2003. There were spring pulses, yet in 2005 egg numbers were relatively high. For Alameda Ck. channel dewatering prior to metamorphosis may be as important a factor in recruitment as survival to hatching. It is possible that in 2003, pulse induced embryo mortality was compensated for by higher tadpole survival to metamorphosis when base flow was higher.
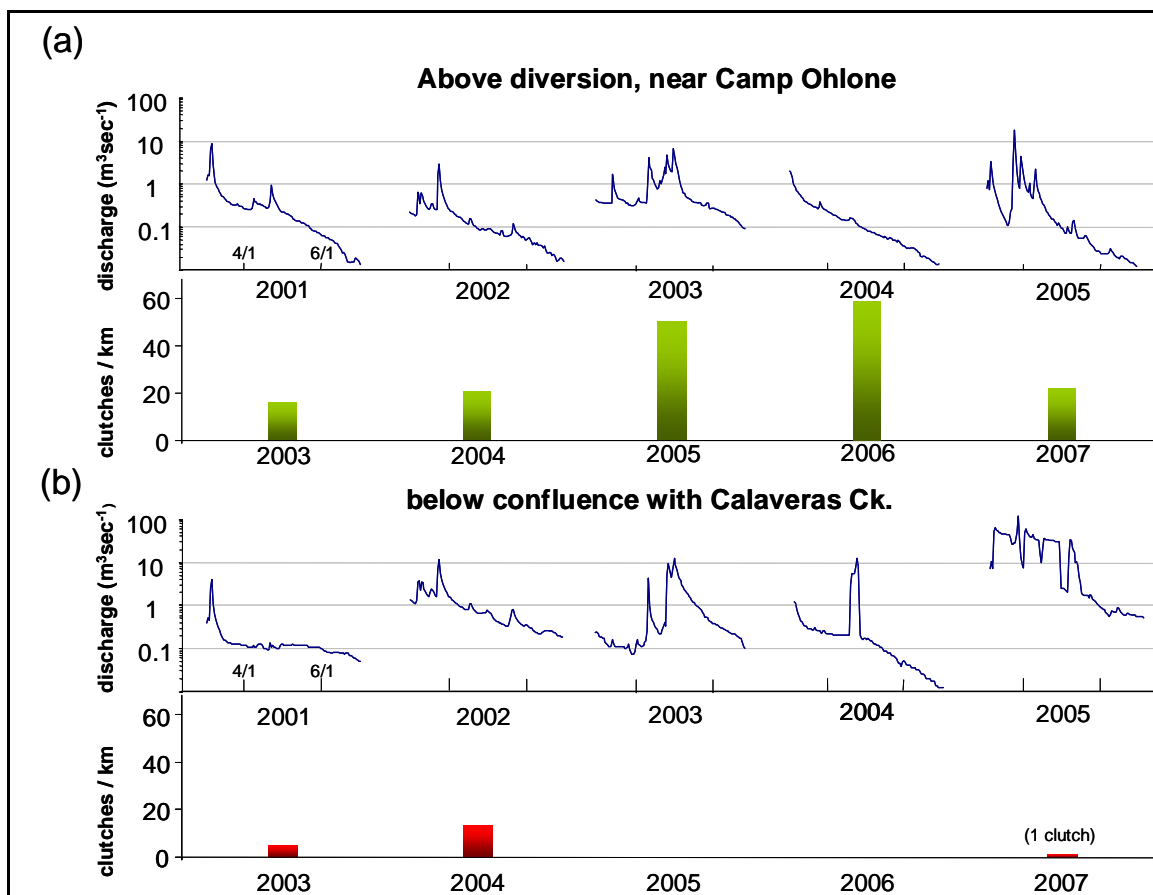


**Figure 3.9. Unregulated (a) and regulated (b) spawning season flow conditions in Alameda Ck. and reproductive output two years later when those individuals would become breeding adults.**

48

## 3.5. Discussion—Recruitment Limitation Hypothesis

Fluctuation in egg mass number in the three study rivers appeared related to past, rather than present, conditions for successful reproduction. The inference derived from this pattern is that survival in the egg and larval life stages is an important factor in *R. boylii* population dynamics. and central to conservation of this species.  For the North Coast Range and Sierran populations, there is a three year lag time between aseasonal pulsed flows that influence egg laying habitat suitability, embryo survival, larval survival and growth, and inter-annual declines in the adult breeding population size. In the Central Coast Range population the lag time may be only two years. This lag time likely represents the time it takes an egg laid in year t to become a breeding female in the year t+3 (NF Feather, SF Eel) or t+2 (Alameda Ck). Sizes of marked and recaptured female frogs in northern (Drennan unpublished data; Wheeler pers. comm.) and central (Gonsolin, unpublished data) California support this growth rate scenario. This type of year class phenomenon in which population numbers are determined by environmental conditions that vary independently of animal density is defined as recruitment limitation (Danilowicz 1997). In the case of *R. boylii*, pulsed flows can cause high egg mass mortality, as was documented in 2005 at the SF Eel whereas gradually descending stage height typically results in high egg mass survival. In the case of the NF Feather, the Cresta population decline began three years after white water boating pulsed flows during egg (2002) and tadpole (2002-2005) seasons were instituted. During the same years populations in the Poe reach had some very high recruitment years. Thus one of the most important consequences of prescribed annually recurring aseasonal pulsed flows is the elimination of 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).

In contrast to recruitment limitation, regulation by density dependent factors (competition and predation) appears to be a dominant process for many amphibian populations, especially lentic associated species (Biek et al. 2002; Govindarajulu et al. 2005; Vonesh and De la Cruz 2002). Some experiments have shown that egg mortality is compensated for when surviving larvae are released from competition resulting in the similar number of individuals reaching metamorphosis (Skelly and Kiesecker 2001). In general, *R. boylii* larvae disperse from the highly concentrated breeding site in the near shore environment as flows decline and more of the channel becomes suitable habitat, such that larval densities do not often approach the densities at which competition is observed (Kupferberg 1997). In one circumstance extremely high tadpole densities were observed. In 2006 on the NF Feather near Flea Valley Ck., breeding commenced during spill, and eggs were deposited in what became isolated off-channel pools after spill cessation. The high density of larvae in these pools (~1000/m2) with no ability to disperse created density dependent effects (larval competition) as resources became limited. The larvae collected (for lab experiments, Chapter 4) from that location at the NF Feather were significantly smaller than those collected from the adjacent low flow channel and smaller than those from other study rivers.

To test the hypothesis that *R. boylii* populations are regulated by recruitment limitation rather than density dependence, a population projection model is being developed as the final element

of this project (expected completion in 2008). This type of model begins with a life table comprised of transition probabilities of survival from one life stage to the next. These transition probabilities can either be fixed or vary in relation to flow regime. The objective of the population modeling effort is to conduct "virtual experiments" with different flow scenarios to examine the relationship between pulse frequency and population viability. When large magnitude (>1000% increase in discharge) spring flows occur at low frequency with long intervals between events, populations rebound. A potential mechanism is that the large old females have sufficient fecundity and reproductive value, so that when they capitalize on benign survival conditions, recruitment is high. Alternatively, 3 year old females that are breeding for the first time may have low future reproductive value. Because it is energetically very costly to breed (Van Wagner 1996), perhaps a significant proportion of females do not survive or do not re-gain sufficient body mass to breed again.

Despite the pattern of associated dips in population growth rate three years after pulsed flows, the overall status of the SF Eel population has not been jeopardized. At the SF Eel, mean daily discharge has exceeded 20 cms, in 7 of 43 (16.3%) years (1946-1970, and 1990-2007) during the breeding season (April 15th on). In contrast, regulated rivers have larger magnitude and more frequent pulse flows, as illustrated by the comparisons between the two Alameda Ck reaches. and the two NF Feather Reaches. One analysis for the NF Feather, Poe reach, shows that spills have occurred in 9 out of the last 35, or 25.7% of years during the likely breeding season (GANDA 2006). For the Cresta Reach, populations occur at much lower densities and with declining population growth rates since spring and summer recreational boating flows were instituted at an annual (100%) frequency. These patterns suggest an important question for future research: What is the shape of the function relating pulse frequency to population growth rate?

With only 5 data points, one from each case study reach, it is not possible to empirically derive the relationships, but three hypothetical functions are illustrated in a conceptual model in Figure 3.11. Rather than using the full historical hydrologic data sets available, only the years corresponding to the years when frog populations were censused, were considered for calculating the pulse frequency. There could be a simple linear inverse relationship (dotted line) between the annual recurrence of pulses that limit recruitment and the persistence of a frog population through time. There could be a step function (solid black line), in which below a certain threshold frequency, factors other than the spring and summer flow regime would determine the frog population growth rate. Alternatively, there could be a sigmoidal function, with the inflection point similarly representing a threshold level of hydrologically driven recruitment limitation that would eventually drive the local frog population to extinction. As more populations will be monitored across the Sierra as part of the compliance phase of new FERC licenses, it may be possible to empirically determine the frequency of pulsed flow which will not further endanger *R. boylii*.
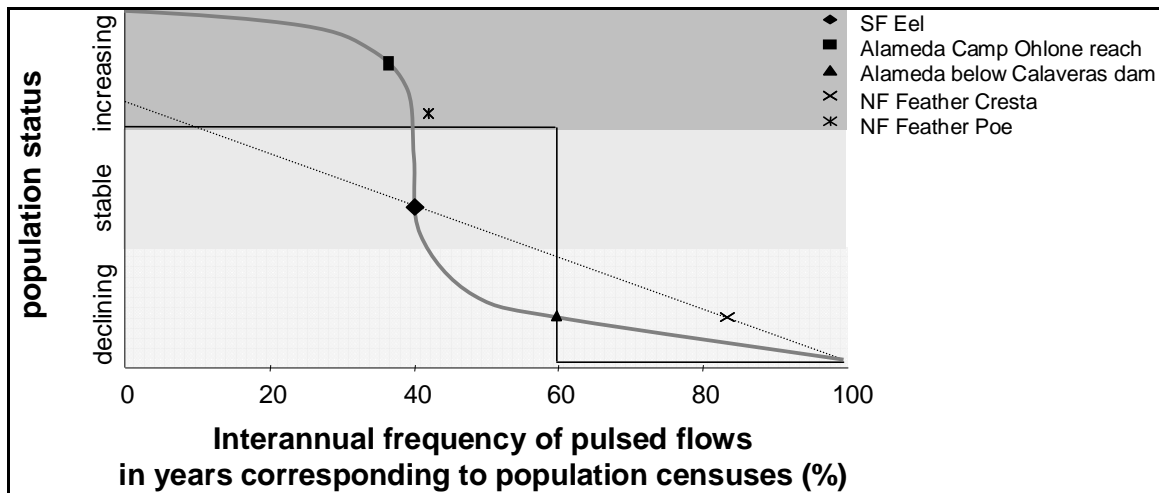
**Figure 3.10. Three hypothetical functions relating breeding and rearing season pulse flow frequency to frog population status.**

Another relationship which cannot be rigorously tested with the currently available data, but which is hinted at, is that large watershed size may inherently yield lower overall population abundance. When comparing numbers of frogs per river km, for large rivers such as the NF Feather, tributaries and breeding locations may be more widely dispersed than in the SF Eel or Alameda Ck., so per kilometer densities appear lower. To examine this possibility, a reference population in an unregulated river of comparable scale is needed for the Sierra Nevada.

To set conservation goals for *R. boylii,* decision makers need to know how many breeding females a population must have to withstand a string of poor recruitment years. Related to setting targets, conservationists need to know how frequently occasional high recruitment years must occur to maintain population viability. Occasional high recruitment years are characteristic of amphibian population fluctuations in general, and help to sustain populations over the long term (Daszak et al. 2005; Meyer et al. 1998). Considering these questions will be complicated by differences in metapopulation structure between regulated and unregulated rivers. For example, in the case study systems, unnatural dispersal barriers occur in the regulated rivers. To re-colonize the Cresta reach, frogs would have to hop upstream around a reservoir from the Poe reach. For Camp Ohlone frogs to re-colonize the Sunol reach, frogs would have to hop downstream through a dry diversion reach. The ongoing monitoring programs at these sites will yield needed information about population recovery rates.

## 3.6. Conclusions

There is statistically significant evidence that aseasonal pulsed flow mortality of vulnerable *R. boylii* life stages has consequences in terms of adult population size. Given the reduced numbers of breeding frogs in regulated reaches documented by the 'among rivers' comparisons, the populations are at great risk of extirpation when there are consecutive years with poor recruitment conditions. Although similar processes of stranding and scouring of egg masses occur in unregulated rivers (documented as the main causes of embryonic mortality in the SF

51

Eel (reported here and in Kupferberg 1996), the populations remain robust, probably because the frequency of mass mortality events is sufficiently low.  The emergent patterns observed within Alameda Ck and the NF Feather, and other regulated rivers reviewed in Chapter 2, support the hypothesis that pulsed flows are a contributing factor in *R. boylii* decline.   The hypothesis is further validated by the results of experiments (Chapter 4) and modeling (Chapter 5) which focus on the processes underlying the patterns.  Together there is a convergence of evidence that hydrologic conditions for sensitive early life stages are central to the conservation of *R. boylii*.

- Annual fluctuations in population growth are not associated with the magnitude of winter peak discharges experienced by juvenile and adult frogs.

- Adult population fluctuations are associated with spring and summer conditions 2-3 years prior, i.e. the pulsed flows that scour egg masses or displace tadpoles.

- Timing of breeding in the spring is not associated with stage height; there is only a very weak trend for frogs to breed later in years with higher water levels. Among years, it is likely that increasing water and air temperature cue the initiation of breeding, not the amount of shallow slow habitat area inundated at the channel margin.

- The magnitude and timing of spring pulse flows have an important influence on whether embryos survive to hatching. While large magnitude pulses scour clutches off of rocks, smaller magnitude pulses later in the season can also cause high mortality.

- Population decline following four years of monthly spring and summer whitewater boating flows in the Cresta reach of the NF Feather corroborates the three year lag time recruitment limitation hypothesis for northern populations of *R. boylii*.

- Divergent population trajectories between an unregulated reach and a reach with spring dam spills in Alameda Ck indicates that a 2-year time lag between recruitment conditions and adult population size may occur.

- Demographic study of *R. boylii* and the development of matrix projection models are needed to explore the sensitivity of population growth rates to pulsed flow frequency.

- One of the most important consequences of prescribed *annually recurring* aseasonal pulsed flows is the elimination of occasional high recruitment years that are a characteristic of amphibian population dynamics in general and which sustain populations over long time periods.

- Statistically significant evidence linking pulsed flows to decline highlights the pressing need for better protection of *R. boylii* and a cautionary approach when dams are being relicensed.

# 4.0  Velocity Manipulation Effects on Larval *Rana boylii*

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**Abstract**

The foothill yellow-legged frog, *Rana boylii*, completes its life cycle in fluvial environments in synchrony with the timing of floods and droughts typical of California's Mediterranean climate. Its life stages occur along a continuum of susceptibility to flow fluctuation: from immobile eggs, to moderately mobile tadpoles, to highly mobile adults. In rivers with dams, vulnerable life stages are subjected to relatively large magnitude and frequency flow fluctuation. To assess the effects of such pulsed flows on tadpoles, a life stage that does not typically experience floods, velocity was manipulated in laboratory flumes and field enclosures. Focal questions were: 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; and, 4) are behaviors in the relatively artificial, yet highly replicated, lab and field enclosure settings consistent with observations from the difficult to replicate, but more realistic, open river manipulations?

Tadpoles across a wide ontogenetic sequence sought refuge in substrate as soon as velocity increased. Behavioral responses and performances were consistent among experimental venues. In a laboratory flume, tadpoles could no longer swim or maintain position under rocks at a mean critical velocity of 20.9 ± 1.6 cm/s. Critical velocity varied inversely with tadpole size and developmental stage, with velocities as low as 10 cm/s causing 25% of tadpoles to be displaced. The most easily displaced individuals were the largest, especially those closest to metamorphosis. In the lab flume without flow refugia, swimming against a 5 cm/s current, tadpoles reached exhaustion at 7.4 ± 2.6 min. For recently hatched tadpoles in the field, there were direct lethal effects of velocities as low as 10 cm/s. While in flow refugia, there were also lethal effects of predation. For tadpoles < 6 weeks old, mortality risk was doubled at elevated, yet sub-critical velocities. The velocities shown to have negative effects in these trials were less than the typical increases in velocity near shore when aseasonal pulsed flows (chapter 2) occur. Many of the negative effects occurred below velocities that can be accurately predicted using a two-dimensional hydrodynamic model (chapter 5). Thus it would be difficult for river managers to design a summer pulsed flow with minimal impact to *R. boylii* tadpoles.  To protect *R. boylii* in regulated rivers, dams should be managed to avoid aseasonal pulsed releases of water.

## 4.1.  Introduction

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. Over-wintering occurs in refugia in tributaries and springs (Nussbaum et al. 1983; Rombough 2006). To evade mortality from discharge fluctuation, 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 the range of *R. boylii* (Kupferberg 1996). This observation is consistent with a recent survey of flow regime adaptations across a broad array of riverine biota which found that traits for avoiding mortality due to flow fluctuation fall into three categories: life-history, behavioral and morphological. To withstand flooding, organisms with an evolutionary history in which large magnitude flooding events occur with a high degree of temporal predictability, generally have life-history and behavioral traits, rather than morphological specializations (Lytle and Poff 2004).

In the process of evaluating the pulsed flow studies done for re-licensing of hydroelectric dams (Chapter 2), it became evident that the extent to which *R. boylii* larval morphology and behavior are adapted to swiftly flowing water was unknown. Under a natural flow regime, discharge gradually declines in early summer, so *R. boylii* tadpoles do not often encounter large magnitude flood events (Chapter 3). One might expect *R. boylii* tadpoles to be susceptible to aseasonal pulsed flows because they lack the highly specialized features for adhesion to rocks or burrowing in rocky substrates, traits seen in anurans whose larvae inhabit turbulent and high velocity habitats (Altig and Johnston 1989, Nodzenski et al. 1989, Richards 2002). Suctorial tadpoles have evolved several times independently among diverse taxonomic groups of frogs (Haas and Richards 1998). For example, *Amolops*, an Asian genus of stream breeding ranid frog that lives in rain forests with no seasonality of precipitation, have tadpoles with an abdominal sucker. Other taxa (e.g. *Litoria* spp.) have specialized cranial musculoskeletal structures allowing them to use their oral discs as adhesive organs (Haas and Richards 1998). Fossorial, or burrowing, tadpoles are eel-like with extra caudal vertebrae extending into the tail (Haas et al. 2006, Handrigan et al. 2007). In contrast, larval *R. boylii's* bodies are not particularly long or thin, the tail is not bony, and the oral disc is notable for features that appear more related to grazing rather than adhesion. The multiple rows of keratinized teeth, or denticles (Zweifel 1955), function primarily to efficiently scrape diatoms and attached algae (Kupferberg 1997), but high speed videography of ranid tadpoles feeding on adnate algae has shown that the denticles can also play an anchoring role (Wassersug and Yamashita 2001). The questions thus arise: To what degree does *R. boylii* morphology serve as a flow adaptation? What behavioral responses do *R. boylii* larvae display when faced with novel aseasonal discharge fluctuation? What are the consequences of increased flow velocity to tadpole survival and growth? These questions were investigated by manipulating velocity conditions of larval *R. boylii* and observing behavioral responses and cumulative impacts. Experiments were conducted in six different venues across a range of spatial and temporal scales in both laboratory and field settings. The venues, study questions, and results are summarized in Table 4.1.

**Table 4.1. Questions, methods, and results of _R. boylii_ velocity manipulations. Bold numbers with the questions identify the report sections where the respective information is presented.**

| Section QUESTIONS | Experimental VENUE | Experimental SCALE | RANGE of MANIPULATION | controlled VARIABLES | un-controlled VARIABLES | RESULTS |
|---|---|---|---|---|---|---|
| **4.2** How do tadpoles behave when velocity increases? | artificial channel (Redwood Sciences Lab, USFS Arcata, CA) | 1.5 m$^2$, 1 hour trials | 0-50 cm/s four stepped intervals, 0-2, 5-8, 16-22, 40-50 | depth, substrate, temperature | no shore, no food velocity spatially heterogeneous | * tadpoles shelter in rocks * 39% displaced at 16-22 cm/s, 100% at 40 cm/s |
| **4.3** At what velocities are tadpoles unable to maintain position? | Brett chamber (UC Davis) | 0.02 m$^2$ 5 min – 1.25 hrs, depending on time to exhaustion | 0-50 cm/s 2 cm/s increments | depth, substrate, temperature tadpole size, stage, source population | no shallow shore no food no large cobbles | * 66% exhausted at 30cm/s * Critical velocity varies with size, and stage |
| **4.4** What are the energetic consequences of refuge use? | flow-through enclosures, SF Eel Alameda Ck | 0.2 m$^2$, 6 wks | 0-12 cm/s control vs. elevated continuous | depth, food, substrate | temperature | * growth and development significantly lower in elevated velocities |
| **4.4** How does refuge use interact with predation | flow-through enclosures SF Eel Alameda Ck | 0.2 m$^2$, 10 weeks | 0-12 cm/s control vs. elevated pulsed differences | depth, food, substrate, predator presence/ absence | temperature spatial heterogeneity | * doubled mortality risk |
| **4.5** Can tadpoles stay in refugia over 18 hrs? | Instream flume Alameda Ck | 2 m$^2$, 18 hour trials | 0-30 cm /sec tadpoles move among velocity patches | depth , substrate | temperature heterogeneity of velocity zones | * 40% swept downstream |
| **4.5** Can tadpoles swim to shore? | drift fence SF Eel | 9 m$^2$, 4 hour trials | 0 - 70 cms in heterogenous patches | shallow shore natural setting | predators | * 70% displaced / not located |
| | Open SF Eel | Unlimited area 20 minutes | unlimited velocity start at 5-10 cm/s | shallow shore present | velocity, substrate, depth | * 80% swept away |

## 4.2. Artificial Stream Channel Manipulation of Velocity

To determine the conditions which cause larvae to alter normal movement and be entrained in the current, velocity and substrate were manipulated in an artificial stream channel.

### 4.2.1. Artificial Stream Channel Methods

The artificial stream facility is located at the Redwood Sciences Lab, Arcata CA. It is a rectangular doughnut-shaped tank with pumps that re-circulate water (Figure 4.1). 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 20 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 intervals. The start times of the trials were 15:32, 20:47, 10:00, 13:25, and 15:54. The channel was illuminated by 6 400 W full spectrum halide lamps suspended above the channel, with the average light intensity at the water surface 6.78 klux (range 6.07-8.14 klux).

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 and Chi-Square analyses using Systat 11 (Wilkinson 2004). Tadpole activity data were subjected to the angular transformation (arcsin √ proportion) to meet ANOVA assumptions (Sokal and Rohlf 1981).

*R. boylii* larvae from the SF Eel were collected Aug. 2, 2005, and transported to the artificial stream. Larvae were also collected from the Mad River, near Arcata CA, on Aug. 4, 2005, for a pilot trial. SF Eel tadpole groups were drawn from a pool of 167 individuals, with a range of developmental stages. Tadpole stage was categorized using characters as defined by Gosner (1960). SF Eel Gosner stage ranged from 29-37, mean ± s.d. = 34.4 ± 1.8. Mad River tadpoles were more developed, at Gosner stages 40-41. Groups were randomly assigned to treatments.

To evaluate the importance of interstitial refugia, two substrate conditions were created. On one side of the flume, 55 cobbles were placed on top of a foam bed. On the opposite side, the filling of interstitial spaces, which can sometimes occur in regulated rivers, was mimicked by carving out an indentation for each rock. Foam was used because fine sediments would damage the pumps. For similar reasons, clean rocks, rather than rocks covered with periphyton were used. Each rock was measured along its intermediate axis to the nearest 0.5 cm. To calculate embeddedness, the difference in height of each rock while resting on a solid surface vs. the same rock's height when placed in, or on, the foam was measured to the nearest 0.5 cm. The median grain size in each treatment was 110 mm. The "embedded" treatment had a 53.3 ± 1.4% difference in rock height and the "unembedded" treatment had a difference of 12.3 ± 1%. 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, $19.2 \pm 2.0$ cm and $19.7 \pm 4.4$ cm, respectively.

Velocity conditions were created by engaging different arrays of pumps: $V_1$ = filter pump only; $V_2$ = filter + chiller pump with valve 2/3 open; $V_3$ = filter + chiller pump with valve fully open and small pump on; $V_4$ = all previous pumps on + large pump. $V_4$ was only used during the pilot trial. To assess the spatial variation in velocity at $V_2$ and $V_3$, measurements arranged in a uniform grid were taken at each flow (a mean of 3 mid-column measurements at each of 12 points). To assess temporal variation in velocity across trials, the probe was mounted at a fixed station on the un-embedded side and readings taken every five minutes during trials. Water temperatures ranged from 20 -21 ºC.
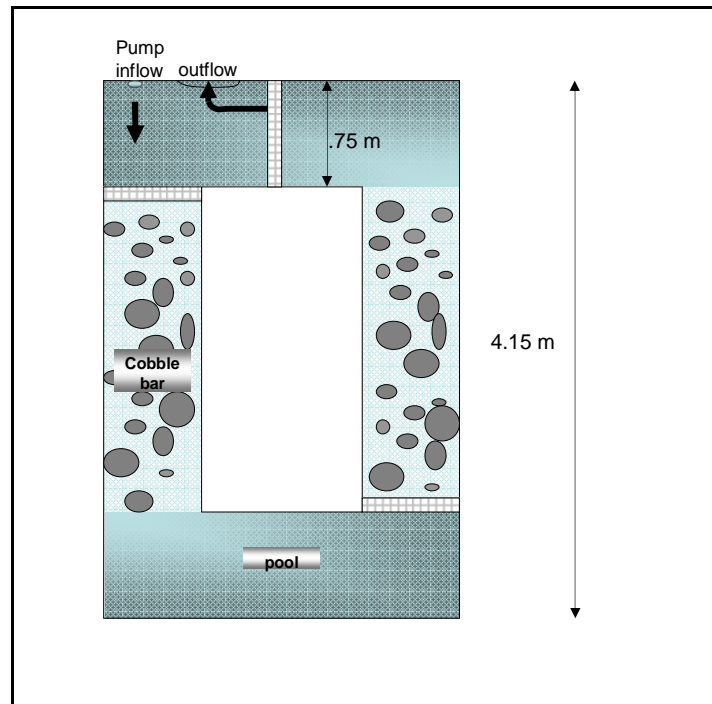


**Figure 4.1. Schematic of artificial channel (top). Light blue rectangles represent rock patches either embedded within or placed on top of foam (bottom, photo credit: S. Kupferberg). Fiberglass mesh (1 mm) screens were placed at the upstream end of each patch and in front of the outflow. Shallow areas are indicated by lighter shading.**

### 4.2.2. Artificial Stream Channel 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 4.2). 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 alternating the positions of the embedded and un-embedded test patches between trials. 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 spatial heterogeneity of velocity conditions (Figure 4.2), 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 4.2. Variation in mid-column velocity (cm/s) as created by four different pump arrays in the artificial stream channel. The "at-a-station" measurements 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) |
|---|---|---|---|---|---|
| Un-Embedded (away from pumps) | $V_1$ = filter only | approx. 1 | 0-2 | $0.95 \pm 0.15$ | 0-2 |
| | $V_2$ = filter + chiller, valve 2/3 open | $4.8 \pm 0.27$ | 4-6 | $6.20 \pm 0.50$ | 3-10 |
| | $V_3$ = filter +chiller, valve fully open + small pump | $19.0 \pm 0.92$ | 13-23 | $17.00 \pm 0.70$ | 16-22 |
| Embedded (near pumps) | $V_1$ = filter only | approx. 1 | 0-2 | | |
| | $v_2$ = filter + chiller, valve 2/3 open | $4.4 \pm 0.6$ | 0-8 | | |
| | $v_3$ = filter +chiller, valve fully open + small pump | $17.0 \pm 1.7$ | 0-26 | | |
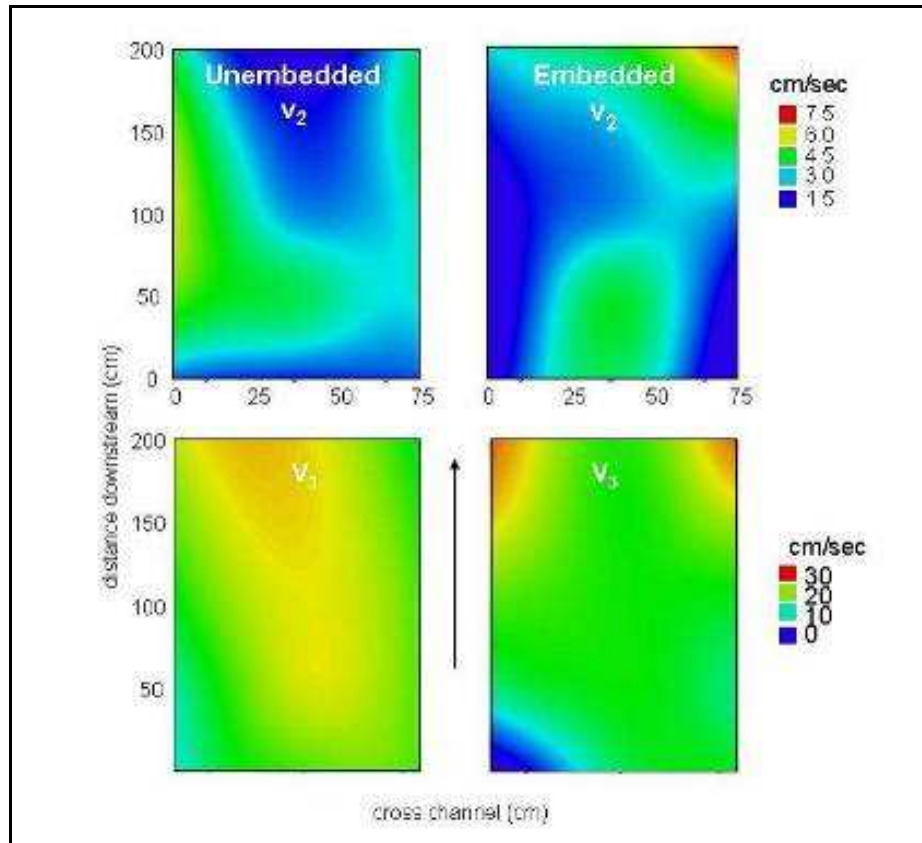
**Figure 4.2. Spatial heterogeneity of velocities in artificial stream channel at $V_2$ (upper charts) and $V_3$ (lower charts). Arrow indicates direction of flow.**

Tadpoles became significantly less active as velocity increased (Figure 4.3). There was no significant effect of embeddedness on the proportion of tadpoles active and there was no interaction between the velocity and embeddedness factors (Table 4.3). Proportionally fewer tadpoles left the artificial cobble bars when velocities were increased as shown by the decreasing slopes of the emigration vs. time lines shown for each of the 10 replicates in Figure 4.4. The mean slope was significantly lower at the two elevated velocities compared to the base flow conditions. There was no effect of substrate embeddedness on rates of emigration from bar to pool and no interaction between substrate and velocity (Table 4.4).

Tadpole response to velocity was consistent among trials even though start times ranged from morning through evening.  Many species of tadpoles are known to have diel shifts in habitat use from day to night (Warkentin 1992, Schley et al 1998, Hampton and Duggan 2003) or change swimming behavior in response to changes in illumination (Beiswinger 1977, Jamieson and Roberts 2000).  However, the trials were conducted under bright artificial lights, so perhaps circadian rhythm effects were minimized or decoupled from the start time of each trial.
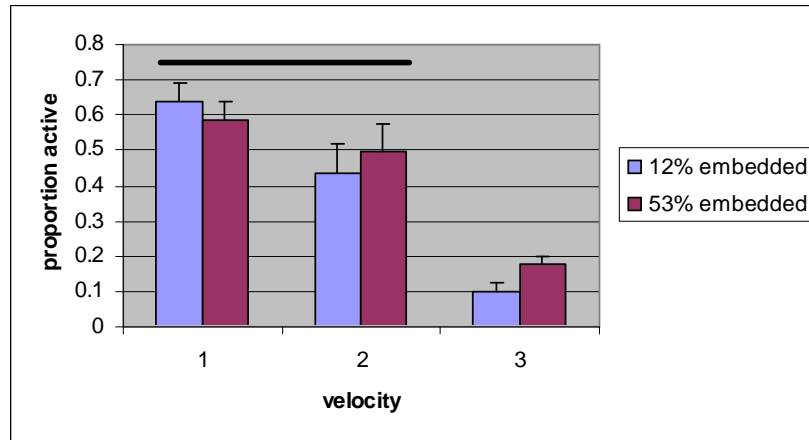
**Figure 4.3. Mean tadpole activity (measured every five minutes) during five paired hour-long trials. Activity at $v_1$ (0-2cm/s) was not significantly different from activity at $v_2$ (5-8 cm/s) (p=0.15). Activity at $v_3$ (16-22 cm/s) was significantly different than at $v_1$ (p<0.001) and $v_2$ (p=0.001).**

**Table 4.3. 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) | | | | | |
| Velocity | | 0.09 | 2,7 | 36.8 | <0.001 |
| Velocity x  Substrate | | 0.74 | 2,7 | 1.2 | 0.36 |
| Analysis of Totals (ANOVA) | | | | | |
| Substrate Embeddedness | 0.023 | | 1 | 0.94 | 0.36 |
| Error | 0.025 | | 8 | | |

Note:  The univariate test of substrate treatment is on the arcsin $\sqrt{}$ % of tadpoles active totaled across velocity time periods 1, 2, and 3.
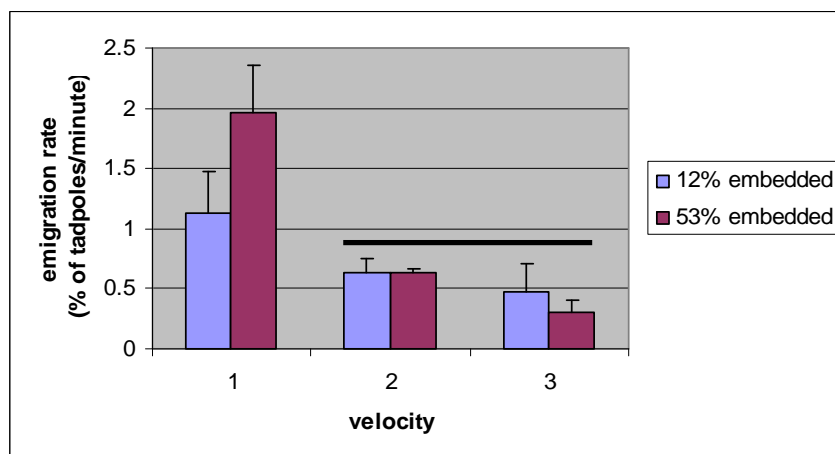


**Figure 4.4. Tadpole movement out of the test patches was significantly lower when velocity was elevated above base  flow conditions, but did not differ significantly between  the two higher velocities (Bonferroni adjusted *p*-values for emigration at $v_1$ vs. $v_2$=0.017, $v_1$ vs. $v_3$=0.008, $v_2$ vs. $v_3$=0.66).**
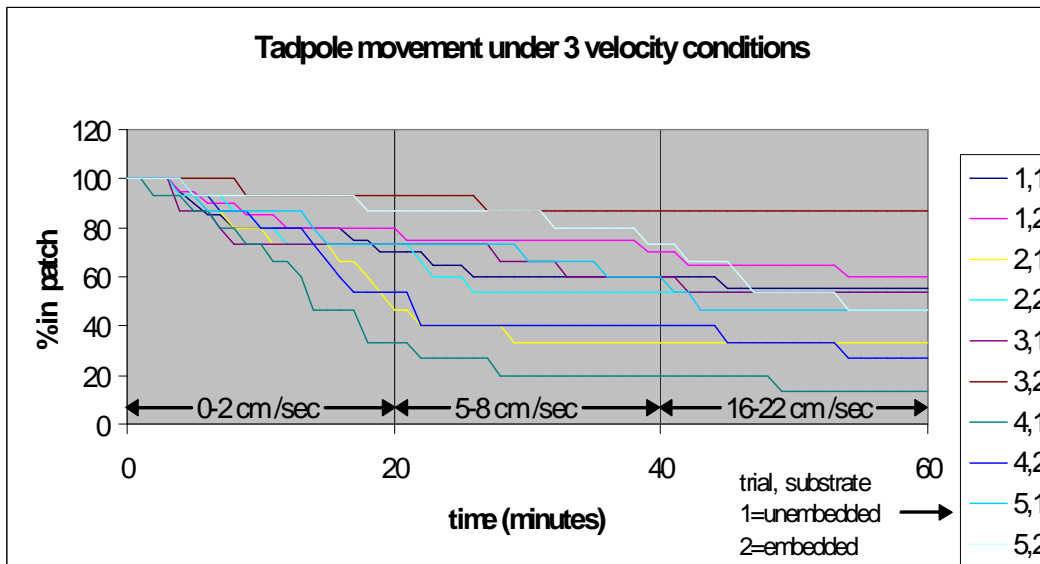
**Figure 4.5. Tadpole emigration from the simulated "cobble bars" to a downstream "pool". Mean slope of the lines in each time period were calculated from least squares regression ($v_1$=1.754, $v_2$=-0.6, and $v_3$=-0.383). Comparisons of these slopes are depicted above in Figure 4.3 and are equivalent to the percent of tadpoles leaving per minute.**

**Table 4.4. 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 $V_2$ and $V_3$, 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 $V_3$ (Figure 4.6). Median burst distance was 0.5m. If bursts are characterized as

short (< 0.5m) versus long (≥ 0.5m), then there was an increase in the proportion of long bursts at $V_2$, but it was not significant ($p$=0.1, Chi Square=4.5, df=2) (Table 4.4).
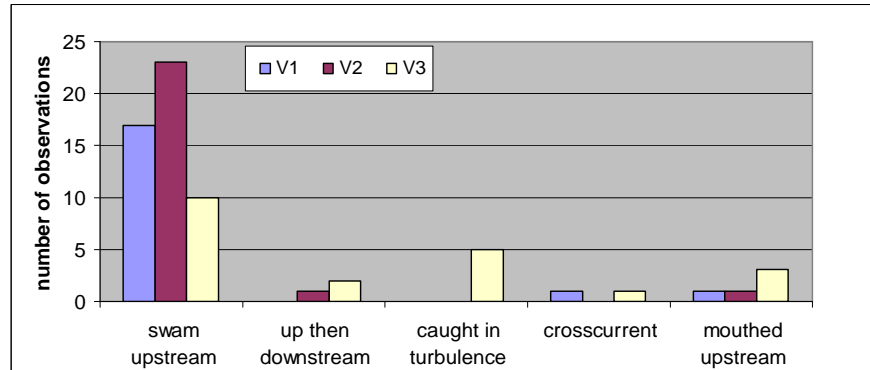


**Figure 4.6. Incidental observations of upstream movement by tadpoles at three velocities.**


**Table 4.5. 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 category | Long bursts<br> # obs. (exp.) | Short bursts<br> # obs. (exp.) | N |
|---|---|---|---|
| 0-2 cm/s | 5 (8.6) | 14 (10.4) | 19 |
| 3-10 cm/s | 14 (10.9) | 10 (13.1) | 24 |
| 16-22 cm/s | 5 (4.5) | 5 (5.5) | 10 |
| Total N | 24 | 29 | 53 |

The results of the flume experiment illustrate the short term behavioral response to seek refuge in the substrate when velocity increased. Many stream-associated tadpoles are essentially fossorial (Handrigan and Wassersug 2007), meaning that they take shelter from the current in cracks and crevices, or in one species actively burrowing in gravel (Haas 2006). These taxa are elongate with relatively small cross-sectional areas, a body shape generally suited to negotiate interstitial spaces (Gans 1975, Nodzenski et al. 1989, Inger & Wassersug 1990). To a modest degree, *R. boylii* tadpoles used this strategy in the flume experiment. At low velocity, tadpoles swam throughout the flume. At the moment the pumps were switched up to the next velocity level and tadpoles experienced increased velocity, they briefly swam against the current, drifted, and then sank or swam to the bottom, where they remained relatively inactive. Although tadpole activity at $V_2$ was not significantly different from $V_1$, there was a significant decrease in emigration from the patch. Similarly the significant differences in activity level between $V_2$ and $V_3$ were not accompanied by significant differences in emigration rate. As velocity increased from $V_2$ to $V_3$ tadpoles sought refuge behind rocks and wiggled down into very small crevices, such as the space between the rocks and the bed foam, or between the pebbles used to fill gaps between the foam bed and the wall of the tank. Some individuals found more protected spots than others, and those that left the patch at $V_3$ did so because they

could no longer maintain their position. Thus the emigration at $V_3$ and $V_1$ are qualitatively different. During the pilot experiment with Mad River tadpoles at $V_4$ (40-50 cm/s), all tadpoles were immediately flushed out of the experimental patches. The critical velocity range between 20-40 cm/s, could not be achieved with the permutations of pump arrays available at the Redwood Sciences Lab facility, so a change in experimental venue was necessary.

To study the critical velocity for displacement and how response varies with developmental stage, this experiment was modified and repeated during 2006 using a smaller scale flume with fine scale velocity control (see next section 4.3).

## 4.3.   Individual Swimming and Sheltering Performance Testing: Measurement of Critical Velocity in a Brett Chamber

Critical swimming velocity ($U_{crit}$) is a measurement of the maximum current velocity at which a tadpole can either swim or maintain its position. Observations were made using a modified Brett-type, re-circulating swimming flume (Brett 1964) at the Center for Aquatic Biology and Aquaculture at UC Davis, July – Sept. 2006. In the main experiment and a secondary experiment, small cobbles and pebbles were provided as substrate to create small scale flow refugia within the chamber (Figure 4.7). In a third ancillary experiment, tadpoles swam in low velocity trials without substrates.

### 4.3.1.  Brett Chamber Methods

Velocities with and without rocks in the chamber were calibrated using an electronic flow meter (Marsh-McBirney, Flomate). Swim chamber dimensions were 9.1 cm in diameter and 24 cm in length. Experiments consisted of replicate trials (Expt I n=57, Expt. II n=13, Expt. III n=8) in which tadpoles were tested individually. Trials were conducted between 9:30 and 21:00 h. Trials were observed remotely on a video monitor via a camera mounted above the chamber, with behavior and location noted throughout the trial. Illumination above the swimming section of the chamber was 500 Lux.

Tadpoles across a range of developmental stages (Gosner 27-41) were collected at each of the three focal watersheds (Alameda Ck July 18, SF Eel Aug 6, and NF Feather Aug 11, 2006). Tadpoles were held in 155 l tanks in a mixture of water from their natal habitat and well water, under a natural photoperiod.  Tadpoles were provided with algae covered rocks from their natal streams and *ad libidum* supplements of dried algae (*Spirulina*) tablets. After swimming trials, tadpole body length, body height, tail length and tail height were measured to the nearest mm, and weighed to the  nearest 0.1 g. Tadpoles were examined with a 10x magnifying lens to determine Gosner stage. In the first Brett chamber experiment all tadpoles swam between 2 and 4 days after being transported to the laboratory. In the second experiment, Alameda Ck tadpoles which had been held in the laboratory for four weeks swam for a second time. These tadpoles grew while in captivity, but because of the relatively low water temperatures (approx. 18˚ C) they did not develop, i.e. did not increase in Gosner stage. The performance of these tadpoles was compared to similarly staged, but significantly smaller, NF Feather tadpoles to tease apart developmental constraints from the effects of body size alone. An example of a developmental constraint as tadpoles approach metamorphosis is the growth of lungs, which

alters buoyancy and surfacing behavior. An example of a size constraint is the increase in drag forces as a tadpole grows. Similar to the Alameda Ck tadpoles in Brett Expt. II, the NF Feather tadpoles used were also swimming for a second trial.

Individual tadpoles were placed in the chamber at 0 cm/s velocity and allowed to acclimate for 5 min. Velocity was increased every 5 min by $3.3 \pm 0.2$ cm/s. When the tadpole tired and was immobile on the downstream end of the tube (impingement), velocity returned to zero. After a 2 min rest, the trial continued, with a return to the first impingement velocity. The protocol continued until a 2nd impingement. Velocity was returned to zero and the tadpole was recovered, measured, and returned to a holding tank.

In the first two experiments, $U_{crit}$ was calculated using the equation: $U_{crit} = U_i + [U_{ij}(T_j \cdot T_i^{-1})]$. $U_i$ is the highest velocity (cm/s) maintained for the prescribed time. In the protocol, time steps were 5 minutes with an average increase in velocity of for each time step interval. $U_{ij}$ is the incremental increase in velocity from $U_i$ to the fatigue velocity, $U_j$, i.e., the velocity at which the tadpole impinges a second time on the downstream end of the swimming chamber. $T_j$ is the time elapsed at the fatigue velocity and $T_i$ is the prescribed swimming time.

Brett Expt. III focused on stamina, rather than $U_{crit}$. Duration of time in which tadpoles could maintain position at 5 cm/s was observed *without* rocks in the chamber. This was the lowest incremental velocity used in Expts. I and II.

The effects of source population and tadpole size on $U_{crit}$ were assessed using Analysis of Covariance (SYSTAT version 11). The size variable used in the analysis was ln(body mass) because it was highly correlated with other measures of size (body length r=0.94, tail length r=0.92) and Gosner stage, (r=0.87). Correlations between trial start time and $U_{crit}$ were calculated assess if there were any diel patterns in performance.

**Figure 4.7. Brett type recirculating flume chamber (upper left) and video monitor (upper right). Close up image of tadpole (circled in lower left) and the direction of flow (arrow) inside the chamber.**

### 4.3.2. Brett Chamber Critical Velocity Results and Discussion

Several factors, which all co-vary, contributed to tadpoles' ability to withstand elevated velocity. Critical velocity varied with developmental stage, body size, and population of origin (Table 4.6, Figures 4.8). Vulnerability appeared to increase as tadpoles approached metamorphosis (Figure 4.9). For many individuals, critical velocities fell within 20 – 40 cm/s, the range that could not be produced in the artificial stream channel given the pump arrays available. There were differences among the source populations, with the populations having larger body size displaying lower critical velocities. Analysis of Covariance (Table 4.7) suggests that population differences alone may be important but were not statistically significant ($p$=0.07). The primary determinant of susceptibility to displacement was tadpole size. There was a positive, but statistically not significant, relationship between the time of day of a trial and tadpole performance (r=0.24, $p$=0.09). Consistent with results from the artificial stream channel experiment, the key behaviors for maintaining position were finding micro-eddies and using mouthparts for sucking on to the substrate or the chamber wall.

The conditions sufficient to sweep tadpoles out of refugia under experimental conditions are lower than velocities observed in the field during real pulsed flows. In the NF Feather, Poe and

Cresta reaches, the mean flow velocity observed at FYLF sites during recreational flows is 31 cm/s (GANDA 2005). Tadpoles are typically found in patches with velocities 0-5 cm / sec. In the Brett chamber (Expt. I), mean critical velocity was approximately 25 cm/s, but velocities as low as 10 cm/s caused 25% of those tadpoles tested to reach exhaustion and be displaced. The duration of the trials (36.34 ± 2.75 minutes to exhaustion in Brett Expt. I) was also much shorter than pulsed flows manufactured for recreation, 12 - 18 hours.

**Table 4.6. Results of Brett Chamber trials with rocks present (Expt. I)**

| Source Population | n | Mean $U_{crit}$ (±1 s.e.) | Gosner stages (range, median) |
|---|---|---|---|
| Alameda Ck | 22 | 16.6 ± 2.2 | 27-41, 34 |
| SF Eel | 17 | 23.6 ± 3.7 | 30-42, 35 |
| NF Feather | 18 | 25.9 ± 3.0 | 28-40, 34 |

**Table 4.7. ANCOVA of Critical Velocity in Brett chamber (Expt. I)**

| Source | Sum of Squares | df | F-ratio | p |
|---|---|---|---|---|
| Population | 694.4 | 2 | 2.8 | 0.07 |
| ln(mass +1) | 2370 | 1 | 19.4 | <0.001 |
| Error | 6463.4 | 53 | | |
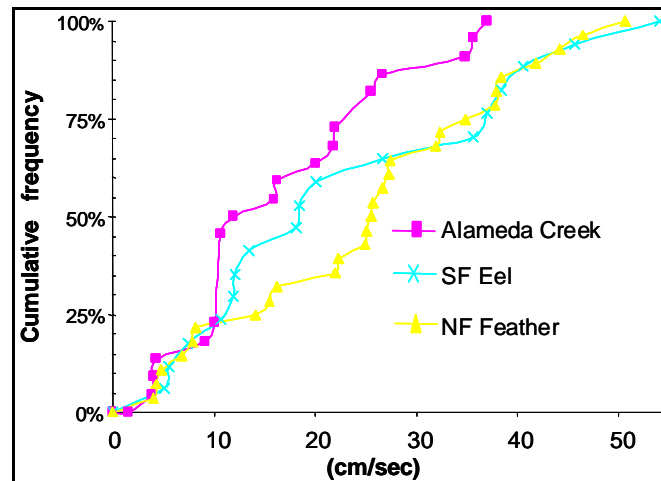


**Figure 4.8. Cumulative distribution of critical velocities of individual tadpoles. tested in a Brett chamber Expt. I flow refugia (i.e. rocks) present. For a given velocity, the height on the curve represents the portion of the test population that could not maintain position. Trial duration = 36.34±2.75 minutes, range 7.08 - 80.28.**
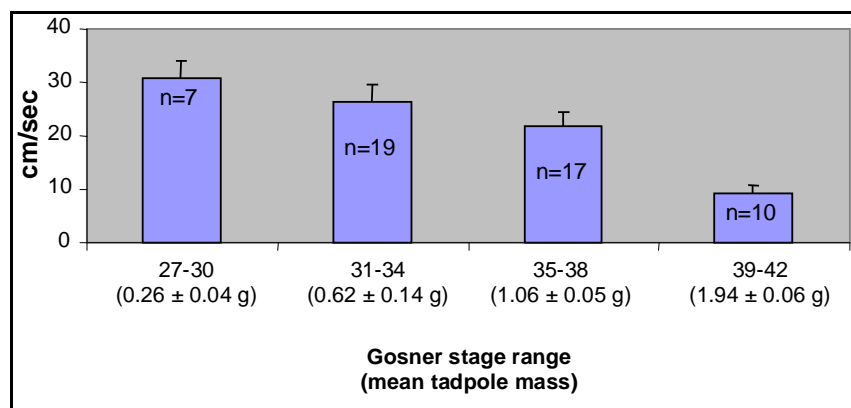
**Figure 4.9. Critical velocity as a function of tadpole size and developmental stage (Brett chamber Expt. I).**

Data from subsequent trials (Brett Expt. II) retesting tadpoles that had been held in tanks for a period of a few weeks and which grew to larger sizes, without much development, corroborate the results of Brett Expt. I that large tadpoles have significantly lower critical velocities than small tadpoles (Table 4.7). In Expt.I, mass was tightly correlated with developmental stage so it is unclear whether bigger tadpoles had poor performance maintaining position in the interstitial spaces among the rocks in the Brett chamber by virtue of their size, or because of morphological changes such as large hind limbs which can increase frontal drag on a stationary tadpole and decrease swimming performance (Dudley et al 1991, Wassersug and Sperry 1977). In addition to the obvious external changes, later stages have internal changes including the development of lungs which affect buoyancy and hardwired neurological behaviors such as surfacing to re-inflate lungs periodically in response to increasing $CO_2$ concentrations (Gdovin et al. 2006).

The pattern of decreasing critical velocity with tadpole size is counter to expectations about performance based on the positive relationship between burst swimming speed and tadpole size (VanBuskirk and McCollum 2000; Wassersug and Hoff 1985) but are consistent with recent work illustrating the importance of the relative proportions of body and tail size (Kaplan 2006) to swimming performance. Generally, there is a positive allometry between the total length of a tadpole and maximum swimming velocity, $U_{max}$, and acceleration, meaning that the rate of increase in speed is proportionally greater than the increase in length that occurs as a tadpole grows and develops (Wilson and Franklin 2000). When comparing tadpoles with a range of body plans, there is a general conclusion that relatively deeper tail fins and tail muscles and smaller bodies facilitate increased burst swimming speed (Dayton e al. 2005). Specifically, with respect to interpreting the results presented here, it is important not to confuse this measure of performance, critical velocity, $U_{crit}$, with $U_{max}$. Poor performance of large, yet still pre-metamorphic, tadpoles in Expts. I and II may be explained by the metabolic costs of swimming faster leading to shorter endurance. Poor performance of large tadpoles may also be due to a smaller strength to weight ratio. Smaller tail area relative to body mass is correlated with lower $U_{crit}$ (Figure 4.10). In other words, the "fat" Alameda Ck tadpoles in Expt. II, may have had over- all larger tails which should lead to better propulsion, but had bigger bodies to propel.

68

In addition to swimming performance, the ability to avoid impingement under the experimental conditions involved other factors such as stamina and mouth suction. Although large size and high burst speed confer a selective advantage in terms of avoiding predation in a low velocity environment (Chovanec 1992) where it is possible to rest after exertion, in a higher velocity environment large size may be disadvantageous because of negative effects on the ability to rest. Larger bodies cannot fit inside the boundary layer of low velocity flow near the river bottom relative to the higher velocities in the water column, or there may be a decrease in mouth suction strength relative to body mass.

It is important to note that the stamina of tadpoles to withstand velocity is short relative to the duration of typical pulsed flows. In the absence of flow refugia (Expt. III), mean (± 1 s.e.) time to impingement at v= 5 cm/s is 7.4 ± 2.6 min, with a maximum of 25 min (Figure 4.11). In the presence of refugia (Expt. I), maximum duration was 85 minutes. Pulsed flows for white water boating have durations on the scale of many hours up to a day or back to back flows on successive weekend days.

**Table 4.8. Critical velocity of relatively larger, but same stage (34-36) tadpoles from Alameda Ck compared to the performance of NF Feather tadpoles in Brett Chamber Expt. II.**

| Variable (mean±1s.e.) | Alameda (n=7) | NF Feather (n=6) | t | df | p |
|---|---|---|---|---|---|
| Ucrit (cm/s) | 11.1±2.4 | 28.1±5.6 | -2.8 | 7 | 0.027 |
| Mass (gm) | 1.73±0.36 | 0.95±0.06 | | | |
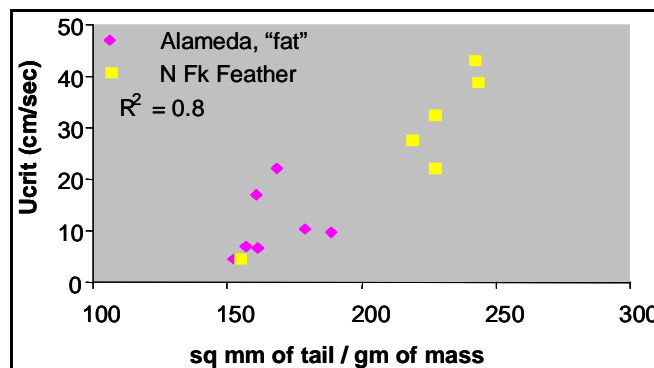


**Figure 4.10. Critical velocity in Brett chamber Expt. II is positively correlated with weight specific tail area.**

69
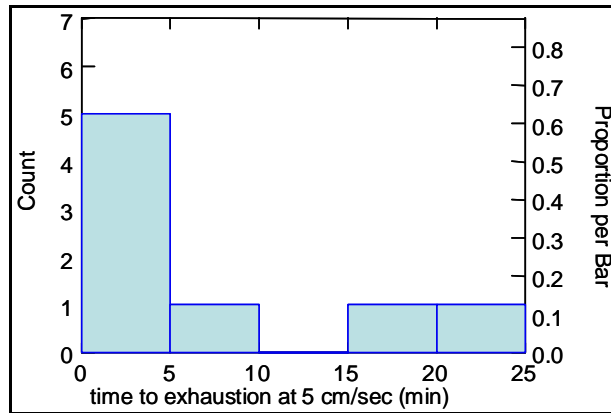
**Figure 4.11. Frequency distribution for time to exhaustion. Tadpoles exposed to 5 cm/s velocity without rocks (Brett Chamber Expt. III). Mean ± 1 s.e.= 7.4 ± 2.6 mins.**

## 4.4. Cumulative Effects of Velocity: Energetic Costs / Predation Risk

To evaluate the cumulative impact of the observed behavioral responses, that tadpoles seek refuge in the interstices and only a small proportion successfully return to their original microhabitat, longer term manipulations focusing on survival and growth were conducted by placing flow-through enclosures in different velocity environments in the SF Eel River and Alameda Ck. As flows declined through time in these unregulated rivers, and as the mesh sides of the enclosures in faster flowing locations became covered with debris, the velocity conditions in treatment enclosures became similar to control enclosures. Then baskets were relocated closer to the thalweg, thus re-imposing the velocity stress. The intervals between relocation of baskets (7-10 days) did not always allow for total return to control conditions, so that the velocity stress imposed should be considered intermediate between episodic and constant. The experimental design assumes that the mechanisms by which sub-critical velocity causes harm are consistent under episodic and constant application. The manipulations were not intended to mimic the pulsed-flow schedule of any particular regulated river, but were carried out to detect effects that might be difficult to discern from natural variation over a single pulsed flow. Another justification for prolonged experiments is that there are some flow alterations that occur over an extended number of days (e.g. see Figure 3.2, the spring hydrographs for the Sunol reach of Alameda Ck, 2005 and 2006) or repeatedly, as in power peaking projects.

In 2005, a pilot trial (Rearing Expt. I) was conducted at the SF Eel. In 2006, Rearing Expts. II and III were conducted to more rigorously replicate the pilot and address questions not previously covered. Specifically, what are the effects of velocity on recent hatchlings? Does the behavioral response to velocity expose tadpoles to increased risk of predation?

### 4.4.1. Methods of Tadpole Rearing

### 2005 Methods

Tadpoles were enclosed in plastic laundry baskets with 1 mm fiberglass mesh glued over the openings and reared in a high or low velocity environment (Figure 4.12). Tadpoles came from a single clutch. At approximately 2-3 weeks post-hatching on July 3, tadpoles were divided among 12 replicates, 25 per enclosure. Mid-way 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.



**Figure 4.12. Flow through rearing enclosures, left shows the interior of a high velocity treatment.**

As stage height declined, velocity differences between the treatments narrowed. Four times during the course of the experiment, at approximately 10 day intervals, enclosures were moved further from shore to re-establish the velocity differences between the two treatments. Depth was 15-20 cm, within the natural range of tadpoles observed at the site. At each movement of enclosures, surface velocity was measured using the float method, timing movement from the upstream to the downstream end of the basket. On two dates the surface flow measurements inside each enclosure were verified using a Marsh Courtney flow meter with surface, mid-column and bottom velocity measurements. Low velocity tadpoles experienced mean mid column velocity = 1.65 ± 0.26 cm/s. In the elevated flow treatment, mean mid-column velocity at time of moving the baskets was 8.8 ± 0.6 cm/sec. Tadpoles were fed *ad libidum*. Enclosures were stocked with rocks covered with algae along with copious loose algae and dried aquarium algae tablets. Temperature data loggers were placed in each enclosure. Water temperature was recorded hourly for the five week duration of the experiment. Tadpole snout–vent length, tail length (mm), weight (mg), and developmental stage were measured on August 8, 2005.

Treatment effects on tadpole size and development in Rearing Expt. I 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 wise error rate of α=0.05.

### *2006 methods*

Rearing and field swimming experiments were repeated at a remote site on the unregulated reach of Alameda Ck (see chapter 3 for full site description). For Rearing Expt. II, 25 full sibling tadpoles were placed in 15 replicate flow-through enclosures, similar to the initial density conditions used in Expt. I. Enclosures were deployed across a range of velocities, from 1 to 13 cm/s. Survival of recent, < 1 week old, full-sibling hatchlings was observed over a two week period, May 12-May 25, 2006.

### *Predators*

In rearing in Expt. III, 22 baskets were placed in pairs (with and without predators) over a range of water velocities. Tadpole density was set at 15/enclosure, to allow comparisons to Expt. I. At seven weeks post-hatching, (6/22/2006), densities were again equalized among enclosures at 5/enclosure. After 7/14/2006 stream stage became too low to maintain the velocity treatment, so data from that date are considered the end point of the experiment. Treatment effects were assessed for both the unequal density period and the end point of the equalized low density period of the experiment.

The predation treatment was modified to reflect the dynamics of a system in which both predators and prey are growing, and in which there are phenological shifts in tadpole susceptibility and invulnerability to benthic macroinvertebrates common at the site. Megalopteran alder fly larvae (*Sialis* sp), 1 per enclosure, were added at the start of the experiment, May 25, 2006, with three-week old tadpoles. When tadpoles outgrew susceptibility to megalopteran larvae, the predators were switched to dragonfly nymphs (*Aeshna* sp), on June 8, 2006. By July 7, tadpoles had outgrown these predators with respect to lethal effects, but there was tail injury.

### *Velocity*

Baskets were set out in pairs (with or without a predator) in a variety of velocity environments dispersed along a sequence of three pools and riffles. At 7 -10 day intervals, enclosures were moved and mesh was scrubbed to re-establish the velocity treatments and maintain depth (15-20cm). Velocity treatments were variable and elevated vs. low and stable. By allowing the mesh screens of the elevated velocity enclosures to clog with detritus and algae, velocity approached control levels. See Figure 4.13 for a typical change in flow due to clogging of mesh. It became difficult to sustain the high velocity treatment past the second week of July because hot weather caused stage to drop dramatically and swift flowing sites were sparse, mostly limited to very shallow riffles inappropriate for basket placement (Figure 4.14).
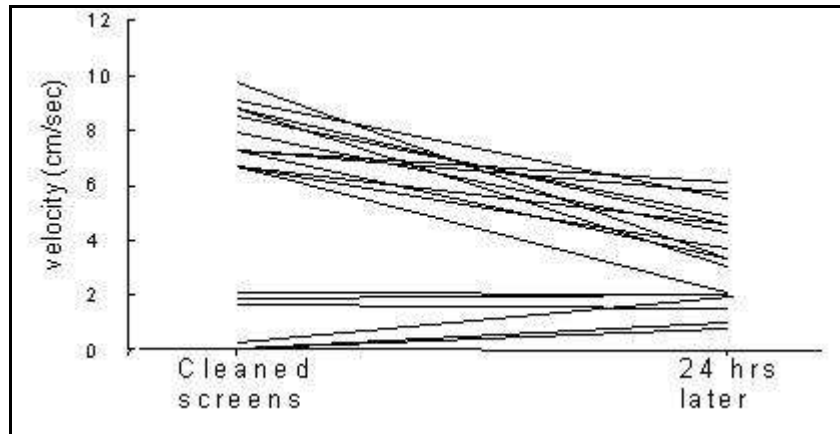
**Figure 4.13. Change in velocity due to clogging of screens.**
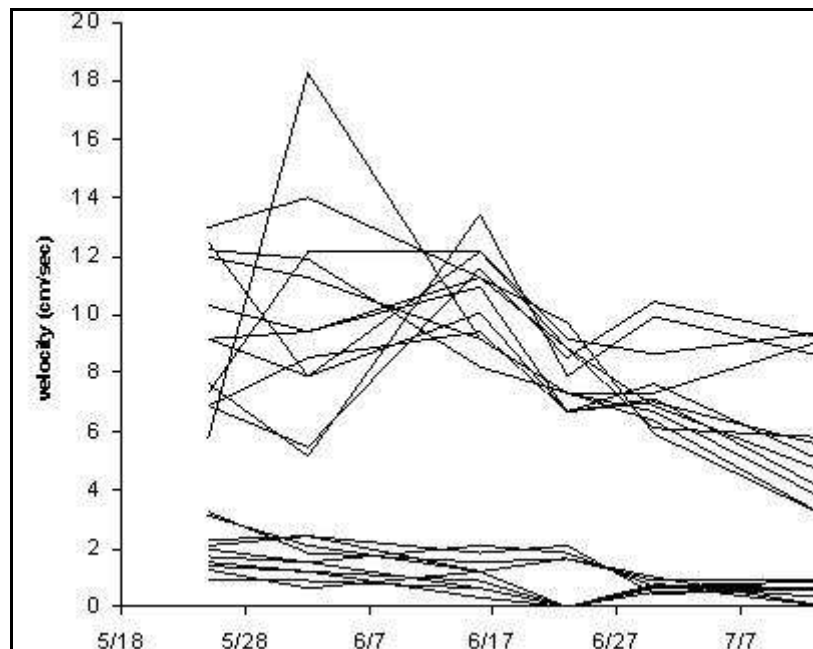


**Figure 4.14. Velocity after enclosures were cleaned and moved during the course of Rearing Expt. III.**

### Feeding and growth

Tadpoles grazed periphyton from rocks and loose algae that were replaced weekly. Tadpoles were weighed and measured weekly or bi-weekly over 10 weeks. Tadpoles were briefly removed from the water to measure length with a ruler. Weight (mg) was measured by placing tadpoles in a tared container of water on a field balance. Tadpoles were weighed in batches until heavy enough to be measured individually, and a mean per capita mass calculated for each enclosure. Tadpole density in Expt. III was set at 15/enclosure, to allow comparisons to Expt. I. At seven weeks post-hatching, (6/22/2006), densities were again equalized among enclosures at 5/enclosure. Treatment effects were assessed for both the high density period and the low density period of the experiment.

### Statistical Analyses

The effect of velocity on hatchling survival in Rearing Expt. II was assessed using linear regression. In Expt. III, predator and velocity effects were evaluated on two response variables, survival and growth. For the first period of the experiment, effects on survival were tested with repeated measures ANOVA, treating the presence vs. absence of a predator and velocity as fixed factors. When growth was the response variable, multiple regression was used with tadpole density (which varied among enclosures due to presence and effectiveness of predators) and velocity as the independent variables. For the second period of the experiment when the treatments did not yield continuous variation in velocity and predator effects, growth data were assessed with two factor ANOVA. Data from all the individuals within each replicate enclosure were pooled by calculating a mean size. Analyses were conducted using Systat 11(Wilkinson 2005).

## 4.4.2. Results and Discussion of Larval Rearing Experiments: Cumulative Effects of Velocity Manipulation

### 2005 pilot larval rearing experiment

Tadpoles raised at elevated velocities were significantly smaller, and less developed than tadpoles reared at low velocity (Table 4.9). On average, elevated velocity tadpoles weighed half as much as low velocity tadpoles.

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 ºC, t=-0.40, *p*=0.97), and tadpoles were fed *ad libidum*. 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.

**Table 4.9. *R. boylii* tadpoles exposed to elevated and variable velocities (Rearing Expt. I) were smaller and less developed than tadpoles reared continuously at low ambient velocities (*p*-values adjusted for multiple comparisons).**

| Response Variable | Low velocity (1.65 ± 0.26 cm/s) n=6 enclosures, 15 larvae/enclosure | Elevated velocity (8.8 ± 0.6 cm/s) 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 |

### 2006 larval rearing experiments—survival effects

Velocity had negative effects on tadpole survival. In rearing Expt. II there were direct lethal effects of velocity on hatchlings, ages 1 to 3 weeks old (Figure 4.15). In Expt. III, where tadpoles were reared in the presence or absence of a predator, there were significant negative effects of

both velocity and predators on survival during the period from three to seven weeks post-hatching (Figure 4.16, Table 4.10). In the absence of predators there was little difference (0.6 fewer tadpoles) in mean survival between the elevated velocity ($\bar{v}$ week0-4=8.3 cm/s) and low velocity ($\bar{v}$ week0-4=1.3 cm/s) enclosures. In contrast, when a predator was present, the velocity effect size was on average a difference of 3.24 tadpoles. This difference suggests that predator and velocity effects may be multiplicative. However, the interaction term in the repeated measures ANOVA (Table 4.10) is not statistically significant ($p$=0.1). The apparent increased vulnerability to benthic predators could be due to two factors. First, tadpoles spend more time under rocks when velocity is elevated so the proximity to predators increases. Second, the elevated velocity tadpoles grow more slowly than the low velocity tadpoles and may thus be more vulnerable by virtue of their small body size, and concomitantly lower burst swimming speeds needed for escape (Wilson and Franklin 2000).
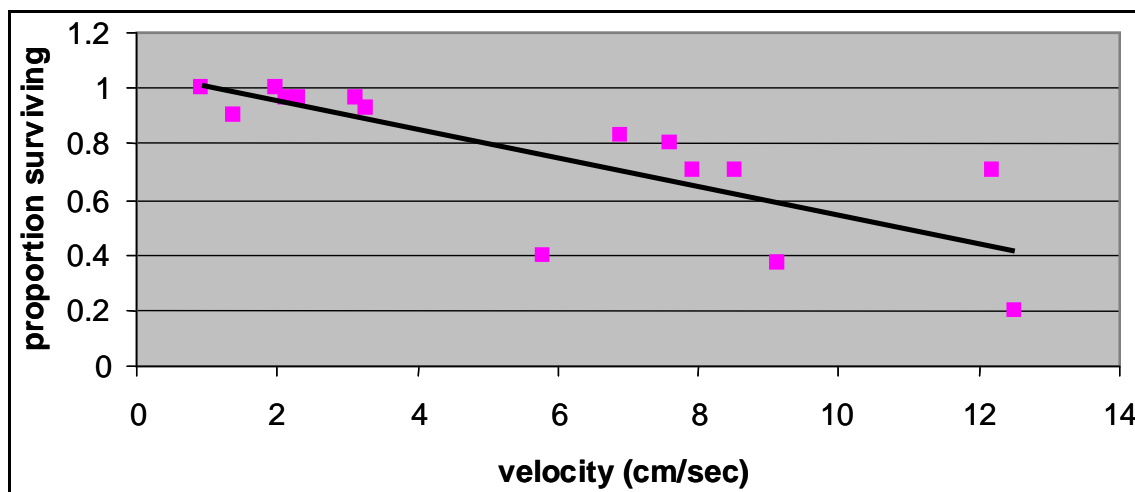


**Figure 4.15. Hatchling tadpole survival over a two week period was significantly negatively affected by velocity inside enclosures during Rearing Expt. II. (F=20, df=1,13, $p$=0.001, $r^2$=0.61).**

**Table 4.10. Repeated measures two way Analysis of Variance of log transformed number surviving (data illustrated in Fig. 4.16 above) over 4 weeks in Rearing Expt. III.**

| Source | Mean Square | Wilks'Lambda | df | F | p |
|---|---|---|---|---|---|
| Analysis of differences (Multivariate ANOVA) | | | | | |
| Time | | 0.42 | 3,16 | 7.4 | 0.002 |
| Time x Velocity | | 0.56 | 3,16 | 4.2 | 0.022 |
| Time x Predator | | 0.49 | 3,16 | 5.6 | 0.008 |
| Time x Velocity x Predator | | 0.74 | 3,16 | 1.9 | 0.172 |
| Between  (ANOVA) | | | | | |
| Velocity | 0.95 | | 1 | 5.5 | 0.03 |
| Predator | 2.49 | | 1 | 14.5 | 0.001 |
| Velocity x Predator | 0.48 | | 1 | 2.8 | 0.11 |
| Error | 0.17 | | 18 | | |
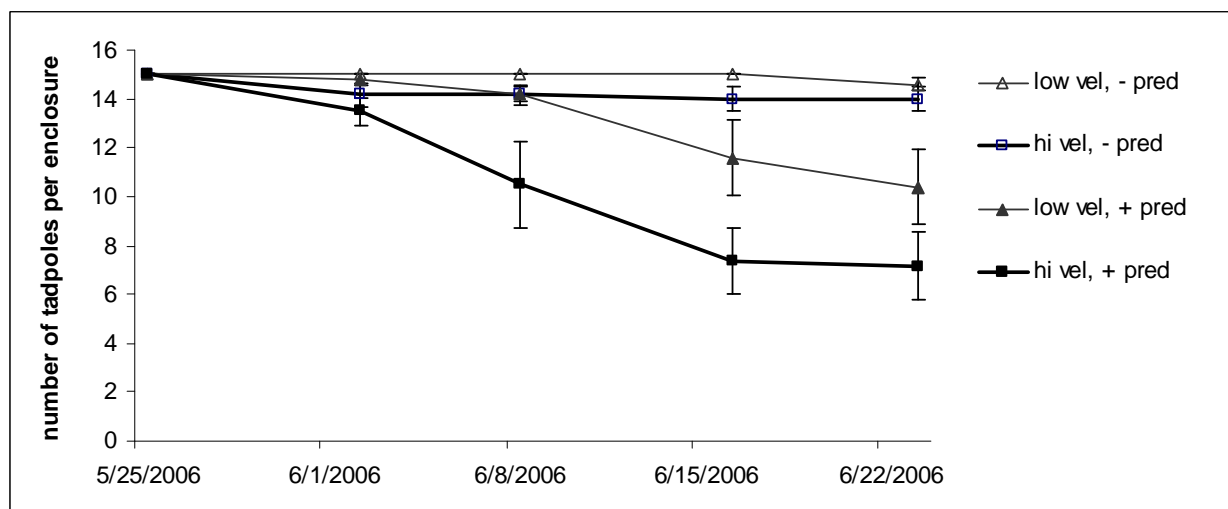


**Figure 4.16. Number of tadpoles surviving from ages 3 to 7 weeks at ambient and intermittently increased velocity in the presence or absence of an insect predator (Rearing Expt. III).**

## *2006 larval rearing experiments—growth effects*

Across the range of velocities created within the enclosures, density effects were observed. This means that when mortality occurred, either due to predators or velocity, the surviving tadpoles responded by growing larger, indicating a release from intraspecific competition (Figure 4.17). Multiple regression analysis (Table 4.11) shows that per capita tadpole mass is negatively affected by both density and velocity.

After densities were equalized among treatments, and the intensity of the velocity treatment was reduced relative to the early weeks of the experiment, growth continued in a similar pattern, with elevated velocity tadpoles being the lightest from week 7 to week 9, but then by week 11, the low velocity tadpoles were lighter (Figure 4.18). Possible explanations for smaller body mass in the low velocity enclosures could include stress, if the water became too stagnant or too warm.
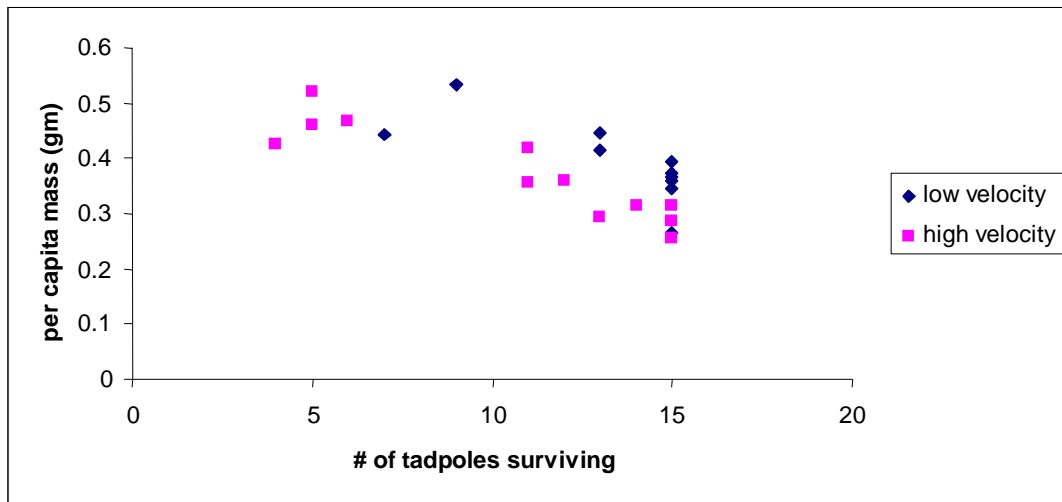


**Figure 4.17. Relationship between density and tadpole mass in rearing Expt. III**

**Table 4.11. Multiple regression of log transformed per capita tadpole mass on 6/30/2006 (data illustrated in Figs. 4.16 and 4.17) in Rearing Expt. III. F=21.4, df=2,19, $p$<0.001, n=22 enclosures.**

| Effect | Coefficient | Std Error | t | p |
|---|---|---|---|---|
| Constant | 0.624 | 0.039 | 16.112 | <0.001 |
| Mean velocity in enclosure | -0.007 | 0.002 | -3.063 | 0.006 |
| Tadpole density in enclosure | -0.017 | 0.003 | -6.403 | <0.001 |
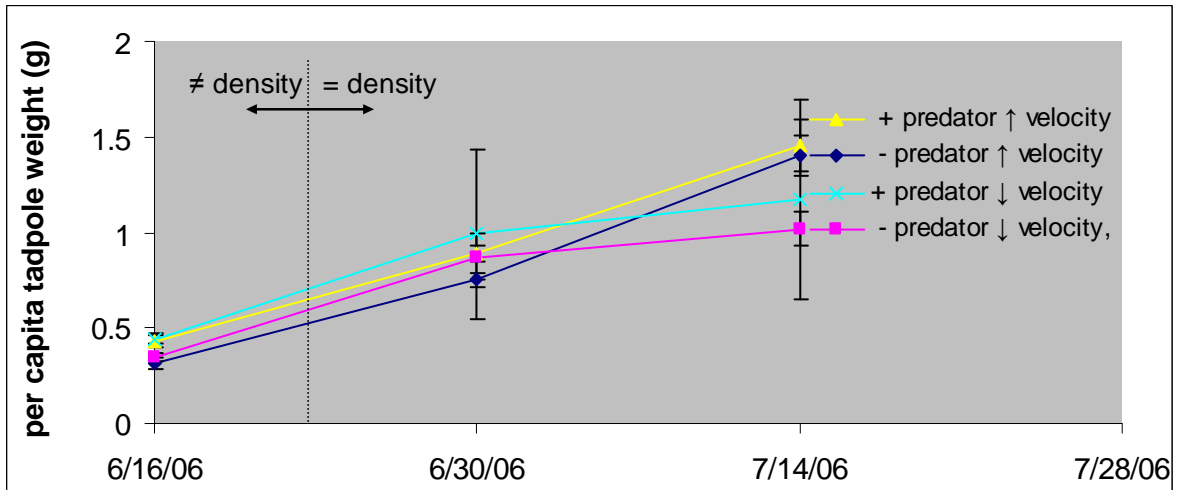
**Figure 4.18. Growth trajectories in Rearing Expt III.**

## 4.5. Velocity Manipulation in the Field: Instream Flume, Drift Fence and Open River Translocation

To assess the feasibility of observing tadpole responses to velocity in settings more natural than the experiments described above, a number of pilot experiments were conducted. These methods were not pursued to a desired level of replication and rigor due to logistical restraints. Setting up and taking down each trial was time consuming and physically difficult. Also in natural settings, late in the summer, when larger tadpoles were present, it was difficult to find swiftly flowing locations at Alameda Ck. At the SF Eel, where higher velocities were available in August, there was a dearth of tadpoles. Concomitant with a warm period, there was also an outbreak of a parasitic copepod, *Lernaea cyprinacea*, which caused mortality and poor condition, such as secondary fungal infections. Thus, there were insufficient numbers of healthy individuals in the field when the flume was set up.

### 4.5.1. Instream Box Flume Methods

A flume box (2m x 1m x 0.5m) was constructed with a plywood bottom, a 12 cm high plywood lip at the base, and vexar window screen mesh side walls. The box was placed in a riffle and stocked with cobbles and gravel to completely cover the bottom of the box. Finer mesh shade cloth was wrapped around the flume box to create a low velocity "baseflow", and then removed in stages to create a higher velocity "pulsed flow". Groups of 20 tadpoles between stages 37 and 40 were stocked in the flume box and allowed to acclimate 20 minutes prior to the pulse. The trials ran overnight for approximately 18 hours, from late afternoon (~16:00) until the following morning (~10:00). Mean tadpole size was 0.92 ± 0.02 g. Median grain size was 32 mm (from Wollman pebble count), maximum 128 mm. Mean velocity, (measured in a regular grid pattern), was 3.3 ± 5.0 cm/s at base flow. In trial 1 the mean pulsed flow velocity was 16.5 ± 0.5 cm/s. In trial 2 the mean pulse velocity was 20.1 ± 2.8 cm/s. The spatial heterogeneity of velocity is depicted in Figure 5.18. During the pulsed flow the flume was open at downstream end. As

tadpoles were entrained in the current they were swept out of the test patch. At the completion of a trial the end screen and fine outer mesh were replaced and tadpoles counted. The tadpoles were so cryptic and difficult to locate in the substrate that it was necessary to completely remove all rocks at the end of the trial to ensure an accurate count of the individuals remaining.
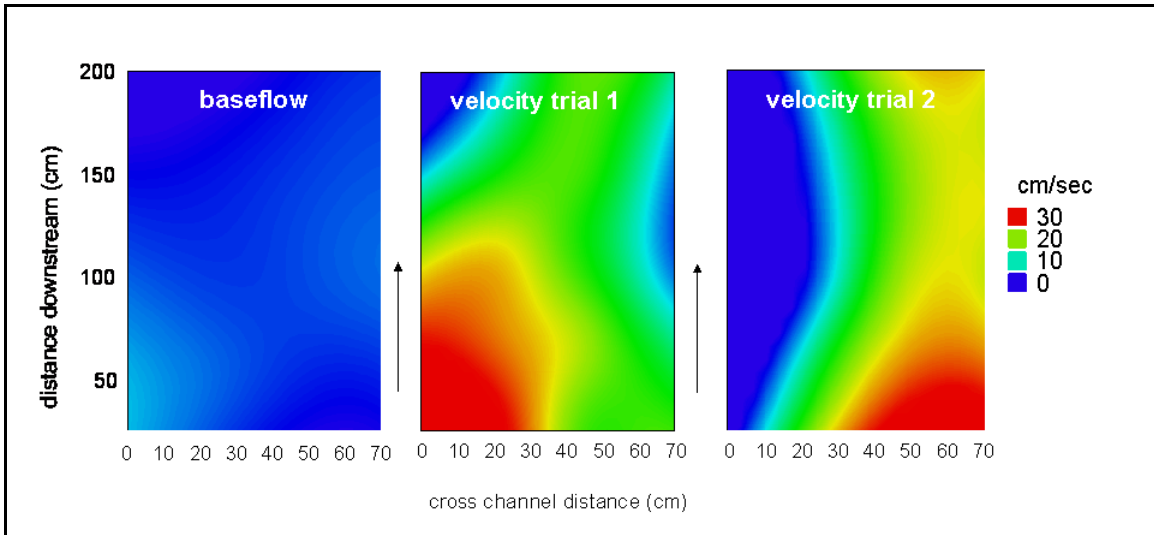


**Figure 4.19. Velocity maps in box flume deployed at Alameda Ck. Arrows indicate direction of flow.**

### 4.5.2. Drift Fence Relocation Methods

To determine whether larvae can return to shore, a pilot manipulation was conducted upstream of a drift fence. A fence was 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 (Fig. 4.18). 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. Tadpole size in this trial was $16 \pm 0.48$ mm total length (mean $\pm$ 1 s.e., n=50). The trial began at approximately 14:00. 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.

Froude number of each grid square was calculated. Froude number is defined as the ratio of inertial to gravitational forces:

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

79

where v is velocity, g is gravity and d is depth. Non-parametric Mann-Whitney U Tests compared the Froude numbers of tadpole present vs. absent grid squares.



**Figure 4.20. Drift fence experiment with flags marking the corners of the 0.5 m2 grid squares.**

### 4.5.3. Open Relocation Methods

During July 2005, pilot trials (n=10) were conducted in which individual tadpoles were moved and observed continuously during mid-day hours when the channel received direct overhead sunlight. Tadpoles were displaced 1-3 m shore, then 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, 12-15 mm SVL, and 30-37 mm total length. Tadpole response was assigned to categories: returns to near shore environment, is swept away/disappears, or finds interstitial refuge. Time and distance to one of these endpoints was noted.

### 4.5.4. Results and Discussion of Relocation Experiments

#### Box flume

Two 18-hour long swimming trials were completed at Alameda Ck (Table 4.12). Displacement rates were 40% and 70% of tadpoles swept downstream, while the remaining tadpoles were able to find refugia and maintain position within the test area. This performance overnight is remarkably consistent with the shorter term performance of Alameda Ck Tadpoles in the Brett chamber (Figure 4.8) where the cumulative frequency curve indicates that in range of approx 20 cm/s conditions, about half of the tadpoles were displaced.

#### Drift Fence and Open Relocation

Almost half of the tadpoles, 24, were relocated at the end of the drift fence trial. The whereabouts of the others was undetermined. None were observed against the drift fence, although fish were present near the fence and predation a possibility. The numbers 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 Figure 4.2.1. Mean Froude number of cells where tadpoles were found was $0.06 \pm 0.01$ (n=13) compared to tadpole absent cells $0.16 \pm 0.04$ (n=24). This difference is statistically significant (Chi-square approximation of Mann-Whitney U=34.54, $df$=1, $p$<0.001). Froude number thus appears to be a good descriptor of tadpole microhabitat. Unfortunately, this range of Froude numbers was below the resolution of values predicted when two-dimensional hydro-dynamic modeling (chapter 5) was applied to the same location where the drift fence was set up. The scale at which tadpoles distribute themselves in the near shore environment is at the level of individual rocks, i.e. in the velocity shadows on the lee sides of cobbles and boulders. A hydrodynamic model's delineation of such fine-scale variation in usable habitat as discharge fluctuates is thus limited by the ability to survey the microtopography of the cobbles and boulders which determine the local velocities.
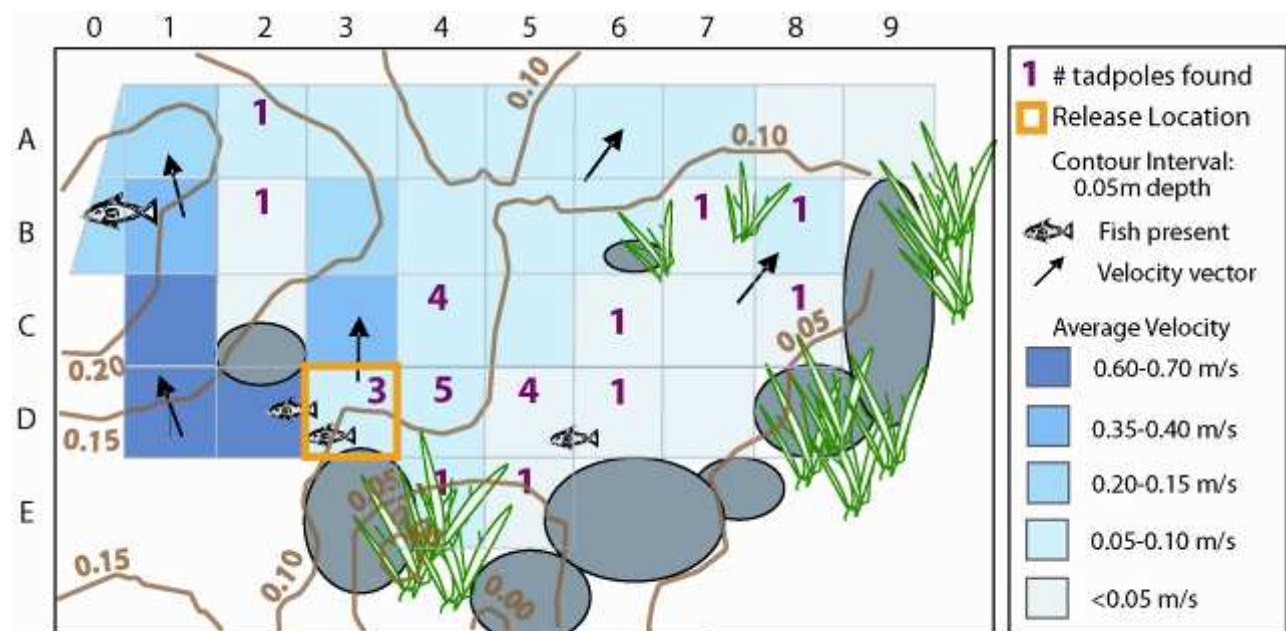


**Figure 4.21. Schematic diagram of drift fence area indicating numbers, locations, depths, and mid-column velocities where tadpoles were found. Fifty tadpoles were released in the square D-3. Area of each grid square is 0.25m$^2$. Ovals represent boulders.**

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 4.12). The mean net distance moved downstream in the drift fence trial was $1.44 \pm 0.24$ m and $0.95 \pm 0.2$ m in the open trial. Unlike swimming in the artificial stream channel, no bursts of upstream swimming

greater than 0.5 m were observed. Most upstream swimming occurred within a few cm of the rocks on the river bottom, apparently within a boundary layer of low flow relative to the water column velocity. Individuals were swept into the current when they came up into the water column.

**Table 4.12. Results of field trials. In-stream flume, drift fence, and open relocation trials lead to 40 to 80% displacement of tadpoles.**

| Final location of larvae | Box flume v=16.5±0.5 | Box flume v=20.1±2.8 | Drift fence v=5-10 cm/s | Drift fence v=5-10 cm/s | Open relocation v=5-10 cm/s | Open relocation v=5-10 cm/s |
|---|---|---|---|---|---|---|
| | Trial 1 (n=20 larvae, in one batch) | Trial 1 (n=20 larvae, in one batch) | Trial 1 (n=50 larvae, in one batch) | Trial 4 (n=14, 1 larva at a time) | distance (m) (mean±1s.e.) | time (min) (mean±1s.e.) |
| Returns to shore | n/a | n/a | 18% | 0% | 0 | 0 |
| Swept away/ disappears | 40% | 70% | 52% | 80% | 0.94 ± 1.0 | 8.8 ± 2.4 |
| Finds refuge | 60% | 30% | 30% | 20% | 1 ± 0.0 | 7.7 ± 2.4 |

In general, the behavior of tadpoles in the open river relocation trials was consistent with the behavior observed in enclosure and laboratory trials. However, the open methods were time intensive and not easily repeatable, yielding few replicates for the effort. These methods were not pursued, but the results are discussed to verify that the responses in the more artificial settings are realistic. With respect to comparing our techniques to those used previously in FERC related studies on the effects of aseasonal pulsed flows, tadpole detectability is a critical issue in evaluating the efficacy of different methods. Estimating detectability and accounting for the errors from the use of uncorrected count data is a subject of growing awareness in conservation (MacKenzie & Kendall 2002; MacKenzie et al. 2003; Schmidt 2004). For the open river experiments, tadpoles could not be reliably detected for prolonged periods. Even in the contained system venues, accounting for all individuals when groups of tadpoles were tested was difficult. It was necessary to remove every rock from the artificial stream channel and flume box and remove tadpoles one by one to get accurate counts at the end of a trial. Visual counts were not reliable indices of actual number, because the tadpoles are extremely cryptic.

For observational studies pre and post-boating flows (GANDA 2005), similar sampling techniques are possible but would be difficult to execute in a rocky stream and would require special statistical techniques for analysis. "Before and After" quadrat counts could be done using a box with a foam perimeter that conforms to the stream bottom preventing tadpole escape. Rocks, if small enough, could be temporarily moved to count tadpoles. Tadpoles could be given time to recover from the disturbance before the box is taken away. Similar counts could be conducted after the pulse. Prior to boating flows, moving rocks and disturbing a study site could confound the disturbance effects of the pulsed flow itself, so counts would need to be compared to the difference in counts from quadrats at a control site not subject to pulsed flows, to account for the quadrat sampling itself, and natural day to day variation in abundance. Such

techniques are necessary to assess the accuracy of tadpole enclosure sampling (Mullins et al. 2004) and determine if counts conducted before and after a pulsed flow have equal rates of detection. Rather than being equal, visual detectability increases post-flow because cover, in the form of algae and detritus, are swept downstream. Because tadpoles are often over-dispersed, even a rigorously conducted quadrat survey will inevitably contain many samples with zero tadpoles. Techniques for making unbiased inferences from such highly variable count data that fit a poisson or negative binomial distribution (rather than a normal distribution) are currently being disseminated in the ecological literature (Ver Hoef and Boveng 2007).

Similarly, it would be difficult to accurately observe individual tadpoles during an aseasonal pulsed flow in an open river as was done in the laboratory flume with a video monitor. *R. boylii* tadpoles have their eyes on the tops of their head and are thus skittish, when observed from above as a snorkeler would. Tadpoles will come out of cover and behave normally if the observer is completely still and observations are made from an oblique angle, not overhead. However, a snorkeler could not maintain such a position in swiftly flowing water and would not be able to follow a tadpole as it moves from rock to rock, or is swept into a turbid water column. In clear water at mid column velocities of only 5-10 cm/s, and depths of 30 cm (open river relocation trials, Table 4.12 ) the longest duration and distance of snorkel observation achieved was 19 min and 1.9 m. To operate a stopwatch, place a marker, or take notes underwater requires momentarily taking one's eyes off the focal animal. In that moment a tadpole can change its position and not be relocated. If the observer is on foot, problems with creating disturbance and turbulence are worse. On the other hand, the laboratory experiments were conducted in settings where tadpoles were viewed remotely via video monitor, or through plexiglass. Observers could call out data to a recorder and not take eyes off focal animals, providing greater accuracy.

In conclusion, the main value of the techniques described in this section (4.5) is to verify consistency between tadpole behavior in the laboratory and in the field. Observations made of tadpoles during an actual pulsed flow in an open river would be difficult to obtain and not reliable. The longer duration of the box flume trials indicates that in very heterogeneous velocity patches, a small portion of tadpoles can locate low velocity refugia and maintain position within a patch over several hours.

## 4.6. Conclusions from Tadpole Experiments

Effects of velocities elevated above natural ambient levels on tadpoles are consistently negative in all the above experiments (Table 4.1). A composite explanation of what happens when an aseasonal pulse occurs emerges from the combined results across the six different venues in which velocity was manipulated. As benthic organisms, larvae use their mouths to hold on to rocks by suction and shelter in cracks and crevices when velocity increases. *R. boylii* larvae lack highly specialized morphologies for adhesion (a ventral sucker) and active burrowing (extra vertebrae and bony tail) seen in anurans that inhabit extremely turbulent environments in streams. If swept into the water column, *R. boylii* tadpoles swim for the bottom or make upstream bursts and then drift or sink to the bottom. They rarely swim cross current. Burst

locomotion may be effective to escape predators, but in the Brett style flume without flow refugia, swimming against a 5 cm/s current quickly leads to exhaustion and impingement. For recently hatched tadpoles there are direct lethal effects of velocities as low as 10 cm/s. While in flow refugia, there are also lethal effects of predation, with risk being doubled at elevated, yet sub-critical velocities. The mean critical velocity for larger tadpoles being swept out of a refuge and swimming to exhaustion is approximately 20 cm/ sec, but velocities as low as 10 cm/ sec caused 25% of tadpoles to be displaced. The most easily displaced individuals are the largest tadpoles and the ones closest to metamorphosis. A summer pulsed flow would exert artificial selection in the exact opposite direction of natural selection which favors large larval body size in terms of risk of predation, post-metamorphic growth rate, and time to reproductive maturity.

The critical velocities observed in the experiments are less than the typical increases in velocity in near shore habitats associated with aseasonal pulsed flows. For example, in the NF Feather recreational flows caused a mean increase of 31 cm/s at *R. boylii* breeding sites (GANDA 2005). Although the ultimate fate of individuals displaced in the field is not known, it is important to note that successful cross-current swimming back to shore was rarely observed.

Tadpoles in the substrate flow refugia 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 (Ibis 2004). 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.

Summary of conclusions and implications for river management:

- *R. boylii* tadpoles across a wide ontogenetic sequence seek refuge in substrate as soon as velocity increases and behavioral responses and performances were consistent among experimental venues. The sheltering response became apparent at velocities as low as 5 cm/sec.

- In a laboratory flume (Brett chamber), tadpoles could no longer shelter under rocks at a mean critical velocity of 20.9 ± 1.6 cm/s.

- Critical velocity varied negatively with tadpole size and developmental stage, with velocities as low as 10 cm/s causing 25% of tadpoles to be displaced. The most easily displaced individuals are the largest, especially those closest to metamorphosis.

- For recently hatched tadpoles in the field, there were direct lethal effects of velocities as low as 10 cm/s.

- In flow refugia, there are lethal effects of predation. For tadpoles < 6 weeks old, mortality risk in rearing enclosures was doubled with a mean increase of approximately 7 cm/sec.

- Velocities causing negative effects in these trials are lower in magnitude than average increases observed in near shore environments during aseasonal pulsed flows.

- The negative effects observed in the artificial stream channel and rearing experiments occurred at velocities below the resolution of conditions predicted by a two-dimensional hydrodynamic model (Chapter 5). Given the typical survey resolution and associated error of 2-D modeling, it would be difficult to design aseasonal pulsed flows benign to *R. boylii* tadpoles.

- The aggregated set of experimental results presented in this chapter (4) adds a link to the robust chain of evidence tying aseasonal pulsed flows to *R. boylii* decline in regulated rivers. The chapter 3.0 data, on the two to three year offset between pulsed flows detrimental to eggs and tadpoles and declines in adult numbers, confirms that the implications of these experimental data are not hypothetical, but of practical importance. As hydro-electric dams are relicensed, *R. boylii* populations will require greater protection from a-seasonal pulsed flows than they are currently receiving if extirpations are to be prevented and currently unoccupied habitats are to be restored to tolerable conditions.

# 5.0  An Assessment of Hydrologic Variability on *R. boylii* Habitat Hydraulics Using 2-Dimensional Hydrodynamic Modeling

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**Abstract**

The accuracy and utility of in-stream hydrodynamic models, while often used to predict fish habitat availability, have rarely been evaluated for other taxa, such as amphibians. In this study, a 2-dimensional model, River2D, was used to evaluate changes in local-scale hydrodynamics and the related changes in habitat suitability and availability for *R. boylii* egg masses and tadpoles. Two study sites in Northern California, one on the unregulated SF Eel and the other on the regulated NF Feather, were selected for modeling. The precision and accuracy of the model in predicting local hydraulics at scales relevant to *R. boylii*, particularly in the near-shore environment where preferred habitat exists, was determined first. Changes in local hydraulics were then related to *R. boylii* habitat suitability using data obtained at the study sites and from concurrent controlled experiments in order to predict habitat quality and availability at the breeding sites under different flow regimes.

Results from the modeling analysis indicate that simulated depths and velocities from River2D generally agreed well with measured field values, with similar error in mid-channel areas and the near-shore environment. Modeled velocities at exact egg locations however were over-predicted, with a mean error (observed-predicted) of -0.04 ± 0.04 m/s. In shallow habitats with large poorly sorted substrates, the resolution of surveyed bed topography (~0.25m$^2$) was not fine enough to depict the microhabitat (<0.25m$^2$) variability in depth, particularly behind large cobbles where eggs were laid. As a result, the model averaged local depths and calculated velocities higher than was observed at point locations behind the cobbles. When coupled with a definition of breeding habitat suitability that encompassed the variability of field-measured values and the range of error within the model output however, the model accurately predicted areas of suitable breeding habitat throughout the survey reach.

Using previously published data and information gathered in this study, the impact of flow changes on habitat availability and suitability was modeled at two study sites representative of *R. boylii* breeding habitat. The sites differ in channel morphology, with the SF Eel site exhibiting a slightly asymmetric wide, shallow cross-section, and the NF Feather site exhibiting an entrenched cross-section with steeply sloping channel banks. At both sites, modeled increases in discharge above typical late spring flows led to decreased habitat availability, with lower discharges providing the greatest weighted usable area. However, in a seasonal pulse modeling experiment where flows increased from various low spring flows to a high spring runoff flow, higher initial discharges provided the greatest buffering capacity against lethal increases in velocity in breeding habitats. At higher initial discharges, larger proportions of suitable breeding habitats are located in shallow overbank areas, so subsequent increases in discharge

result in relatively smaller increases in depth and velocity. In a modeled aseasonal pulse scenario, higher initial discharges also provided the greatest buffering capacity in larval rearing habitats; however, only 20-30% of the suitable habitat in the SF Eel site and <5% of the suitable habitat in the NF Feather site remained suitable during the pulse regardless of initial flow level due to the low tolerance of tadpoles to even small increases in velocity. In both the spring pulse and aseasonal pulse scenarios, the SF Eel study site provided 2-3 times the buffering capacity of the NF Feather site. These differences between sites were surmised to be due to the differences in channel morphology. The steep channel banks at the NF Feather site provide little refuge from increased velocities as flows increase, while the shallow overbank areas at the SF Eel site provided refuge from high velocities as flows fluctuated.

Management of *R. boylii* may benefit from model-based methods such as those used in this study as long as the limitations and inherent error in 2D modeling are understood and taken into account. A 2D model can simulate mesohabitat-scale conditions for multiple life stages as well as evaluate habitat suitability at a reach-scale; however, the precision of the model is not high enough at typical topographical resolutions to differentiate point velocities in shallow microhabitat locations with coarse substrate where eggs may be located.

## 5.1. Introduction

In-stream flow modeling is thought to offer an alternative to intensive field surveys at different flows as a method for determining the location and amount of suitable habitat for aquatic species under different water flow conditions. In-stream flow models have been used extensively for predicting available fish habitat (Bovee 1982; Milhous et al. 1989), but rarely has their accuracy and utility been evaluated for other taxa, such as amphibians (see Bockelmann et al. 2004 and Tomsic et al. 2007 for assessments of benthic macroinvertebrate habitat suitability). Two-dimensional (2D) hydrodynamic modeling is a potentially useful method for evaluating hydraulic habitat data commonly collected for in-stream flow studies (e.g. depth, velocity, substrate size) in relation to the observed utilization and tolerances of *R. boylii* egg and larval life stages. Hypothetical flow scenarios can be created specific to the types of conditions that might occur during a seasonal or aseasonal pulse, and the results can be evaluated in a variety of ways that inform specific questions of interest. While quantitative one-dimensional (1D) models that use habitat suitability curves to estimate habitat quality for given flow conditions have been used widely to predict effects of high flows on fisheries (Bovee 1982; Milhous et al. 1989), a finer scale approach that can better predict hydraulics in near-shore habitat is necessary for *R. boylii*. Although a 1D model could predict whether clutches would be stranded as discharge declines for example, it could not predict cross-sectional variation in velocity across a large-scale roughness feature such as a point bar (Osborne et al. 1988; Ghanem and Hicks 1992). For *R. boylii*, this is particularly important as oviposition and rearing sites are generally located within a meter or two of shore, at the upper end of point bars or in shallow side pools. A 2D model that calculates both longitudinal and cross-sectional velocity distributions is more likely to accurately simulate flow patterns in meso-scale habitats (Ghanem et al. 1996; Crowder and Diplas 2000). When combined with knowledge of the biological response and physical

tolerances of egg and larval life stages, 2D modeling may provide an additional analytical tool for resource managers to assess how changes in flow affect *R. boylii*.

The primary goal of the modeling effort was to assess the ability of a commonly used and freely available 2D hydrodynamic model, River2D (Steffler and Blackburn 2002), to evaluate changes in hydraulic habitat (depth and velocity) for egg and larval life stages of *R. boylii*. Specific questions addressed include: Is the precision of the model adequate in near-shore locations to address habitat suitability for *R. boylii*? How do breeding / rearing habitat availability and connectivity change as discharge fluctuates? What are the hydraulic impacts of a seasonal (spring) flow pulse on breeding habitat and an aseasonal (summer) flow pulse on rearing habitat?

## 5.2. Methods

### 5.2.1. Study Sites

Two study sites were selected for the modeling analysis, one within the egg census survey reach on the unregulated SF Eel, and one within the Poe reach on the regulated NF Feather. Both study sites were located at established breeding areas where previous surveys routinely documented high numbers of breeding and rearing individuals (Kupferberg 1996, GANDA 2004a,f), and where habitat types occur that are similar in character to other known breeding and rearing areas.

The SF Eel study site is located at an elevation of 390m approximately 0.5km upstream of Fox Creek and approximately 4.5km upstream of Ten-mile Creek, the downstream end of the egg census reach (Figure 5.1). The study site is 110m in length and encompasses one riffle-pool sequence. The upstream end of the site is constrained by a bedrock outcrop that creates a mid-channel scour pool followed by a shallow depositional run. Just downstream, a high-gradient riffle empties into a deep bedrock pool along the outside of a bend, across from a large cobble bar located along the inside of the bend. The site includes the most populous breeding area on the SF Eel, with 33.6±4.2 clutches per year (range=9-78), representing 6.7% of the 1992-2007 annual mean reproductive output (Kupferberg 1996). Breeding/oviposition areas are typically located along the shallow margin of the run and on the shallow upstream end of the cobble bar (Kupferberg 1996). Substrates range from small cobbles in the run to large cobble and small boulders on the bar to bedrock along portions of the stream banks and in the pools. Sedges line the water's edge, but common riparian vegetation such as willows and alders is limited. Annual flows illustrate a natural runoff hydrograph typical of unmanaged northern Coast Range rivers (Figure 5.2).

The NF Feather study site is located at the confluence with Flea Valley Creek adjacent to the town of Pulga at an elevation of 415m. The site is at the upstream end of the Poe reach approximately 1.5km downstream of the Poe dam (Figure 5.1). The study site is 150m in length and also encompasses one riffle-pool sequence. The upstream end of the site is located at the mid-point of a large vegetated cobble bar along the right bank just above a high-gradient riffle that empties into a mid-channel scour pool. Downstream of the pool, the channel transitions into a deep run with a large steep-faced cobble-boulder bar along the left bank. Flea Valley

Creek enters on the right bank and a shallow overbank area dominated by boulders, cobbles and sedges is located just downstream. The site encompasses a *R. boylii* breeding area that has been monitored since 2001 (GANDA 2004a) with 18.9±7.0 clutches per year, representing 35% of the 2003-2007 reproductive output at the known sites on Poe. Breeding/oviposition areas typically occur along the right bank downstream of the creek and along the upstream portion of the left bank cobble bar. In some years, oviposition sites have also been located along the upstream right bank cobble bar towards the water's edge where vegetation is less dense. Substrates range from large cobble and small boulder in the bars to large boulders along the channel banks and in the main channel. Sedges line the water's edge throughout the site, while willows, alders and blackberries cover the channel banks. Annual flows in the study site reflect the highly managed nature of the NF Feather system (Figure 5.2).

Photos of both study sites are included in Appendix C.
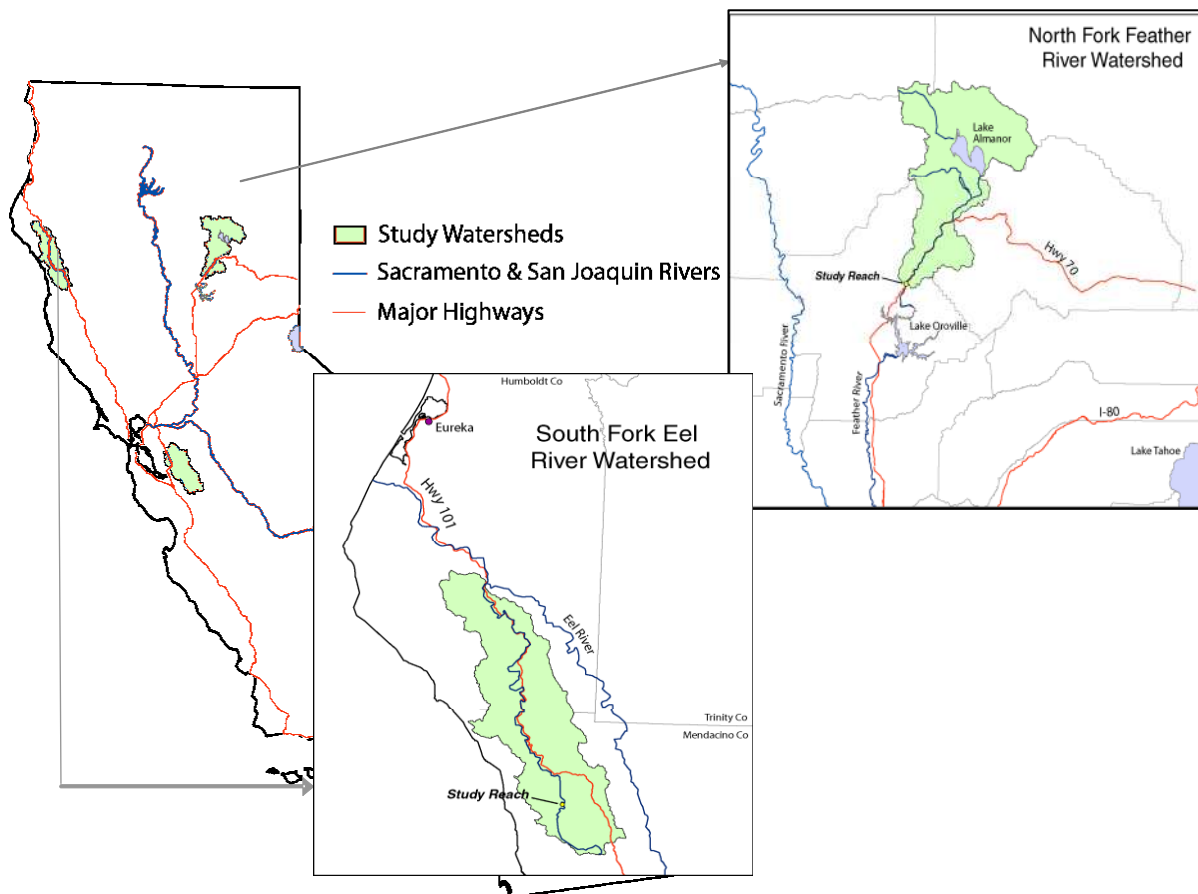


**Figure 5.1. Location of study reaches within the South Fork Eel and North Fork Feather watersheds in northern California (Teale Data Center 1999)**
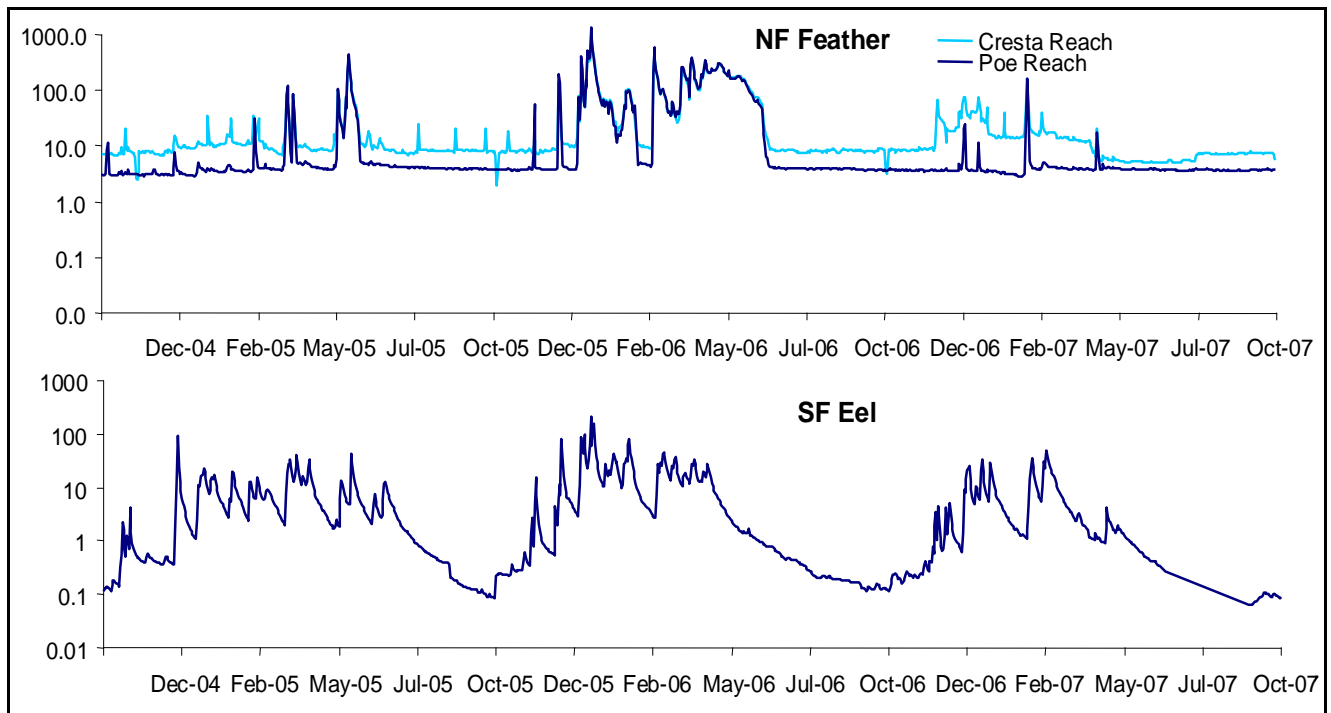
**Figure 5.2. Mean daily discharge (cms) for water years 2005-2007 in the NF Feather (top) and SF Eel (bottom).**

### 5.2.2. Topographic Data Collection and Hydrodynamic Modeling

Topographic surveys of each study reach were completed in fall 2005 and winter 2006. At the NF Feather study site, high winter and spring flows in February, 2006 and May, 2006 rearranged the stream banks and bar deposits in the vicinity of the Flea Valley Creek confluence. Additional topographic surveys were completed in summer and early fall 2006 to accurately reflect the channel topography present when eggs were laid in June, 2006. Although high spring flows also occurred at the SF Eel study site, the topography changed minimally and additional topographic surveys were not needed.

Topographic surveys were completed at each study site (survey reach) using a robotic total station and a GPS-RTK (Global Positioning System – Real Time Kinematic) survey system (Topcon models GTS-802A and Hiper Lite Plus, respectively). While the GPS-RTK was the preferred survey instrument due its rapid data collection, varied conditions within the study sites, including heavy vegetation, steep canyon walls and deep water, necessitated the additional use of a total station. Surveys were completed in a grid format at resolutions ranging from approximately 2m by 2m in simple mid-channel or high floodplain areas to 0.25m by 0.25m in the near-shore and channel margin areas where egg and tadpole habitats typically occur. In locations where large boulders or other flow-influencing features existed, the density of survey points increased (up to 0.10m by 0.10m) to reflect the topography of the feature. A total of 4847 points were surveyed across 3832 m$^2$ in the SF Eel study reach, resulting in an average density of 1.3 pts/ m$^2$. In the NF Feather study reach, 7602 points were surveyed across

12596 m$^2$ in the NF Feather study reach, resulting in an average density of 0.6 pts/ m$^2$. An average substrate roughness in the form of roughness height, k$_s$, was estimated in the field for each primary geomorphic feature (e.g. pool, bar, riffle) and then assigned to each survey point on that feature. Roughness values ranged from 4.5 on the cobble/boulder bars to 2.0 in the pools for both survey reaches.

Hydrologic calibration and validation data was collected for the model at each site at low or base flows in fall, at high winter flow in January and February, and at spring flow in May and June when eggs were present in the channel. Table 5.1 details the various dates and discharges when data was collected. On the SF Eel, a total of 3 discharges were surveyed as planned, with the spring discharge used for model calibration, the low and high discharges used for model validation, and the egg locations used for validation of general habitat suitability conditions. On the NF Feather, due to unusual late-season high flows, frogs did not begin oviposition at base flow or a moderate spring flow as in previous years, but laid eggs at a high discharge several days before flows were steeply reduced to base flow by upstream project operations. This resulted in a loss of half the egg masses due to desiccation, and collection of egg mass location data only when flows had returned to base flow. As a result, only 2 discharges were surveyed, a moderate winter flow in late January and base flow in spring when eggs were still present. Model calibration was completed using base flow conditions and model validation was completed with the winter flow data. Egg locations were used to verify habitat suitability conditions at both base flow and the simulated high spring discharge.

**Table 5.1. Dates and discharges when calibration and validation data was collected for each study site.**

| River | Date | Discharge (cms) | Discharge (cfs) | Data Use |
|---|---|---|---|---|
| SF Eel | 10/22/2005 | 0.15 | 5 | model validation |
| | 2/21/2006 | 2.5 | 88 | model validation |
| | 5/15/2006 | 1.45 | 51 | model calibration, egg mass habitat suitability validation |
| NF Feather | 1/26/2006 | 15.7 | 555 | model validation |
| | 6/20/2006 | 4.4 | 155 | model calibration |

The hydrodynamic modeling was completed using River 2D, a two-dimensional, depth averaged finite element model that is freely available and used by the California Fish and Game Department, U.S. Fish and Wildlife Service and others in fish habitat evaluation studies (Steffler and Blackburn 2002; Tiffan et al 2002; Hanrahan et al. 2004; Gard 2005). The model is designed specifically for use with natural streams and rivers; 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, inflow discharge and downstream boundary conditions in the form of water surface elevation (Steffler and Blackburn 2002). Field measurements of water surface

elevation, depth and velocity taken at low- and high-flows provide data for calibration and validation purposes.

The topographic data and associated substrate roughness heights were used to create a two-dimensional finite element computational mesh consisting of a triangulated irregular network or TIN. At each computation node, bed elevation and roughness height were calculated based on a linear interpolation of the underlying surveyed topographic data and associated roughness heights. Similar to the topography survey, the density of the mesh varied with channel bed complexity. In simple mid-channel regions, node spacing was approximately 1.5 m, while in the near-shore areas, node spacing increased to an average of 0.25 m. Over large boulders, the node spacing was increased further if needed to reflect the topography. The computational domain was extended one channel width at the upstream end of each study site in order to minimize the effect of inflow boundary conditions on hydraulic characteristics. Once the computational mesh was generated, smoothed and checked for anomalies, the hydrodynamic model was run until convergence between the inflow and outflow discharges was achieved (commonly defined as a difference of less than 1% (Waddle et al. 2000)). Output from the model included a simulated water depth, water surface elevation, velocity, and flow direction for each node.

For calibration, measured water surface elevations, depths and velocities were compared to simulated values for a single flow at each study site. Water surface elevations at the upstream and downstream boundaries and along the water's edge at the bank were compared, and the downstream boundary elevation was adjusted if needed until average predicted water surface elevations were within 3-5 cm of measured values. Point measurements of depth and mean-column velocity (estimated as the instantaneous velocity at a depth of 0.6 times the total depth averaged over a 60-second time interval (Harrelson et al 1994)) were taken throughout the channel and near-shore environment using a top-set wading rod and Marsh-McBirney Flo-Mate meter. Comparisons between the spatial location of the water's edge and the point measurements of depth and velocity were then evaluated to determine local areas of deviation. Adjustments to the mesh density, underlying bed topography (primarily smoothing) and roughness values were made to minimize differences between measured and simulated depth and velocity values (Crowder and Diplas 2000).

Once calibrations were complete, the model output was validated with empirical data from additional measured discharges. At each validation discharge, measurements of water surface elevations at the downstream boundary and along the water's edge, depths and velocities across two monumented cross-sections, and random point measurements of depth and velocity in the channel were compared.

Flow simulations were run at a series of discharges ranging from base or low summer flows to winter flood flows. The goal was to encompass a range of flows typical of each study site in an average year. Simulations required downstream boundary conditions from a stage-discharge relationship that was either empirically derived or calculated from known water surface elevations, depending on the study site. Nodal output files from the flow simulations

containing data on geographic location (nodal coordinates), predicted depth and velocity were input into GIS for analysis.

## 5.3. Results – Model Output and Error

### 5.3.1. South Fork Eel River

Water depths and velocities predicted by River2D generally agreed with depths and velocities measured at the SF Eel study site (Table 5.2). Comparisons between empirical and simulated values show mid-channel locations have the lowest percent error while depth at the water's edge had the greatest percent error. In the mid-channel environment at the calibration flow of 1.45 cms, the percent error in predicted depth and velocity averaged 11% and 25%, respectively. This is comparable to error reported in previous 2D modeling studies (21% for depth, 29% for velocity over gravel substrate in Pasternack et al. 2006; see also discussion in Tiffan et al. 2002) and reflects both error in surveying bed topography and limitations within the model assumptions.

At measured locations in the near-shore environment, modeled values had high percent error in comparison to mid-channel locations, ranging up to 350% for predicted velocity at egg locations (Table 5.2). Calculations of percent error in these shallow, slow-moving areas however do not necessarily reflect the ability of the model to provide biologically significant information. For example, the percent error between an observed velocity of 1 cm/s versus a simulated velocity of 3 cm/s equates to 200% error, even though the difference in velocities is only 2 cm/s. Therefore, analysis of the error or difference between modeled and surveyed values provided a better gage of model accuracy in the near-shore oviposition environment. Mean error for depth and velocity in near-shore locations at the calibration flow of 1.45 cms was $0.04 \pm 0.08$ m and $0.04 \pm 0.13$ m/s, respectively (Table 5.2). These mean values were not statistically different from mean error in the mid-channel (t=-0.144, p=0.89 for depth; t=-0.161, p=0.87 for velocity), although variability in velocity error in the near-shore was greater than in the mid-channel (F=5.699, p=0.02) (Figure 5.3). At the validation discharge of 2.5 cms, mean error for depth was lower than mean error at the calibration discharge of 1.45 cms, while mean error for velocity in the mid-channel was slightly higher (Table 5.2). This under-prediction of velocity in the mid-channel environment was not significantly different from mean velocity error in the near-shore (t=1.495, p=0.14), and because depths in the mid-channel were accurately predicted (Figure 5.3), likely reflects inherent model error due to the assumption of steady state flow (Pasternack et al., 2006).

**Table 5.2. Comparison of modeled and surveyed points at each calibration and validation discharge. All values are metric (depth = m, velocity = m/s). Mid-channel, near-shore, egg location and edge of water datasets are subsets of the all points datasets. Percent error is calculated as ((modeled-surveyed)/surveyed)*100 for each point. Error is calculated as (surveyed-modeled) for each point.**

| River | Discharge (cms) | Dataset | Hydraulic characteristic | Mean (+/- SD) of surveyed points | Mean (+/- SD) of modeled points | Mean Percent Error | Mean Error (+/- SD) (surveyed-modeled) |
|---|---|---|---|---|---|---|---|
| South Fork Eel | 1.45 | all points | depth (m) | 0.18 (+/- 0.23) | 0.16 (+/- 0.23) | 266 | 0.02 (+/- 0.08) |
| | | | velocity (m/s) | 0.08 (+/- 0.16) | 0.09 (+/- 0.12) | 181 | -0.01 (+/- 0.07) |
| | | mid-channel | depth | 0.56 (+/- 0.19) | 0.53 (+/- 0.19) | 11 | 0.03 (+/- 0.06) |
| | | | velocity | 0.21 (+/- 0.16) | 0.19 (+/- 0.11) | 25 | 0.02 (+/- 0.07) |
| | | near-shore | depth | 0.23 (+/- 0.15) | 0.19 (+/- 0.16) | 174 | 0.04 (+/- 0.08) |
| | | | velocity | 0.19 (+/- 0.16) | 0.17 (+/- 0.21) | 182 | 0.03 (+/- 0.13) |
| | | egg locations | depth | 0.10 (+/- 0.06) | 0.07 (+/- 0.06) | 45 | 0.03 (+/- 0.04) |
| | | | velocity | 0.02 (+/- 0.03) | 0.05 (+/- 0.05) | 350 | -0.04 (+/- 0.04) |
| | | edge of water | depth | 0.0 (+/- 0.0) | 0.01 (+/- 0.10) | 778 | -0.02 (+/- 0.10) |
| | | | velocity | 0.0 (+/- 0.0) | 0.01 (+/- 0.02) | 84 | -0.01 (+/- 0.08) |
| | 2.5 | all points | depth | 0.42 (+/- 0.32) | 0.41 (+/- 0.35) | 243 | 0.01 (+/- 0.08) |
| | | | velocity | 0.24 (+/- 0.28) | 0.20 (+/- 0.18) | 66 | 0.04 (+/- 0.14) |
| | | mid-channel | depth | 0.67 (+/- 0.23) | 0.67 (+/- 0.23) | 8 | -0.01 (+/- 0.06) |
| | | | velocity | 0.35 (+/- 0.26) | 0.27 (+/- 0.14) | 43 | 0.07 (+/- 0.16) |
| | | near-shore | depth | 0.35 (+/- 0.19) | 0.33 (+/- 0.21) | 90 | 0.02 (+/- 0.07) |
| | | | velocity | 0.24 (+/- 0.29) | 0.21 (+/- 0.19) | 87 | 0.03 (+/- 0.14) |
| | | edge of water | depth | 0.0 (+/- 0.0) | -0.05 (+/- 0.14) | 1143 | 0.05 (+/- 0.14) |
| | | | velocity | 0.0 (+/- 0.0) | 0.01 (+/- 0.05) | 78 | 0.00 (+/- 0.04) |
| | 0.15 | cross-sections | depth | 0.18 (+/- 0.11) | 0.14 (+/- 0.08) | 24 | 0.04 (+/- 0.05) |
| | | | velocity | 0.05 (+/- 0.04) | 0.07 (+/- 0.04) | 110 | -0.02 (+/- 0.02) |
| North Fork Feather | 4.4 | all points | depth | 0.40 (+/- 0.32) | 0.36 (+/- 0.31) | 249 | 0.04 (+/- 0.10) |
| | | | velocity | 0.15 (+/- 0.18) | 0.18 (+/- 0.18) | 149 | -0.02 (+/- 0.13) |
| | | mid-channel | depth | 0.67 (+/- 0.18) | 0.63 (+/- 0.18) | 11 | 0.04 (+/- 0.08) |
| | | | velocity | 0.25 (+/- 0.17) | 0.30 (+/- 0.13) | 78 | -0.04 (+/- 0.14) |
| | | near-shore | depth | 0.37 (+/- 0.19) | 0.32 (+/- 0.17) | 40 | 0.06 (+/- 0.08) |
| | | | velocity | 0.15 (+/- 0.17) | 0.14 (+/- 0.16) | 188 | 0.01 (+/- 0.15) |
| | | edge of water | depth | 0.0 (+/- 0.0) | -0.01 (+/- 0.13) | 800 | 0.00 (+/- 0.13) |
| | | | velocity | 0.0 (+/- 0.0) | 0.02 (+/- 0.09) | 220 | -0.02 (+/- 0.09) |
| | 15.7 | all points | depth | 0.30 (+/- 0.27) | 0.30 (+/- 0.34) | 524 | -0.01 (+/- 0.16) |
| | | | velocity | 0.19 (+/- 0.25) | 0.19 (+/- 0.20) | 184 | 0.00 (+/- 0.14) |
| | | mid-channel | depth | 0.51 (+/- 0.21) | 0.53 (+/- 0.28) | 32 | -0.02 (+/- 0.15) |
| | | | velocity | 0.35 (+/- 0.27) | 0.35 (+/- 0.19) | 85 | 0.00 (+/- 0.19) |
| | | near-shore | depth | 0.33 (+/- 0.16) | 0.32 (+/- 0.21) | 40 | 0.01 (+/- 0.13) |
| | | | velocity | 0.17 (+/- 0.19) | 0.15 (+/- 0.13) | 274 | 0.02 (+/- 0.13) |
| | | edge of water | depth | 0.0 (+/- 0.0) | 0.0 (+/- 0.19) | 1474 | 0.00 (+/- 0.19) |
| | | | velocity | 0.0 (+/- 0.0) | 0.02 (+/- 0.05) | 238 | -0.02 (+/- 0.05) |
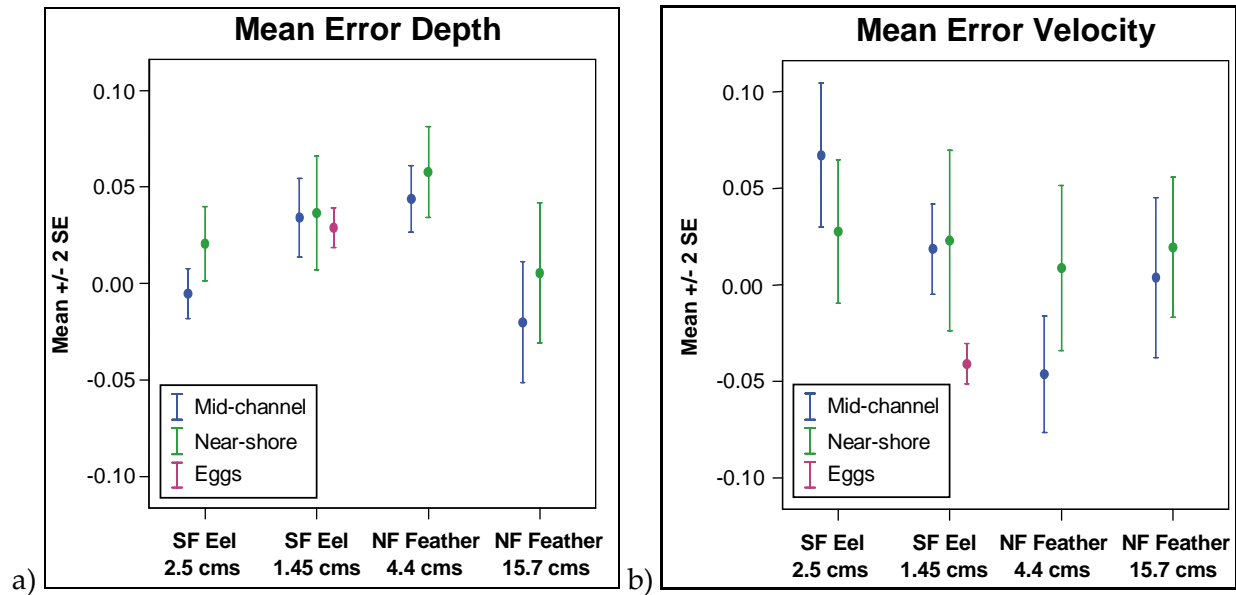
**Figure 5.3. Mean error in surveyed versus modeled a) depths and b) velocities within various environments in the each survey reach at calibration and validation discharges.**

Graphical comparisons of measured depth and velocity values show that while the model performed well in the mid-channel and near-shore environments, it over-predicted velocity and slightly under-predicted depths at egg locations. Figure 5.4 shows surveyed versus modeled depths and velocities on the SF Eel at 1.45 cms in various channel locations to illustrate the difference in prediction error for egg locations (see Appendix D for graphical comparisons illustrating the range of error at all discharges at both study sites). The mean error for velocity at egg locations was also significantly different than the mean error for velocity in the greater near-shore environment (t=2.665, p=0.01) (Figure 5.3b). Eggs are most often attached to the downstream lee-side of cobbles and boulders where point velocities are low due to eddy effects. If the surveyed topography input to the model does not explicitly detail the boulder, calculations of velocity and depth within the grid cell containing the egg mass will be averaged as if the boulder was not present. When present, the boulder obstructs flow reducing velocities and increasing depth downstream; therefore calculations of the same flow volume through the grid cell without the boulder results in over-predicted velocities and under-predicted depths at the egg point location. However, because the flow volume is calculated from grid cell to grid cell over an averaged topographic bed surface, average depth and velocity conditions throughout the larger mesohabitat area are correctly predicted. This is likely the case for the oviposition area at this study site. While topographic surveys were completed at an average resolution of 0.25 m$^2$ in this area, the large cobble and small boulder substrate could not be finely detailed. As a result, precise predictions of velocity and depth at point oviposition locations at the study site were subject to error (over-predicted velocity, Figure 5.4b), but general hydraulic conditions throughout the near-shore and mid-channel environments were accurate (Figure 5.4a).
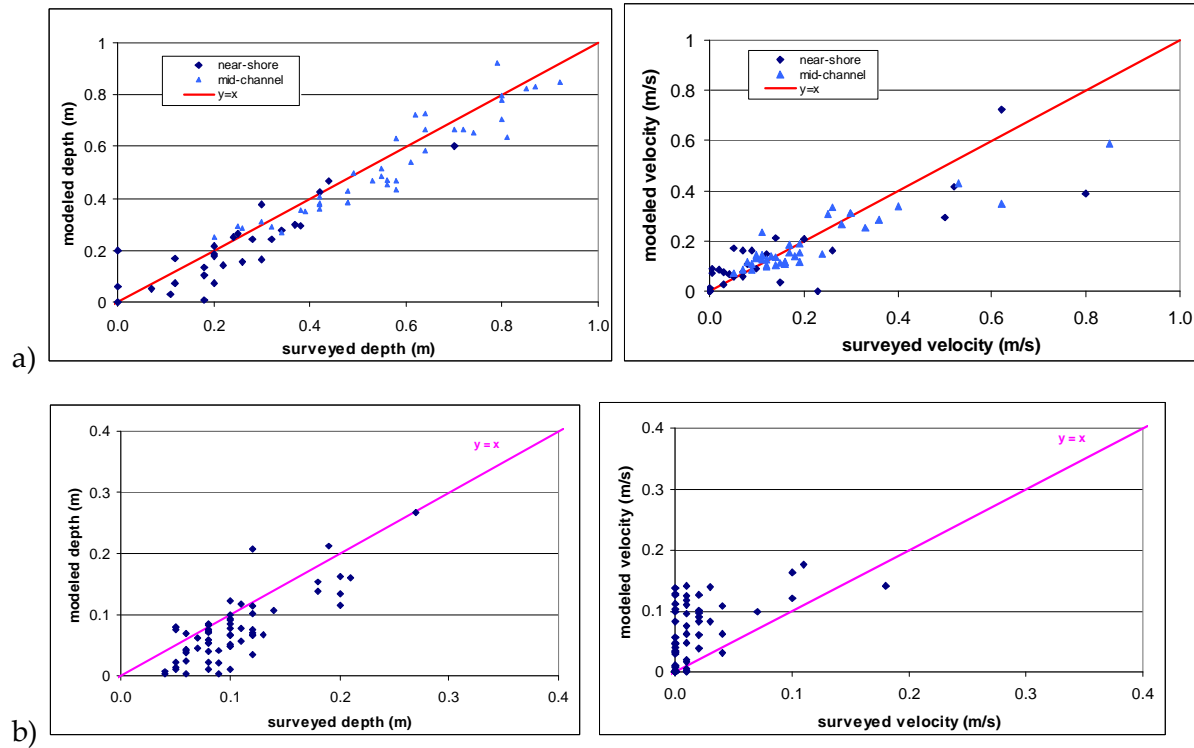
**Figure 5.4. Surveyed versus modeled depths and velocities on the SF Eel at 1.45 cms for a) mid-channel and near-shore locations and b) egg locations.**


### 5.3.2. North Fork Feather River

At the NF Feather study site, predicted values generally agreed with observed values in a pattern similar to the SF Eel site; however, the percent error between modeled and surveyed velocities in the mid-channel was greater (Table 5.2). Mean error in depth and velocity were similar between mid-channel and near-shore locations, with the exception of velocity in the mid-channel at the calibration flow of 4.4 cms, which was significantly different than in the near-shore (-0.05 ± 0.14 m/s mid-channel vs. 0.01 ± 0.15 m/s near-shore) (t=-2.144, p=0.03) (Figure 5.3). The larger percent error in modeled velocities in the mid-channel and the over-prediction of velocity in the mid-channel at 4.4 cms is likely due the abundance of large boulders in the channel substrate. In the near-shore, the topographic survey resolution was greater than in the mid-channel (approximately 0.25 m² grid versus 2 m² grid on average), so boulders in the mid-channel were likely not well delineated. As discussed above in relation to egg locations, the result is an averaged topographic surface that under-predicts depth and over-predicts velocities near the boulders. Although mean error was higher in the mid-channel at the NF Feather site at 4.4 cms, the model correctly routed flow throughout the survey reach, as shown by the low mean error in the near-shore environment (see also graphical comparisons in Appendix D). At the higher validation discharge (15.7 cms), where greater depths reduce the influence of substrate boulders on the flow, mean error was low in both the mid-channel and near-shore (Figure 5.3).

At both study sites, River2D simulated water depths and velocities that generally agreed with measured values at the calibration and validation flows. Percent error in the model results for mid-channel areas were similar to results reported in other studies that used 2D model simulations to assess physical in-stream habitat (Pasternack et al. 2006), and in general, mean error in predicted depths and velocities was low. In locations where substrates were poorly sorted and the resolution of the surveyed topography was not fine enough to delineate protruding cobbles and boulders, the model under-predicted depth and over-predicted point velocities. At both study sites, mean errors in the near-shore environment were generally small and similar to mean errors in the mid-channel, but should be considered in the context of depths and velocities actually used by *R. boylii*. An assessment of whether the mean error was small enough to adequately predict habitat suitability depends on how broadly or narrowly suitability is defined and is presented below in section 5.4.1.

## 5.4.   Applications of the Hydrodynamic Models

### 5.4.1. Defining Habitat Suitability in the Context of Model Error

In a broad sense, 'habitat suitability' is the extent to which a habitat patch provides the correct abiotic conditions and biotic factors for a particular species or life stage to survive, grow or successfully reproduce depending on the life stage of interest. Abiotic conditions are nested in a hierarchy from small to large spatial and temporal scales, where microhabitat physical characteristics such as velocity, depth and substrate are nested within larger scale features such as mesohabitat morphology (tens of meters in river length), channel slope and reach morphology (hundreds of meters) and proximity to floodplain or tributary habitats (thousands of meters) (Frissell et al. 1986; Imhof et al. 1996). Biotic factors such as abundance of resources (algae for tadpoles, insects for adult frogs), density of competitors and distribution of predators similarly vary at fine and broad spatial scales (Power et al. 1988; Poff 1997). Figure 5.5 shows a conceptual framework for the relationship between abiotic and biotic environmental factors and *R. boylii* egg and larval habitat suitability.
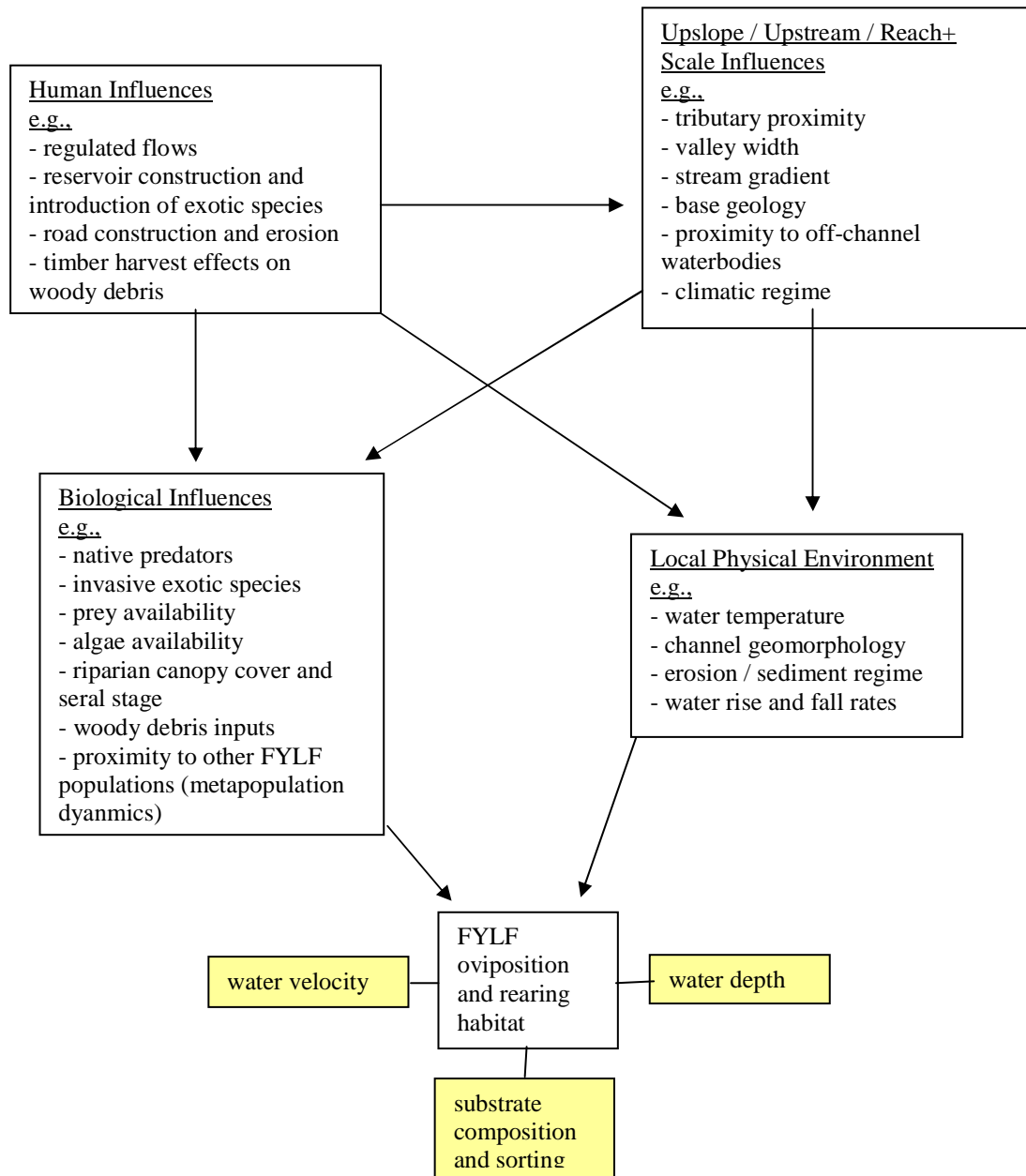
**Figure 5.5. Conceptual framework for FYLF oviposition/rearing habitat associations in the context of other biotic and abiotic environmental influences. Highlighted (yellow) boxes depict variables included in hydraulic habitat suitability criteria.**

In studies of the relationship between in-stream flow conditions and specific lotic taxa however, 'habitat suitability' is often narrowly defined in terms of the hydraulic characteristics of depth, velocity and substrate. Hydrodynamic modeling has been widely used to evaluate the effects of changes in flow and local hydraulic characteristics on various fish species habitat (e.g. salmonid breeding and fry rearing habitat) (Ghanem and Hicks 1992; Jowett 1997). Habitat suitability criteria then are the specific ranges of depth, velocity and substrate conditions that provide the

link between model output and biological significance for a certain life stage (Bovee 1982; Stalnaker et al. 1995). Local hydraulic conditions have been shown to be key selective factors for *R. boylii* sub-populations among creeks in the Yuba River watershed (Yarnell 2005), and in our three case study watersheds, frog population fluctuations appear linked, at least in part, to flow-related effects on recruitment (see chapter 3). Therefore use of a 2D hydrodynamic model to describe how hydraulic habitat suitability for egg and tadpole life stages varies with discharge can be informative. However, it is important to note that the physical habitat conditions defined by the model output are: (a) only one aspect of the greater habitat suitability required for maintenance of frog populations, and (b) must be framed within the inherent errors and limitations of the hydrodynamic model.

Currently, validated habitat suitability criteria for *R. boylii* do not exist, and it was outside the scope of this research project to undertake this extensive task. While the first step in establishing habitat suitability criteria, to collectively analyze data on hydraulic habitat associations included in existing studies, has been undertaken for an ongoing re-licensing project (see study plans for the DeSabla-Centerville re-licensing project, FERC# 803), this work is not yet complete. A proposal has been submitted to design and conduct a validation study in 2008 that builds on the results from the DeSabla-Centerville effort and aims to establish habitat criteria reflective of preference and unbiased by habitat availability. As a result, the habitat suitability criteria used in the model simulations presented below are based on data reviewed and obtained within this study. Specifically, criteria for suitable oviposition habitat are based on empirical data obtained at each study site, and criteria for suitable larval habitat are based on the experimental results presented in chapter 4. Implications of using different habitat criteria are discussed in section 5.5.

For egg masses, suitable habitat criteria were based on the range of surveyed total depths and mid-column velocities at egg locations in the SF Eel study site in 2006 (n=73 egg masses), with consideration given to the range in error observed in the model output. Surveyed depths ranged from 0.05 – 0.27 m. The maximum error between observed and simulated depths for 90% of the values at egg locations was 0.09 m; therefore a definition of suitable depths for eggs as 0.0 – 0.4 m would encompass both the full range of observed depth conditions at the SF Eel study site and the potential error in the model output. Although measured depths and velocities at egg locations in the NF Feather site could not be obtained, monitoring studies in the Poe reach (reviewed in chapter 2) show the average total depth at egg masses was 0.3 m, with 90% of the observations occurring at less than 0.52 m (n=102 egg masses) (Appendix A, GANDA 2004a,f). In order to maintain consistency between definitions of habitat suitability at each study site, this slightly higher range in depths was incorporated and suitable depth habitat for eggs was defined as 0.0 – 0.5 m.

Surveyed mid-column velocity at eggs in the SF Eel study site in 2006 ranged from 0.0 – 0.18 m/s; however, the maximum measurement of 0.18 m/s was statistically an outlier. The remaining surveyed values were 0.11 m/s or less and 90% were 0.04 m/s or less. These values are similar to those reported in several FERC-related studies summarized in chapter 2. On the Pit River, mean mid-column velocity was 0.034 ± 0.045 m/s (range 0.0-0.17 m/s, n=33 egg

masses) (Appendix A, PIT1), and data from monitoring studies on the Poe reach of the NF Feather showed mid-column velocities ranging from 0.0 – 0.08 m/s (Appendix A, GANDA 2004a,f). The precision of the 2D model in the near-shore environment was not high enough to accurately distinguish velocities less than 0.05 m/s (mean error = 0.04 ± 0.04 m/s on SF Eel), and the maximum error between observed and simulated velocities for 90% of the values at egg locations on the SF Eel study site was 0.1 m/s. Therefore, suitable velocities for eggs was defined as 0.0 – 0.1 m/s, encompassing the range of observed velocities at the SF Eel study site, the mean velocities observed in other studies reviewed in chapter 2, and the range in potential error in model output. All depths and velocities defined as 'suitable' were assigned a suitability criteria value of 1.0, while all other depths and velocities were assigned a suitability of zero.

Suitable habitat for tadpoles was defined from observed conditions in previous studies reviewed in chapter 2 and the experimental results presented in section 4. On the Poe River reach on the NF Feather, monitoring studies reported observed depths for tadpoles ranging from 0.0 – 0.75 m, and velocities ranging from 0.0 – 0.05 m/s, with 90% of the values less than 0.42 m and at 0.0 m/s, respectively (Appendix A, GANDA 2004a,f). Behavioral data collected during the artificial stream channel experiment (section 4.1) showed tadpoles exhibiting 'normal' behavior (freely swimming about and foraging on algae on rock surfaces or floating mats) at velocities less than 0.05 m/s. Suitable depth habitat for tadpoles was defined as 0.0 – 0.5 m in total depth, reflecting the depths at which 90% of tadpoles were observed on the Poe reach and the average absolute difference of 0.08 m between observed and simulated depths at the NF Feather study site. Similarly, suitable velocity habitat was defined as 0.0 – 0.05 m/s; however, as discussed above, mean error in near-shore velocity predictions from the model was 0.04 ± 0.045 m/s, thus precise determinations of habitat locations above or below a 0.05 m/s threshold could be problematic. Therefore, the analysis of tadpole habitat response to changes in flow was completed using 'tolerable' habitat conditions, where 'suitable' habitat conditions are a subset of tolerable conditions.

Tolerable habitat for tadpoles was defined from the experimental results as areas where velocities were high enough to preclude 'normal' behavior, but low enough to allow tadpoles to seek refuge in the substrate without being swept away over short periods (minutes to hours). Specifically, tolerable velocities were defined as 0.0 – 0.1 m/s, reflecting the range of velocities where sub-lethal negative effects were observed in the rearing experiments (section 4.3). Over longer periods (hours to days), tadpoles in 'tolerable' conditions (0.0 - 0.1 m/s) have increased risks of predation and lower growth than tadpoles in 'suitable' conditions (0.0 - 0.05m/s). Velocities greater than 0.1 m/s were defined as 'intolerable'. Results from the Brett chamber experiment (section 4.2) indicate that 0.1 m/s was a critical velocity where 25% of tadpoles were unable to maintain position and were swept downstream. Although 50% of tadpoles observed in the Brett Chamber experiment were able to maintain their position at velocities up to 0.20 – 0.25 m/s, there is no data available at this time to indicate what type of effect a loss of 50% of a tadpole cohort would have on long-term population dynamics. Therefore the more conservative value of 0.1 m/s was chosen as the critical velocity defining the threshold for intolerable habitat conditions. To maintain simplicity and similarity with definitions of egg habitat suitability, all

depths defined as suitable and velocities defined as tolerable were assigned a suitability criteria value of 1.0, while all other depths and velocities were assigned a suitability of zero.

Although River2D outputs a variety of hydraulic parameters, such as Froude number and shear stress, depth and velocity were the most useful in quantifying appropriate egg and larval habitat suitability. Froude number (see definition in section 4.4.2) has been shown to be useful for quantitatively delineating large-scale mesohabitats (pool, riffle, run) (Panfil and Jacobson 2005), and did delineate micro-scale habitat preferences in the larval drift fence experiment (section 4.4). However, when Froude number was plotted throughout each study site in River2D, areas of suitable habitat were not distinguishable. Large-scale features such as the run, riffle and pool were distinguished (e.g. high velocity-low depth in riffle versus low velocity-high depth in pool), but edge-habitat along the run (low velocity-low depth) was not differentiated from the mid-channel portion of the run (moderate velocity-moderate depth). Similarly, shear stress varied across the large-scale features in the study sites, but did not vary within some habitats such as between the edge-habitat of a pool and the center of a pool. When compared with the locations of occupied suitable habitat in each site, which occur within low velocity-low depth locations, neither Froude number nor shear stress accurately delineated the suitable habitat. A simple combination of depth and velocity best distinguished suitable from non-suitable habitat.

### 5.4.2. Suitable Habitat Availability and Connectivity as Discharge Changes

#### 5.4.2.1. Habitat Availability

Results from several FERC re-licensing studies showed that comparisons of suitable habitat availability as discharge increased varied widely depending on the site location and the method used to determine suitable habitat area; however, the general trend across most re-licensing studies indicates that suitable habitat decreases with increasing discharge (detailed in section 2.2). Although there is insufficient data to make conclusions as to why this trend may occur on regulated rivers, one hypothesis is that regulated hydrographs dominated by flat base flows and lacking moderate magnitude discharges with gradually receding limbs may create channel cross-sections with steep bank slopes that provide less shallow edgewater habitat (Shields et al. 1994). As high magnitude flows quickly recede, coarse bedload in motion often rapidly deposits in steep-faced unconsolidated bars high on the channel banks; sustained low flows can then gradually erode smaller material at the base of the bars and along the low flow banks creating a U-shaped low flow channel inset below a coarse floodplain. If subsequent discharges are rarely large enough to remobilize the perched floodplain sediments, vegetation can become established forcing erosion to occur within the low flow channel and perpetuating the steep channel banks. Previous research on the SF Eel showed that *R. boylii* breeding locations had wider, shallower cross-sections than random cross-section locations, resulting in more stable depth and velocity in the near-shore environment as discharge changed (Kupferberg 1996). Using results from the 2D model and the definition of habitat suitability discussed above (section 5.4.1), total suitable habitat area was compared across the full range of modeled flows at each study site.

Calculations of suitable habitat area from the 2D model were most similar to the 'shifting polygon' method described in section 2.2.1. and used in the Spring Rivers 2002 study. In this method, areas of suitable habitat were delineated independently at each study flow, thus suitable habitat 'shifted' throughout the reach as discharge fluctuated. Similarly, using the 2D model output, polygons of suitable habitat were delineated at each flow based on the depth and velocity conditions at each model node and summed across the reach. In some re-licensing studies, only "occupied" suitable habitat was assessed, so a subset of the total suitable nodes was also delineated as occupied in the modeled reaches for comparison. Occupied suitable habitat was defined as all nodes between the furthest upstream and downstream egg locations in the longitudinal direction and all nodes between the minimum and maximum flow boundaries in the cross-sectional direction. Figure 5.6 shows the percent change in suitable habitat as flow increased from base flow to each modeled flow.



a)



b)
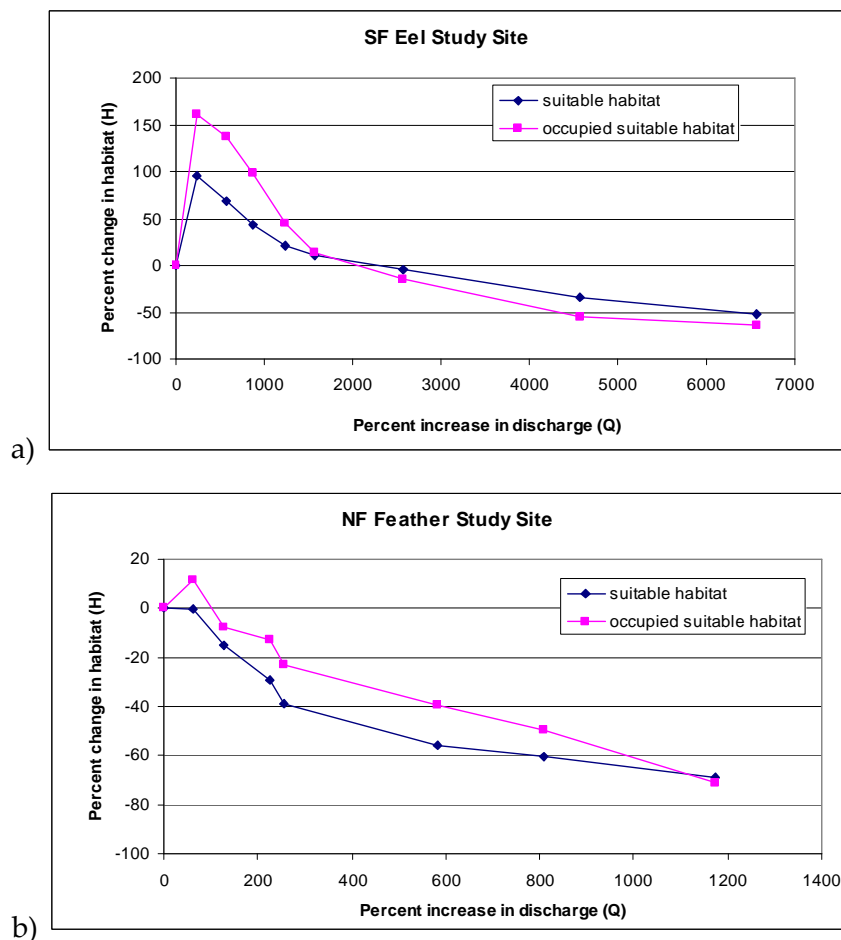
**Figure 5.6. Percent change in suitable and occupied suitable habitat as flow increases from base flow to each modeled flow for a) SF Eel study site and b) NF Feather study site. Percent increase at each point is calculated as %$\Delta$Q = (((Qtest – Qbase)/Qbase)*100) and %$\Delta$H = (((Htest – Hbase)/Hbase)*100).**

At the SF Eel study site, both suitable and occupied suitable habitat increased at low to moderate discharge increases above the summer low flow (0.15 cms), but then decreased at successively higher discharges (Figure 5.6a). This pattern is similar to the pattern observed in the Spring Rivers 2002 study where suitable habitat initially increased as discharge increased, than decreased and leveled off at higher discharges. A slightly similar pattern occurred with occupied suitable habitat in the NF Feather study site, although the initial increase in habitat was very small and habitat decreased in larger proportions as flow increased (Figure 5.6b). Availability of suitable habitat in the NF Feather site was highest at baseflow, and similarly declined at successively higher discharges.

These differences in habitat availability between the two study sites are a reflection of differing channel morphology. The SF Eel study site has wide, shallow or slightly asymmetrical channel shapes that provide more stable depth and velocity conditions across at least a subset of flow fluctuations (Figure 5.7). The NF Feather site has steeply faced banks along the water's edge that create less total shallow, low velocity edgewater habitat (Figure 5.8). When discharge fluctuates within the main low-flow channel, depths and velocities are less stable. A comparison of the annual hydrographs for each study site (Figure 5.2) shows that the regulated NF Feather is dominated by flat baseflows (i.e., minimum flows required by license agreements in regulated rivers) through the summer and large peak magnitude storms with steep recession limbs in the winter and early spring. Intermediate flows that promote cobble bar scour and gradual redeposition of sediment as flows slowly recede are lacking on the NF Feather, but present on the SF Eel. Based on the model, while the NF Feather study site has proportionally twice the cobble bar area (calculated as percent of total reach with exposed cobble and small boulder deposits at low flow) than the SF Eel site (41% vs. 20% of the total study area, respectively), it provides roughly half the suitable habitat area at all modeled discharges (Figure 5.9).
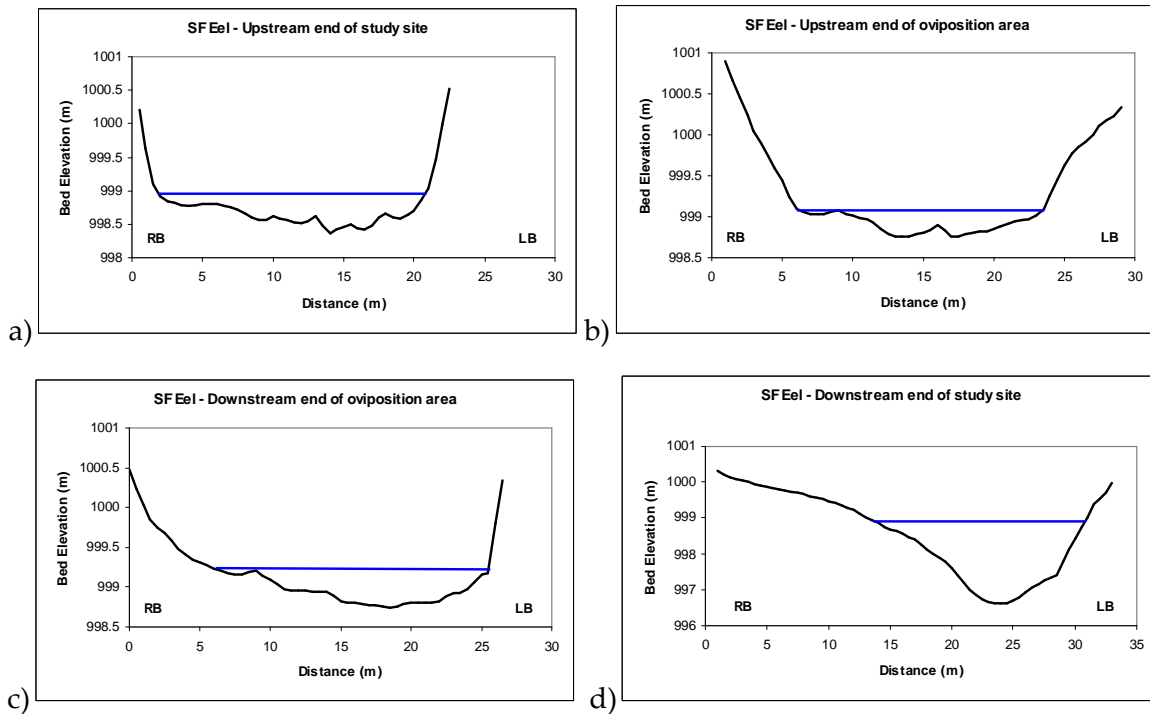
**Figure 5.7. Representative cross-sections for the SF Eel study site ranging from most upstream (a) to downstream (d). Blue line represents depth at 1.45 cms, the discharge at oviposition in 2006.**
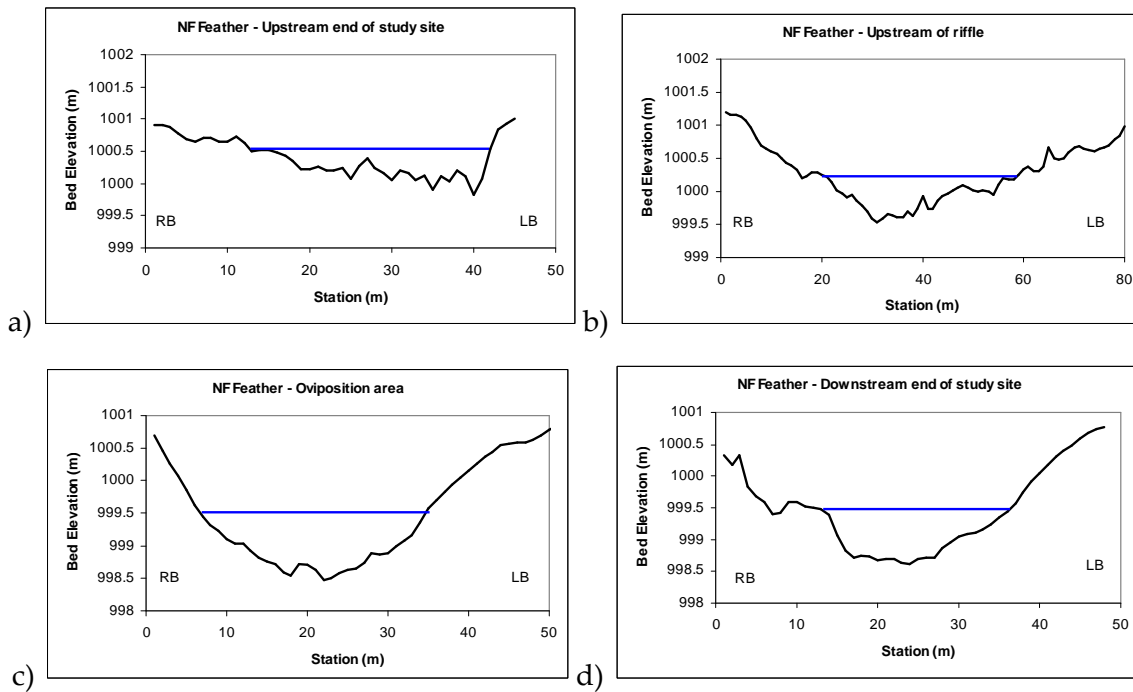


**Figure 5.8. Representative cross-sections for the NF Feather study site ranging from most upstream (a) to downstream (d). Blue line represents depth at baseflow (4.4 cms), the discharge at oviposition in most years.**
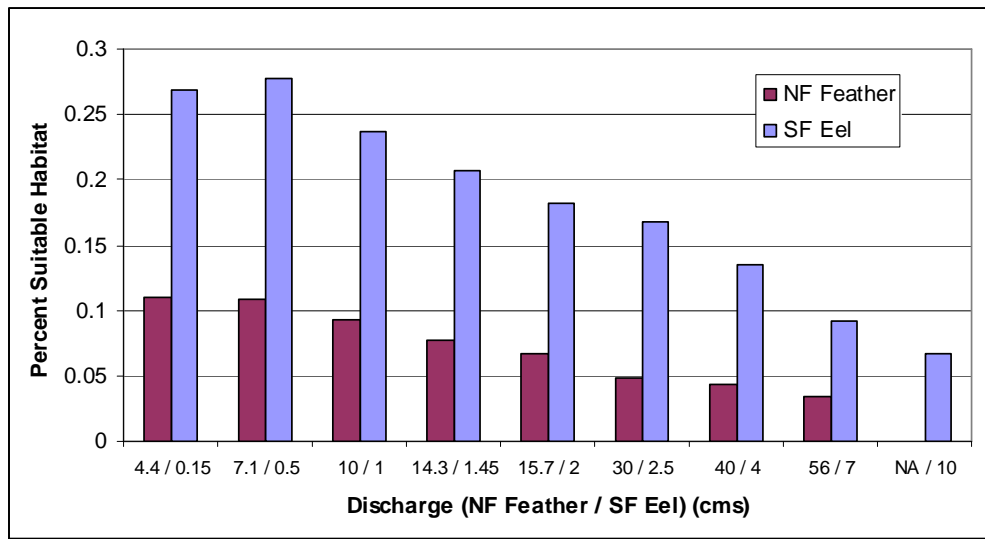
**Figure 5.9. Suitable habitat in each study reach at each modeled flow expressed as a percent of the total reach area.**

### 5.4.2.2. Habitat Connectivity

While informative, comparisons of habitat suitability across flows may not take into account the spatial location of that habitat throughout the survey reach. As flows fluctuate, previously suitable habitats may become unsuitable while previously unsuitable locations may become suitable resulting in little overall change in total suitable habitat area. If these habitats are not hydrologically connected and thus access to the newly created habitats is precluded, then realized total suitable habitat area may decrease. As flows decrease through the season, a lack of connectivity between suitable egg habitat and suitable tadpole habitat may lead to stranding of individuals.

Several metrics for evaluating spatial relationships in GIS have been shown to be useful in previous studies exploring habitat connectivity, such as nearest neighbor analysis and contingency analyses (Johnston 1998). However, these metrics generally provide a measure of connectivity across a complex landscape at a single point in time. Temporal changes in habitat type across a landscape can be evaluated using a variety of change analyses; however, these techniques focus on changes through time at a specific spatial location. Simple techniques to quantify connectivity across both space and time are lacking. Connectivity of suitable habitats as flows fluctuate through the season can be assessed qualitatively in GIS however. While River2D cannot explicitly model standing water that is disconnected from the main channel flow, it models variations in wetting and drying in shallow areas by incorporating groundwater equations. Areas of very shallow patchy flow that may 'blink' in and out as flow fluctuates can be delineated. A simple visual assessment of the locations of suitable habitat as discharge changes (either continuously in a video output from River2D or discretely in a series of

106

snapshots in GIS) can provide information on which areas within the survey reach remain connected throughout the season.

Figure 5.10 shows suitable habitat at the unregulated SF Eel study site at each modeled flow from 1.45 cms (2006 egg-laying discharge) decreasing to low summer baseflow (0.15 cms). In general, the majority of suitable habitat remained connected along the water's edge as flows decreased. Suitable habitat adjacent to the steep riffle at the river right edge of the cobble bar (facing downstream) was patchy where individual microhabitats were intermittently suitable depending on the flow. The patch of suitable habitat where the eggs were located on the river right bank adjacent to the run upstream of the riffle maintained connectivity to suitable habitat as flow decreased, and directly connected to the largest patch of highest suitability habitat at the lowest base flow. Two additional large patches of suitable habitat at 1.45 cms, at the upstream river right end of the survey reach and along the river right cobble bar adjacent to the pool at the downstream end, also remained connected to suitable habitat as flows decreased, however they connected to less suitable habitat at the lowest modeled flow.



a)

South Fork
Eel River
Q = 1.0 cms

b)

Legend

0.5m contour

Egg mass

Combined
Suitability Index

1.00
0.90
0.80
0.70
0.60
0.50
0.40
0.30
0.20
0.10
0.00

Distance
10.0 m

South Fork
Eel River
Q = 0.5 cms

c)
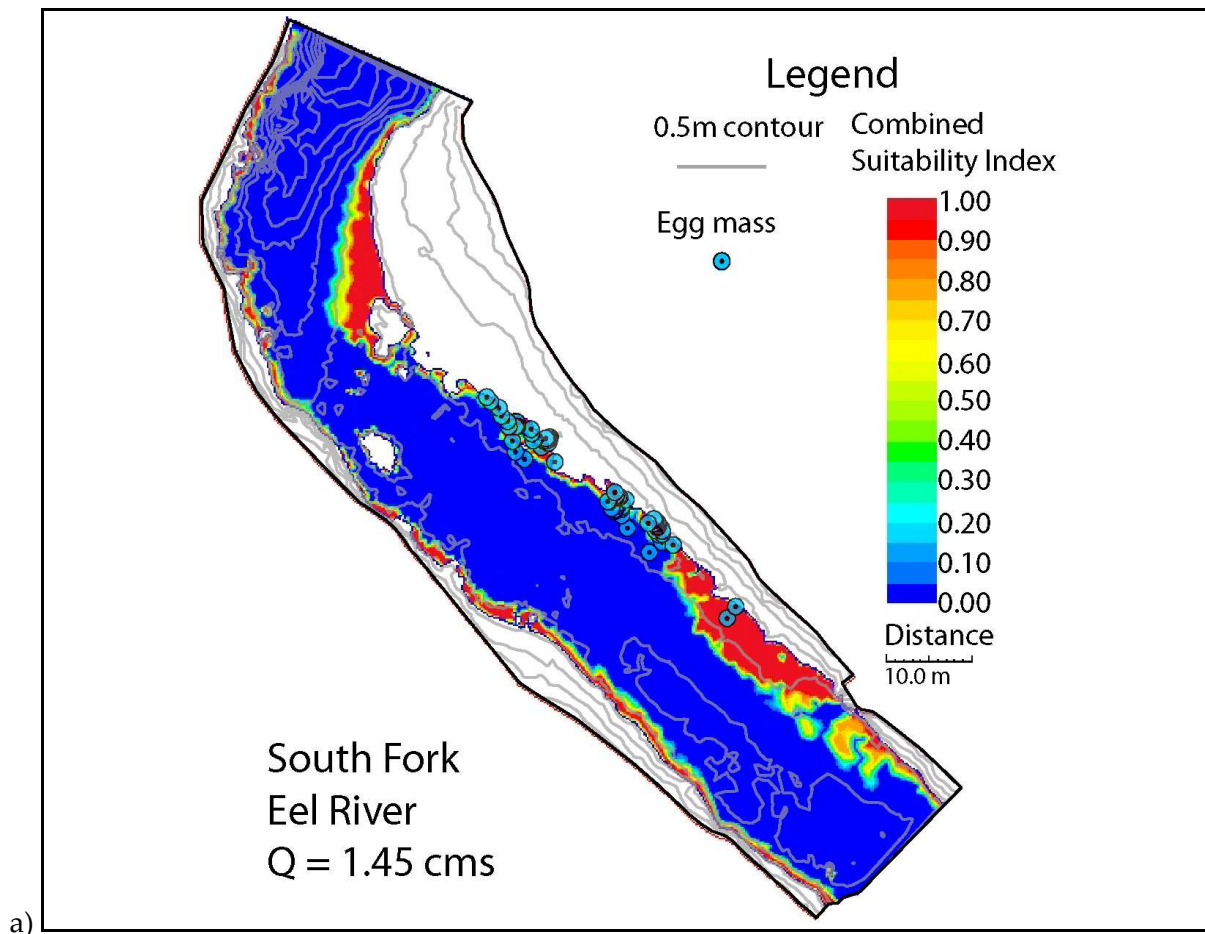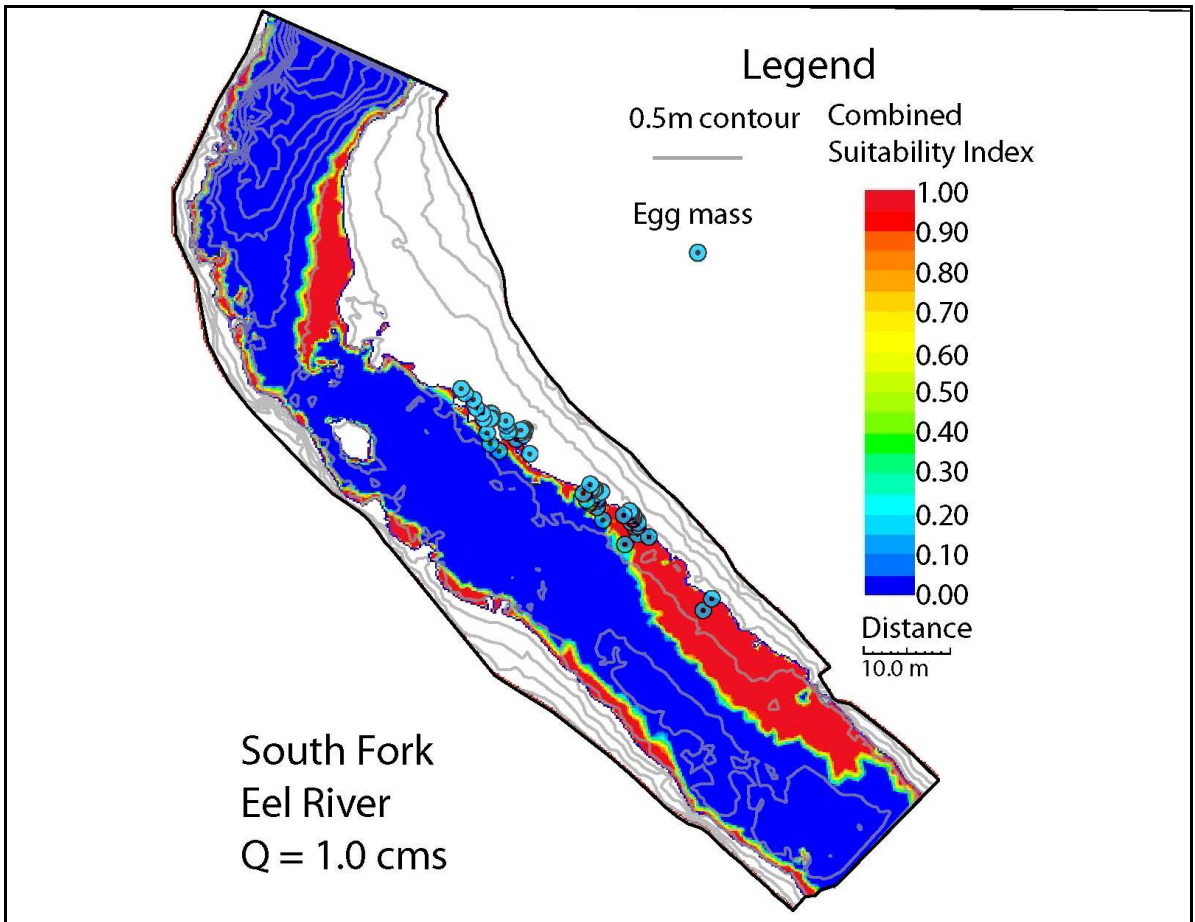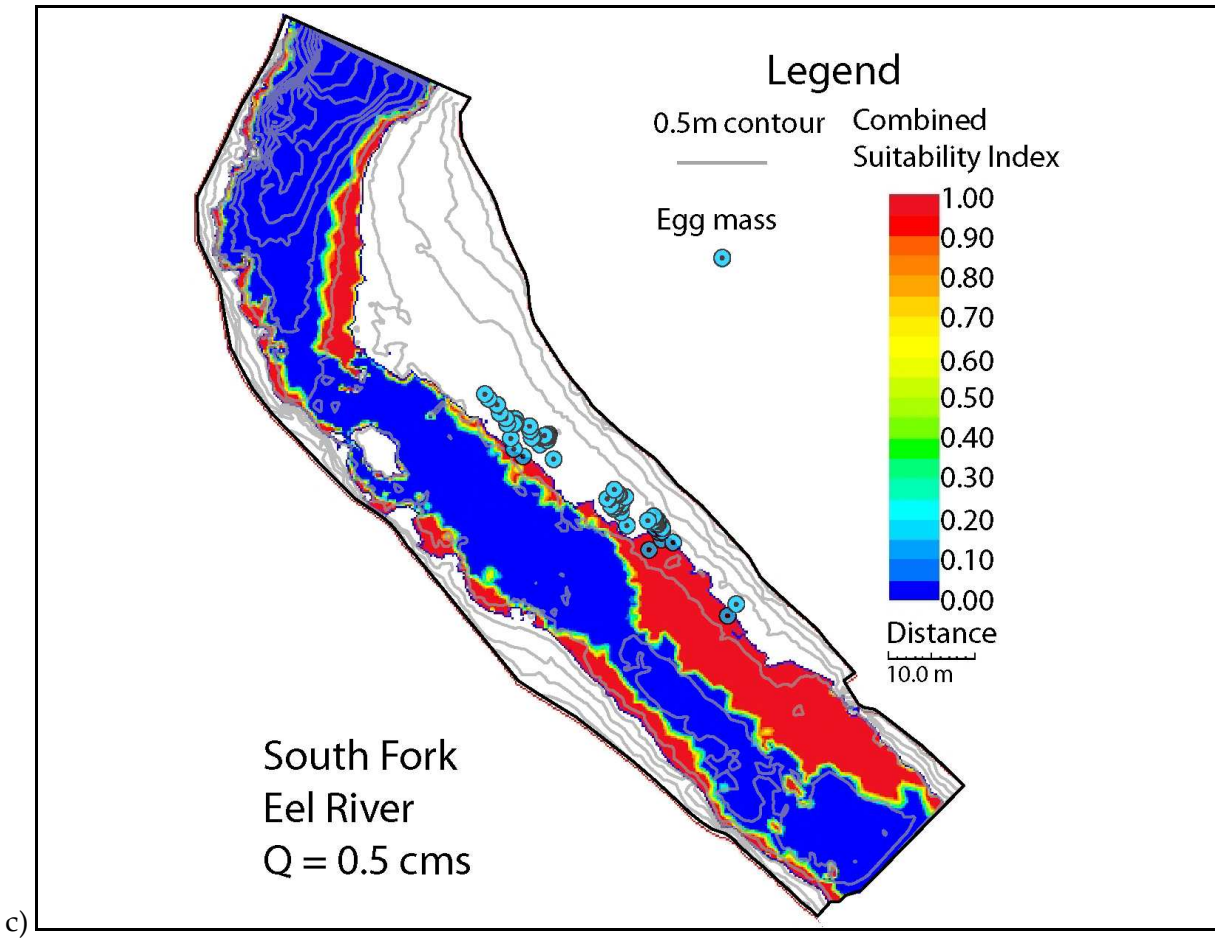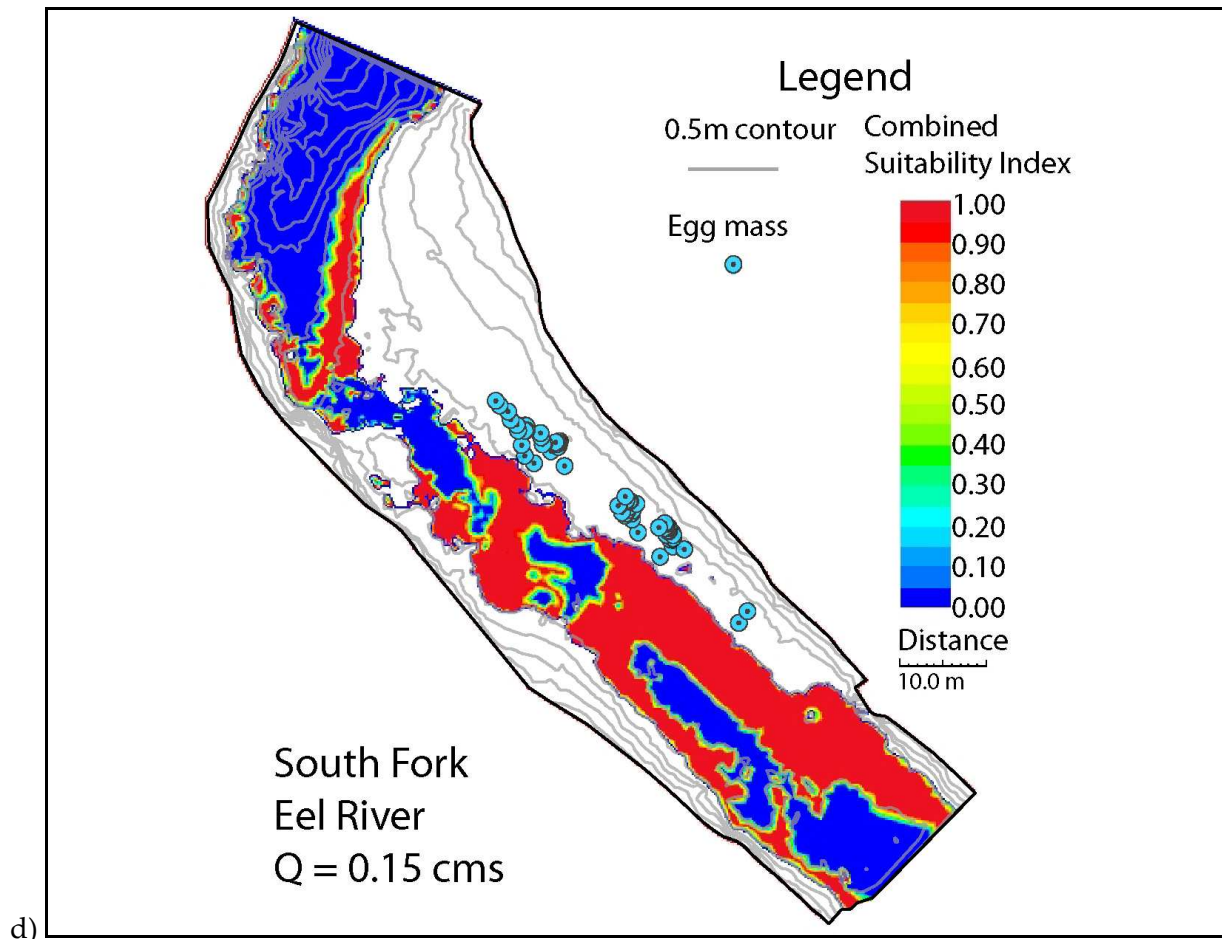
**Figure 5.10. Suitable habitat at the SF Eel study site at each modeled discharge decreasing from a) 1.45 cms (2006 egg-laying discharge) to b) 1.0 cms, c) 0.5 cms, and d) 0.15 cms (low summer flow). Background shows 0.5m contours; Overlaid colors depict habitat suitability (high suitability in red to low suitability in blue) and the extent of flow; Light blue dots indicate egg locations.**

At the NF Feather study site flows are regulated to a minimum in-stream baseflow throughout the late spring and summer; however, high spring runoff can occasionally occur into the breeding season forcing individuals to lay eggs above baseflow discharge, as was the case in 2006. Figure 5.11 shows suitable habitat at each modeled flow from 30.0 cms (discharge at which all egg masses along river right bank were laid) decreasing to the baseflow of 4.4 cms (discharge at which four egg masses on the river left bank were laid). In general, the majority of the suitable habitat along the main channel below the riffle remained connected in a narrow band along the water's edge as flows decreased; however, suitable habitat upstream of the riffle along both banks was patchy and intermittent. The habitat on the river right bank where most of the eggs were laid maintained connectivity as flows decreased, and was connected to the largest patch of suitable habitat downstream of the riffle at baseflow. At moderate discharges, a large patch of suitable habitat appeared along the river left bank at the upstream end of the

110

cobble bar and remained suitable as flows decreased to baseflow. Eggs were not laid in this location in 2006, but the area was utilized in 2007 when discharge at oviposition was 4.3 cms.



a)

North Fork
Feather River
Q = 15.7 cms

Legend

0.5m contour

Egg mass

Combined
Suitability Index

1.00
0.90
0.80
0.70
0.60
0.50
0.40
0.30
0.20
0.10
0.00

Distance

10.0 m

b)

North Fork
Feather River
Q = 10.0 cms

Legend

0.5m contour

Egg mass

Combined
Suitability Index

1.00
0.90
0.80
0.70
0.60
0.50
0.40
0.30
0.20
0.10
0.00

Distance
10.0 m

c)

North Fork
Feather River
Q = 7.1 cms

Legend

0.5m contour

Egg mass

Combined
Suitability Index

1.00
0.90
0.80
0.70
0.60
0.50
0.40
0.30
0.20
0.10
0.00

Distance

10.0 m

d)

e)

**Figure 5.11. Suitable habitat at the NF Feather study site at each modeled discharge decreasing from a) 30.0 cms (2006 egg-laying discharge) to b) 15.7 cms, c) 10.0 cms, d) 7.1 cms, and e) 4.4 cms (baseflow). Locations of eggs in 2006 are shown as light blue dots; eggs laid along the river right bank (left side of figures) were laid at 30.0 cms, the 4 eggs laid on the river left bank were laid at 4.4 cms. Background shows 0.5m contours; Overlaid colors depict habitat suitability (high suitability in red to low suitability in blue) and the extent of flow.**

In an unregulated system, lack of connectivity between suitable egg and tadpole habitats as flows gradually decrease through the season may provide one explanation for why some suitable egg habitats are unoccupied. There are a variety of reasons why habitats with suitable depth, velocity and substrate conditions may be unoccupied including but not limited to presence of predators, presence of heavy vegetation or canopy cover that limits direct sunlight,

unstable hydraulic conditions as flows fluctuate, or simply that habitat is not a limiting factor. As flows decreased at the SF Eel study site, the downstream patch of suitable but unoccupied egg habitat eventually connected to a large deep pool where predatory fish reside. The upstream patch of suitable but unoccupied habitat was shaded for the majority of the day by a large redwood tree in the right bank. At the NF Feather study site, the large patch of suitable but unoccupied habitat at the upstream end of the left bank cobble bar was filled with silt by late summer and was shaded by a large overhanging tree. A spatial evaluation of how hydraulic conditions change as flows fluctuate that includes the position of riparian vegetation and other potentially influential environmental features, may help to resolve the question of why some suitable sites are unoccupied and thus provide a broader context for what defines 'suitable habitat' for *R. boylii*.

### 5.4.3. Scenarios in Hydropower Re-licensing

In regulated river systems (those with hydropower dams), the process of re-licensing can provide an opportunity to change flow management and operation procedures to reduce negative effects on sensitive aquatic taxa, such as *R. boylii*. Specifically, the magnitude of a minimum in-stream flow ('baseflow'), timing and ramping of spring spills, and the timing and magnitude of aseasonal pulse flows, such as recreational boating releases, have potential negative effects on particular *R. boylii* life stages and their habitat (Sections 2 and 3). Differing levels of baseflow may provide differing amounts of available breeding and rearing habitat depending on channel cross-section shape, substrate composition and extent of riparian vegetation. Once eggs are laid at a certain flow level in spring, controlled and uncontrolled spills could create velocities sufficient to scour eggs. On the other hand, eggs laid during a late spring spill event could be stranded after rapid cessation of spill and the return to minimum baseflow. Aseasonal flow pulses that rapidly increase discharges above established baseflow may force previously suitable habitats to become unsuitable due to increased local velocities. The potential effects of each of these management scenarios on *R. boylii* could be evaluated using hydrodynamic models coupled with appropriate definitions of habitat suitability and information on demographic outcomes. To illustrate, three scenarios common in hydropower re-licensing proceedings were explored using the 2D model developed in this study and the habitat suitability definition described above (section 5.4.1): the effects of a spring spill on oviposition habitat, an evaluation of breeding habitat suitability at various baseflow discharges and the effects of an aseasonal recreational pulse flow on rearing habitat.

### 5.4.3.1. Effects from Spring Spills

In unregulated systems, naturally occurring late spring storm events can result in significant loss of eggs due to scour from increased local velocities and can have significant impacts on a season's cohort (see discussion of 2005 SF Eel data in sect 3.3.1). In regulated systems, controlled and uncontrolled spills during late spring after oviposition has begun can have similar impacts and may occur with greater frequency. To determine the potential impact of sudden increases in flow on oviposition habitat, a series of spring pulses was simulated for both study sites using the 2D model.

Three pulses varying from low spring discharges to a high spring discharge were modeled at each study site. On the NF Feather, the lowest three modeled flows (4.4, 7.1, and 10.0 cms) were increased to 30.0 cms. The lowest flow, 4.4 cms, was the minimum baseflow required in 2006, and in most years since 2000 when monitoring began, was the discharge at which oviposition occurred. On the SF Eel, spring egg-laying discharges for the last decade ranged from 0.7 cms to 11.0 cms. Three of the lower modeled flows within this range (1.0, 1.45 and 2.0 cms) were selected, and an increase from each to 7.0 cms, a typical high spring discharge, was modeled.

For each simulated pulse, the change in velocity at each suitable node was determined and the percent of total nodes falling into one of three velocity categories was calculated. Velocity categories were based on the observed rates of egg scour in the Spring Rivers 2002 (Appendix A) flow study (refer to section 2.3.1 for details): velocity increases up to 0.1 m/s had 10% of eggs cumulatively scoured, increases up to 0.4 m/s had approximately 45% cumulative scour, and velocities greater than 0.4 m/s had approximately 50% and potentially greater cumulative scour. Table 5.3 summarizes the change in velocity within suitable habitats as discharge increased from each low flow to the high flow at each study site.

**Table 5.3. Summary of change in velocity category at suitable nodes as discharge is increased from a low spring flow to a high spring flow. Velocity categories based on approximate loss of eggs due to scour observed in Spring Rivers 2002 (Appendix A) study: <0.1 m/s = ~10% cumulative loss; 0.1-0.4 m/s = ~45% cumulative loss; >0.4 m/s = ≥50% cumulative loss.**

| Study Site | Change in Flow (cms) | Mean Increase in Velocity (m/s) | % of nodes <0.1m/s | % of nodes 0.1 - 0.4m/s | % of nodes >0.4m/s |
|---|---|---|---|---|---|
| SF Eel | 1.0 to 7.0 | 0.25 | 23.36 | 60.24 | 16.39 |
| | 1.45 to 7.0 | 0.21 | 28.44 | 60.84 | 10.73 |
| | 2.0 to 7.0 | 0.21 | 34.55 | 53.24 | 12.20 |
| NF Feather | 4.4 to 30.0 | 0.55 | 1.32 | 27.56 | 71.11 |
| | 7.1 to 30.0 | 0.48 | 2.66 | 36.14 | 61.20 |
| | 10.0 to 30.0 | 0.41 | 5.06 | 48.90 | 46.04 |

At both study sites all three simulated pulses resulted in a majority of the suitable breeding habitat becoming unsuitable with velocities greater than 0.1 m/s (Figure 5.12). At the SF Eel study site, only 23-35% of the breeding habitat remained suitable or was 'buffered' from increased velocities associated with the pulse. At the NF Feather study site, <5% of the breeding habitat was buffered. At both sites, the highest modeled low flows had the largest 'buffering capacity', defined as the highest percent of suitable nodes with little to no change in velocity (lowest velocity category). 'Buffering capacity' could also be quantified in a less conservative

manner as the percent of suitable nodes remaining below 0.4 m/s; using this definition, the highest low flow at the NF Feather study site and the mid-level low flow at the SF Eel study site provided the greatest buffering capacity.



a)



b)
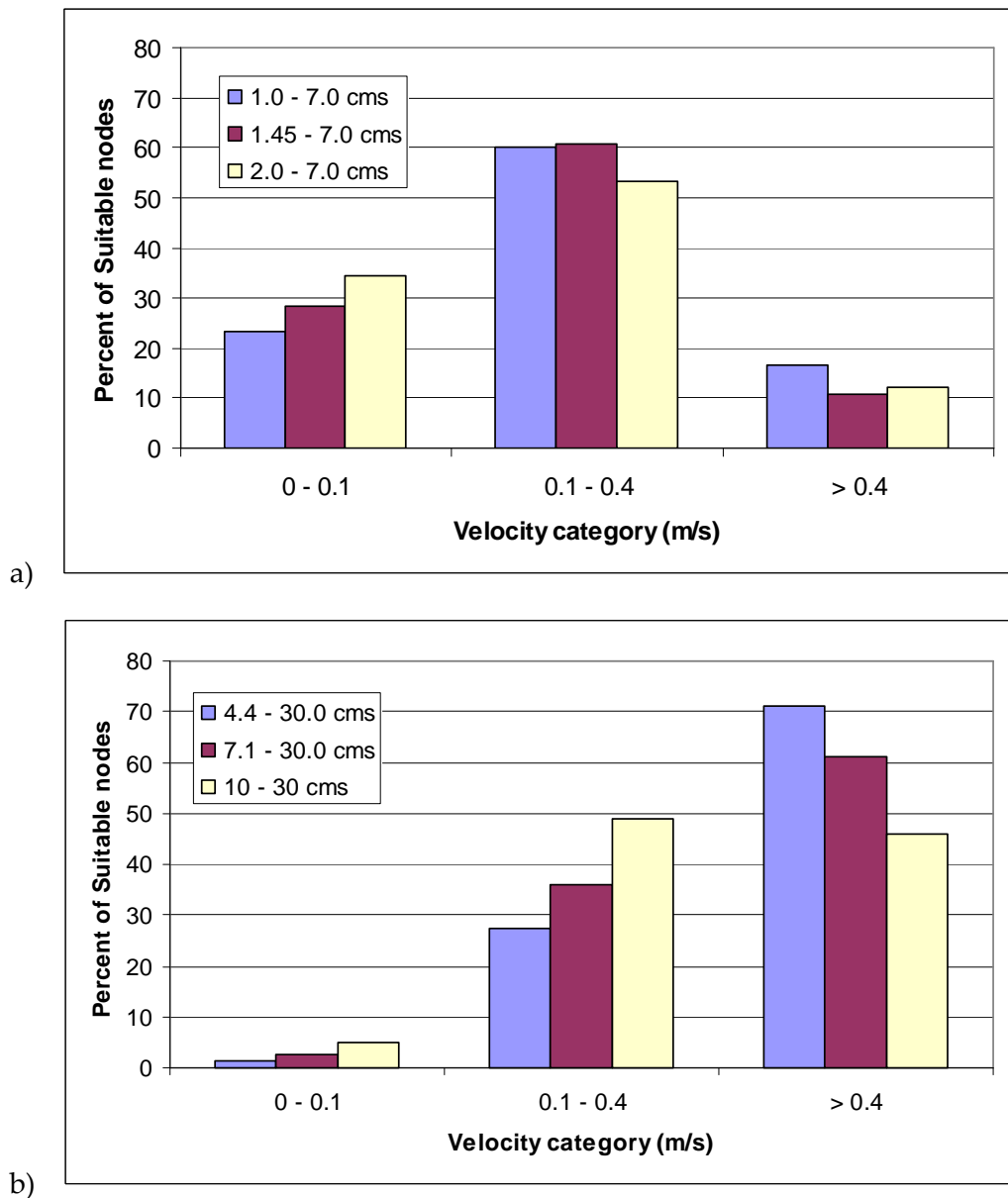
**Figure 5.12. Percent of suitable nodes at each low spring flow for a) SF Eel study site and b) NF Feather study site in each velocity category when flow is increased to a high spring discharge. For example, on the SF Eel, 60% of suitable nodes at 1.0 cms show an increase in velocity from <0.1 m/s to 0.1-0.4 m/s at 7.0 cms. Velocity categories represent ranges associated with observed scour of eggs on the Pit River (Spring Rivers 2002): <0.1 m/s = ~10% cumulative loss of eggs; 0.1-0.4 m/s = ~45% cumulative loss; >0.4 m/s = ≥50% cumulative loss.**

Regardless of the initial low flow discharge however, the SF Eel study site appeared to provide a greater inherent buffering capacity than the NF Feather study site. Only 10-20% of the suitable nodes at the SF Eel study site increased to >0.4 m/s, while 45-70% of the suitable nodes at the NF Feather study site increased to >0.4 m/s depending on the initial level of discharge. These large changes in velocity as discharge increased at the NF Feather study site were likely due to the steep channel banks and narrow, deep cross-sectional shape of the main channel.

The spatial distribution of velocity changes associated with the middle initial discharge pulse for each study site is shown in Figure 5.13. The locations with the largest buffering capacity (lowest velocity change category) at the NF Feather study site overlap with observed occupied suitable habitat. These locations also have connectivity with large areas of suitable larval habitat suggesting both buffering capacity and connectivity may be important in differentiating occupied from unoccupied suitable habitat. However this is not the case at the SF Eel. The occupied suitable habitat along the right bank upstream of the riffle shows low to moderate buffering capacity with velocities increasing from 0.1 to 0.4 m/s and greater than 0.4 m/s during the simulated pulse. The locations with the lowest change in velocities are primarily in eddies adjacent to the deep downstream pool and the upstream scour pool. While both these eddy locations provide suitable habitat in terms of flow (see Figure 5.10), other non-flow related factors, such as predation in the large downstream pool or shading by overhanging vegetation in the upstream eddy, may limit suitability for larval rearing. On the unregulated SF Eel where high spring pulses are infrequent, connectivity to suitable larval habitat may be more important for oviposition site selection than buffering capacity.

Legend

0.5m contour

Egg mass

Category of
Velocity Increase

< 0.10 m/s

0.10 - 0.40 m/s

> 0.40 m/s

Distance

10.0 m

South Fork
Eel River

a)
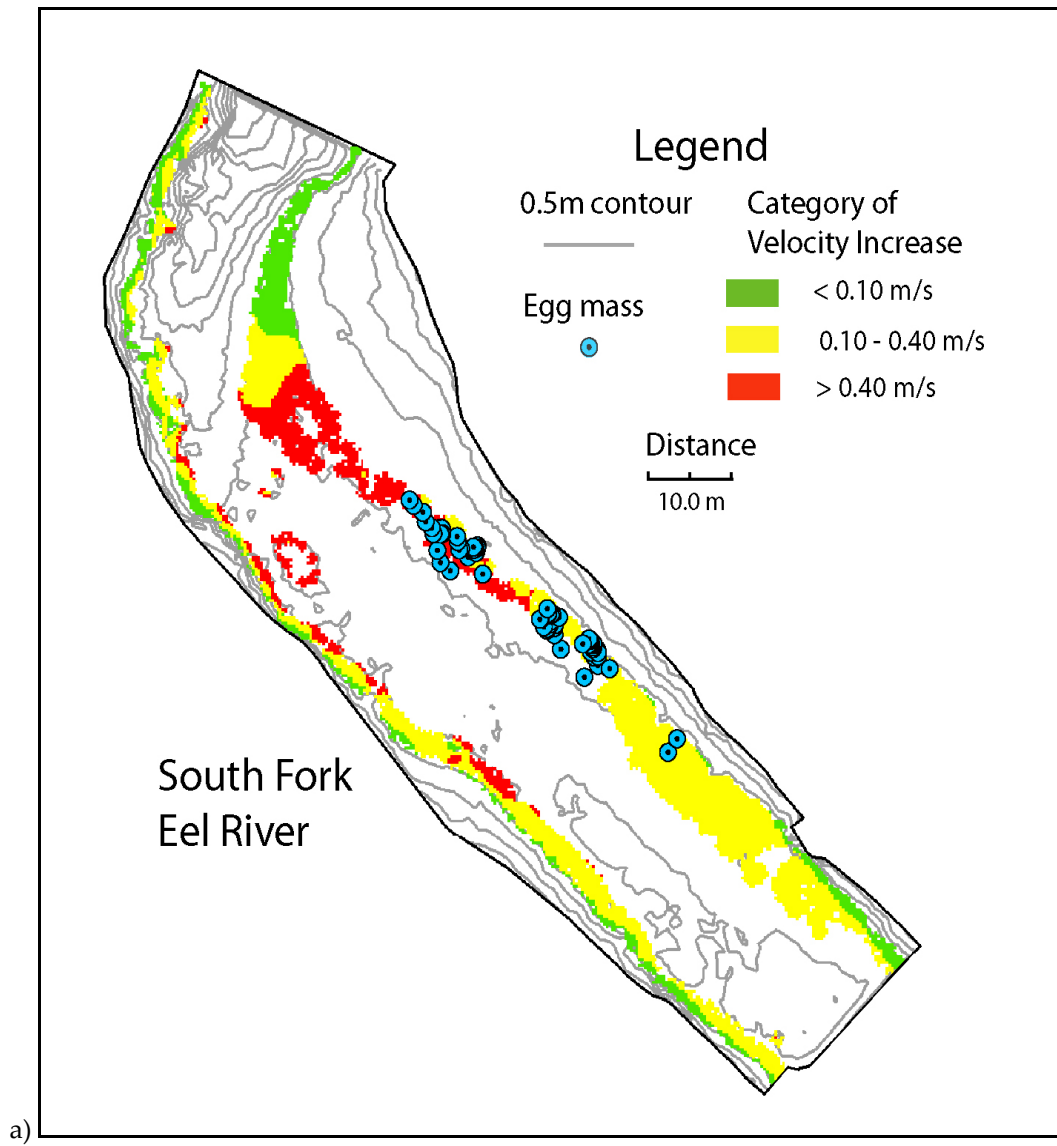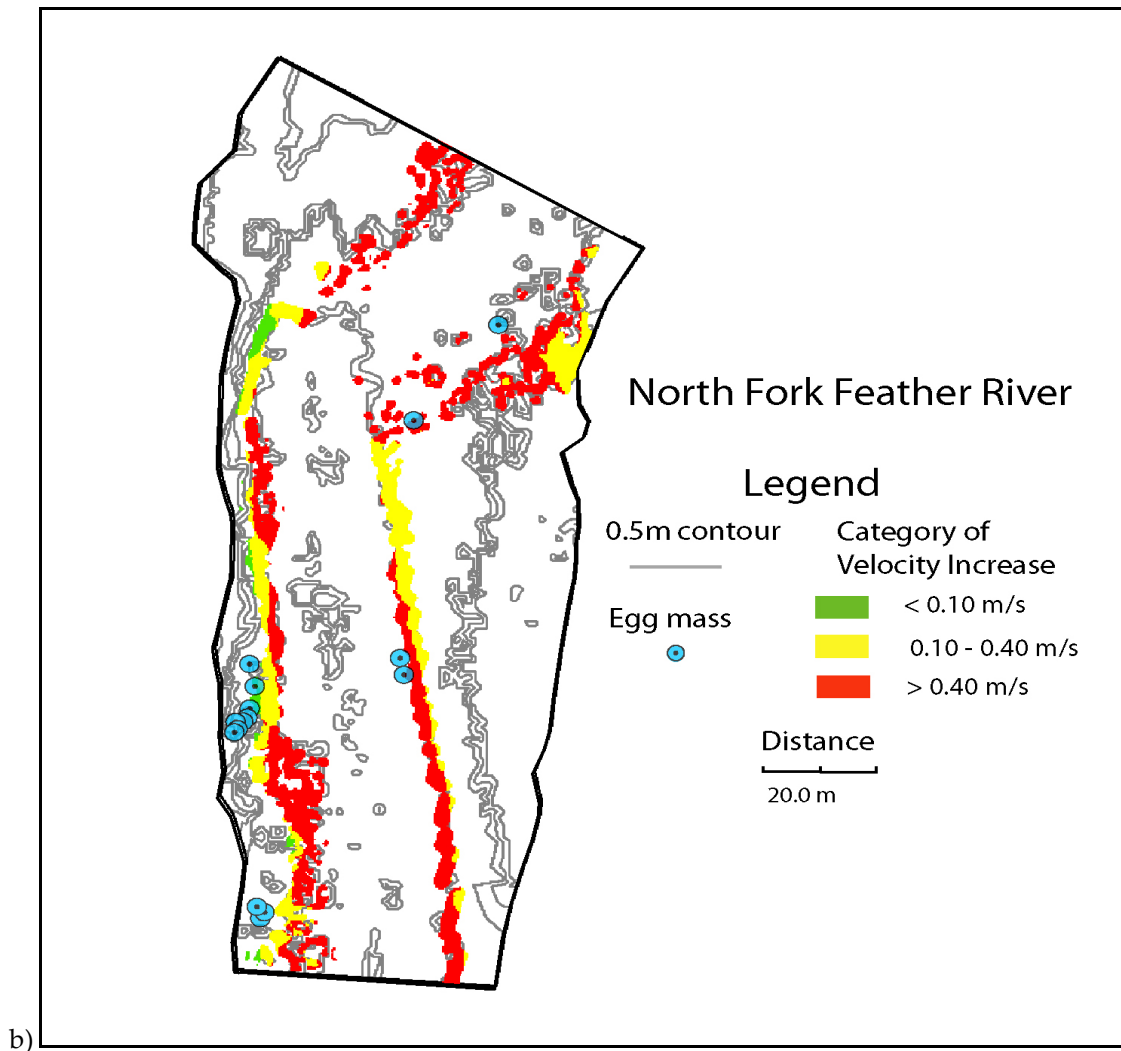
**Figure 5.13. Distribution of suitable oviposition nodes differentiated by velocity category in a modeled spring pulse scenario. a) SF Eel study site; discharge increased from 1.45 cms to 7.0 cms; b) NF Feather study site, discharge increased from 7.1 cms to 30.0 cms. Background shows 0.5m contours. Overlaid colors depict the category of velocity increase. Locations of eggs in 2006 are shown as light blue dots.**

### 5.4.3.2. Selection of Baseflows

The selection of a minimum required flow or baseflow in regulated systems is a complex and highly debated decision that managers, scientists and stakeholders must make when negotiating license conditions. An important factor in the decision is an assessment of the amount of habitat each potential baseflow provides to aquatic species. Calculations of weighted usable area (WUA; a measure of suitable habitat area at a given discharge) from the output of 1D or 2D modeling are a common way to quantify available habitat for aquatic species and life stages of interest (Stalnaker et al. 1995). An analysis of WUA in regard to selecting baseflows was completed only for the regulated NF Feather as the unregulated SF Eel is a free-flowing river with annual variability in the descending limb of the hydrograph. Using the habitat

121

suitability criteria defined above (sect 5.4.1.) for *R. boylii* egg masses, WUA of breeding habitat at three potential baseflows was calculated for the NF Feather study site directly in River2D. The lowest 3 modeled flows were selected (4.4, 7.1, and 10.0 cms), the lowest of which (4.4 cms) was the minimum flow required in 2006. Figure 5.14 shows the WUA for the three potential baseflows.
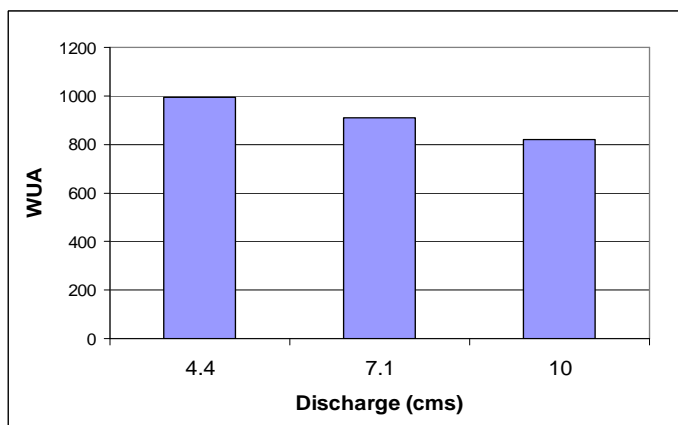


**Figure 5.14. Weighted Usable Area for potential baseflows at the NF Feather study site calculated using River2D.**

The largest WUA occurred at the lowest modeled discharge as would be expected given lower flows generally provide more shallow habitat throughout the channel. For *R. boylii* however, the amount of habitat available may be less of a critical factor than the ability of the available habitat to remain hydraulically stable or 'buffer' against changes in flow.

Although the lowest potential baseflow had the largest WUA, the highest tested baseflow had the largest buffering capacity in the spring spill analysis above. If the management goal for determining the level of baseflow was to limit impacts of flow fluctuation on *R. boylii* breeding habitat and reduce the risk of egg scour, the highest baseflow level providing the greatest buffering capacity might be selected. However, if spring pulses were uncommon and breeding habitat was limited in availability, the baseflow with the greatest WUA might be selected. In either case, such decisions would need to be assessed on a river by river basis in conjunction with other aquatic species needs.

### 5.4.3.3. Effects of Aseasonal Pulsed Flows

*R. boylii* is one of many native aquatic species that has adapted its life history strategy to the stable, non-fluctuating summer baseflows typical of California's Mediterranean environment. Results from the field and flume manipulations presented in section 4 showed that tadpoles are not adapted to withstand large increases in velocity. To determine the effects of an aseasonal pulsed flow on tadpoles, a series of flows that increased from a low flow (same discharges as assessed in section 5.4.3.1) to a representative high flow suitable for recreational boating were modeled; the subsequent velocity increases within suitable tadpole habitats were then evaluated.

During the first few weeks following hatching, tadpoles are vulnerable to increased velocities at the egg mass site (see section 4.3) until they develop sufficiently to disperse into adjacent suitable habitats. Once in these suitable habitats, tadpoles remain susceptible to increased velocities throughout the low-flow summer season until they reach metamorphosis in early fall and have the potential to leave the shallow stream margin. Their susceptibility to increased velocities varies with Gosner stage such that later stages are the most susceptible (Figure 4.9); however, in order to simplify the assessment of modeled velocities for tadpoles, the rate of tadpole loss as determined from the Brett chamber experiment (section 4.2) was averaged for three categories of increased velocity. Based on the cumulative frequency plot of tadpole loss versus critical velocity when tadpoles fatigue (Figure 4.10), the average critical velocity for each quartile of loss was calculated: 25% of tadpoles were lost at 0.1 m/s, 50% at 0.18 m/s, 75% at 0.32 m/s and 100% at 0.43 m/s. These data were used to create three categories of increased velocity, each associated with an average percent of tadpole loss: 0.0-0.1 m/s = ~25% loss; 0.1-0.25 m/s = ~50% loss; and >0.25 m/s = ~75%+ loss.

To assess the impact of an aseasonal pulse, such as a recreation flow, on tolerable tadpole habitat, an increase in discharge from each of the three modeled low flows to a typical boatable flow was modeled at each site (7.0 cms on SF Eel, 30.0 cms on NF Feather). For each model run, the change in velocity at each tolerable node was determined and the percent of total nodes falling into one of the three velocity categories associated with tadpole loss was calculated. Based on the experimental results discussed in section 4, most tadpoles respond to increasing velocity by swimming straight down into the substrate rather than laterally to another potentially suitable patch. Therefore, as velocities increased to the higher discharge, it was assumed that tadpoles either remained in their initially tolerable habitats or were swept downstream and lost. Any nodes that were initially unsuitable or dry, but became tolerable as flow increased were not included in the assessment.

Similar to the assessment of increased velocities on suitable egg habitat, the highest initial discharges had the lowest percent loss of tadpoles when discharge was increased (Table 5.4; Figure 5.15). However, the difference between the two study sites of the percent of tolerable nodes falling into the highest velocity category was much more pronounced. While only 25-45% of tolerable nodes at the unregulated SF Eel study site became highly unsuitable (>75% tadpole loss), 75-90% of the nodes at the regulated NF Feather site became highly unsuitable. Although both study sites showed increased velocities at most nodes, the NF Feather site had larger magnitude increases. As mentioned above, the large changes in velocity magnitude at the NF Feather study site were surmised to be due to the entrenched nature of the channel that provides steep banks.

**Table 5.4. Summary of change in velocity category at tolerable nodes as discharge is increased from a low flow to a summer boatable flow. Velocity categories based on loss of tadpoles observed in field and flume experiments: <0.1 m/s = 25% loss; 0.1-0.25 m/s = ~50% loss (0.18m/s = 50%); >0.25 m/s = ~75%+ loss (0.32 m/s = 75%).**

| Study Site | Change in Flow (cms) | Mean Increase in Velocity (m/s) | % of nodes <0.1m/s | % of nodes 0.1 - 0.25m/s | % of nodes >0.25m/s |
|---|---|---|---|---|---|
| SF Eel | 1.0 to 7.0 | 0.25 | 23.18 | 30.21 | 46.42 |
| | 1.45 to 7.0 | 0.21 | 28.08 | 44.35 | 27.21 |
| | 2.0 to 7.0 | 0.21 | 33.87 | 34.30 | 31.14 |
| NF Feather | 4.4 to 30.0 | 0.55 | 1.32 | 6.73 | 91.95 |
| | 7.1 to 30.0 | 0.48 | 2.66 | 11.86 | 85.48 |
| | 10.0 to 30.0 | 0.41 | 5.06 | 21.40 | 73.54 |

a)



b)
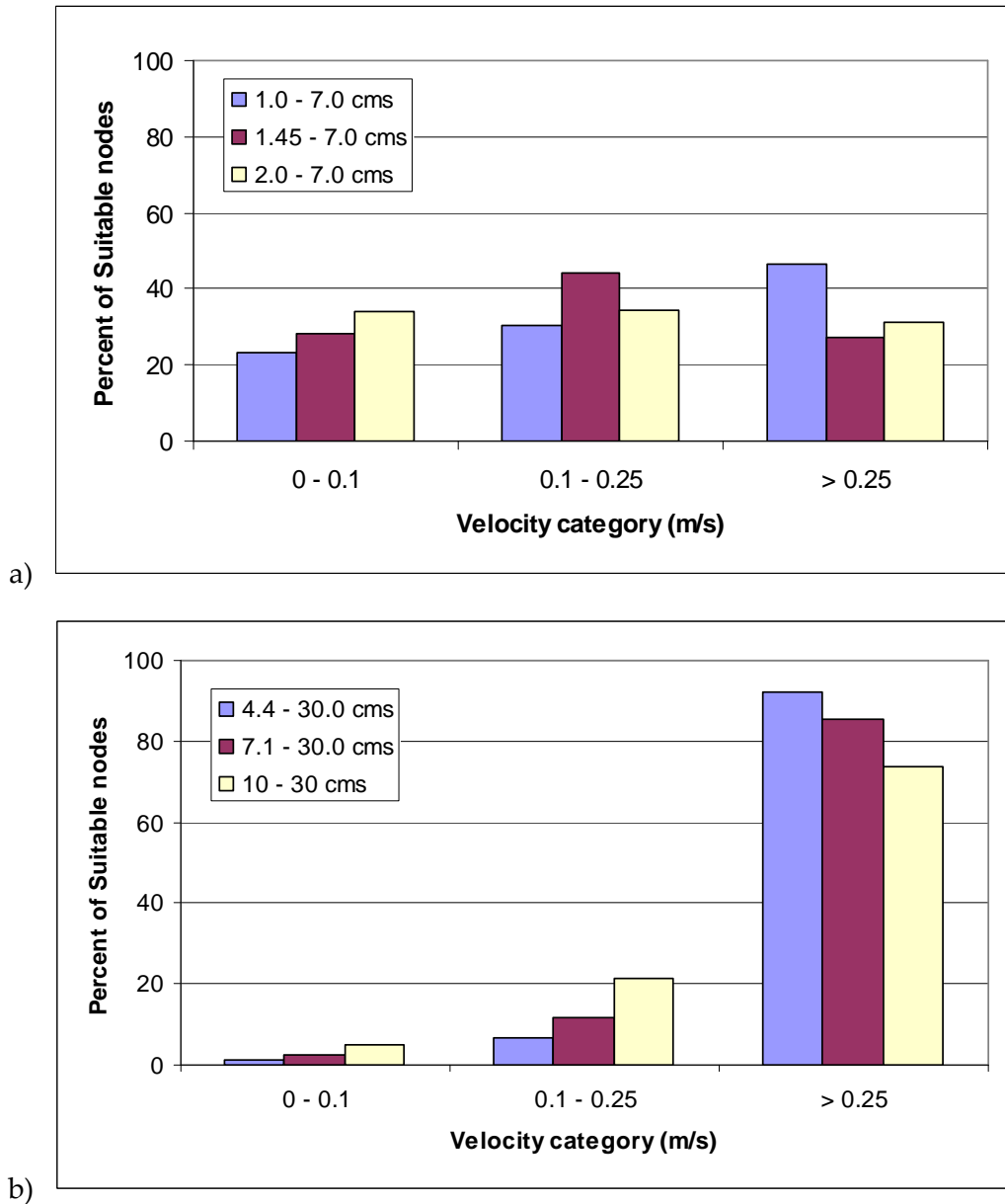
**Figure 5.15. Percent of tolerable nodes at each initial low flow for a) SF Eel study site and b) NF Feather study site in each velocity category when flow is increased to a summer boatable discharge. For example, on the SF Eel, 30% of tolerable nodes at 1.0cms show an increase in velocity from <0.1 m/s to 0.1-0.25 m/s at 7.0 cms. Velocity categories represent ranges associated with observed loss in field and flume tadpole experiments (section 4): <0.1 m/s = ~25% loss of tadpoles; 0.1-0.25 m/s = ~50% loss; >0.25 m/s = ~75% loss.**

## 5.5. Conclusions and Management Implications

Although in-stream flow models have been used extensively to evaluate fish habitat, this methodology has not previously been applied to assessments of amphibian habitat. Analysis of changes in hydraulic habitat as flow fluctuates with a 2D hydrodynamic model is useful for *R. boylii* in particular, due to their reliance on near-shore in-stream habitat conditions for reproduction.

The 2D model used in this study performed reasonably well, depending upon the nature and scale of management questions addressed. For questions regarding relative change in local hydraulic habitat conditions, such as potential for scour from a high pulse flow in occupied breeding habitat or flows that cause entrainment or exhaustion of tadpoles, the model provided useful information. However, the model was not useful in predicting exact impacts to microscale habitats due to low precision in point velocities. For example, the model could not predict "suitable" tadpole habitat, defined as 0.0-0.5 cm/s, but the model could resolve "tolerable" tadpole habitat, defined as 0.0-0.1 m/s. As a result, the 2D model proved well-suited for evaluation of the general reach-scale response of hydraulic habitat to variation in flow conditions, and could be used as a viable management tool for testing the relative impact of flow scenarios. Questions framed at a larger scale, such as predictions of frog distribution or determining impacts to frog population dynamics would require a different methodology. When used in conjunction with other assessment tools, such as empirical field observations and experimental studies where the level of precision is finer than what is achievable with a 2D model, the modeling approach, which allows for extrapolations through space and time beyond what can be achieved by experiments, is an informative tool for resource managers.

Several modeled flow scenarios were completed to explore various questions of interest relating to *R. boylii* habitat availability and connectivity as discharge fluctuates. As discharge increased across the full range of modeled flows at each study site, breeding habitat availability gradually decreased, similar to results from empirical flow manipulations reviewed in chapter 2; however, differences in channel morphology between the two modeling study sites affected the proportions of change in habitat availability such that the NF Feather site provided less suitable habitat due to entrenchment of the channel. As discharge decreased from a spring flow at oviposition to a low summer flow, a qualitative evaluation of habitat connectivity showed high density occupied suitable breeding habitat connected to large areas of suitable rearing habitat in both study sites. Low density occupied habitat at the NF Feather site connected to small areas of suitable rearing habitat, and unoccupied suitable breeding habitats at both sites connected to either small areas of suitable rearing habitat or unsuitable rearing habitats.

Several modeled flow scenarios were also completed to explore questions of interest relating to typical flow regimes prescribed in hydropower re-licensing proceedings. In a natural spring pulse scenario, 25-30% of suitable breeding habitat on the SF Eel site and <5% of the breeding habitat on the NF Feather site remained suitable or were 'buffered' from the pulse. At the NF Feather site, occupied breeding habitat overlapped with buffered habitats; however, at the SF Eel site, occupied breeding habitat overlapped with moderately buffered habitat where velocity increases were associated with moderate rates of egg scour. Results from the spring pulse

scenario and connectivity analysis suggest both buffering capacity and connectivity to suitable rearing habitat may be important in differentiating occupied from unoccupied suitable breeding habitat at the NF Feather study site, but connectivity may be more important than buffering capacity at the SF Eel study site where spring pulses are infrequent. In a comparison of breeding habitat suitability at various baseflows in the regulated study site, the lowest tested baseflow had the largest weighted usable area, but the highest tested baseflow had the largest buffering capacity. In an aseasonal pulse flow scenario, 25-45% of suitable rearing habitat at the SF Eel study site and 75-90% of suitable rearing habitat at the NF Feather site resulted in velocity increases associated with >75% tadpole loss. Differences between the sites in buffering capacity against flow increases were largely due to differences in channel morphology. Although both sites had velocity increases throughout the majority of suitable habitat areas as flows increased, channel entrenchment at the NF Feather site resulted in much greater increases in velocity in the near-shore environment. An understanding of how various channel morphologies create more or less susceptibility to changing near-shore habitat conditions as flows fluctuate should be incorporated into flow regulation considerations.

Perhaps the largest limitation of a 2D modeling approach for assessing impacts on *R. boylii* from various flow regimes is the necessity of incorporating compatible hydraulic habitat suitability criteria for each life stage. If the question of interest requires defining habitat suitability at a scale finer than the precision of the model, a different methodology should be used. Likewise, different definitions of suitability might provide different results. For example, in the spring pulse modeling scenario discussed in section 5.4, if a larger range of velocities (e.g. 0.0-0.15 m/s) had been determined to provide suitable habitat, discrete quantifiable results such as available habitat area and the percent of habitat falling within a suitable velocity category would change. However, relative changes between flows and the degree of impact comparatively between flows would remain the same. The habitat suitability criteria used in this study were determined to be acceptable for these specific study sites, but they may not be applicable in other river reaches or watersheds. As a result, it is essential to understand the precision, accuracy and limitations of the model, frame questions of interest in a manner appropriate to the known characteristics of each life stage and interpret the model results appropriately within the narrow scope in which they apply. If these distinctions are not understood and model results are applied carelessly in water management, risks to *R. boylii* may be higher than desired.

# 6.0  Conclusions and Recommendations

## 6.1.  Conclusions

The combined results of the literature review, pulse frequency analyses, mechanistic experiments with tadpoles, and hydrodynamic modeling support the hypothesis that aseasonal pulsed flows have contributed to the decline of the foothill yellow-legged frog (*Rana boylii*). *Rana boylii* has evolved several adaptations to the Mediterranean climate and associated hydrologic regime (wet winters and dry summers) of California rivers.  Most prominent among their adaptations is that the multi-staged life cycle of *R. boylii* occurs in synchrony with the natural flow regime.  The timing, magnitude, duration, frequency and rate of change of water discharge are all relevant factors.  The multiple disparate lines of evidence explored in this report lead to the fundamental conclusion that **aseasonal pulse flows adversely affect *R. boylii* by creating stressful or fatal velocity conditions for the relatively immobile early life stages**. A second fundamental conclusion is that **within regulated rivers, flow management can be improved to meet—or reduce the impact on—the life history needs of *R. boylii***.

The specific conclusions include:

- Adults generally breed and lay eggs in areas where the river channel morphology reduces the impact of scour during natural spring run-off pulses. Breeding locations do not experience as much velocity change with change in stage as other locations. Adults select egg laying sites within areas that have low water velocities and relatively shallow water depths and often attach eggs to large substrates that provide protection from variable water velocities.

- Based on 2D hydrodynamic modeling, it appears that occupied suitable breeding sites also have the characteristic of being connected to suitable rearing areas as flows decline throughout the summer. That is, recently hatched tadpoles would be able to follow the receding shoreline, without becoming trapped in isolated pools that may dry or become lethally hot, into suitable areas with potentially lower predation risks and high algal production.

- Reviews of previous studies and the case study data revealed that significant losses of *R. boylii* egg masses have occurred due to both scouring (pulse flows after egg laying) and stranding/desiccation (eggs laid during spring release and flows dropped suddenly). Thus, in regulated rivers, timing and magnitude of spring pulses can be manipulated to reduce impacts.

- Experiments show that tadpoles respond to increases in water velocity and depth by seeking refuge in stream substrates. This response, while potentially protective in the short-term, may result in losses to predation by fish if tadpoles are displaced to the water column or are forced to stay under rocks where predators like crayfish and other aquatic invertebrates dwell. In laboratory experiments, displacement of tadpoles from substrate refugia was observed at relatively low water velocities (10-20 cm/s) over short

periods of time (< 2 hours). Larger (older) tadpoles are more susceptible to increases in velocity than smaller (younger) ones.

- Tadpoles are also stranded by summer pulse flows and 2D hydrodynamic modeling demonstrates the importance of hydraulic connectivity and channel shape in this process, along with pulse magnitude. Future research focusing on how slow the change in discharge, and over how narrow a range, should take into account factors such as bank slope, particle size, sorting, and embeddedness. For a small tadpole (< 1 cm) even moderately sized cobbles and boulders could be obstacles to following a receding shoreline. Recommendations for benign ramping rates will thus be quite site specific.

- Post-metamorphic life stages (juveniles and adults) may be less at risk from pulsed flows, due to their greater mobility. However, if manufactured pulsed flow events are decoupled from fall rain events, which might cue frog migration to off-channel over-wintering sites, these life stages may still be susceptible. Such issues, which integrate *R. boylii's* use of multiple habitats at a watershed-scale, remain open for future research.

- Long-term population censuses show that population dynamics appear to be driven by successful egg laying and tadpole rearing which is strongly related to spring and summer flow conditions. This relationship is only apparent when incorporating a two (Central Coast streams) or three (Northern Coast and Northern Sierra streams) year lag time, representing time to maturity, into the analyses.

- Reviews of previous studies indicated that change in suitable habitat area as discharge changed was extremely site specific.  In this report, areas of suitable habitat can be modeled for both egg and tadpole life stages, but given the limitations of fine scale surveying technology, error in precision of point water velocities in shallow microhabitats with coarse substrate  may lead to higher than desired risk to these life stages if model results are used carelessly in water management.


## 6.2   Recommendations for Management of California Rivers

This section provides recommendations for managing riverine water releases with the goal of maintaining robust populations of *R. boylii* and restoring populations at risk.  Even though these approaches are focused on *R. boylii*, they may benefit other aquatic species with similar evolutionary histories and seasonal adaptations.  Species that are currently successful in regulated river reaches may be negatively affected by these recommended management approaches.  Thus, effects on other species should be evaluated prior to implementation.  Also, while these changes to water release regimes should be beneficial, there are other factors which may influence the overall success of new management approaches for *R. boylii* populations, such as:  (1) distribution of exotic predatory species; (2) proximity to robust *R. boylii* populations and tributary refugia; (3) recent alteration of channel morphology due to regulated flows, (4) water temperature regimes, etc.  These factors should be evaluated simultaneously to aid in the interpretation of the effectiveness of changes to flow regimes.

Based on the work in this study, management options fall in three main categories – options for river reaches in which *R. boylii* is currently present and at risk, options for reaches where they are apparently stable, and approaches for evaluating the efficacy of restoring populations to reaches where they are mysteriously absent or with known extirpations. Since the majority of regulated river reaches contain at risk populations and this study focused on effects of pulsed flows, the bulk of the following recommendations are for that category.

<u>Populations At Risk</u>

- Minimize fluctuations in flows during the oviposition and tadpole rearing periods. This includes both short-term (on the order of hours) and longer term (on the order of a few days) pulsed flows. This can be accomplished in one of two ways: (1) direct population monitoring or (2) precautionary date-setting.

    o In direct population monitoring, surveys would begin prior to the earliest known oviposition dates. Once breeding and oviposition were detected, pulsed flows would be stopped and flows would be maintained at a steady rate or dropped at a rate slow enough to prevent stranding of egg masses and to allow tadpoles to follow a receding shoreline through the rearing season until metamorphosis. Natural hydrographs for individual rivers could be evaluated to provide potential ramping rates.

    o In precautionary date-setting, dates would be set based on previous monitoring data. Several years of monitoring in a variety of water year types (e.g. warm/dry, cold/wet) would be necessary to provide valid boundaries for setting dates. The spring date would be buffered by setting it substantially earlier than the earliest known oviposition date. After that date, pulsed flows would be stopped and flows would be maintained at a steady rate or dropped at a rate slow enough to prevent stranding of egg masses and to allow tadpoles to follow a receding shoreline through the rearing season until the fall date. The fall date (post-metamorphosis) would be set based on previous observations of the latest date upon which most metamorphosis has occurred or after the first fall rains, whichever comes later. Periodic monitoring would still occur into the future to confirm the validity of these dates.

- Raise minimum flows (baseflows) to buffer the effects of pulsed flows.

- Habitat modeling (either 1 or 2-dimentional approaches) can provide a starting point for examining the connectivity between breeding/oviposition and rearing locations as discharge fluctuates and estimating the effects of pulsed flows on near shore depths and velocities. This information is useful for setting flow conditions during FERC re-licensing, with the following caveats. If base flows are increased, post-license studies will be needed on water temperature changes and riparian vegetation/ channel morphology effects which could affect *R. boylii* growth/survival and habitat suitability,

respectfully. Also, the nature of the relationship between *R. boylii* population stability and habitat suitability/area needs to be quantified. Specifically,

o The hypothesis of a positive relationship between habitat area containing suitable velocities and depths (defined in habitat models as "weighted usable area") and *R. boylii* population size or stability has not been tested yet. Though it is assumed that more suitable habitat within a regulated river will be beneficial to this species, there is evidence (either observational or experimental) that several factors may be limiting, including: (1) other abiotic conditions such as temperature, (2) community level interactions such as competition for algal resources and predation by non-native taxa, and (3) metapopulation structure such as the distance between tributaries used by adults, and reservoirs or diversion reaches that may act as barriers to dispersal and re-colonization. Before habitat modeling is broadly applied to evaluating the license conditions needed by *R. boylii* in hydroelectric projects, the importance of "weighted usable area" must be quantitatively placed in the context of other key determinants of frog distribution and abundance.

Apparently Stable Populations

- For populations that are apparently **not** at risk in regulated river reaches, flows should be managed to simulate the natural (pre-regulation) hydrographs. The most important components to maintain are the winter flood peaks and historic spring run-off patterns (Trush and McBain 2007). Flow release pattern should differ for different water year types.

River Reaches With Extirpated Populations

- The analytical methods of this report can be used as tools to evaluate the potential success of repatriation of *R. boylii* to river reaches where there have been known extirpations or where frogs are absent, but present in contiguous reaches.

    o Breeding/oviposition and tadpole rearing season pulsed flow frequency analysis can be used to assess the potential for reproductive success.

    o Hydrodynamic habitat modeling of proposed re-introduction locations can be used to assess whether potential breeding/oviposition sites would remain connected to tadpole rearing sites under the existing flow regime.

## 6.3. Recommendations for FERC-Related Studies and Future Research

Through reviews of recent study reports, field and laboratory experiments, and hydrodynamic modeling, this study has identified the aspects of aseasonal pulsed flows that negatively influence pre-metamorphic life stages (eggs and larvae) of this *Rana boylii*. This study has also

begun to illuminate the mechanisms of these effects and the potential for large scale population responses. However, information gaps do remain and are identified below.

- Future FERC re-licensing or other studies on *R. boylii* would be improved by:

    o 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.

    o Presenting sampling effort (e.g., number sites, search time, or area) clearly in text and figures.

    o Including bankfull width or upstream drainage area in evaluations of habitat area.

    o Using consistent life stages that are clearly defined.

    o Improving abundance/population estimates through the use of more rigorous field techniques such as mark-recapture or multiple visits over short time periods.

    o Integration of biological, hydrological, temperature, and geomorphological studies in the field and development of a synthesis of all study results prior to setting license conditions. The consequences of decisions made during the re-licensing process will be more clear if relationships between focal species and current (and predicted) variation in other biotic (e.g. predators/prey) and abiotic (e.g., temperature, hydrology) elements could be stated explicitly based on such integrated studies.

- As identified in Chapter 2, 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. In such research, particular attention should be paid to determining what environmental conditions may cue recently metamorphosed frogs to leave mainstem channels for tributaries and other off channel water bodies (e.g. seeps and springs).

- 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 is being pursued during 2007 and 2008.

- Apart from revealing differences in regulated and unregulated rivers, data collection and analyses for Chapter 3 also revealed the lack of a reference population of *R. boylii* for the Sierra Nevada bioregion. Long-term monitoring of one (or more) representative populations of *R. boylii* in an unregulated Sierran river would provide a context for year to year variation seen in regulated rivers. A peer-reviewed generalized survey and monitoring protocol for *R. boylii* is also needed.

- Field and flume experiments (Chapter 4) revealed energetic/predatory consequences for tadpoles occupying high velocity environments. Water temperature was not manipulated in these experiments, but it is a characteristic that can vary spatially, especially in large rivers. More work is needed to examine the consequence for tadpoles that displaced into higher velocity areas that are likely to have cooler water temperatures.

- Assessments of suitable breeding and rearing habitat, whether via 2D hydrodynamic modeling (Chapter 5) or some other static method, require a comprehensive and validated definition of habitat suitability criteria. A review of existing habitat association data began in 2006 and initial criteria will be completed in 2007, but validation of these criteria across various regions and watershed sizes is needed.

- Two-dimensional hydrodynamic modeling (Chapter 5) provides a method for assessing habitat conditions in a limited length of stream reach. There is a need for research on how modeling results gained from these short segments of rivers can be extrapolated to larger scales. There is also a related need to better understand how *R. boylii* is distributed within and among heterogeneous habitats along large sections of rivers and in associated tributaries (i.e. the metapopulation dynamics of the species). For example, how many highly suitable breeding areas and how many tributary refugia are needed within a section of river to sustain a local population of *R. boylii*?

## 6.4. Commercialization Potential

Not applicable to this study.

## 6.5. Benefits to California

The benefits of this research are multi-faceted in their scale and scope and they are fundamental to the conservation of *R. boylii*, a California Species of Special Concern. Review of statewide data and past FERC related study reports provided an overall assessment of the impacts of pulsed flows from hydroelectric projects on this species at risk. In addition, shortfalls of studies were identified and recommendations made for improvements to future FERC related and other studies of *R. boylii* and other riverine biota. Results obtained from analysis of biological and hydrological data from case study rivers along with field and laboratory experiments on tadpoles fill key knowledge gaps regarding the patterns of negative effects of aseasonal pulse flows on *R. boylii*. 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. These results have also contributed to better understanding of the mechanisms and critical water velocities at which tadpoles may be displaced during pulsed flow releases. The assessment of 2D hydrodynamic modeling in this study identified appropriate scenarios and likely error rates for modeling habitat of *R. boylii* and other aquatic 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 re-licensing projects.

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# 8.0 Glossary

| | |
|---|---|
| α | Statistical error rate; 0.05 is typical. |
| Adult | Large individuals (2–3+ years old) that exhibit secondary sexual characteristics |
| Allometry | A phenomenon whereby parts of the same organism grow at different rates, or in general refers to the effects of size on shape. |
| ANOVA | Analysis of Variance |
| BACI | Before—After—Control—Impact |
| Bonferroni adjustments | These are statistical corrections made to correct for multiple comparisons. |
| CD | Critically Dry Year |
| cfs | Cubic feet per second (ft$^3$/s), a measure of flow rate |
| cms | Cubic meters per second (m3/s), a measure of flow rate |
| D | Dry year |
| *df* | Degrees of Freedom, usually equal to sample size minus 1 |
| *F* Ratio | A statistical ratio in analysis of variance (ANOVA) ; the variation explained by a set of treatments or factors in relation to the unexplained (error) variation |
| FERC | Federal Energy Regulatory Commission; the government body that licenses hydroelectric projects |
| Flume experiments | Trials conducted within a channel that is typically constructed for experimentation |
| Froude number | The Froude number is calculated from stream depth and velocity, and is a good indicator of habitat type. |
| Fluvial | Riverine |
| GIS | Geographic information system |
| Heterogeneity | Spatial complexity |
| Hydrograph | A graphical representation of the discharge or stage of a stream as a function of time at a fixed location, often a gaging station. |
| IFIM | Instream Flow Incremental Methodology |

| | |
|---|---|
| Interstitial substrate | Areas of small, narrow spaces among rocks and other items within a streambed |
| 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) |
| Lambda ($\lambda$) | Annual proportional change in population, such that $\lambda = 1$ indicates stability, values $> 1$ indicate growth, and values $< 1$ indicate decline |
| Lek | A lek is a breeding aggregation in which males defend small territories which contain no resources and "put all their effort into self advertisement" (Krebs and Davies 1991, p.274). For *R. boylii*, advertisements are underwater acoustic displays. |
| Longitudinal gradient | Slope of streambed along the direction of streamflow |
| Microrefugia | Small areas of refuge |
| n | Sample size, as in the number of trials, or the number of individuals observed. |
| NF | North Fork |
| Ontogeny | Developmental life history or stages of an organism |
| Oviposition | Egg laying |
| *p* | Probability test statistic; numbers closer to 0.0 indicate stronger relationship |
| Pulsed flow | Temporary increase in stream flow |
| Q | Discharge or flow |
| $r^2$ | Coefficient of determination; numbers close to 1 represent a stronger relationship |
| Recruitment | The amount by which a population changes in size during one stage or over one interval in time, such as recently metamorphosed young of the year frogs growing to become adults of reproductive size. |
| Scouring | Removal of egg masses from substrate |
| s.d. | Standard deviation, a measure of variability in sample data |

| s.e. | Standard error, a measure of variability for population mean, such that the range of the mean plus or minus 1.96 times the standard error encompasses 95% of the values observed |
| --- | --- |
| SF | South Fork |
| Thalweg | The deepest part of a stream's channel |
| USFS | United States Forest Service |
| Young of the Year | Post-metamorphic animals seen only in the late summer and fall (approximately August–October); easily distinguished due to small size at that time of year |

# Appendix A

Catalog of Study Reports Used for Analyses in Chapter 2 and Referenced in Section 7

(Reports in italics were not reviewed in detail)

| Report Number | Authors / Contact info | Licensee[1] | FERC # | Report / Study Title | Year of Report | Years of Study | River | Reach | Surveys[2] | Flow Effects[3] | Months of flows | Habitat[4] |
|---|---|---|---|---|---|---|---|---|---|---|---|---|
| ALC1 | S. Bobzien and J. Didonato , East Bay Regional Park District, 2950 Peralta Oaks Ct., Oakland, CA 94605 | SFPUC | na | The Status of the California Tiger Salamander (*Ambystoma californiense*), Calfornia Red-Legged Frog (*Rana draytonii*), Foothill Yellow-Legged Frog (*Rana boylii*), and Other Aquatic Herpetofauna in the East Bay Regional Park District, California. | 2007 | 2000-2006 | Alameda Ck (*R. boylii*) | Camp Ohlone, Sunol Visitor Center | y | e (quali-tative) | seas-sonal | y |
| BIG1 | Entrix, Inc. 7919 Folsom Blvd., Suite 100, Sacramento, CA 95826 | SCE | 67, 120, 2085, 2175 | Combined Aquatics Working Group Amphibian and Reptile Report CAWG-8 Draft Technical study Report | 2004 | 2003 | Big creek, Jose Creek | multiple reaches | y | n | na | y |
| DSC1 | Stillwater Sciences 2855 Telegraph Ave., Suite 400 Berkeley, CA 94705 | PG&E | 803 | DeSabla-Centerville Hydroelectric Project FERC Project No. 803, Draft Licence Application (DLA) Vol. IIB, Exhibit E (Section 6.3 Fish and Aquatic Resources) | 2007 | 2006 | Butte Creek, West Branch Feather | multiple reaches | y | n | na | y |
| MOK1 | Jones and Stokes, 2600 V Street, Sacramento, CA 95818-1914 916-737-3000 | PG&E | 137 | Mokelumne River Project FERC 137: Evaluation of summer short-term power generation water releases on FYLF (*Rana boylii*) and their habitat in the NF Mokelumne River 2003 | 2004 | 2003 | NF Mokelumne | Salt Springs-Tiger Creek | y | l, m, h | 9 | y |
| MOK2 | Ibis Environmental Services, 340 Coleman Dr., San Rafael, CA 94583 | PG&E | 137 | Results of 2001 surveys for FYLF (*Rana boylii*) in the Mokelumne River Project Area. | 2002 | 2001 | NF Mokelumne | Salt Springs-Tiger Creek | y | n | na | y |

| Report Number | Authors / Contact info | Licensee[1] | FERC # | Report / Study Title | Year of Report | Years of Study | River | Reach | Surveys[2] | Flow Effects[3] | Months of flows | Habitat[4] |
|---|---|---|---|---|---|---|---|---|---|---|---|---|
| MOK3 | Ibis Environmental Services, 340 Coleman Dr., San Rafael, CA 94583 | PG&E | 137 | Results of 2002 surveys for FYLF (*Rana boylii*) in the Mokelumne River Project Area. | 2003 | 2002 | NF Mokelumne | Salt Springs-Tiger Creek | y | n | na | y |
| MOK4 | Ibis Environmental Services, 340 Coleman Dr., San Rafael, CA 94583 | PG&E | 137 | Results of 2003 surveys for FYLF (*Rana boylii*) in the Mokelumne River Project Area. | 2004 | 2003 | NF Mokelumne | Salt Springs-Tiger Creek | y | n | na | y |
| *MOK5* | *Bruce McGurk* | *PG&E* | *NA* | *Mokelumne Stream Flow Data and Report* | *1999* | *1997-1999* | *NF Mokelumne* | *multiple gaging stations* | *n* | *n* | *na* | *n* |
| MOK6 | Ibis Environmental Services, 340 Coleman Dr., San Rafael, CA 94583 | PG&E | 137 | Brief Summary of Amphibian Surveys Mokelumne River Project -2001-2004 Preliminary Findings and Implications for Future Operations associated with Recreation and Pulse Flow Releases | 2004 | *2001-2004* | NF Mokelumne | Salt Springs-Tiger Creek | y | l, yoy | 5,6,7,8 | *n* |
| NFF1 | EA Engineering, Science, and Technology, 1850 Gateway Blvd., Suite 220, Concord, CA 94520 | PG&E | 2107 | Results of preliminary surveys for foothill yellow-legged frogs (*Rana boylii*) and an evaluation of the effects of test flows on foothill yellow-legged frogs and associated habitat, along the NF Feather within the Poe Project Area [in 2000] | 2001 | 2000 | NF Feather | Poe | y | yoy, j, h | 9 | y |
| NFF2 | Garcia and Associates, 2601 Mission St., Suite 600, San Fransicso, CA 94110 | PG&E | 2107 | Results of 2000-2002 surveys of foothil yellow-legged frogs (*Rana boylii*) on the NF Feather and Selected Tributaries within the Poe Project | 2004 | 2000, 2001, 2002 | NF Feather | Poe | y | yoy, j, h | 9 | y |
| NFF3 | Garcia and Associates, 2601 Mission St., Suite 600, San Fransicso, CA 94110 | PG&E | 2107 | Results of 2003 surveys of foothil yellow-legged frogs (*Rana boylii*) within the Poe Project Area, NF Feather | 2004 | 2003 | NF Feather | Poe | y | e (in disc. only) | na | y |
| NFF4 | Garcia and | PG&E | 2107 | Results of 2002 study | 2003 | 2002 | NF Feather | Poe | n | h* | 9 | y |

| Report Number | Authors / Contact info | Licensee[1] | FERC # | Report / Study Title | Year of Report | Years of Study | River | Reach | Surveys[2] | Flow Effects[3] | Months of flows | Habitat[4] |
|---|---|---|---|---|---|---|---|---|---|---|---|---|
| | Associates, 2601 Mission St., Suite 600, San Fransicso, CA 94110 | | | evaluating the availability, extent, and quality of foothill yellow-legged frog (*Rana boylii*) habitat within the Poe Reach at the existing flow level and at four higher flows | | | | | | | | |
| NFF5 | Garcia and Associates, 2601 Mission St., Suite 600, San Fransicso, CA 94110 | PG&E | 2107 | Results of 2004 study evaluting impacts of elevated flows on foothill yellow-legged frog (*Rana boylii*) habitat in the Poe Reach, NF Feather | 2004 | 2004 | NF Feather | Poe | n | h* | 4 | y |
| NFF6 | ECORP Consulting, Inc. 1376 Lead Hill Blvd., Suite 130 Roseville, CA 95661 | PG&E | 1962 | Results of 2001 for foohtill yellow-legged frog (*Rana boylii*) on the NF Feather and selected tributaries within the Rock-Cresta Project Area | 2002 | 2001 | NF Feather | Rock Creek, Cresta | y | n | na | y |
| NFF7 | Garcia and Associates, 2601 Mission St., Suite 600, San Fransicso, CA 94110 | PG&E | 1962 | Results of 2002 surveys and monitoring for foothill yellow-legged frogs (*Rana boylii*) within the Rock Creek-Cresta project area, NF Feather, recreation and pulse flow biological evaluation | 2004 | 2002 | NF Feather | Rock Creek, Cresta | y | e, l, yoy, j, a | 6,7,8, 9 | y |
| NFF8 | Garcia and Associates, 2601 Mission St., Suite 600, San Fransicso, CA 94110 | PG&E | 1962 | Results of 2003 surveys and monitoring for foothill yellow-legged frogs (*Rana boylii*) within the Rock Creek-Cresta project area, NF Feather, recreation and pulse flow biological evaluation | 2004 | 2003 | NF Feather | Rock Creek, Cresta | y | e, l, yoy, j, a | 6,7,8, 9 | y |
| NFF9 | Garcia and Associates, 2601 Mission St., Suite 600, San Fransicso, CA 94110 | PG&E | 2107/ 1962 | Identifying Climatic and Water Flow Triggers Associated with the Onset of Breeding in a Foothill Yellow-legged Frogs (*Rana boylii*) Population in the NF Feather, California: First Year Interim Report | 2004 | 2004 | NF Feather | Poe, Cresta | y | n | na | n |

| Report Number | Authors / Contact info | Licensee[1] | FERC # | Report / Study Title | Year of Report | Years of Study | River | Reach | Surveys[2] | Flow Effects[3] | Months of flows | Habitat[4] |
|---|---|---|---|---|---|---|---|---|---|---|---|---|
| NFF10 | Garcia and Associates, 2601 Mission St., Suite 600, San Fransicso, CA 94110 | PG&E | 1962 | Results of 2004 Surveys and Monitoring for Foothill Yellow-Legged Frog (Rana boylii) within the Rock Creek-Cresta Project Area, NF Feather and 2002-2004 Recreation and Pulse Flow Biological Evaluation Summary | 2005 | 2002-2004 | NF Feather | Cresta | y | l, yoy, h | 6,7,8, 9,10 | y |
| PIT1 | Spring Rivers Ecological Sciences, LLC, P.O. Box 153, Cassel, CA 96016 530 335-5446 | PG&E | 233 | Foothill Yellow legged Frog (*Rana boylii*) Egg Mass, Tadpole, and Habitat Surveys in the Pit 4 Reach in 2003 | 2004 | 2003 | Pit | Pit 4 | y | h | extra polat ed | y |
| PIT2 | Spring Rivers Ecological Sciences, LLC, P.O. Box 153, Cassel, CA 96016 530 335-5446 | PG&E | 233 | Foothill Yellow-Legged Frog (*Rana boylii*) Studies in 2002 for PG&E's Pit 3, 4, and 5 Hydroelectric Project (FERC No. 233) | 2003 | 2002 | Pit | Pit 3,4,5 | y | e, l, h* | 5, 8 | y |
| *PIT3* | *R2 Resource Consultants, Inc.* | *PG&E* | *233* | *Pit River Habitat Mapping: Results of the "August 2002 Demonstration Flow Study"* | *2003* | *2002* | *Pit* | *Pit 3,4,5* | *n* | *n* | *5, 8* | *n* |
| PIT4 | S. Kupferberg | PG&E | 233 | Appendix A-2 to Forest Service Comments to to the FERC DEIS, Forest Service revised preliminary 4(e) conditions, PG&E – PIT 3, 4, and 5 hydroelectric project No. 233 | 2003 | 2002 data redo | Pit | Pit 4 | n | e, l,h | 5,8 | y |
| *PIT5* | *Hardin-Davis, Inc., 460 SW Madison Ave., Suite 7, Corvallis, OR 97333* | *PG&E* | *233* | *Pit River 2-Dimensional Instream Flow Study, Draft Final Report* | *2003* | *2002* | *Pit* | *Pit 3,4,5* | *n* | *n* | *8* | *n* |
| SFF1 | Stillwater Sciences 2855 Telegraph Ave., Suite 400 Berkeley, CA 94705 | SFWPA | 2088 | South Feather Power Project, FERC Project No. 2088, Draft License Application, Special-Status Amphibians and Aquatic Reptiles Study | 2006 | 2004-2005 | South Fork Feather | multple | y | e (quali-tative) | seas-onal | y |
| STA1 | ECORP Consulting, | PG&E | 2130 | Results of the 2003 Foothill | 2004 | 2003 | MF and SF | Philadelphi | y | h* | 6,7,8, | y |

APD A-4

| Report Number | Authors / Contact info | Licensee[1] | FERC # | Report / Study Title | Year of Report | Years of Study | River | Reach | Surveys[2] | Flow Effects[3] | Months of flows | Habitat[4] |
|---|---|---|---|---|---|---|---|---|---|---|---|---|
| | Inc. 1376 Lead Hill Blvd., Suite 130 Roseville, CA 95661 | | | Yellow legged Frog (*Rana boylii*) and Mountain yellow legged frog (Rana muscosa) studies at the Spring Gap - Stanislaus project | | | Stanislaus | a, Camp Nine, Sand Bar, Spring Gap | | | 9,10 | |
| STA2 | | Tri-Dam | 2005 | Exhibit E - Environmental Report from Final License Application for Beardsley/Donnells Project | 2002 | 2000-2001 | MF Stanislaus | Beardsley-Donnells | y | n | na | y |
| TRI1 | A. J. Lind, H.H.Welsh, Jr., R. A. Wilson  USDA Forest Service, PSW, Redwood Sciences Lab, Arcata,CA | BOR | na | The effects of a dam on breeding habitat and egg survival of the foothill yellow-legged frog (*Rana boylii*) in northwestern California (Published in 1996 in Herpetological Review 27(2):62-67) | 1996 | 1991-1994 | Mainstem Trinity River | Lewiston Dam, to confluence with NF Trinity | y | e | 4,5,6 | y |
| UAR1 | Devine Tarbell & Associates, Inc., Sacramento CA and Stillwater Sciences, Davis, CA | SMUD / PG&E | 2101/ 2155 | Amphibian and Aquatic Reptiles Technical Report, Sacramento Municipal Utility District, Upper American River Project (FERC No. 2101) and PG&E Chili Bar Project (FERC No. 2155) | 2005 | 2002, 2003, 2004 | Silver Creek and SF American | 13 reaches surveys, 7 for fhyl frogs | y | n | na | y |
| *UAR2* | *Devine Tarbell & Associates, Inc., Sacramento CA and Stillwater Sciences, Davis, CA* | *SMUD / PG&E* | *2101/ 2155* | *Channel Morphology Technical ReportSMUD Upper American River Project (Ferc Prohject no. 2101) and Pacific Gas and Electric Company Chili Bar Project (FERC No. 2155)* | *2005* | *2002, 2003, 2004* | *Silver Creek and SF American* | *multiple* | *n* | *n* | *na* | *n* |
| UAR3 | Devine Tarbell& Associates, Inc., Sacramento Ca, Stilllwater Sciences, Davis, CA | SMUD | 2101 | Amphibian Habitat Test Flow Technical Report, Sacramento Municipal Utility District, Upper American River Project (FERC No. 2101) | 2004 | 2003 | Silver Creek | Camino Adit and near confluence with SFAR | n | h* | 10, 11 | y |
| *UAR4* | *Devine Tarbell & Associates, Inc., Sacramento CA and* | *SMUD / PG&E* | *2101/ 2155* | *Hydrology Technical Report, Sacramento Municipal Utility District, Upper American River* | *2005* | *Histo rical flows* | *Upper SF American and* | *multiple* | *n* | *n* | *na* | *n* |

| Report Number | Authors / Contact info | Licensee[1] | FERC # | Report / Study Title | Year of Report | Years of Study | River | Reach | Surveys[2] | Flow Effects[3] | Months of flows | Habitat[4] |
|---|---|---|---|---|---|---|---|---|---|---|---|---|
| | *Margaret Hanaford, P.E. Jamestown, CA* | | | *Project (FERC No. 2101) and Pacific Gas and Electric Company Chili Bar Project (FERC No. 2155)* | | *from 1975-2001* | *associated tributaries* | | | | | |
| UAR5 | ECORP Consulting, Inc. 1376 Lead Hill Blvd., Suite 130 Roseville, CA 95661 | EID | 184-065 | Speical-Status Amphibian Surveys for EID Project 184, El Dorado County, CA | 2002 | 2002 | Upper SF American, Silver Fork American and tribs | 8 reaches surveyed | y | n | na | y |
| UAR6 | ECORP Consulting, Inc. 1376 Lead Hill Blvd., Suite 130 Roseville, CA 95661 | EID | 184-065 | Results of the 2004 (Year 1) Amphibian Monitoring Program for Foothill Yellow-legged Frog and Mountain Yellow-Legged Frog | 2005 | 2004 | SF American Alder Creek and Kyburz Dam | Reach 1 and 2 | y | e,l drop-pin flows | 6 | y |
| UAR7 | Garcia and Associates, 2601 Mission St., Suite 600, San Fransicso, CA 94110 | EID | 184 | Results of 2005 Surveys for Foothill Yellow-Legged Frog (*Rana boylii*) on the South Fork American River, El Dorado County, California for the Eldorado Hydroelectric Project (FERC no. 184) | 2007 | 2005 | Upper SF American, Silver Fork American and tribs | Upper SF American, Silver Fork American and tribs | y | n | na | y |

[1] Licensees: PG&E=Pacific Gas and Electric Company, SFPUC= San Francisco Public Utilities Commission, SFWPA=South Feather Water and Power Agency, SMUD=Sacramento Municipal Utility District, EID=El Dorado Irrigation District, SCE=Southern California Edison

[2] Survey (data): y=yes, n=no.

[3] Flow effects (data): e=eggs, l=larvae, yoy-young of the year, j=juvenile, a=adult, h=habitat (*=quantitative), n=flow effects not evaluated.

[4] Habitat (data): y=yes, n=no.

# Appendix B

Methodology for compiled hydrologic record at the SF Eel Angelo Reserve gaging station (Power and Dietrich, unpublished data)

Synthesis of Angelo/Branscomb Station

By Mary Power, Bill Dietrich 10/2004

We used a USGS generated rating curve for the Branscomb station to estimate discharge (Q, cms) from stage readings from the Branscomb gaging station that we reactivated in April 1990. For lower flows, (stage, S (m) < 0.5528), $Q = 57.397 \, S^{4.4285}$, $r^2 = 0.97494$. For higher stages, $Q = 16.180 \, S^{2.2924}$, $r^2 = 0.99944$. To estimate discharge when records from the re-activated Branscomb gaging station were not available (before April 1990, or during gaps due to our instrument's failure), we developed regressions between the USGS Branscomb record and discharge at the USGS Elder Creek gaging station (USGS 11475560) during three years (1967-1979) when both were monitored by the USGS: Branscomb discharge (cms) = 0.0886 (Elder discharge, cms)$^{1.16}$, $r^2 = 0.98$, n = 1096. Elder Creek is a tributary of the SF Eel in our study area, and is gaged at a station 4 km from the Branscomb gaging station. We also developed regressions with a downstream monitoring site on the SF Eel at Leggett (USGS 11475800), which has been monitored by the USGS since 1965. We selected the regression with Elder Creek for our synthetic hydrograph for SF Eel at Branscomb during gaps in our record, as it gave better predictions of Branscomb low flow discharge than did the regression with mean daily discharge at Leggett, which dropped less rapidly than at Branscomb during low flow. Instantaneous peak discharges, however, were better correlated between Branscomb and Leggett than Branscomb and Elder, so we used the following regression to estimate peak discharges for gaps in our record. Discharge (cfs) at Branscomb = 0.0044 (Discharge at Leggett)$^{1.05}$, $r^2 = 0.97$, n = 6). The peak discharge in 1997 had to be estimated by regression with Elder Creek, however, as the Leggett gage was not recording during that event.

# APPENDIX C

Photos of SF Eel and NF Feather Modeling Study Sites



**Photo 1. Upstream view of SF Eel study site standing on cobble bar along river right bank. Picture taken 10/22/05 at 0.15 cms.**

**Photo 2. Downstream view of SF Eel study site standing on cobble bar along river right bank. Picture taken 10/22/05 at 0.15 cms.**



**Photo 3. Downstream view of NF Feather study site. Flea Valley Creek enters on right; oviposition area is downstream along right bank. Picture taken 10/8/05 at baseflow (4.4cms).**

**Photo 4. Upstream view of NF Feather study site, standing on river right bank at downstream end of site. Picture taken 10/8/05 at baseflow (4.4cms).**



**Photo 5. View of Flea Valley Creek and river right bank after high flows scoured and redeposited sediments at the tributary confluence. Picture taken 1/26/06 at 15.7 cms (validation flow).**

# APPENDIX D

**Graphical depictions of hydrodynamic model results and error.**

Graphs (a-d) of simulated depth and velocity vectors during low and peak magnitudes of a spring pulse flow at each study site.
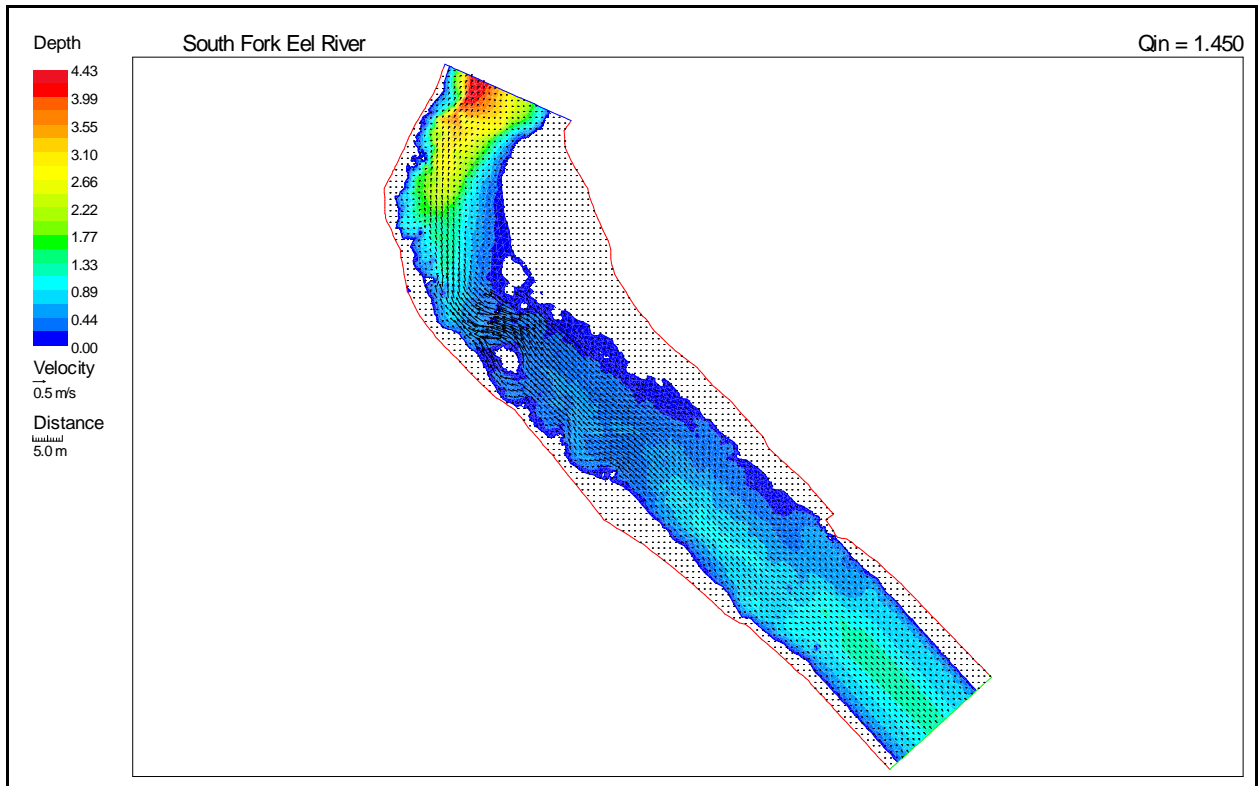


a) 1.45 cms on South Fork Eel
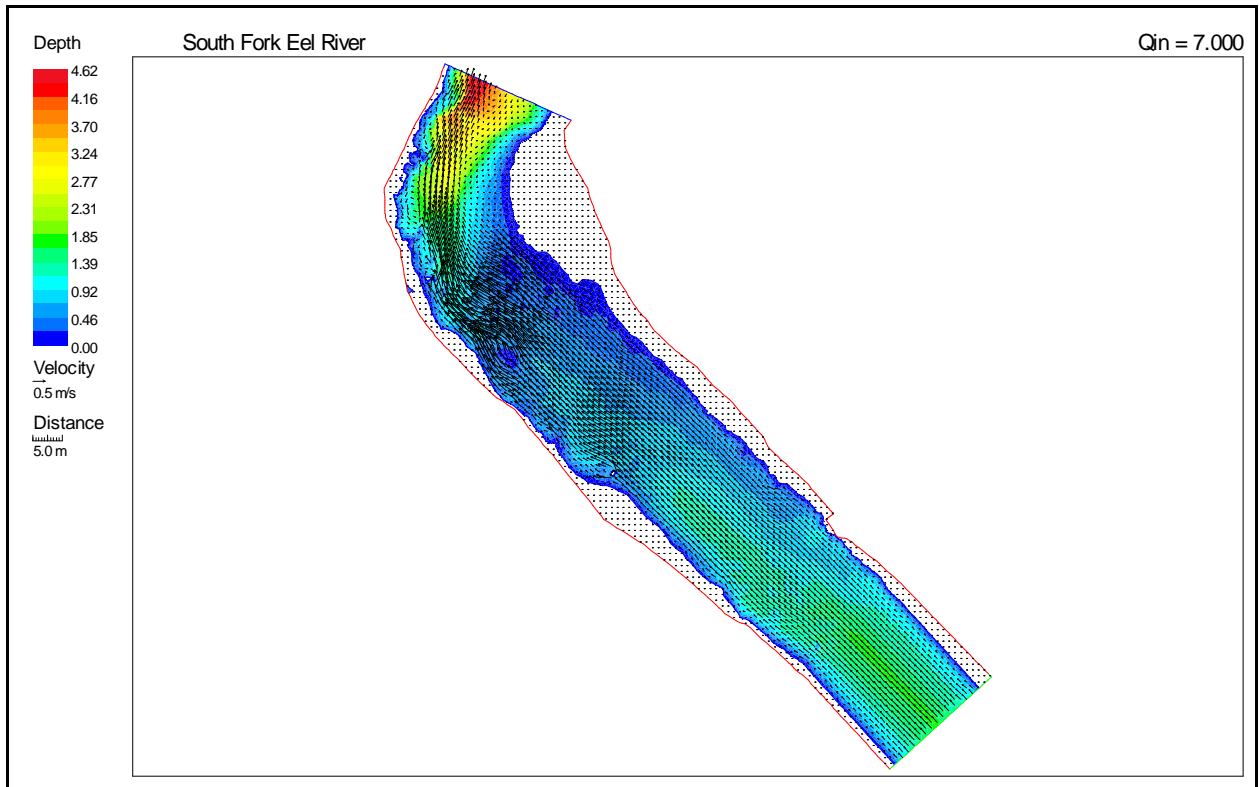
b) 7.0 cms on South Fork Eel
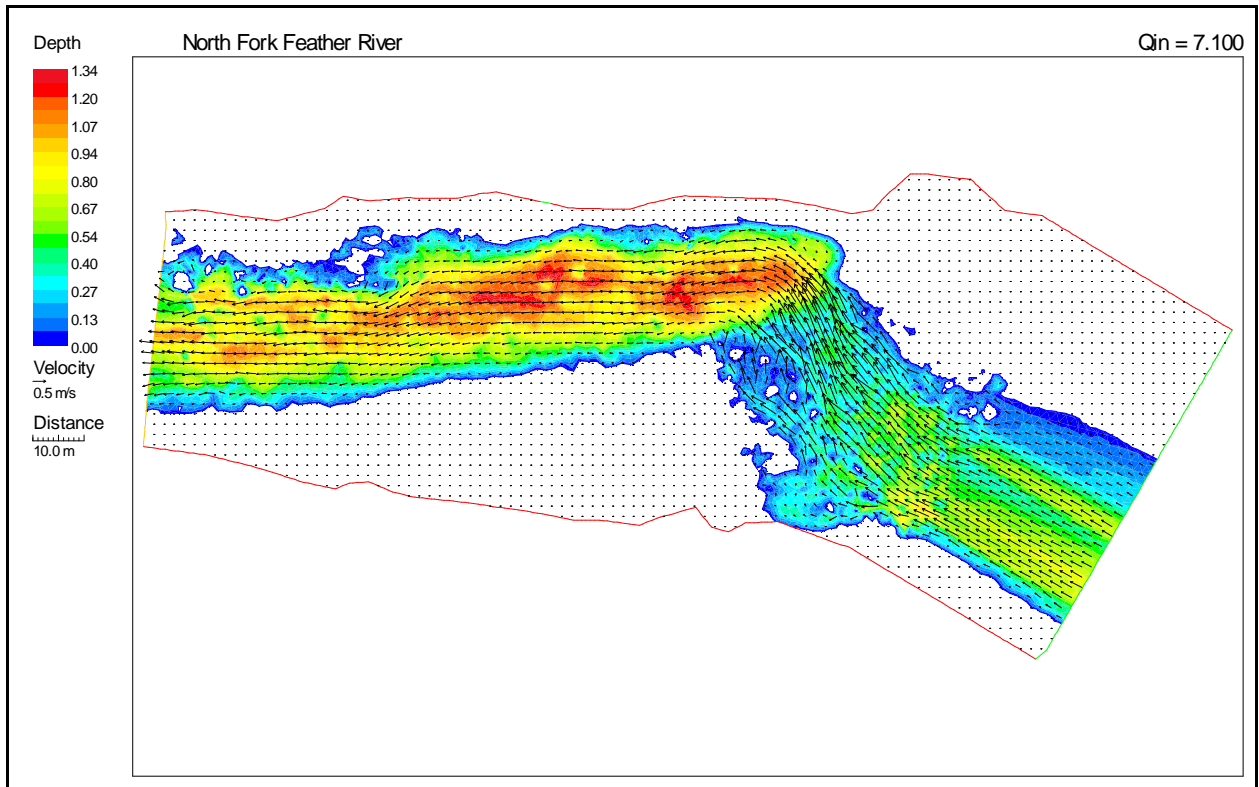
c) 7.1 cms on North Fork Feather
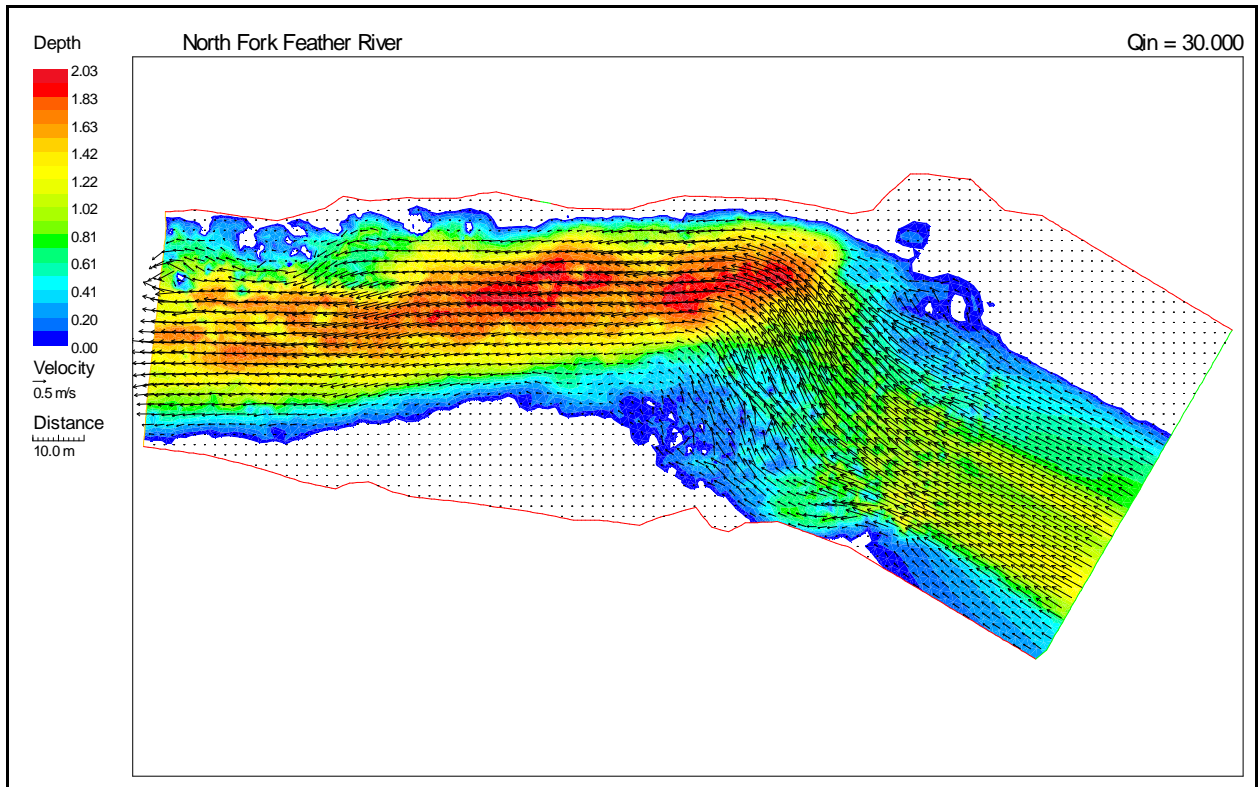
d) 30.0 cms on North Fork Feather

Graphical comparisons between simulated and observed point depths and velocities for calibration and validation discharges at each study site.

**SF Eel-calibration data, all points-1.45 cms**
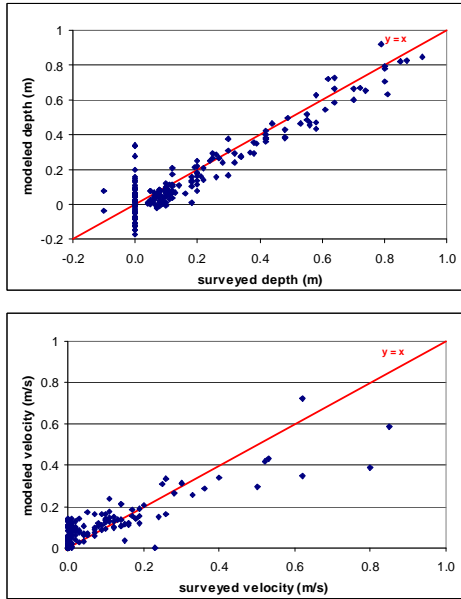


**SF Eel-calibration data, mid-channel-1.45 cms**
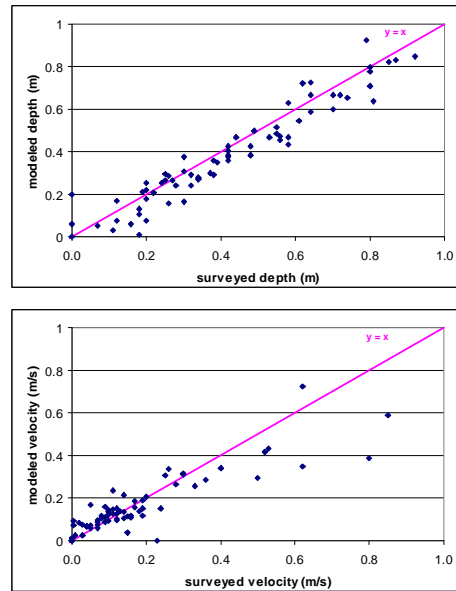


**SF Eel-calibration data, monumented cross-sections-1.45 cms**
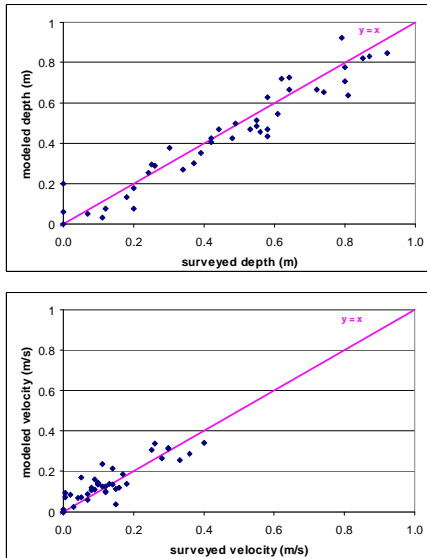


**SF Eel–Oviposition locations-1.45 cms**
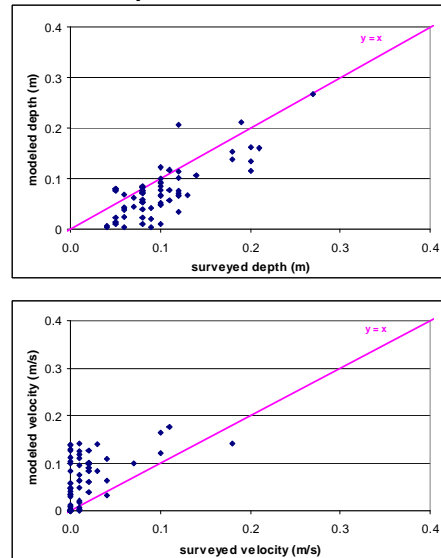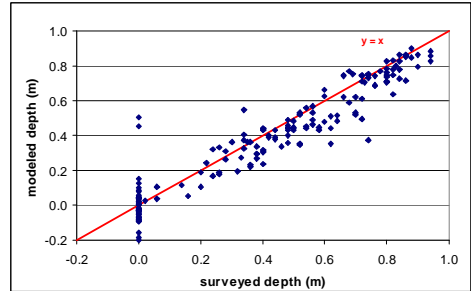
## SF Eel - validation data, all points - 2.5 cms
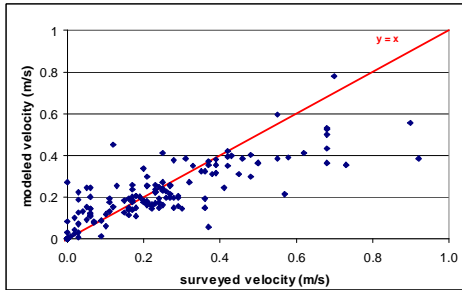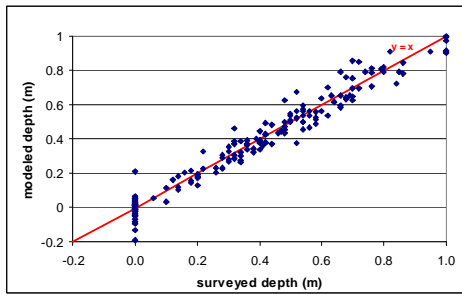


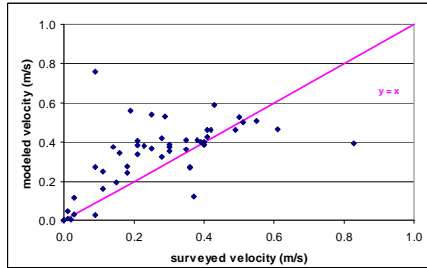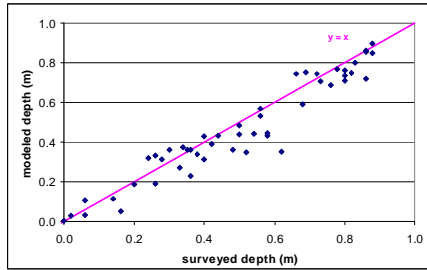## SF Eel-validation data, monumented cross-sections - 2.5 cms
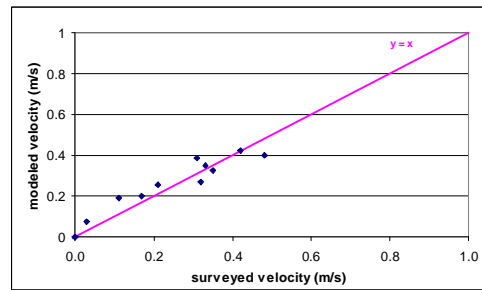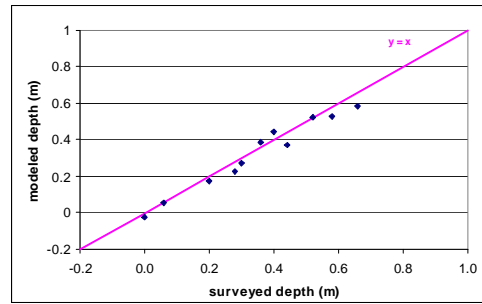


## SF Eel-validation data, monumented cross-sections - 0.15 cms
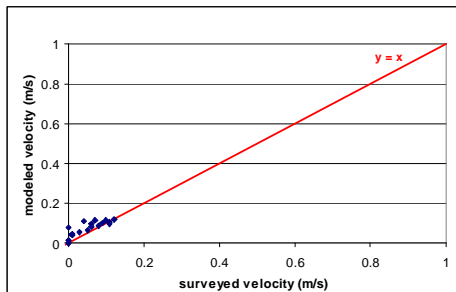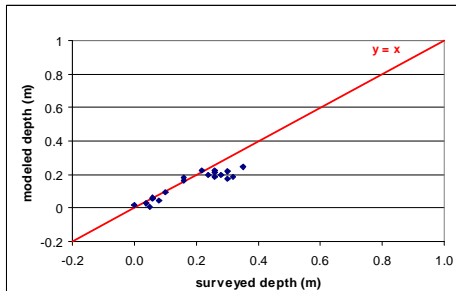


## NF Feather-calibration data, all points - 4.4 cms
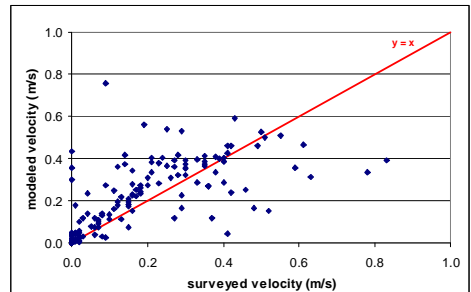
**NF Feather-calibration data,**
**monumented cross-sections - 4.4 cms**

**NF Feather - validation data, all points - 15.7 cms**