Spatial Heterogeneity of *Rana boylii* Habitat: Physical Processes, Quantification and Ecological Meaningfulness

By

SARAH MUNRO YARNELL
B.S. (University of California, Davis) 1995
M.S. (University of California, Davis) 2000

DISSERTATION

Submitted in partial satisfaction of the requirements for the degree of

DOCTOR OF PHILOSOPHY

in

Hydrologic Sciences

in the

OFFICE OF GRADUATE STUDIES

of the

UNIVERSITY OF CALIFORNIA

DAVIS

Approved:

Committee in Charge

2005

Table of Contents

CHAPTER 3: The Influence of Relative Sediment Supply on Riverine Habitat Heterogeneity..97

List of Figures

List of Tables

DISSERTATION ABSTRACT

Analysis of the heterogeneity of stream habitat and how biological communities respond to that complexity are fundamental components of ecosystem analysis that are often overlooked. The Foothill Yellow-legged Frog (*Rana boylii*) is known to associate with various stream habitats throughout its lifecycle and thus may require some degree of habitat complexity at a larger reach scale for a population to persist. The physical processes driving stream hydraulic and geomorphic conditions, such as the relationship between the sediment supply and transport capacity, likely influence the degree of habitat heterogeneity that results. Through a series of three studies, this project addressed the relationships between stream habitat heterogeneity, the supply/capacity ratio, and the physical habitat requirements of *R. boylii*.

R. boylii habitat associations were quantified throughout a single season to obtain insight into local hydraulic and geomorphic conditions preferred by each lifestage. The best predictors of habitat associations by lifestage were velocity and substrate size, two key characteristics of geomorphic units such as riffles and pools. Results indicated *R. boylii* occurred in stream reaches with a variety of geomorphic habitats suitable to multiple lifestages. The spatial heterogeneity of geomorphic units was then quantified using several indices from landscape ecology. Indices of spatial composition, such as Shannon's Diversity Index, were found to correlate well with frog abundance, while indices of spatial configuration, such as Contagion, were not significant. Lastly, Shannon's Diversity Index, as an ecologically meaningful spatial metric, was compared with a supply/capacity ratio calculated for each study reach in order to assess how relative sediment supply correlated with varying degrees of habitat heterogeneity. Results indicated that in simple channels where only flow and alluvial sediment interacted to create bed topography, maximum heterogeneity occurred with a moderate relative sediment supply. In complex channels where structural elements, such as large woody debris and boulders, created local scour and deposition, habitat heterogeneity increased as the percent of structural elements increased. Project results imply restoration practices and land use changes that affect the relative sediment supply and local geomorphic processes in a stream may directly impact the suitability of habitat complexity required by *R. boylii*.

ACKOWLEDGEMENTS

How can anyone get through four years of field work, classes, endless literature reviews, orals and phenomenally long hours in front of a computer without the help and support from others? Simple, it can't be done! First and foremost, I would never have had the motivation to actually finish this without my family. The love and encouragement from my husband, Bryan, my mom, Karen, my dad and my brother, along with their sense of humor, endless patience and thoughtful insight, continually propelled me forward. Coupled with a few fantastic unforgettable rafting trips over the years, I somehow managed to keep slogging through making progress. A large part of my success is also due to my wonderfully supportive advisors, Jeff Mount, Peter Moyle and Eric Larsen. I can't thank them enough for their constant support and insight as I struggled to understand the complex interactions of watershed dynamics. They were never put off by my endless questions or frustration in learning to understand.

Funding for this project was provided by U.S. Geological Society Water Resources Division and UC Davis Department of Geology. I extend special thanks to Lorrie Flint and Jenny Curtis of USGS for their support over the years and for their general belief that whatever I did for my research would turn out to be useful and interesting. I have enormous gratitude for my field assistants who put up with long hikes, hot days, hard work and cool swims in the river: Tanya Blacic, Aaron Thurston, Austin Roelofs, Audra Loyal, and Jeff Malinowski. I'd also like to thank my fellow grad students and colleagues for their time, support, laughter, ideas and creative input: Tanya Blacic, Kaylene Keller, Mark Rains, Joan Floresheim and Chris Hammersmark.

CHAPTER 1: Stream Habitat Associations of the Foothill Yellow-legged Frog (*Rana boylii*): the Importance of Physical Heterogeneity

Abstract

Previous studies on the life history of the Foothill Yellow-legged Frog, *Rana boylii*, indicate that different age classes have distinctly different geomorphic and hydraulic habitat requirements. However, many gaps in knowledge remain regarding the physical habitat preferences of each life stage, particularly at multiple spatial scales and in highly disturbed Sierran streams. This study focused on the habitat associations of several small sub-populations of *R. boylii* in the Yuba River watershed in the northern Sierra Nevada. Specific objectives included 1) quantifying physical microhabitat associations for each lifestage throughout an entire season, 2) determining habitat preferences at the reach-scale, including preferences for reach types, stream locations near tributaries and reaches with greater valley width, and 3) assessing whether reaches with greater habitat heterogeneity are preferred over reaches with less geomorphic complexity.

Visual encounter surveys were completed monthly between May and October, 2003 on four tributaries in the Yuba River watershed to collect data on individual lifestages, local physical microhabitat characteristics and reach-scale morphologic characteristics. The data were analyzed using a variety of statistical techniques including logistic regression, canonical correspondence analysis and paired mean tests. Velocity, depth and substrate were the most significant microhabitat characteristics that distinguished habitat associations by lifestage. As velocity and depth increased, the likelihood of observing successively older lifestages increased, with the exception that sub-adults were associated with high velocity, low depth habitats. The degree of sorting and size of substrate was also important in distinguishing younger lifestages from older lifestages. In general, regression models that included both hydraulic and substrate characteristics performed significantly better than models that included only velocity or depth. At the reach-scale, *R. boylii* showed distinct habitat preferences for certain reach morphologies and a preference for locations nearer to tributary confluences. Although reach type preferences varied across creeks, within each creek, the reach types with a greater variety of microhabitats had higher population densities than expected. These results indicate that due to the complexity of habitats required by each lifestage throughout the *R. boylii* lifecycle, individuals are occupying reaches with higher physical habitat heterogeneity, where a greater diversity of habitats is available in a relatively shorter section of stream.

Introduction

The Foothill yellow-legged frog (*Rana boylii*) is a small stream-dwelling frog native to California and southern Oregon that has received attention over the past decade as one of several native amphibians in rapid decline (Jennings and Hayes 1994); Jennings 1996; California Department of Fish and Game 2004). Largely confined to gravel and cobble streams at mid-elevations, *R. boylii* have been particularly vulnerable to introduced species and large-scale land use disturbances, such as dams and mining (Kupferberg 1996; Lind et al. 1996). While it is widely acknowledged that populations have diminished throughout their range over the past century (Moyle 1973; Nussbaum et al. 1983; Hayes and Jennings 1986), only recently has detailed information regarding their life history characteristics and habitat preferences become known.

Prior studies on coast range populations (Kupferberg 1996; Lind et al. 1996) and limited field studies in small Sierran populations (Van Wagner 1996; Yarnell 2000) have shown that *R. boylii* habitat preferences are strongly tied to geomorphic characteristics of a stream. In the coast range populations, oviposition sites were limited to channel locations with asymmetric channel shape, coarse substrate and specific hydraulic conditions, while Van Wagoner (1996) found significant correlations between age class and mesohabitat type. A follow-up study by Yarnell (2000) found process-based geomorphic measures worked well to describe habitat preferences of juveniles and adults; the most preferred habitats for juveniles combined seasonally dynamic channel shape with limited substrate mobility. While these findings indicate that different age classes have distinctly different geomorphic and hydraulic habitat requirements, many gaps in knowledge still remain regarding habitat preferences of each life stage, particularly in highly disturbed Sierran streams.

Considerable evidence exists suggesting the availability and quality of the physical habitat affects the arrangement and nature of biological communities (reviews in Poole 2002; Ward et al. 2002). Physical stream habitat is defined as the combination of structural and hydraulic features that are dynamic both in time and space, thus serving as the natural link between geomorphic processes and biologic response. Assessments that fully characterize the physical habitat therefore can provide not only information on the structure of the associated biological communities, but can provide information needed for river restoration, flow regulation and monitoring (Maddock 1999). Greater variation and diversity in the physical habitat has also been shown to increase aquatic species diversity (Beisel et al. 2000; Brown 2003) and individual species success and survival (Power 1992; Strayer 1999; Torgersen and Close 2004). *R. boylii*, with its distinctive variability in lifestage-specific habitat requirements, may respond to and even directly benefit from increased habitat heterogeneity.

R. boylii generally live within limited sections of streams, often moving no more than 500-1000m in a season (Van Wagner 1996). However, the processes that create and maintain aquatic habitat operate at greater spatial and temporal scales (Frissell et al. 1986; Newson and Newson 2000). Stream systems are commonly described in terms of the watershed, segment, reach and sub-reach (mesohabitat or microhabitat) spatial scales, each of which is dependent on the larger scale processes above it and contributes to the characteristics of the smaller scale below. This framework allows for logical categorization at multiple scales of both the processes driving change and the responses observed (Frissell et al. 1986). Studies that incorporate features and processes at a variety of spatial and temporal scales provide a more complete understanding of species habitat requirements and potential effects of alterations to that habitat. *R. boylii* is highly adapted to the annual fluctuations in discharge common to California's Mediterranean climate (Kupferberg 1996; Lind and Welsh 2005). As flows decrease through the year, seasonal selection in habitat may change with the changing physical habitat conditions. As a result, physical habitat preferences may be reflected at a variety of spatial scales, such as the microhabitat, reach and segment scales, as individuals move between breeding, foraging and overwintering habitats.

This study focuses on habitat preferences of several small sub-populations of *R. boylii* in the Yuba River watershed in the northern Sierra Nevada. Specific objectives included 1) quantifying physical microhabitat associations for each lifestage throughout an entire season, 2) determining habitat preferences at the reach-scale, including preferences for reach types, stream locations near tributaries and reaches with greater valley width, and 3) assessing whether reaches with greater habitat heterogeneity are preferred over reaches with less geomorphic complexity. The goal of this research was to determine if R. boylii show a quantifiable preference for stream reaches with higher habitat heterogeneity in terms of specific geomorphic and hydraulic channel features.

Methods

Study Area and Survey Segment Selection

Populations of *R. boylii* currently exist across the northern Sierra Nevada, but the majority are located between the Stanislaus River watershed to the south and the Feather River watershed to the north (Jennings and Hayes 1994). The Yuba River Drainage is located just south of the Feather River Basin in Nevada County (figure 1.1). Within the Yuba River watershed, populations are sporadically located both along the main forks and in their tributaries. Although a thorough documentation of the range and size of populations within the Yuba basin has not been completed, previous studies by California State Parks and U.S. Forest Service have documented many of the sub-populations along the South Yuba River, the Middle Yuba River and their tributaries (Yarnell 1999; Yarnell 2000, pers. comm. A. Carlson, U.S. Forest Service).

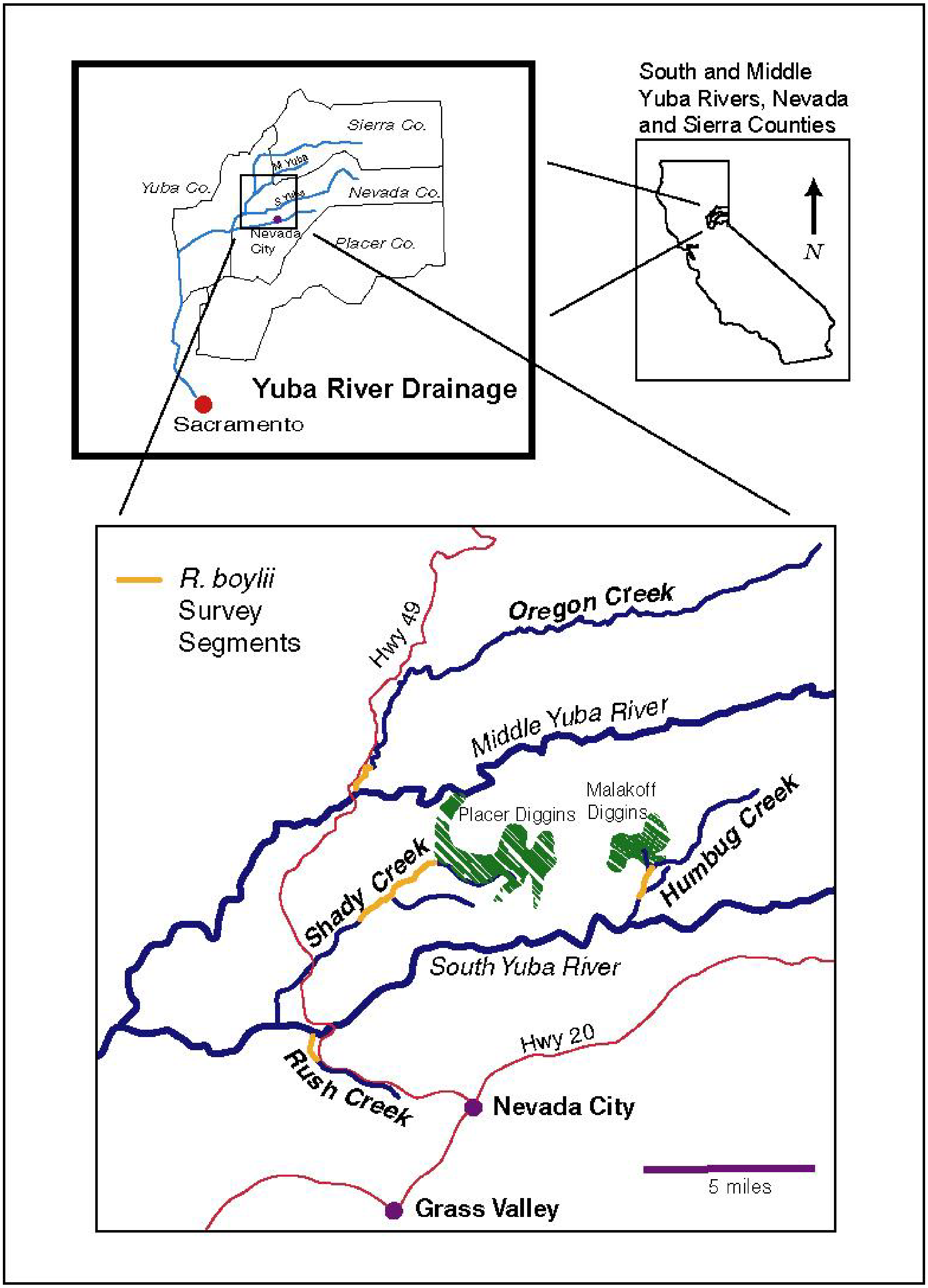


Figure 1.1. Microhabitat study location map showing study creeks and survey segments.

Four tributaries were selected for study, each known to sustain small populations of *R. boylii*: Shady Creek, Rush Creek and Humbug Creek on the South Yuba River and Oregon Creek on the Middle Yuba River (figure 1.1). These creeks vary both in terms of stream habitat availability and occupation by *R. boylii*. Shady Creek has the highest population density and individuals reside year-round within the creek. Oregon Creek has been known to occasionally support breeding but the majority of individuals observed in the lower reaches of the creek are subadults and adults (pers. comm. A.Carlson, U.S. Forest Service). Individuals have been documented breeding in the Middle Yuba River just upstream of the confluence with Oregon Creek (Lind et al. 2003, pers. comm. A. Carlson, U.S. Forest Service). As a result, the lower reaches of Oregon Creek largely provide summer foraging and overwintering habitat for adults, while eggs and tadpoles rear in the Middle Yuba River. Rush and Humbug Creeks are also generally known to support only sub-adult and adult lifestages, but breeding has been occasionally documented in both creeks at very low levels (1-2 egg masses total) (Yarnell 1999). While breeding has not been specifically documented in the South Yuba River near these creeks, it is likely that, as on Oregon Creek, individuals converge near the mouth of the tributary to breed in the South Yuba River in spring.

The four study creeks are similar to most mid-elevation Sierran drainages, having moderate to steep slopes, confined valleys with occasional bedrock outcrops, narrow disconnected riparian zones, coarse substrates and cascade, step-pool, and riffle-pool morphologies (after the classification of Montgomery and Buffington 1997). All four creeks have been subject to various land uses including mining (in-stream, hydraulic and high banking), logging and development. Shady Creek differs from the other study creeks in that it continues to recover from extensive past aggradation of hydraulic mining debris. Some reaches with steeper slopes have recovered to the original bedrock surfaces, but the majority of reaches continue to degrade through vast piles of tailings leaving remnant terraces behind. These four creeks represent common stream habitats that are known to support *R. boylii* populations elsewhere in the northern Sierra Nevada, such as the North Fork American River and its tributaries (pers. comm. S.Kupferberg), Bear River and its tributaries (pers. comm. A.Carlson, U.S. Forest Service), and Clear Creek (Van Wagner 1996). Table 1.1 summarizes the main habitat characteristics of the selected survey segments on each creek.

Creek	**Total Drainage Area (km^2)**	**Total Elevation Range (m)**	**Survey Segment Length (km)**	**Reach Morphologies**	**Dominant Channel Morphology**	**Dominant Riparian Type**	**Dominant Substrate Types**
Shady	37.58		3.2	Riffle-pool, Plane Bed, Braided	Riffles, Runs, Gravel Bars, Shallow Pools	Willow thickets with open gravel bars	Cobble, Gravel, Sand
Humbug	27.75		1.8	Cascade, Step-pool, Forced Riffle-pool	Plunge Pools, Boulder Steps, Coarse Bars, High Gradient Riffles	Mature alders	Cobble, Boulder
Rush	14.56		1.2	Cascade, Step-pool, Bedrock	Plunge Pools, Boulder Steps, Cascades, Coarse Bars	Mature alders	Boulder, Cobble
Oregon	19.08		1.5	Cascade, Step-pool, Bedrock	Plunge Pools, Boulder Steps, Cascades	Mature alders	Boulder, Bedrock, Cobble

Table 1.1. Habitat characteristics of survey segments for each creek.

Survey segments were selected in areas known to consistently support *R. boylii* including those sites were breeding was previously observed. Segments ranged in length from 1.2 km to 3.2 km and incorporated as many reach morphologies and habitat types common to that creek as possible. The goal was to select segments with enough length and diversity to adequately assess reach-scale habitat associations, but short enough to be surveyed in one 8-10 hour day.

Rana boylii Sampling

R. boylii visual encounter surveys (Heyer et al. 1994) were completed on each creek once per month from the start of breeding season in May through the end of foraging season in October. Surveys consist of walking each survey segment upstream during mid-day, visually identifying frogs and documenting data specific to each frog observation. Individuals were categorized based on lifestage; and details on their size, location and habitat associations were recorded. Subadults were identified based on snout-to-vent length (35mm or less), while adults were identified by standard sexual dimorphism traits such as size and presence or absence of swollen joints (Zweifel 1955). *R. boylii* are strictly stream inhabitants and are usually found within 1-2 meters from the stream margin (Zweifel 1955; Nussbaum et al. 1983). Individuals are often sited perched on the edge of rocks protruding from the water surface or sitting partially submerged in the water at the stream margin. To obtain the most accurate results and document the highest proportion of the population, two observers were required to span the width of the creek and banks.

Habitat Description

At each individual frog observation, a series of physical habitat characteristics were recorded. Table 1.2 summarizes the variables measured. A variety of quantitative and qualitative variables were chosen in an effort to determine how well each type of parameter performed in describing habitat associations. Although most previous research on *R. boylii* has been qualitative in nature (Zweifel 1955; Van Wagner 1996), several recent studies have used discrete quantitative variables to assess hydraulic variables such as depth and velocity

(Kupferberg 1996; Yarnell 2000; Lind and Welsh 2005). While the use of quantitative variables is undoubtedly more objective and repeatable, there is some value to assessing the applicability of subjective qualitative variables (such as 'pool') in describing aspects of the habitat that may not be accounted for in a single quantitative variable (such as velocity) (Hawkins et al. 1993). Therefore, an assessment of both qualitative and quantitative variables may provide some insight to both the applicability of the measures and the habitat associations of the different lifestages.

Variable	Variable Type	Variable Range	Measurement Method	Statistical Analysis
Local Depth	Quantitative	+/- 0.05 m	Depth taken at point in water where individual was observed, or average depth of habitat unit individual was next to if out of the water	Logistic Regression, CCA, Descriptive
Local Velocity	Quantitative	+/- 0.1 m	Velocity taken at point in water where individual was observed, or average velocity of habitat unit individual was next to if out of the water	Logistic Regression, CCA, Descriptive
Channel Width	Quantitative	+/- 0.25 m	Average width of water surface of habitat unit individual was observed in or next to	Logistic Regression, CCA, Descriptive
Dominant Substrate	Categorical	Bedrock, Boulder, Cobble, Gravel, Sand, Silt	Size of substrate individual was observed attached to or perched on	Logistic Regression, CCA, Descriptive
Degree of Substrate Sorting	Categorical	Well-sorted, Moderately-sorted, Poorly-sorted	Degree of sorting of particles immediately surrounding the dominant substrate	Logistic Regression, CCA, Descriptive
Cover Class	Categorical	0-25%, 25-50%, 50-75%, 75-100%	Cover was defined as any vegetation occurring in the vertical space located immediately above the water surface	Logistic Regression, CCA, Descriptive
Geomorphic Unit	Categorical	Pool, Run, Riffle, Rapid, Bar, Step, Bedrock Chute	Units identified based on common definitions found in the literature	Logistic Regression, Descriptive
Hydraulic Unit	Categorical	Standing Water, Scarcely Perceptible Flow, Smooth Surface Flow, Upwelling, Rippled, Unbroken Standing Wave, Broken Standing Wave, Chute, Freefall	Units identified based on definitions described in Thompson et al (2001)	Logistic Regression, Descriptive
Reach Type	Categorical	Cascade, Step-pool, Plane Bed, Riffle-pool, Braided, Bedrock	Types identified based on definitions described by Montgomery and Buffington (1997)	Logistic Regression, Descriptive
Riparian Type	Categorical	Cobble Bar, Pure Willow, Willow/Alder mix, Mature Riparian	Categories represent stages of riparian succession; following methods described in Lind and Welsh (2005)	Descriptive
Mesohabitat Type	Categorical	Cascade, Step-pool, Side Channel Pool, Pool, High Gradient Riffle, Low Gradient Riffle, Other	Types identified based on definitions described by USFS R5	Descriptive

Table 1.2. Habitat variables measured at each frog observation.

Some reach-scale characteristics were also noted in an effort to assess larger scale preferences for habitat. The location of each frog observation was recorded in the field using a handheld GPS and a topographic map. This data was incorporated into GIS where preferences for reach morphology (measured as reach type), valley morphology (measured as valley width) and tributary influx (measured as distance to nearest tributary) were assessed. Differences between observed and expected frog distributions were statistically analyzed using chi-square and one-sample t-tests; these methods are further described below. Unlike the microhabitat data, which was collected at each observation, the reach-scale data incorporated both presence and absence of individuals and therefore can be interpreted as habitat preferences rather than habitat associations.

Statistical Analyses

The associations of each lifestage with the microhabitat characteristics were analyzed using several statistical methods. Initially, all data was assessed descriptively to elucidate general trends in association. Histograms of each variable by lifestage were examined for general patterns of association and scatter plots of the quantitative variables versus lifestage were explored for obvious trends in the data. The data was evaluated both seasonally (subsets of spring: May-June, summer: July-August, and fall: September-October) and annually (full dataset: May-October). Logistic regression was used to determine which microhabitat variables were significant in predicting the probability of observing certain lifestages. Canonical Correspondence Analysis (CCA) was then used to explore the relationship between lifestage structure and the environment as described by the significant variables.

Logistic Regression

Unlike linear regression, logistic regression requires limited assumptions regarding normality or homoscedasticity (Hosmer and Lemeshow 1989; Trexler and Travis 1993). Specifically, logistic regression only requires that observations are independent and that explanatory variables are linearly related to a log transform of the response. The heterogeneous distribution of organisms across the environment often does not meet the standard assumptions of normality or linearity among predictors and response variables that are required by linear regression (Hirzel and Guisan 2002). As a result, the logistic modeling approach has been used to predict species-habitat relationships at a variety of scales (Knapp and Preisler 1999; Torgersen et al. 1999; Torgersen and Close 2004).

The logistic model describes the predicted probability of an event occurring in the following manner:

$$\text{Prob(event)} = 1/(1+e^{-Z})$$

where Z is the linear combination $Z = B_0 + B_1X_1 + \ldots + B_pX_p$ and p is the number of independent variables. When the model is rewritten in terms of the log of the odds (a logit), it can be analyzed as a linear model:

$$\log(P/(1-P)) = B_0 + B_1X_1 + \ldots + B_pX_p$$

where P is the probability of an event occurring. The parameters of the logistic model are estimated using the maximum likelihood method, where the coefficients that increase the odds of the observed results are selected. The model uses the selected coefficients and the logit transformation of a binary response variable to predict the probability of an event occurring in relation to categorical or continuous explanatory variables (Norusis 2004).

While logistic regression does have only limited assumptions, it is sensitive to multicollinearity among predictor variables (Tabachnick and Fidell 2001). Therefore, a non-parametric cross-correlation analysis was completed to assess all pairwise correlations between the microhabitat variables. Any pair of variables with a significant correlation value (Spearman's Rho > 0.300; $p < 0.01$) was assessed and the least descriptive variable of the pair was excluded from the logistic analysis. The logistic model was applied using the SPSS v 12.0 software package (SPSS 2003) and run using the forward stepwise automated model-building algorithm. P-values were calculated for each coefficient and if a term did not reduce deviance significantly ($p > 0.05$), it was removed from the model.

To determine the probability of observing a certain lifestage given the microhabitat characteristics, each lifestage was modeled in relation to the others as a binary response (table 1.3). Each lifestage was modeled in succession of age (e.g. 'tadpole versus older than tadpole' rather than 'tadpole versus not tadpole') in order to reflect the seasonal variation in lifestage assemblage (eggs only exist in spring, tadpoles only exist in summer). As a check on the results from these seasonally-based models, a series of models in reverse succession (e.g. adult versus younger than adult, etc) were also run using the full annual dataset. The results from each set of models agree well and provide a comprehensive description of the associations between lifestage and physical microhabitat characteristics.

Lifestage	Dataset evaluated	Parameters entered into stepwise algorithm
Eggs vs. older	Spring	Velocity, Depth, Dominant Substrate, Degree of Sorting, Cover
Tadpoles vs. older	Summer	Velocity, Depth, Width, Dominant Substrate, Degree of Sorting, Cover
Tadpoles vs. eggs	Annual	Velocity, Depth, Dominant Substrate, Degree of Sorting, Cover

Subadults vs. older (a)	Fall	Velocity, Depth, Width, Dominant Substrate, Degree of Sorting, Cover
Subadults vs. older (b)	Fall	Velocity, Depth, Width, Dominant Substrate, Cover
Subadults vs. younger	Annual	Velocity, Depth, Dominant Substrate, Degree of Sorting, Cover
Adults vs. younger	Annual	Velocity, Depth, Dominant Substrate, Degree of Sorting, Cover
Adult males vs. adult females	Annual	Velocity, Depth, Width, Dominant Substrate, Degree of Sorting, Cover

Table 1.3. Summary of logistic regression models tested.

Canonical Correspondence Analysis (CCA)

While logistic regression was useful in describing lifestage-habitat associations in a predictive model form, CCA described the relationship of each lifestage with respect to each microhabitat variable separately and along environmental gradients. CCA was preferred over other multivariate ordination techniques because of the unimodal response of each lifestage to the microhabitat variables observed in the descriptive analyses (McCune and Grace 2002). CCA also provided a method to visually explore the relationship between lifestages and the suite of microhabitat variables as well as a way to ascertain the strength of correlation between each lifestage and physical variable.

CCA as applied in this analysis constrained an ordination of a lifestage structure matrix by a multiple linear regression on the microhabitat variables in an environmental matrix (TerBraak 1986; McCune and Grace 2002). As a result, the analysis disregarded any community structure that was unrelated to the environmental variables, and the variance explained by the environmental axes describes only that related to the variables included in the analysis. The effect of each variable on the explanation of variance was tested used a Monte Carlo permutation test ($p < 0.10$; 1000 random permutations), where the null hypothesis was that samples were randomly associated with the microhabitat data.

(TerBraak and Verdonschot 1995). The data were analyzed for annual variation using the full dataset and seasonally using the 2-month subsets. The two substrate measures and cover class were entered in the analysis as categorical variables after they were manually recoded into n-1 binary dummy variables. The analysis was completed using CANOCO 4.0 (TerBraak and Smilauer 1998).

Reach-scale Statistical Analyses

Reach type, distance to nearest tributary and valley width were incorporated into ArcGIS 8.3 (ESRI 2002) in mapped form to facilitate comparison with the observed frog distributions from each monthly survey. Reach type was a continuous line segment overlay based on data collected in the field during the August frog surveys. Reach types were recorded as each survey progressed upstream, and reach breaks were mapped using a handheld GPS. Reach break points were imported into ArcGIS and used to create a continuous line overlay for each creek. Tributary junctions were mapped in ArcGIS as a point overlay based on identification from the topographic map and verification in the field. Valley width was calculated from 7.5’ USGS topographic maps and imported as a point overlay, where each point represented the average valley width for 50m of stream length. Frog points were then compared to these mapped overlays using the spatial join function and geoprocessing tools in ArcGIS.

The reach type layer was overlaid with each frog distribution layer to determine an associated reach type for each frog point. These data were compared with the reach type data collected during each survey at each frog observation point in the field. On Humbug, Rush and Oregon creeks there were no discrepancies between the mapped reach type and the reach types assigned to each frog in the field. On Shady creek, an average of 9% of the frog points were assigned a different reach type during each survey than were determined from the mapped reach types. The overwhelming majority of these points were located near reach break points were reach types changed from one type to another. Reach breaks were generally not well defined in the field and often occurred over a small transition zone, so small discrepancies over the course of the entire survey period would be expected. For consistency, the mapped reach types were analyzed in relation to the observed frog points.

A Chi-square test was completed to compare the observed versus expected number of frogs found in each reach type. The 'expected' distribution of frog points was determined based on the testable hypothesis that frogs were equally spaced throughout the survey segment on each creek. Therefore, the percent of frogs observed in each reach type should be proportional to the percent of availability of that reach type in the survey segment. The availability of each reach type was determined using ArcGIS and statistically compared to the observed percent of frogs in each reach type. Tests were completed on the annual dataset for each creek and on the seasonal datasets for Shady and Humbug Creeks. The sample sizes on Rush and Oregon creeks were too small to allow for seasonal analyses.

The distance to nearest tributary statistic for each observed frog point was determined using the spatial join feature in ArcGIS. Each frog point was joined with the nearest tributary junction point and the observed distance to the tributary was recorded in an output table. Like the expected reach type distribution, the expected distance to nearest tributary was determined based on the assumption that frogs were equally spaced throughout the survey segment. To calculate the expected distance, an overlay of evenly distributed points spaced 50m apart was created for each survey segment. These points were then spatially joined with the tributary junction points and the distance to tributary was recorded in an output table. The mean expected distance to tributary and the mean observed distance to tributary were compared using a one-sample t-test (SPSS 2003). The tests were completed on the annual datasets from each creek and the seasonal datasets for Shady and Humbug creeks.

Valley width was calculated by hand from 1:24K topographic maps, averaged over a stream distance of 50m, and mapped in ArcGIS as a series of evenly distributed points. These mapped points were used as the expected distribution of valley widths under the same testable hypothesis that frogs were evenly spaced throughout the survey segment. The valley width for each observed frog point was determined by completing a spatial join between the observed frog points and the evenly distributed valley width points. Each frog point was assigned the valley width of the closest evenly distributed point, which were always less than 25m and generally only about 10m away. The mean expected valley width was then compared with the mean observed valley width using a one-sample t-test (SPSS 2003). As with the other tests, the annual dataset for each creek and the seasonal datasets for Shady and Humbug were analyzed.

Results

Population densities varied widely between the four study creeks (table 1.4). With 90% of the total number of observations, Shady Creek had significantly higher population densities than any of the other study creeks. As discussed above, Shady Creek supports all lifestages throughout the season, while predominantly sub-adults and adults occur on the other creeks. As a result, statistical analyses of lifestage–microhabitat associations were only completed on Shady Creek. However, the microhabitat associations on Shady Creek were qualitatively compared with the adult and subadult microhabitat associations on the other study creeks in order to see if trends were similar across creek systems.

Survey Date (2003)	Creek	Total Observations	Distance Surveyed (km)	Population Density (#/km)
May 20	Shady	40	3.2	12.5
June 3	Shady	130	3.2	40.6
July 3	Shady	62	3.2	19.4
August 15	Shady	90	3.2	28.1
September 12	Shady	142	3.2	44.4
October 15	Shady	114	3.2	35.6
June 10	Humbug	3	1.8	1.7
July 9	Humbug	5	1.8	2.8
August 14	Humbug	10	1.8	5.6
September 18	Humbug	13	1.8	7.2
October 13	Humbug	12	1.8	6.7
June 13	Rush	1	1.2	0.8
July 11	Rush	5	1.2	4.2
August 12	Rush	1	1.2	0.8
September 17	Rush	3	1.2	2.5
October 14	Rush	3	1.2	2.5
June 12	Oregon	3	1.5	2.0
July 10	Oregon	1	1.5	0.7
August 13	Oregon	0	1.5	0.0
September 16	Oregon	0	1.5	0.0
October 9	Oregon	2	1.5	1.3

Table 1.4. Summary of *R. boylii* population density for each survey.

Microhabitat Associations on Shady Creek

On average, 96 individuals were observed on Shady Creek during each monthly survey, with the largest numbers noted during the late summer months when tadpoles and young of the year subadults were most prevalent. A total of 42 egg masses were counted in June, an average of approximately 150 tadpoles per month were observed between July and September, and an average of 70 newly metamorphosed subadults were recorded in

September and October. An average of 33 adults were observed each month, of which on average 15% were male, 32% were female and 53% were of an undeterminable sex. The percent of male adults observed decreased through the season as the presence of swollen joints/glands, the primary identification trait for males, decreased.

An initial analysis of the frequency of each lifestage associated with each categorical microhabitat variable revealed a few general trends (table 1.5). Frogs were observed with the highest frequency in the most prevalent habitats on Shady Creek: habitats with open cover canopies (cover class = 1), mixed alder/willow riparian types, and riffles with poorly sorted gravel and cobble substrates. However, eggs were most often found in open riparian areas with little to no vegetation, attached to boulders or cobbles in pools with scarcely perceptible flow. Tadpoles were found at riffle margins and in pools with smooth surface flow or scarcely perceptible flow, while subadults were observed with the highest frequencies in shallow riffles with poorly sorted gravel substrates. In addition to the prevalent habitats, adults were observed with moderate frequencies in higher velocity habitats such as riffles and cascades with cobble substrates.

Variable		Total Observations	Lifestage					
			Egg	Tadpole	Subadult	Adult Female	Adult Male	Adult Unknown
Geomorphic Unit	Pool	81	10	46	7	6	4	8
	Riffle	294	6	60	103	43	18	64
	Run	33	5	11	10	1	3	3
	Step	0	0	0	0	0	0	0
	Cascade	1	0	0	0	0	0	1
	Bar	74	0	4	30	14	5	21
	Bedrock	3	2	1	0	0	0	0
Hydraulic Unit	Freefall	0	0	0	0	0	0	0
	Chute	0	0	0	0	0	0	0
	Broken Stnd Waves	3	0	0	2	0	0	1
	Unbroken Stnd Waves	15	0	0	4	4	0	7
	Rippled	313	3	50	114	52	21	73
	Upwelling	0	0	0	0	0	0	0
	Smooth Surface Flow	57	9	15	18	1	7	7
	Scarcely Percp Flow	76	10	44	9	6	2	5
	Standing Water	22	1	13	3	1	0	4
Reach Type	Cascade	11	0	0	1	2	0	8
	Step-pool	0	0	0	0	0	0	0
	Plane Bed	231	12	49	83	33	0	54
	Riffle-pool	33	2	11	1	1	15	3
	Bedrock	0	0	0	0	0	0	0
	Braided	211	9	62	65	28	15	32
Canopy Cover	0-25%	352	18	76	122	46	23	67
	25-50%	65	2	24	14	6	6	13
	50-75%	57	3	20	13	6	1	14
	75-100%	12	0	2	1	6	0	3
Riparian Type	gravel/cobble bar	52	13	0	11	9	8	11
	pure willow	26	0	9	13	1	0	3
	willow/alder mix	364	10	106	111	48	20	69
	mature riparian	44	0	7	15	6	2	14
Dominant Substrate Size	Silt	0	0	0	0	0	0	0
	Sand	9	0	4	3	0	1	1
	Gravel	240	1	40	113	28	14	44
	Cobble	230	19	77	34	36	15	49
	Boulder	7	3	1	0	0	0	3
Degree of Sorting	Poorly Sorted	54	0	21	15	9	2	7
	Moderately Sorted	225	1	31	111	27	12	43
	Well Sorted	207	22	70	24	28	16	47

Table 1.5. Frequency of each lifestage with categorical microhabitat variables on Shady Creek.

To determine which variables were suitable for inclusion into the statistical analyses, a non-parametric cross-correlation analysis was completed. Riparian type was significantly correlated with cover class and reach type, hydraulic unit was strongly correlated with velocity and geomorphic unit, and geomorphic unit was significantly correlated with velocity (table 1.6). The remaining variables were either not significantly correlated or had Spearman's rho values of less 0.300 indicating a weak correlation. Riparian type was a less specific descriptor than cover class and reach type, so riparian type was excluded from the statistical analyses. Cover class and reach type were not correlated, so both parameters were retained. Velocity as a quantitative variable was a preferable measure for both modeling and gradient analysis, so both hydraulic unit and geomorphic unit were also excluded from the statistical analyses.

	Correlated Variable	**Spearman's rho**	**p-value**
Riparian Type	Cover Class	0.478	< 0.001
Riparian Type	Reach Type	0.300	< 0.001
Hydraulic Unit	Velocity	0.733	< 0.001
Hydraulic Unit	Geomorphic Unit	0.650	< 0.001
Geomorphic Unit	Velocity	0.540	< 0.001

Table 1.6. Correlated variables resulting from the cross-correlation analysis.

Logistic Regression

The most statistically significant microhabitat parameters that distinguished lifestages in the models were velocity, depth and substrate (both dominant size and degree of sorting) (table 1.7). However, the significance and direction of association (positive or negative) of each predictor variable varied depending on which lifestages were analyzed. Due to the fact that the response variable must be binary, each lifestage was assessed in relation to either one other lifestage or all lifestages older or younger as applicable. Therefore no single model was developed to assess all lifestages, but rather a suite of models resulted, each specific to a lifestage (table 1.3).

The most significant predictor that distinguished eggs from all older lifestages was dominant substrate, followed by velocity and depth. As the size of substrate increased, the likelihood of observing egg masses increased, and if the substrate was boulder, the odds of observing egg masses versus other lifestages were significantly higher. Eggs were negatively associated with velocity and depth, such that as velocity and depth decreased, the likelihood of observing eggs increased. The model performed very well and correctly reclassified 93% of the original data as egg or older.

Velocity was the only significant predictor to enter the stepwise model that distinguished tadpoles from older lifestages, such that decreasing velocities increased the likelihood of observing tadpoles versus subadults or adults. However, the model performed well, correctly reclassifying 83% of the original data. The model to distinguish tadpoles from eggs also performed well with dominant substrate as the most significant predictor such that finer grained substrates (sand and gravel) increased the odds of observing tadpoles. The degree of substrate sorting entered the stepwise model on step 2 and depth entered on step 3. Poorly sorted and moderately sorted substrates relative to well sorted substrates increased the likelihood of observing tadpoles, and for a given substrate, increasing depth increased the odds of observing tadpoles versus eggs. The egg vs. tadpole model correctly reclassified 83% of the data.

Lifestage	Variables Included in Stepwise Model	Standardized Coefficients	Wald Chi-square	p-value	Omnibus Test Chi-square	Nagerkelke R2	% correctly reclassified
Eggs vs older	Dominant Substrate (gravel/cobble/boulder relative to sand)	19.227 / 23.086 / 43.472	11.104	0.063			
	Velocity	-21.893	12.496	< 0.001			
	Depth	-22.817	3.462	0.011			
model summary				*< 0.001*	*142.231*	*0.832*	*92.9*
Tadpoles vs older	Velocity	-13.544	44.42	< 0.001			
model summary				*< 0.001*	*78.925*	*0.548*	*82.9*
Tadpoles vs eggs	Dominant Substrate (gravel/cobble/boulder relative to sand)	-19.355 / -21.133 / -26.822	21.664	< 0.001			
	Degree of Sorting (poorly/moderately sorted relative to well sorted)	3.683 / 4.025	13.292	0.001			
	Depth	24.389	6.902	0.009			
model summary				*< 0.001*	*87.957*	*0.597*	*83.1*
Subadults vs older (a)	Degree of Sorting (poorly/moderately sorted relative to well sorted)	2.564 / 2.793	22.847	< 0.001			
	Depth	-25.66	15.698	< 0.001			
	Velocity	-5.869	15.192	< 0.001			
	Dominant Substrate (cobble relative to gravel)	-1.328	8.883	0.003			
model summary				*< 0.001*	*131.619*	*0.592*	*81.2*
Subadults vs older (b)	Dominant Substrate (gravel relative to cobble)	2.329	37.897	< 0.001			
	Depth	-23.048	16.548	< 0.001			
	Velocity	-5.851	17.682	< 0.001			
model summary				*< 0.001*	*102.645*	*0.489*	*79.0*
Subadults vs younger	Velocity	10.106	42.728	< 0.001			
	Dominant Substrate (gravel/cobble/boulder relative to sand)	-0.902 / -2.07 / -22.5	19.304	< 0.001			
	Degree of Sorting (poorly/moderately sorted relative to well sorted)	2.002 / 0.815	30.077	< 0.001			
	Depth	-16.415	15.237	< 0.001			
model summary				*< 0.001*	*203.317*	*0.555*	*78.4*
Adults vs younger	Velocity	5.974	77.214	< 0.001			
	Depth	13.32	34.384	< 0.001			
	Degree of Sorting (poorly/moderately sorted relative to well sorted)	-1.064 / -0.632	15.149	0.001			
	Dominant Substrate (gravel/cobble/boulder relative to sand)	0.330 / 1.000 / -0.120	9.384	0.025			
model summary				*< 0.001*	*177.84*	*0.366*	*77.3*

Table 1.7. Results of logistic regression modeling. Variables are listed in order of inclusion in the stepwise algorithm. Positive standardized coefficients indicate a positive association between that variable and the lifestage of interest, while negative coefficients indicate a negative association. Wald Chi-square tests the significance of each variable within the model, and Omnibus Chi-square tests the significance of the resulting final model.

Two models were run to determine which habitat parameters best distinguished subadults from the other lifestages. Each model had the same four predictors, but with different significance values. Subadults were best distinguished from adults with a model that had degree of substrate sorting entered on the first step, depth as the second most significant predictor, velocity entered on the third step and dominant substrate size entered on the last step. Poorly sorted substrates relative to moderately and well sorted substrates greatly increased the odds of observing subadults versus adults, and subadults were negatively associated with depth such that decreasing depth increased the likelihood of subadults. Given the degree of substrate sorting and depth, subadults were negatively associated with velocity and more likely to be observed on gravel than cobble. This model performed well, correctly reclassifying 81% of the original data. The second model differed from the first in that degree of substrate sorting was not included as a potential predictor. As a result, dominant substrate became the most significant predictor and entered the model on the first step followed by depth and velocity. This smaller model has less predictive power than the full model ($R^2 = 0.489$, 79% correctly reclassified), but illustrated the importance of some measure of substrate as a significant distinguishing habitat characteristic for subadults.

Subadults were best distinguished from eggs and tadpoles with a model where velocity was the most significant predictor, followed by dominant substrate size, degree of substrate sorting, and depth in successive steps. As velocity increased, the odds of observing a subadult versus younger lifestages increased, and subadults were much more likely to be associated with smaller substrate sizes (sand and gravel) than larger cobbles or boulders. Subadults were positively associated with poorly sorted and moderately sorted substrates relative to well sorted substrates, and as depth decreased for a given substrate and velocity, the likelihood of observing subadults versus eggs or tadpoles increased. This model also performed well when compared with models with fewer possible predictors.

Several significant predictors distinguished adults from all younger lifestages. Adults were positively associated with velocity and depth such that as both variables increased, the likelihood of observing adults increased. Degree of sediment sorting entered the model on step 3 such that well sorted substrates were more likely than moderately sorted and much more likely than poorly sorted substrates to be associated with adults. Dominant substrate was the last significant predictor to enter the model where the odds of observing adults versus younger lifestages were greatest for cobble-sized substrates relative to sand, slightly positive for gravel relative to sand and decreased for boulders relative to sand. This model performed moderately well with 77% of the original data correctly reclassified. The stepwise algorithm could not create a significant model ($p<0.05$) that would distinguish adult males versus adult females.

In summary, several habitat characteristics were significant predictors of lifestage-habitat associations. Present in every model, except that which distinguished eggs from tadpoles, velocity was the most significant predictor of lifestage. As velocity increased, the likelihood of observing successively older lifestages increased. Depth was the next most significant predictor, present in every model except that which distinguished tadpoles from older lifestages. As depth increased, the likelihood of observing older lifestages increased; except for subadults, who were negatively associated with increasing depth. Substrate was an important predictor for distinguishing the younger lifestages from the older lifestages. Eggs had a positive association with boulders, while tadpoles and subadults were positively associated with gravel. Cobble substrates relative to sand and gravel increased the likelihood of observing adults. Well-sorted substrates were positively associated with eggs and adults, while poorly sorted substrates were positively associated with subadults. In some models, dominant substrate size was a better predictor than degree of substrate sorting (e.g. eggs vs. older, SA vs. younger), while in others degree of substrate sorting was a better predictor (e.g. SA vs. older, adults vs. older). In all models except tadpoles versus older, some measure of substrate increased the predictive power of the model when combined with one or both hydraulic variables.

Canonical Correspondence Analysis

Of the six microhabitat variables (channel width, local depth, local velocity, cover class, dominant substrate size and degree of substrate sorting) analyzed in relation to each of the lifestages, velocity, depth and the two substrate measures were found to be significant in explaining variation within the data. In general, the CCA results support the results of the logistic regression analysis.

The full annual dataset was analyzed in relation to the dominant four lifestages (eggs, tadpoles, subadults and adults). Figure 1.2 shows the CCA biplot of the influence of environmental variables on the lifestage assemblage. The first axis is determined predominantly by velocity, while the second axis is correlated with dominant substrate (specifically cobble and gravel) and degree of substrate sorting (specifically poorly sorted). These two axes explain 23.1% of the variance in the lifestage data and are of high significance ($p < 0.01$, Monte-Carlo permutation test). Eggs were strongly associated with low velocity and boulders, and negatively associated with gravel. Tadpoles were moderately associated with low velocity, while subadults were strongly associated with poorly sorted gravel substrates and negatively associated with cobbles. Adults were strongly associated with high velocity and cobbles, and negatively associated with poorly sorted gravel substrates.

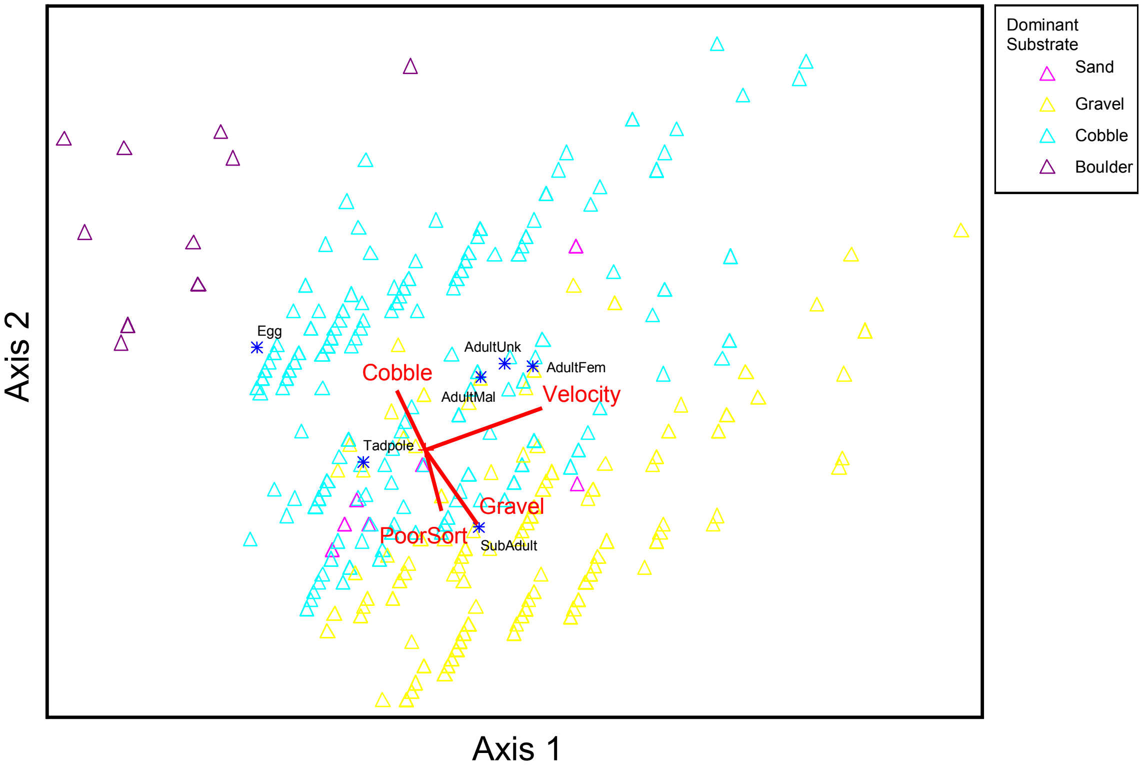
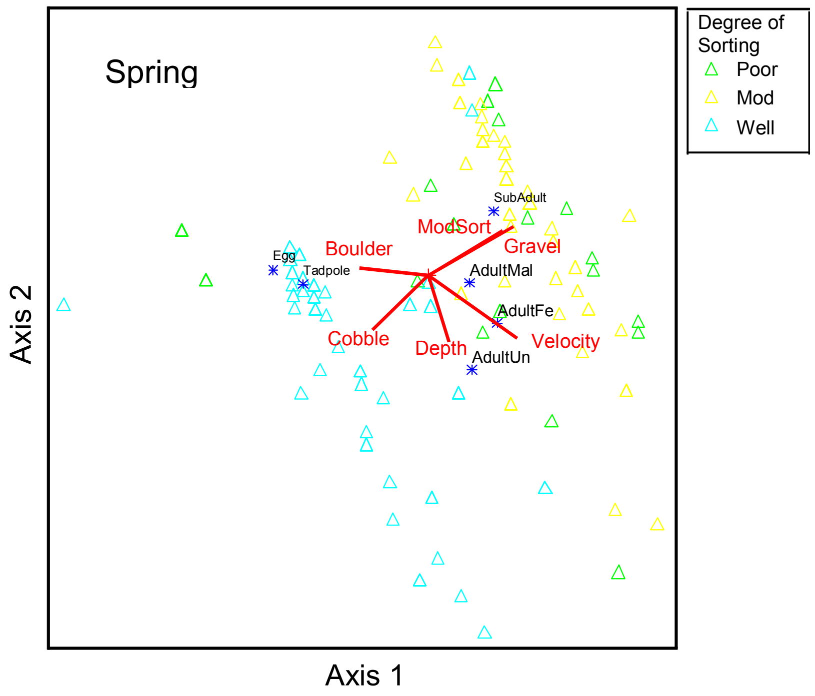


Figure 1.2. CCA biplot of the annual influence of environmental variables on the full lifestage assemblage of Shady Creek. All individuals observed on Shady Creek throughout the survey period (May – October) were included in the data. Color overlay represents dominant substrate size. Depth and cover class are represented on Axis 3 (not shown).

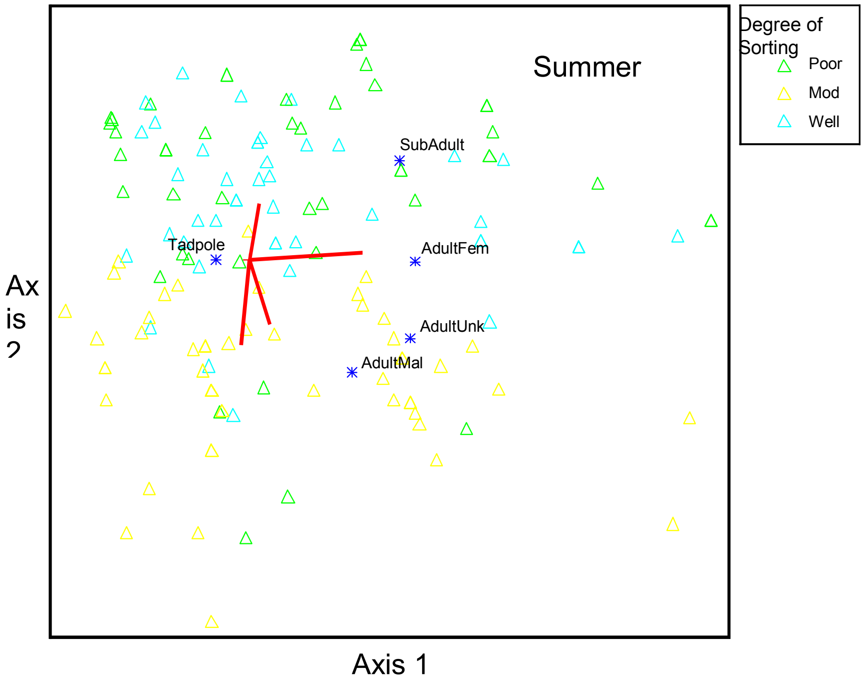
The results of the seasonal CCA analyses were similar to the annual analysis in that velocity and substrate were the primary distinctions between lifestages. However the seasonal associations varied slightly, particularly in relation to the various adult lifestages (figure 1.3). In May and June, adult males were associated with moderate velocities and depths and negatively associated with boulders and cobbles, while adult females were strongly associated with high velocity and adult unknowns were strongly associated with high depth. In July and August, adult males became associated with high depth and moderately sorted cobbles, while adult females and adult unknowns remained associated with high velocities and high depths, respectively. Subadults remained associated with gravels as in May and June, but became associated with low depth and high velocities. By September and October, adult males were strongly associated with high depths and cobbles, while adult females and adult unknowns were moderately associated with high velocities, cobbles and high depths. Subadults were strongly associated with poorly sorted gravel and low depth. Tadpoles remained associated with low velocities throughout each of the seasons.

In summary, egg masses were most strongly associated with low velocities and boulders, and negatively associated with fine or poorly sorted substrates. Tadpoles were initially in similar habitats to eggs in May and June, but by summer were associated most strongly with low velocity habitats regardless of substrate or depth. Subadults were generally associated with low depths and smaller substrates, particularly poorly sorted gravel. In July and August when sub-adults were largest (before tadpoles are metamorphosing), they were associated with moderate to high velocities in addition to low depths and fine substrates.

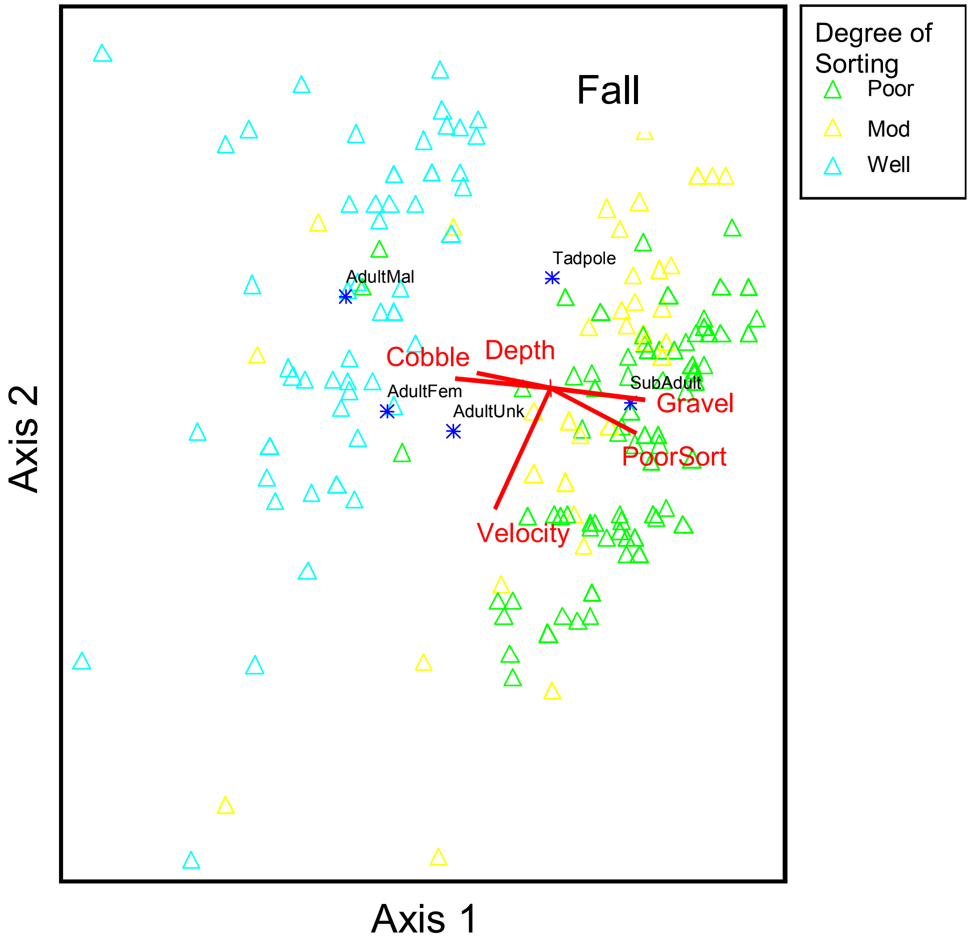
Adults in general preferred higher velocities, higher depths and coarser cobble substrates. The adult unknowns generally fell between the adult male and adult female habitats, some seasons closer to one, some closer to the other. Adult females were consistently associated with high velocities and high depths year-round. There was some association with cobble substrates in the late summer months, but substrate associations were neutral the remainder of the year. Adult males were generally associated with high to moderate depths, cobbles and high velocities. There was an association with less coarse substrates in May and June, but the remainder of the year their association with cobbles was strong. Width and cover were not significant factors in any of the analyses.



1.3a) Spring dataset



1.3b) Summer dataset

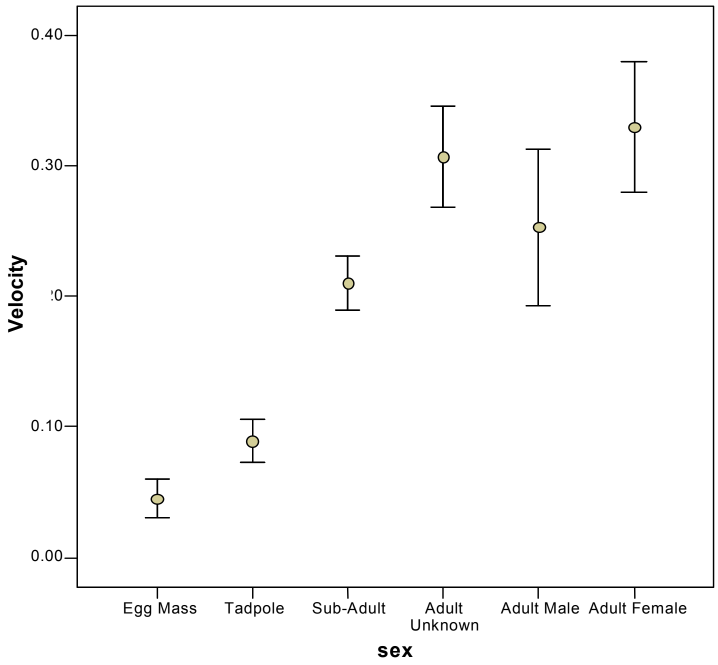


1.3c) Fall dataset

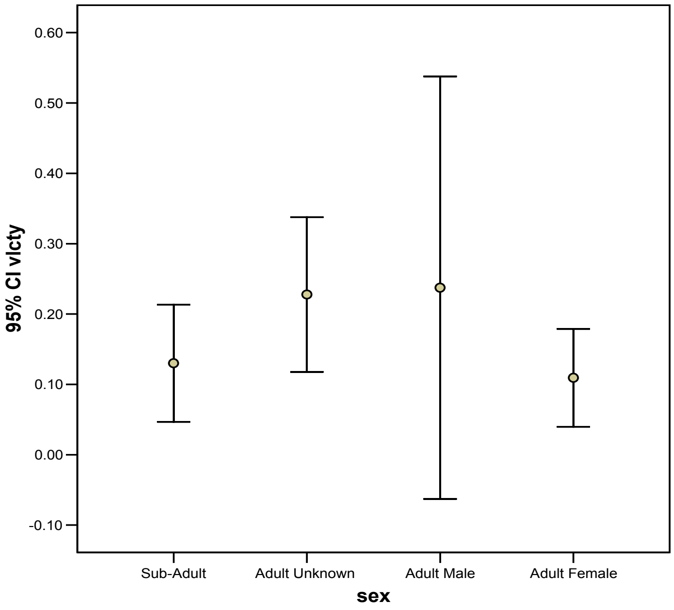
Figure 1.3. CCA biplots of the seasonal influence of environmental variables on the full lifestage assemblage of Shady Creek: a) Spring (May/June) dataset, b) summer (July/August) dataset, c) fall (September/October) dataset. Color overlay represents degree of substrate sorting: poorly (‘Poor Sort’), moderately (‘Mod Sort’) or well sorted (‘Well Sort’).

Microhabitat Associations on Other Study Creeks

The available habitats on Humbug, Oregon and Rush Creeks were more varied than those on Shady Creek, often with large boulder and bedrock substrates, partial to full canopy cover and a mature riparian zone. Steeper reach morphologies provided a variety of microhabitats that were rare or absent from Shady Creek, such as steep boulder cascades, deep plunge pools, and coarse boulder bars and steps. As a result, individuals were observed in coarser substrates and in denser canopy cover. Given the differing available habitat however, most lifestages were observed in generally similar habitat conditions, particularly with respect to hydraulic parameters. As velocity increased and substrate size increased, the number of observations of adults increased. The most notable exception was that adult females were observed in lower velocity habitats along with sub-adults, while the adult males and adult unknowns were observed in high velocity habitats (figure 1.4). Figure 1.5a shows the distribution of individuals in each geomorphic unit type on Humbug Creek. Adult females were observed overwhelmingly in pools, while adult males and adult unknowns were equally observed in riffles and cascades. On Shady Creek, adult females were observed most often in riffles presumably because the number of pools, particularly deep scour pools, was limited.



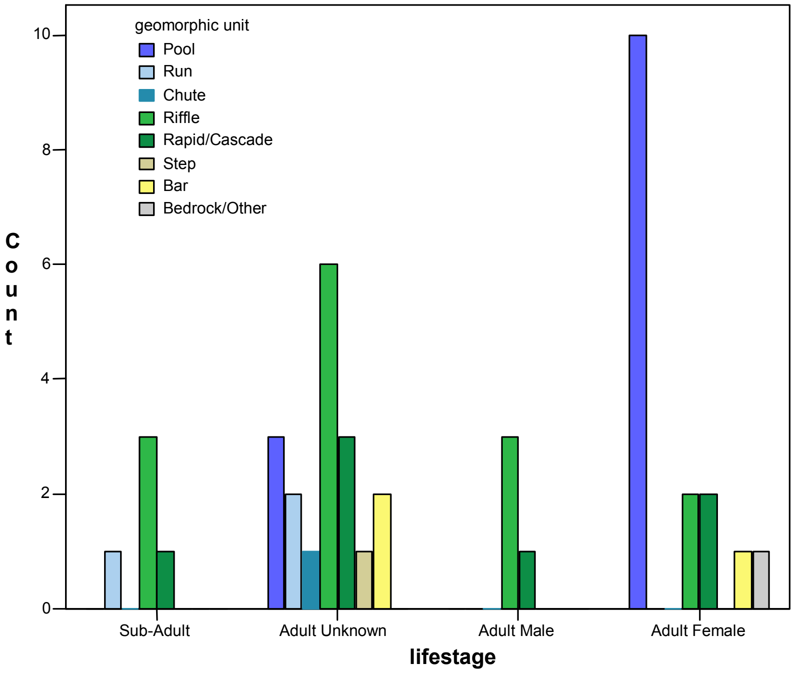
1.4a) Shady Creek



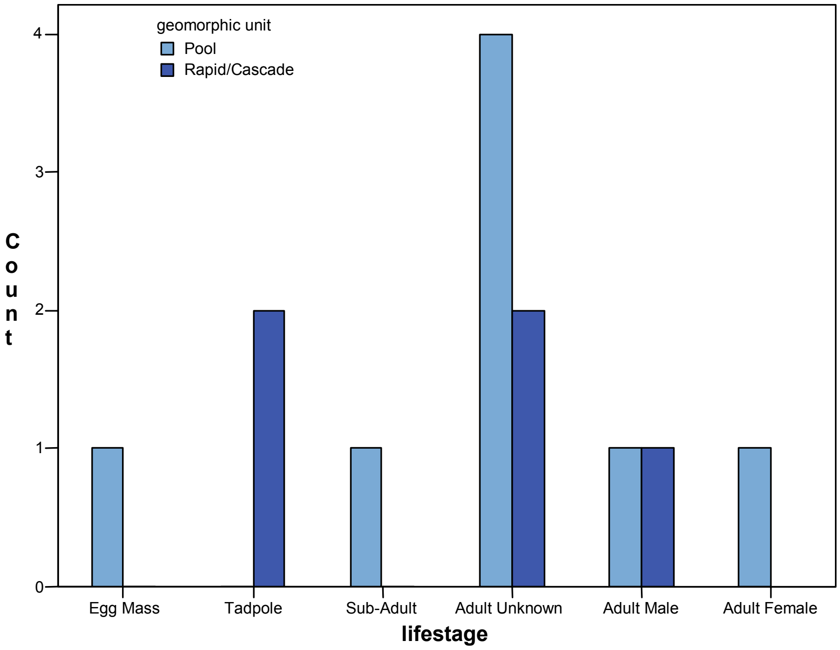
1.4b) Humbug Creek

Figure 1.4. Mean velocity at each observation by lifestage at a) Shady Creek and b) Humbug Creek. Error bars show 95% confidence intervals.

On Humbug Creek, subadults were observed most often in lower velocity riffles with cobble-sized substrate, while adult males were observed in a wide variety of habitats, but most often in higher velocity riffles and rapids with cobble and boulder substrates. Adult females were observed most often in low velocity pools with cobble substrates. Adult unknowns were observed in a wide variety of habitats as well, generally similar to either male or female preferences. Rush Creek had similar habitat associations to Humbug Creek with the females observed in slow moving pools, while the adult males and adult unknowns were observed in pools, cascades and rapids (figure 1.5b). The one egg mass found on Rush creek was located in a gently flowing shallow pool with cobble substrate and low canopy cover. This is similar to the habitats where eggs were observed on Shady Creek. Only six individuals were observed on Oregon Creek, but the female and two sub-adults were observed in pools, while the other adults were observed in rapids and cascades. Like Rush Creek, Oregon creek was dominated by boulder, cobble and bedrock substrates, and most individuals were observed on boulders.



1.5a) Humbug Creek



1.5b) Rush Creek

Figure 1.5. Geomorphic unit type associations by lifestage for a) Humbug Creek and b) Rush Creek.

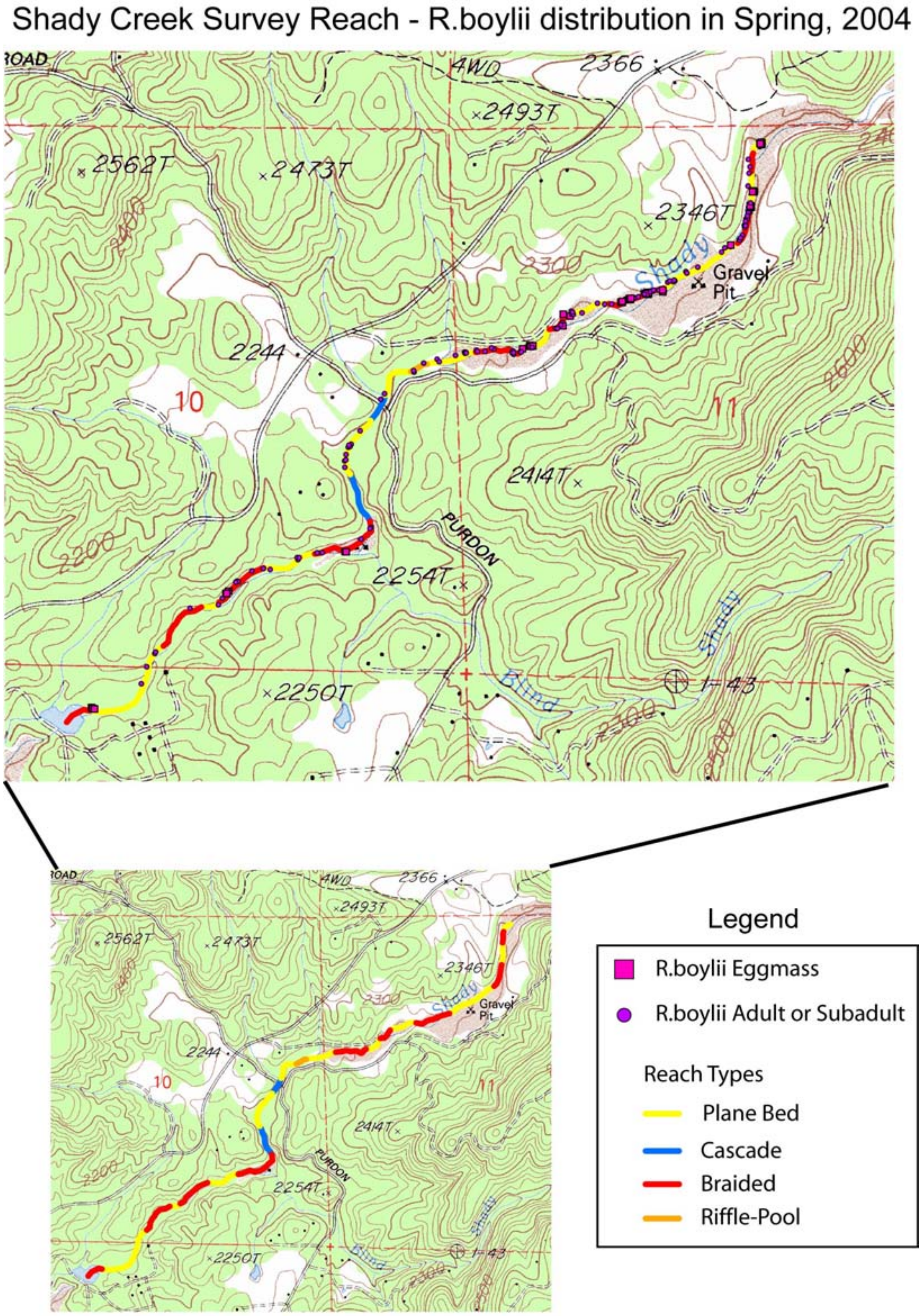
Reach-scale Habitat Associations

Three reach-scale characteristics were analyzed in detail using GIS to determine preferences on all creeks for reach morphology (measured as reach type), valley morphology (measured as valley width) and tributary influx (measured as distance to nearest tributary) (figure 1.6). Results from the Chi-square and one-sample t-tests revealed statistically significant habitat preferences on Shady, Humbug and Rush creeks. Due to the small sample size on Oregon Creek statistical analyses could not be completed, but individuals did show similar preferences to frogs on Humbug Creek.

Comparisons of observed versus expected reach-scale characteristics for all lifestages in the annual datasets revealed distinct habitat preferences for reach type on each creek and a preference for locations nearer to tributary confluences. While the preference for reach type varied by creek, the preference for locations near tributaries was consistent across Humbug, Rush and Oregon creeks. A preference for greater than average valley width was not statistically significant on Humbug Creek, but it was moderately significant on Shady and Rush creeks. Surprisingly, valley width correlated with distance to tributaries only on Rush Creek. On Humbug and Oregon creeks, the stream canyons were so narrow that tributary inputs had only moderate geomorphic impact on the main stream. Valley widths were larger at the tributary confluence, but the increased width did not translate up or downstream for more than 50-100m. These small distances were unlikely to appear in statistical analyses.

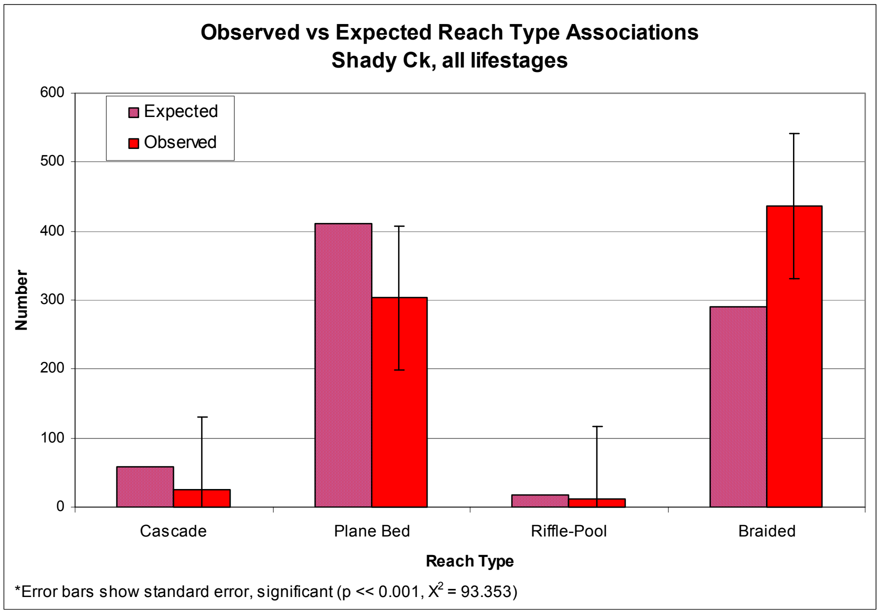
Analysis of the annual datasets revealed general habitat preferences for certain reach types, while the seasonal datasets provided some insight into the movements of adults throughout the season. On Shady Creek, frogs of all lifestages throughout the year were consistently observed in braided reaches more often than would be expected if individuals were evenly disbursed along the creek and in plane bed reaches less than expected (figure 1.7a, table 1.8). Individuals were also observed less than expected in cascade reaches, but were generally neutral with regard to riffle-pool reaches. Unlike the other study creeks, these habitat preferences were consistent across lifestages and were significant to highly significant for every lifestage.

On Humbug Creek, adults were observed more often than expected in riffle-pool reaches and less often in cascade and bedrock reaches (figure 1.7b); however, only adult females were statistically significant in this trend (table 1.8). Adult males and subadults on Humbug were generally noted in each reach type in proportion to the availability of that reach type. In a similar fashion, adults on Rush Creek were observed more than expected in step-pool reaches, less than expected in bedrock reaches and as expected in cascade reaches (figure 1.7c). Only grouped adults (all adult lifestages) had the statistical power to be significant as sample sizes were too small to separate out lifestages. Individuals on Oregon Creek were observed slightly more often than expected in cascade reaches (figure 1.7d), but the sample size was too small for statistical analysis.

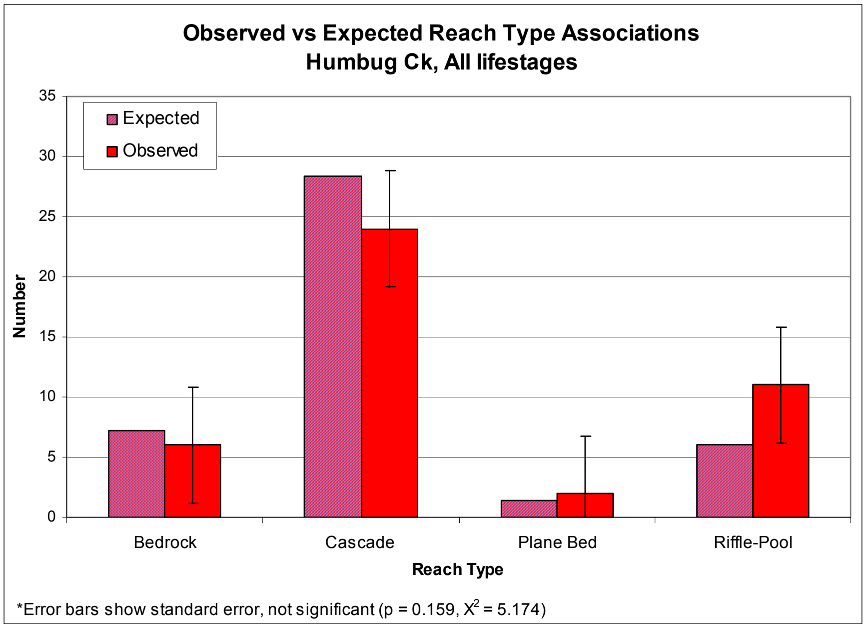


Shady Creek Survey Reach - R.boylii distribution in Spring, 2004

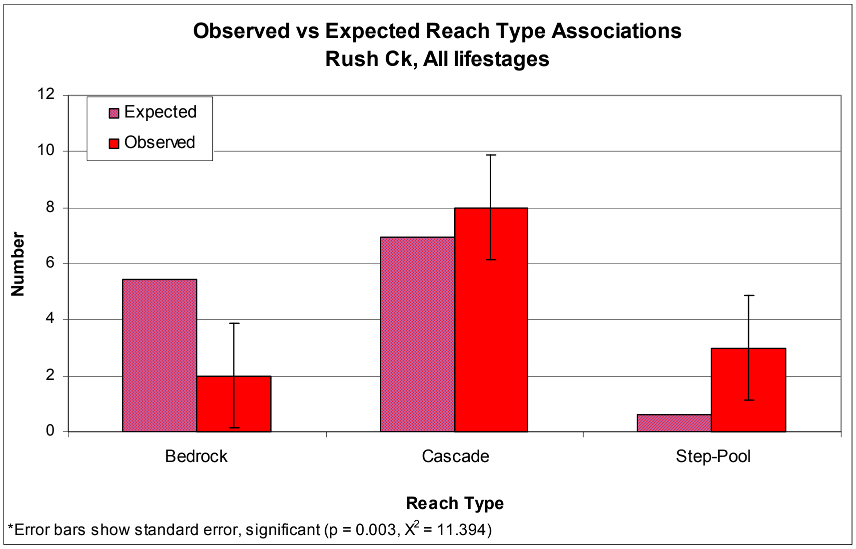
Figure 1.6. Example GIS output showing survey segment, population distribution and mapped reach type.



1.7a) Shady Creek

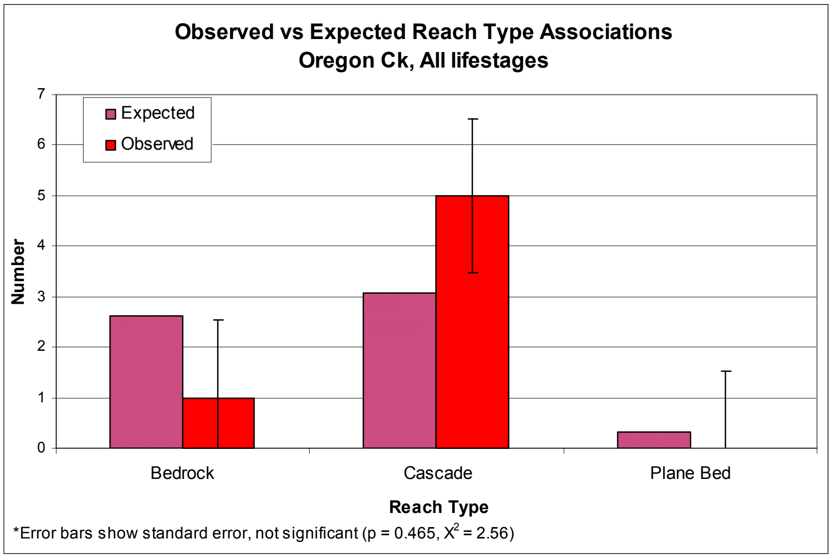


1.7b) Humbug Creek


Observed vs Expected Reach Type Associations
Rush Ck, All lifestages

*Error bars show standard error, significant (p = 0.003, X^2 = 11.394)

1.7c) Rush Creek


Observed vs Expected Reach Type Associations
Oregon Ck, All lifestages

*Error bars show standard error, not significant (p = 0.465, X^2 = 2.56)

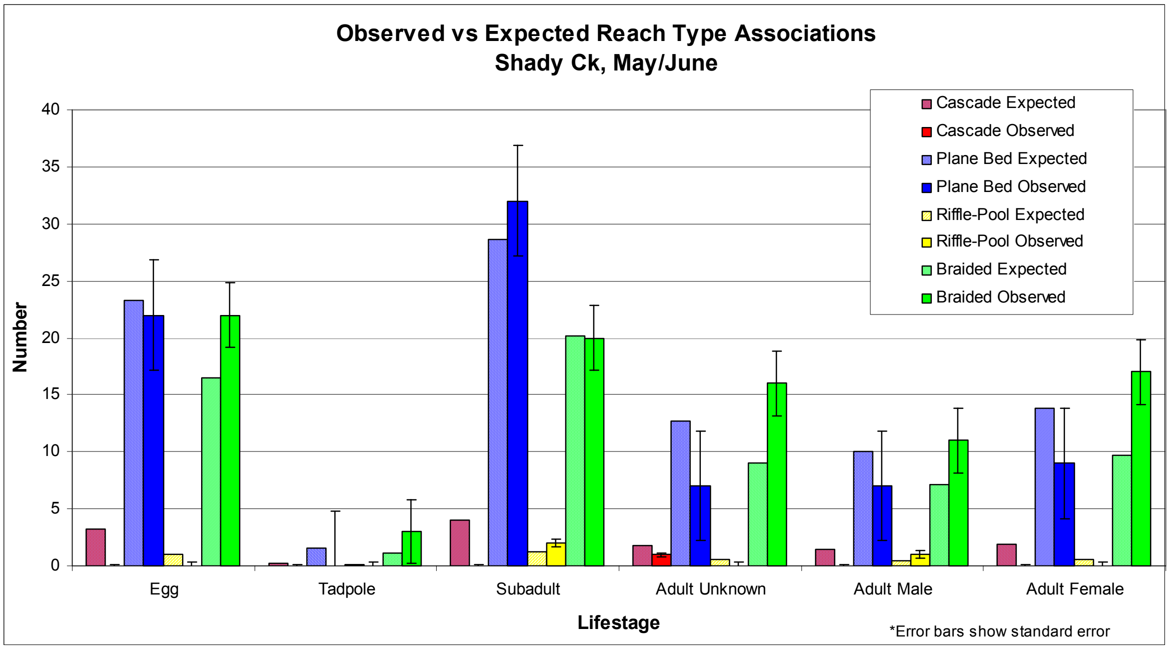
1.7d) Oregon Creek

Figure 1.7. Annual observed versus expected preference for reach type on a) Shady Creek, b) Humbug Creek, c) Rush Creek and d) Oregon Creek.

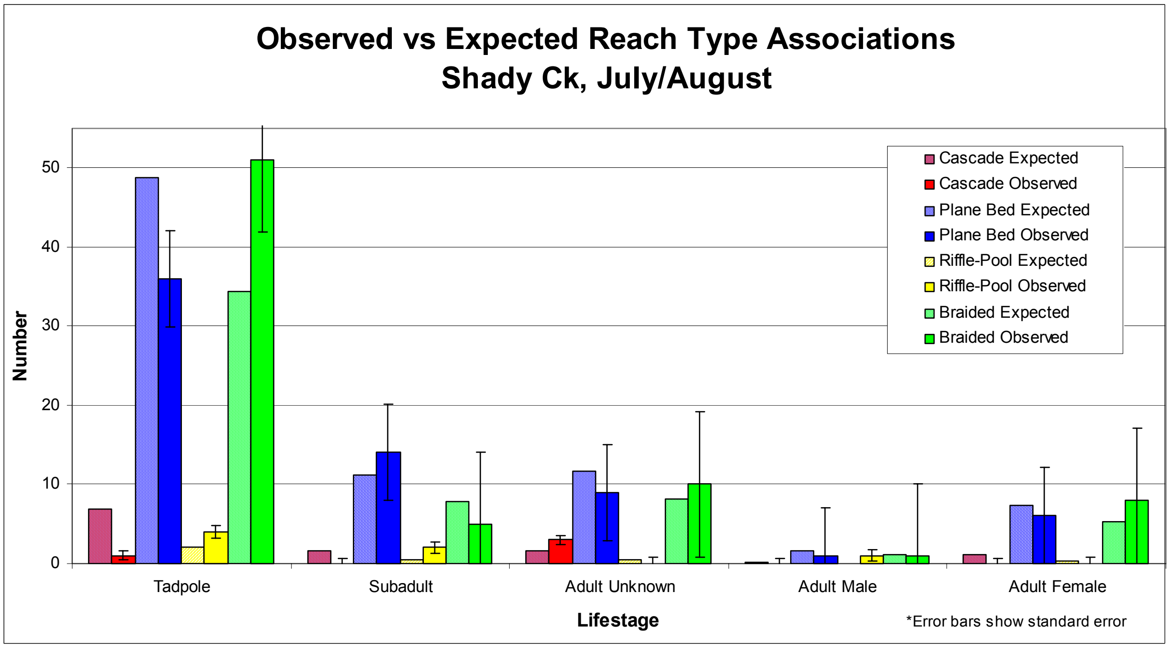
Creek	Dataset	Lifestage	p-value	Chi-square
Shady	Annual	All	**<< 0.001**	93.353
		Egg	**0.001**	6.245
		Tadpole	**< 0.001**	27.570
		Subadult	**< 0.001**	36.890
		Adult Unknown	**0.003**	16.340
		Adult Male	**0.065**	7.290
		Adult Female	**0.002**	17.170
		All Adults	**< 0.001**	31.700
Humbug	Annual	All	0.159	5.174
		Subadult	0.958	1.058
		Adult Unknown	0.901	1.603
		Adult Male	0.969	0.912
		Adult Female	**0.027**	12.630
		All Adults	0.165	7.850
Rush	Annual	All	**0.003**	11.394
		All Adults	**0.038**	6.530
Shady	Spring	Egg	**0.100**	6.245
		Tadpole	0.171	5.005
		Subadult	0.171	5.005
		Adult Unknown	**0.061**	9.005
		Adult Male	0.149	5.332
		Adult Female	**0.022**	9.678
		All Adults	**< 0.001**	23.675
Shady	Summer	Tadpole	**< 0.001**	20.492
		Subadult	**0.037**	8.460
		Adult Unknown	0.630	2.590
		Adult Male	**0.003**	13.670
		Adult Female	0.375	3.108
		All Adults	0.486	2.444
Shady	Fall	Tadpole	**0.034**	8.680
		Subadult	**<< 0.001**	56.910
		Adult Unknown	**0.048**	7.900
		Adult Male	0.799	1.007
		Adult Female	0.107	6.090
		All Adults	**0.005**	13.016
Humbug	Summer	All	0.615	1.798
Humbug	Fall	All	**0.015**	10.439

Table 1.8. Chi-square statistics for observed versus expected *R.boylii* distribution by reach type. Bold type indicates statistical significance less than 0.100. Sample sizes were too small on Rush Creek to test each lifestage separately.

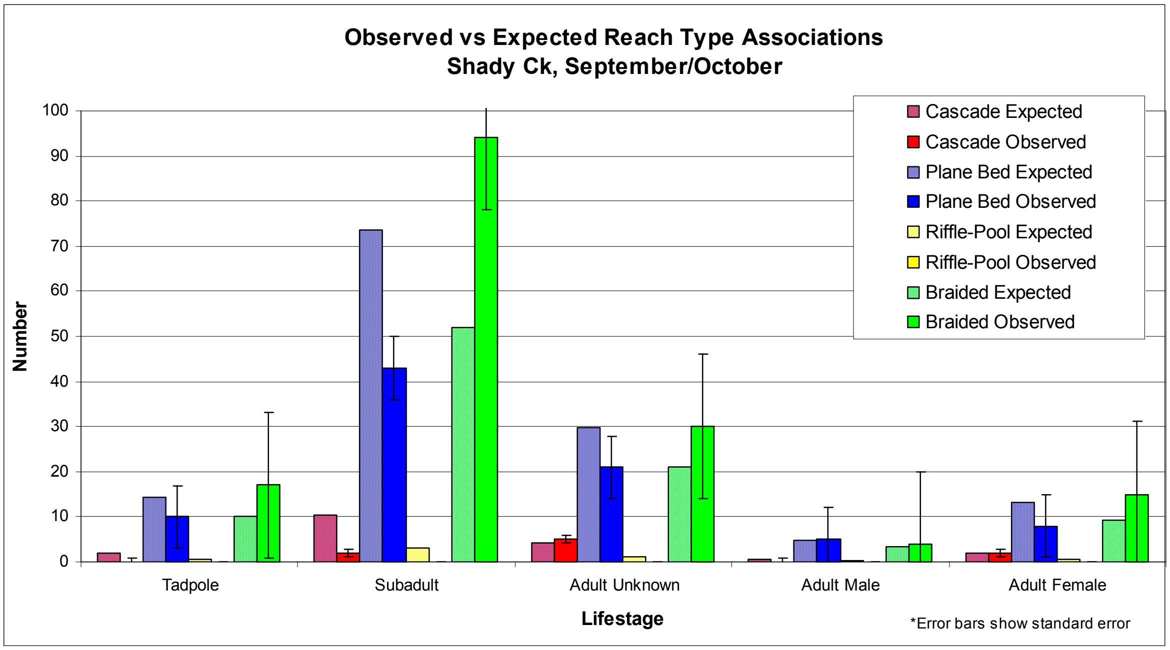
While the general preferences shown in the annual datasets for Shady and Humbug creeks were reflected in the seasonal data sets, adults in particular showed variation in reach type preferences depending on the season. During the spring breeding season, both adults and eggs on Shady Creek were observed in braided reaches much more than expected and plane bed reaches less than expected, while subadults were observed in all reach types proportional to the availability (figure 1.8a). By summer, however, tadpoles remained in the braided reaches rather than the plane bed reaches, while adults showed no preference for reach type; subadults were observed more often in plane bed and riffle-pool reaches than braided reaches (figure 1.8b). This change in reach type preference indicates movement by both the adults and subadults throughout the summer foraging season. In fall, preferences for braided reaches over plane bed reaches were significant for all lifestages once again (figure 1.8c, table 1.8). Analysis of the seasonal data on Humbug Creek showed no preference for reach type during the summer, but a significant preference for riffle-pool reaches over cascade or bedrock reaches in fall.



1.8a) Spring dataset



1.8b) Summer dataset



8c) Fall dataset

Figure 1.8. Seasonal observed versus expected preference for reach type on Shady Creek: a) Spring, b) Summer, c)Fall.

Figure 1.9 shows the observed versus expected mean distance to tributary for each study creek. Frogs on Shady Creek were observed further than expected from tributary junctions, while frogs on the other study creeks were observed closer than expected to tributaries. The difference between the means was statistically significant on Shady, Humbug and Rush creeks (table 1.9). The seasonal dataset for Shady and Humbug creeks revealed the same trends as the annual dataset with each season except spring on Shady Creek showing statistical significance. Individuals on Oregon Creek were observed closer to tributaries than the expected average mean distance; however, the sample size was too small for statistical analysis.

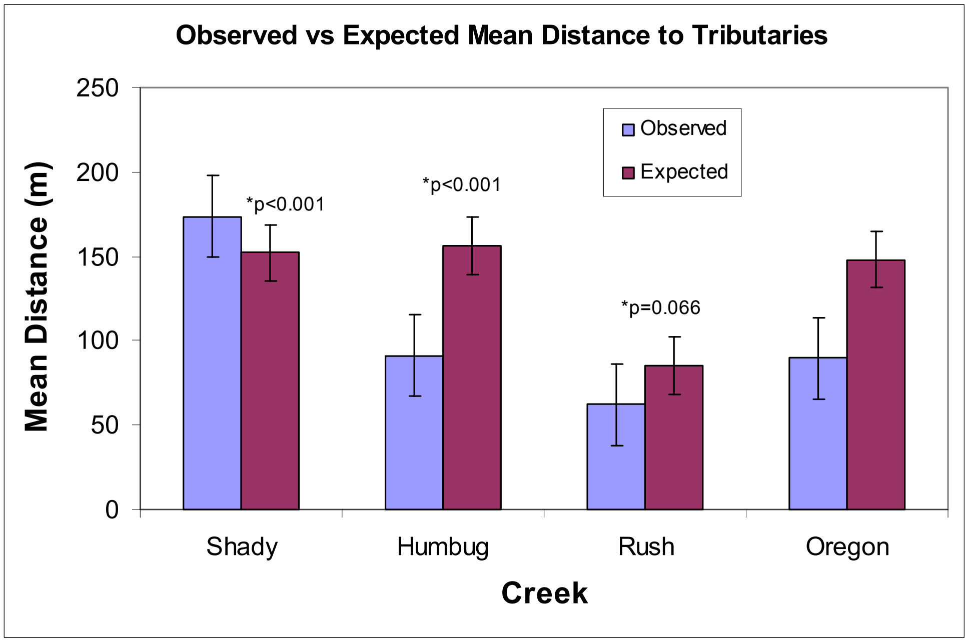


Figure 1.9. Observed versus expected mean distance to nearest tributary for each study creek.

Creek	Dataset	p-value	t value
Shady	Annual	**<0.001**	4.965
	Spring	0.109	1.611
	Summer	**0.014**	2.481
	Fall	**<0.001**	4.200
Humbug	Annual	**<0.001**	-5.509
	Summer	**<0.001**	-4.369
	Fall	**0.002**	-3.410
Rush	Annual	**0.066**	-2.039

Table 1.9. One sample t-test statistics for observed versus expected mean distance to nearest tributary. Bold type indicates statistical significance less than 0.100. Sample sizes were too small on Rush Creek and Oregon Creek to test each season separately.

Frogs on Humbug Creek did not show a preference for valley width ($p > 0.10$), but did on Shady and Rush creeks (figure 1.10). Individuals on both Shady and Rush creeks were observed more often than expected in stream locations with wider than average valley width ($p = 0.023$, $t = 2.286$; $p = 0.076$, $t = 1.959$; respectively). Preferences for valley width were not significant in the Humbug Creek seasonal datasets or the summer and fall datasets for Shady Creek. In spring on Shady Creek, however, individuals did show a preference for stream locations with wider than average valley width (p = 0.001, t = 3.296).

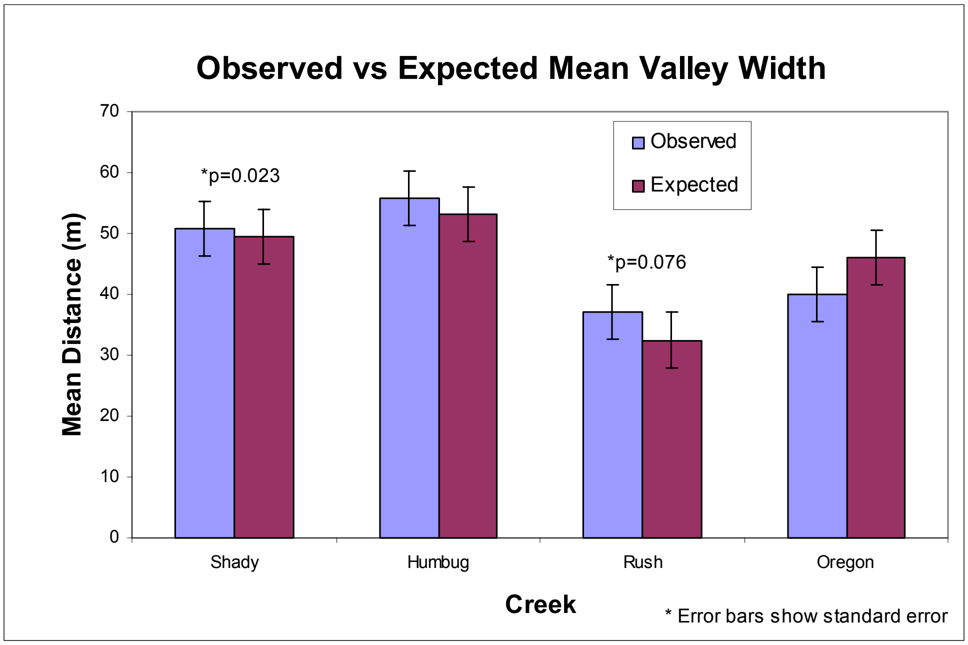


Figure 1.10. Observed versus expected mean valley width for each study creek.

Discussion

Microhabitat Associations

The results from the statistical analyses indicate that hydraulic parameters, specifically velocity, depth and substrate size, are the most useful predictors of habitat associations by lifestage for *R. boylii*. On Shady Creek, velocity accounted for 48% of the explained variance observed between all lifestages (using CCA). Generally, as individual size increased, the association with higher velocities increased. When velocity was evaluated in combination with other hydraulic parameters, such as depth and substrate, the ability to predict individual lifestage-habitat associations greatly increased. The combination of velocity and depth indicated general patterns of association for each lifestage (figure 1.11) and were useful in predicting habitat associations for pre-metamorphosis lifestages. However, evaluating the combination of velocity, depth and substrate through logistic regression modeling resulted in an average of 82% of lifestage-habitat associations correctly predicted.

Although depth and velocity are usually correlated with substrate size in most stream environments, lifestage associations with substrate, depth and velocity on Shady Creek were not correlated. Rather, lifestages were often observed in association with habitats where substrate size did not reflect the given depth and velocity conditions. For example, eggs were often found attached to coarse substrates in low velocities and depths, and subadults were often observed on smaller substrates such as gravel and small cobble, but in shallow, high velocity flows. These associations suggest *R. boylii* may require specific microhabitat conditions that are the result of previous high flows. High velocities scour and transport finer material downstream leaving coarse cobbles and boulders behind. Only when flows subsequently decrease will a microhabitat of low velocity, low depth and coarse substrate required for successful oviposition emerge.

The patterns of depth and velocity associations on Shady Creek are similar to those observed on the other study creeks, with the exception of adult females. On Shady Creek, adult females were observed in high velocity, high depth habitats (figure 1.4), while on the other study creeks, females were observed in high depth, low velocity habitats. This exception on Shady Creek may be due to the absence of deep, slow pools. The few relatively deep habitats on Shady Creek (maximum of 0.3m) were generally created by local scour around willows rather than larger scale scour that would result in a slow mid-channel pool or backwater habitat. Due to the high sediment load, any slow-moving deep pools created by high annual flows would quickly fill up with sand and gravel due to decreased velocities. Therefore only those habitats that had enough velocity to continue to scour even in low flow, such as small eddies, could maintain a greater than average depth. If adult females were seeking habitats with higher depth for cover from predators, those few habitats on Shady Creek would necessarily be associated with moderate velocity as well. The three other study creeks were not subject to such high sediment loads and therefore would be able to maintain slow-moving deep pools year-round. Thus, the strong association of females with high velocity versus high depth on Shady Creek may indicate an adaptive behavior to the lack of deep pools that provide protective cover.

On Shady creek, moderate to high velocities create surface turbulence in the form of ripples and small standing waves, which have been known to provide cover for in-stream aquatic organisms (Allouche and Gaudin 2001). Adult females may be utilizing surface turbulence as a form of cover, as well as using the high velocities as a simple escape mechanism. During surveys, females were often seen jumping into swift currents that quickly carried them downstream towards overhanging vegetation or large cobbles where they could hide underwater.

The observed microhabitat associations on all four creeks generally agree with results from previously published studies. Kupferberg (1996) found that *R. boylii* selected breeding sites with specific hydraulic parameters such that negative effects from fluctuating discharges were minimized. Specifically, she found that eggs had the highest survival rates in locations with lower than average depth and velocity and higher than average width. Lind and Welsh (2005) furthered this study by examining breeding sites across the northern California coast range and the northern Sierra Nevada. Their results indicate *R. boylii* optimize reproductive success by selecting breeding sites that are wide, shallow, low velocity and with cobble-sized substrate. The results on Shady Creek show a similar association between eggs, low velocity, coarse substrate, and low depth. While Shady Creek with its extensive hydraulic tailings differs in habitat availability from the South Fork Eel River (Kupferberg 1996) and the other streams previously studied, the fact that *R. boylii* were observed in breeding sites with the same hydraulic parameters suggests these habitat characteristics may be essential limiting factors for reproductive success regardless of the nature or location of the stream.

Little data exists on the habitat associations of older lifestages; however, the data from this study complements data from two previous studies examining *R. boylii* life history. Van Wagner (1996) found subadults most commonly occupied riffle and glide habitats, while adult females were most often observed in pools, and adult males occupied a wide range of habitats that included runs, riffles, glides and pools. In an attempt to better define these observed associations quantitatively, Yarnell (2000) used hydraulic geometry relationships to describe associations between channel shape and lifestage. She found subadults were most often observed in small narrow channels with a wide, shallow overbank area where channel width increased rapidly as discharge increased. Adults conversely were observed most often in channels that were wide but deep where depth and velocity increased rapidly as discharge increased. Neither study described the habitat associations of tadpoles.

The results from Shady Creek support these findings, indicating that habitats with higher velocity and depth were more likely to be associated with adults, while shallow habitats were more likely to support subadults. In late summer, subadults on Shady Creek were associated not only with low depths, but increasing velocities, as would be found in mesohabitat types like riffles and glides. Most adults were observed in high depth and high velocity habitats that have comparable hydraulic conditions to mesohabitats like runs and scour pools. The data therefore suggest adults and subadults on Shady Creek are associating with habitats similar to those observed by Van Wagoner (1996).

Of the microhabitat variables that were not significant predictors of lifestage, cover class was the most surprising. Previous studies have indicated adult *R.boylii* are often observed in partially shaded stream habitats (Zweifel 1955; Van Wagner 1996), while eggs and tadpoles are generally found in open, sunny habitats (Kupferberg 1996; Lind et al. 1996). In both the logistic regression modeling and the CCA analysis, cover class was not a significant factor in delineating lifestages on Shady Creek. It may be that so much of Shady Creek is open with little canopy cover, individuals may not have access to canopied areas in numbers that would statistically distinguish the various lifestages. Given that the overwhelming majority of all age individuals were observed in open reaches with 0-25% canopy cover, further study of the amount of canopy cover available on Shady Creek might reveal whether individuals are preferentially selecting open canopied habitats or, more likely, simply occupying those habitats available.

Reach-scale Associations

Reach type (Montgomery and Buffington 1997) was a useful indicator of reach-scale habitat preferences in this study and served as a good indicator of microhabitat availability. Statistically significant associations of *R. boylii* with specific reach types on each creek revealed not only a likely preference for habitat characteristics at a larger scale than the immediate microhabitat, but a preference for stream locations with a certain combination of microhabitats. On Shady Creek, braided reaches were preferentially used by all lifestages over other available reach types. The multi-channeled nature of the braided reaches provided an abundance of exposed channel bars, scour pools in locations were channels converged or moved around vegetation, shallow gently flowing riffles and faster riffles and runs. Within this diversity of habitat types, microhabitat conditions for each lifestage occurred. Similarly, on Humbug and Rush creeks, riffle-pool and step-pool reaches were the most heavily used reach types, each providing a greater amount of pool and bar habitat than either bedrock or cascade reaches. While the results from the microhabitat analysis indicated that adult females prefer single habitats, such as pools, perhaps pools next to bars may provide additional benefit by providing a basking location immediately next to cover. This type of combination of microhabitats would have to be assessed at the larger reach-scale. The reach type classification provides not only an appropriate measure for that scale, but serves as an indicator of the types of microhabitat available throughout the reach.

The analysis of reach type preference within the seasonal datasets provided additional insight regarding lifestage preferences and movement of individuals between habitats throughout the year. As the lifestages progressed from eggs through metamorphosis, microhabitat associations changed to successively faster flowing habitats with varying substrates and depths; however, the apparent preference for reach type remained consistent. Eggs, tadpoles and subadults strongly used braided reaches throughout the year, while adults showed varying associations with microhabitat and preferences for reach type depending on season. The variability in adult habitat may indicate movement throughout the foraging season similar to that found by Van Wagoner (1996).

The lack of variability in reach type preference for the younger lifestages may then indicate decreased movement, either by choice or necessity. Braided reaches provide the variety of habitats required for each of the younger lifestages and therefore may be preferred so that movement upstream or downstream is minimized. Decreased movement is inherent to eggs and young tadpoles simply due to their limited mobility, but limited movement by older tadpoles and newly metamorphed subadults may decrease energy expenditure and reduce the risk of exposure to predators, thereby increasing survival rates. If this were the case, braided reaches would provide a significant benefit towards increased survival over less diverse reaches such as cascades and plane bed reaches where costs of movement between habitats would be greater.

The results from comparing observed versus expected distance to tributaries on Humbug, Rush and Oregon creeks agrees with data collected from other studies that show a preference by *R. boylii* for stream habitats closer to tributary junctions (Kupferberg 1996; Van Wagner 1996). Tributaries often provide overwintering habitat and refuge from high winter and spring flows on larger streams. However, Lind and Welsh (2005) did not find a preference for tributary locations on Hurdygurdy Creek, a northern California coastal stream with an established *R. boylii* population. Rather, oviposition sites were commonly located in braided reaches where water temperature and algal growth were greater. They surmised the lack of association with tributaries was due to the relatively small size of Hurdygurdy Creek and the limited number of perennial tributaries.

While Shady Creek provides substantially different habitat conditions than Hurdygurdy Creek, several similarities exist. Tributaries on Shady Creek, while technically perennial, are usually reduced to very low levels in late summer as flows enter the subsurface and travel interstitially through the gravels. As a result, surface flow input from tributaries is often insignificant in late summer and fall. In addition, the wide, open nature of Shady Creek and the tendency for braiding at high flows provides an abundance of refuge habitat in the adjacent floodplains and low terraces. Flows rarely get deep, turbulent or fast at high water as width increases substantially faster than depth. Therefore, like Hurdygurdy Creek, there is no need for refuge habitat in higher elevation tributaries. In addition, the data on Shady Creek indicate a strong preference by all lifestages for stream locations with wider than average valley widths. Braided reaches commonly occur in these wider valley sections suggesting the open conditions of braided reaches provide an increased benefit over the potential refuge of tributaries.

On Rush Creek, individuals showed a preference for stream locations with both wider than average valley width and less than average distance to nearest tributary. However, these two characteristics were also correlated such that valley width was greatest at tributary junctions ($R^2 = 0.37$, $F = 12.93$, $p = 0.002$). Grant and Swanson (Grant and Swanson 1995) found stream reaches near tributary confluences had wider valley floors with larger floodplains. It’s unclear from the data whether the true preference is for stream locations close to tributaries, for areas with greater valley width or both. As discussed above, tributaries can provide refuge habitat during high flows, but wider reaches on Rush Creek also tended to have less canopy cover and more hours of direct sunlight. On Humbug Creek, valley width did not correlate with distance to tributaries, and individuals only showed a significant preference for tributary location. In this case, stream locations near tributary confluences may provide greater benefits than reaches with greater valley width. Valley width was generally constant on Humbug Creek varying only slightly near tributaries or in reaches with less bedrock control. Therefore, variations in habitat type or direct sunlight may be related to factors other than valley width on Humbug Creek.

Habitat Heterogeneity

Physical habitat heterogeneity (the spatial variation of physical properties between habitats) has long been believed to influence biologic processes in stream ecosystems both directly in terms of species richness and diversity (Palmer et al. 1996; Downes et al. 2000) and indirectly as the result of watershed disturbance processes (Resh et al. 1988; Townsend et al. 1997; Wootton 1998; Poole 2002). Specifically, greater heterogeneity in stream habitat can increase both aquatic species diversity (Beisel et al. 2000; Brown 2003) and individual species success and survival (Power 1992; Strayer 1999; Torgersen and Close 2004). For *R. boylii*, increased habitat heterogeneity at the reach scale can provide substantial benefits for each lifestage, particularly from eggs through metamorphosis. Reaches with higher heterogeneity provide a greater diversity of habitat suitable to each of the lifestages, provide a greater variety of habitats with multiple functions (e.g. cover, forage, basking and breeding) and provide a greater variety of refugia as flows fluctuate throughout the season.

Results from a concurrent study (see chapter 2) showed that diversity in stream habitat type and spatial variation in those habitats can be quantified using a variety of habitat heterogeneity indices. These indices were shown not only to reflect the spatial diversity of channel structures at the reach-scale, but to be ecologically meaningful as well. Using data on *R. boylii* from the same four study creeks within the Yuba River basin, reach types with the highest habitat heterogeneity were the most preferred by *R. boylii*. Interestingly, reach types were not consistent in their level of measured heterogeneity across each of the tributaries and thus did not correlate with *R. boylii* abundance across creeks. Rather, the reach type with the highest heterogeneity of those available within that creek was the reach type most preferred by *R. boylii* in that drainage (refer to results in chapter 2). Results regarding reach type preference from this microhabitat study and potential reasons for those preferences as discussed above agree well with the results from the concurrent study. *R. boylii* are largely selecting reaches with higher physical habitat heterogeneity, where a greater diversity of habitats is available in a relatively shorter section of stream.

The association of all lifestages for stream locations near tributary confluences and greater valley width also agrees with the concept that reaches with greater heterogeneity provide optimal habitat for *R. boylii*. Benda et al (2003) found that heterogeneity in channel morphology increased near tributary confluences prone to debris flows. Debris and alluvial inputs from tributaries are forms of watershed disturbance and act to increase habitat diversity by depositing large woody debris, inducing sediment deposition behind larger boulders and forming wider valley floors. Just as increased complexity in habitat types induces increased species richness by providing a greater variety of niches (Ward et al 2002), so too does increased habitat heterogeneity provide the variety of habitats needed by *R.boylii* throughout their lifecycle.

The results from this study have direct implications for conservation and restoration practices. Because *R. boylii* habitat requirements vary across multiple spatial and temporal scales, streams where natural disturbance processes create a high diversity of physical habitats within a stream reach will have the highest benefit for long-term reproductive success. Specifically, reaches where a variety of velocity, depth and substrate conditions exist provide an increased likelihood that in any given year, regardless of the flow conditions, the required habitat conditions will exist for multiple lifestages. This is especially true for vulnerable lifestages such as eggs and tadpoles that have very specific microhabitat conditions. Stream reaches with a greater geomorphic diversity are more likely to contain the low velocity, shallow depth, coarse substrate habitat required for oviposition in both low flow and high flow years than a uniform stream reach where the right habitat may exist only at certain flows. Therefore, restoration practices in altered streams that maximize the variability in flow and sediment that create geomorphic disturbance will likely maximize the diversity of physical habitats available directly benefiting *R. boylii*.

Works Cited

Allouche, S. and P. Gaudin (2001). Effects of avian predation threat, water flow and cover on growth and habitat use by chub, *Leuciscus cephalus*, in an experimental stream. *Oikos* 94(3): 481-492.

Beisel, J. N., P. Usseglio-Polatera and J. C. Moreteau (2000). The spatial heterogeneity of a river bottom: a key factor determining macroinvertebrate communities. *Hydrobiologia* 422: 163-171.

Brown, B. L. (2003). Spatial heterogeneity reduces temporal variability in stream insect communities. *Ecology Letters* 6(4): 316-325.

Downes, B. J., P. S. Lake, E. S. G. Schreiber and A. Glaister (2000). Habitat structure, resources and diversity: the separate effects of surface roughness and macroalgae on stream invertebrates. *Oecologia* 123(4): 569-581.

ESRI, Inc. (2002). ESRI ArcGIS ver.8.3. www.esri.com., ESRI Inc.

Frissell, C. A., W. J. Liss, C. E. Warren and M. D. Hurley (1986). A Hierarchical Framework For Stream Habitat Classification - Viewing Streams in a Watershed Context. *Environmental Management* 10(2): 199-214.

Grant, G. E. and F. J. Swanson (1995). Morphology and processes of valley floors in mountain streams, western Cascades, Oregon. Natural and anthropogenic influences in fluvial geomorphology. J. E. Costaet al, American Geophysical Union Geophysical Monograph. 89: 83-101.

Hawkins, C. P., J. L. Kershner, P. A. Bisson, M. D. Bryant, L. M. Decker, S. V. Gregory, D. A. McCullough, C. K. Overton, G. H. Reeves, R. J. Steedman and M. K. Young (1993). A Hierarchical Approach to Classifying Stream Habitat Features. *Fisheries* 18(6): 3-12.

Hayes, M. P. and M. R. Jennings (1986). Decline of Ranid Frog Species in Western North-America - Are Bullfrogs (*Rana catesbeiana*) Responsible? *Journal of Herpetology* 20(4): 490-509.

Heyer, W. R., M. A. Donnelly, R. W. McDiarmid, L. C. Hayek and M. S. Foster, Eds. (1994). Measuring and monitoring biological diversity: Standard methods for amphibians. Biological Diversity Handbook Series. Washington D.C., Smithsonian Institution Press.

Hirzel, A. and A. Guisan (2002). Which is the optimal sampling strategy for habitat suitability modelling? *Ecological Modelling* 157: 331-341.

Hosmer, D. W. and S. Lemeshow (1989). Applied Logistic Regression. New York, NY, John Wiley & Sons.

Jennings, M. R. and M. P. Hayes (1994). Amphibian and reptile species of special concern in California. Final Report. Rancho Cordova, California Department of Fish and Game Inland Fisheries Division.

Knapp, R. A. and H. K. Preisler (1999). Is it possible to predict habitat use by spawning salmonids? A test using California golden trout (*Oncorhynchus mykiss aguabonita*). *Canadian Journal of Fisheries and Aquatic Sciences* 56: 1576-1584.

Kupferberg, S. J. (1996). Hydrologic and geomorphic factors affecting conservation of a river-breeding frog (*Rana boylii*). *Ecological Applications* 6(4): 1332-1344.

Lind, A. J., J. B. Bettaso and S. M. Yarnell (2003). Natural History Notes: *Rana boylii* and *Rana catesbeiana* Reproductive Behavior. *Herpetological Review* 34(3): 234-235.

Lind, A. J. and H. H. Welsh (2005). Multi-scale oviposition site choice by the foothill yellow-legged frog (*Rana boylii*) in California: Responses to a stochastic environment. *Journal of Herpetology*. In press.

Lind, A. J., H. H. Welsh and R. A. Wilson (1996). The effects of a dam on breeding habitat and egg survival of the foothill yellow-legged frog (*Rana boylii*) in northwestern California. *Herpetological Review* 27(2): 62-67.

Maddock, I. (1999). The importance of physical habitat assessment for evaluating river health. *Freshwater Biology* 41(2): 373-391.

McCune, B. and J. B. Grace (2002). Analysis of Ecological Communities. Gleneden Beach, OR, MJM Software Design.

Montgomery, D. R. and J. M. Buffington (1997). Channel-reach morphology in mountain drainage basins. *Geological Society of America Bulletin* 109(5): 596-611.

Moyle, P. B. (1973). Effects of introduced bullfrogs, *Rana catesbeiana*, on the native frogs of the San Joaquin Valley, California. *Copeia* 1973: 18-22.

Newson, M. D. and C. L. Newson (2000). Geomorphology, ecology and river channel habitat: mesoscale approaches to basin-scale challenges. *Progress in Physical Geography* 24(2): 195-217.

Norusis, M. J. (2004). SPSS 12.0 Guide to Data Analysis. Upper Saddle River, NJ, Prentice Hall.

Nussbaum, R. A., J. Brodie, E.D. and R. M. Storm (1983). Amphibians & reptiles of the Pacific Northwest. Univeristy Press of Idaho.

Palmer, M. A., P. Arensburger, A. P. Martin and D. W. Denman (1996). Disturbance and patch specific responses: The interactive effects of woody debris and floods on lotic invertebrates. *Oecologia* 105(2): 247-257.

Poole, G. C. (2002). Fluvial landscape ecology: addressing uniqueness within the river discontinuum. *Freshwater Biology* 47(4): 641-660.

Power, M. E. (1992). Habitat Heterogeneity and the Functional-Significance of Fish in River Food Webs. *Ecology* 73(5): 1675-1688.

Resh, V. H., A. V. Brown, A. P. Covich, M. E. Gurtz, H. W. Li, G. W. Minshall, S. R. Reice, A. L. Sheldon, J. B. Wallace and R. C. Wissmar (1988). The Role of Disturbance in Stream Ecology. *Journal of the North American Benthological Society* 7(4): 433-455.

SPSS, Inc. (2003). SPSS 12.0 for Windows: Base, Regression Models and Advanced Models. Chicago, IL, SPSS Inc.

Strayer, D. L. (1999). Use of flow refuges by unionid mussels in rivers. *Journal of the North American Benthological Society* 18(4): 468-476.

Tabachnick, B. G. and L. S. Fidell (2001). Using Multivariate Statistics. Boston, MA, Allyn and Bacon.

TerBraak, C. (1986). Canonical Correspondence Analysis: A New Eigenvector Technique for Multivariate Direct Gradient Analysis. *Ecology* 67(5): 1167-1179.

TerBraak, C. and P. Smilauer (1998). Canoco reference manual and user's guide to Canoco for Windows, Software for Canonical Community Ordination (version 4). Ithaca, NY, Microcomputer Power.

TerBraak, C. and P. Verdonschot (1995). Canonical correspondence analysis and related multivariate methods in aquatic ecology. *Aquatic Sciences* 57(255-289).

Torgersen, C. E. and D. A. Close (2004). Influence of habitat heterogeneity on the distribution of larval Pacific lamprey (*Lampetra tridentata*) at two spatial scales. *Freshwater Biology* 49(5): 614-630.

Torgersen, C. E., D. M. Price, H. W. Li and B. A. McIntosh (1999). Multiscale thermal refugia and stream habitat associations of chinook salmon in northeastern Oregon. *Ecological Applications* 9(1): 301-319.

Townsend, C. R., M. R. Scarsbrook and S. Doledec (1997). The intermediate disturbance hypothesis, refugia, and biodiversity in streams. *Limnology and Oceanography* 42(5): 938-949.

Trexler, J. C. and J. Travis (1993). Nontraditional Regression Analysis. *Ecology* 74: 1629-1637.

Van Wagner, T. J. (1996). Selected life-history and ecological aspects of a population of foothill yellow-legged frogs (*Rana boylii*) from Clear Creek, Nevada County, California. Master's Thesis. Department of Biological Sciences. Chico, California State University, Chico: 143.

Ward, J. V., K. Tockner, D. B. Arscott and C. Claret (2002). Riverine landscape diversity. *Freshwater Biology* 47(4): 517-539.

Wootton, J. T. (1998). Effects of disturbance on species diversity: A multitrophic perspective. *American Naturalist* 152(6): 803-825.

Yarnell, S. M. (1999). Foothill Yellow-legged Frog Population Data and Fluvial Geomorphic Data for Spring, Shady and Humbug Creeks, Nevada County, CA. Final Report. Grass Valley, Ca, California Dept of Parks and Recreation, Gold Rush District: 15.

Yarnell, S. M. (2000). The influence of sediment supply and transport capacity on Foothill Yellow-legged Frog habitat, South Yuba River, California. Master's Thesis. Geology. Davis, CA, University of California, Davis: 241.

Zweifel, R. G. (1955). Ecology, distribution and systematics of frogs of the Rana boylii group. Berkeley, CA, University of California Publications in Zoology.

CHAPTER 2: Quantifying Physical Habitat Heterogeneity in an Ecologically Meaningful Manner: A Case Study of the Habitat Preferences of the Foothill Yellow-legged Frog (*Rana boylii*)

Abstract

Geomorphic features of four creeks tributary to the South Yuba River, Nevada County, California known to support populations of Foothill Yellow-legged Frog (*Rana boylii*) were evaluated to determine relative frog abundance and degree of habitat heterogeneity. Spatial heterogeneity indices from landscape ecology were used as objective measures to quantify habitat variability. Four spatial indices quantifying spatial composition (patch shape, diversity, richness and evenness) and two indices quantifying spatial configuration (contagion and interspersion) were calculated for each study reach. Results from multiple linear regression analyses showed indices of spatial composition correlated well with frog abundance, while indices of spatial configuration were not significant. The most significant regression model contained only Shannon's Diversity Index as the best predictor of frog abundance such that as the diversity in geomorphic units throughout the reach increased, relative frog abundance increased. These findings indicate *R. boylii* selects stream reaches with increased geomorphic complexity that provide habitats suitable to each lifestage, habitats with multiple functions (e.g. cover, forage, basking and breeding) and a greater variety of refugia as flows fluctuate throughout the season. Spatial heterogeneity indices are useful in quantifying aquatic habitat heterogeneity, and when shown to be ecologically meaningful can be useful for quantifying habitat in river restoration or conservation practices.

Introduction

Physical habitat heterogeneity influences biologic processes in stream ecosystems both directly in terms of species richness and diversity (Palmer et al. 1996; Minshall and Robinson 1998; Downes et al. 2000) and indirectly as the result of watershed disturbance processes (Resh et al. 1988; Townsend et al. 1997; Wootton 1998; Poole 2002). Specifically, greater heterogeneity in stream habitat can increase both aquatic species diversity (Beisel et al. 2000; Brown 2003) and individual species success and survival (Power 1992; Strayer 1999; Torgersen and Close 2004). The quantification of stream habitat heterogeneity; however, has been highly variable. Methods are inconsistent across disciplines and definitions are often lacking. As a result, the term is used in the literature as a catch phrase to encompass a broad array of concepts ranging from spatial variation in flow to habitat patch richness.

Discrete definitions and repeatable methods for quantifying habitat heterogeneity through the use of spatial indices have been developed over the last decade in the field of landscape ecology (Turner et al. 1994; Li and Reynolds 1995); however, their use has been primarily limited to large-scale regional studies of terrestrial landscapes. Some researchers have suggested applying concepts from landscape ecology to riverine ecology (Ward et al. 2001; Poole 2002; Ward et al. 2002), and several recent studies have incorporated common landscape indices into benthological studies (Palmer et al. 2000; Cardinale et al. 2002; Boyero 2003). As the use of landscape indices has increased however, prominent landscape ecologists were prompted to publish cautionary statements regarding the proper use of common indices (Li and Wu 2004). One primary complaint was that landscape indices and associated map data were sometimes used without testing their ecological relevance, potentially leading to erroneous or meaningless interpretations of results. Li and Wu (2004) recommended incorporating exploratory correlation analyses that generate causal hypotheses and using indices that have close associations with ecological processes into studies to help alleviate this problem.

This study addresses several of the key ideas and concepts presented above by examining the spatial heterogeneity of physical habitat of *Rana boylii*, a river-dwelling frog native to California and southern Oregon. *R. boylii* has been found to require a wide variety of geomorphic and hydraulic conditions throughout its complex lifecycle (Kupferberg 1996; Lind et al. 1996; Yarnell 2000) and may occupy stream reaches with high physical heterogeneity, both in terms of habitat composition and spatial configuration. Landscape indices that quantify various aspects of stream habitat may help to elucidate *R. boylii* associations with spatial patterns in habitat.

Incorporating suggestions from Li and Reynolds (1995), indices were selected that represent the number and proportions of habitat types, the spatial arrangement of habitats, and habitat shape. Addressing the concerns of Li and Wu (2004), the scale of study was conducted at the stream reach (based on reach types defined by Montgomery and Buffington 1997) in order to link geomorphic processes creating channel morphology and the biologic response of *R. boylii* to its physical habitat. Analyses focused on correlating the heterogeneity of geomorphic features within a reach type to the relative abundance of *R. boylii* within that reach type. A concurrent study on the microhabitat preferences of *R. boylii* (chapter 1) showed that frogs associate both with specific geomorphic features and certain reach types depending on lifestage and season. The study hypothesis is that reaches with the greatest diversity of habitats and greater interspersion and juxtaposition of patches will support the greatest abundance of *R. boylii*.

Background

Classification of stream habitat into discrete units that reflect both the physical processes creating channel morphology and the biologic response of aquatic species has been a heavily studied and debated topic across multiple academic disciplines. As the literature on how to best describe and assess in-stream channel habitat has grown in recent years, scientists have attempted to merge multiple views into a more holistic framework that addresses the processes which drive watershed ecology (Newson and Newson 2000; Thomson et al. 2001; Poole 2002). Two primary concepts have emerged as essential to stream channel habitat assessment: classification of the stream spatially within a hierarchical framework, and incorporation of the processes that create, maintain and destroy channel habitat. A hierarchical framework allows for logical categorization at multiple scales of both the processes driving change and the responses observed, such that each sequentially smaller spatial scale is dependent on the larger scale processes above it and contributes to the characteristics of the smaller scale below (Frissell et al. 1986). Process-based classifications provide information not only on the conditions currently existing within the channel, but also on how changes in the watershed or landscape will affect the channel morphology and hydrology.

Few stream habitat classification schemes fully incorporate these two themes; however, Montgomery and Buffington (1997) proposed a process-based reach type classification that incorporates the most commonly described geomorphic channel features (pool, riffle). Reach types are based on the dominant geomorphic units observed and range in occurrence along a gradient corresponding to slope. This classification has been shown to be ecologically meaningful (Montgomery et al. 1999) and easily fits within a hierarchical watershed framework (Montgomery et al. 1996; Montgomery 1999). Therefore, the scale of inquiry for the study was the reach-scale and study reaches were classified by reach type after the methods of Montgomery and Buffington (1997).

The composition of geomorphic units within each study reach was evaluated as a mosaic of patches using methods common to the field of landscape ecology. The concept of viewing a river or stream as a 'landscape' has only recently emerged in the literature as stream ecologists have turned to methods used by landscape ecologists to quantify and describe the inherent spatial complexity of riverine habitat (Palmer et al. 2000; Ward et al. 2001; Wiens 2002). The term 'habitat heterogeneity' has become a popular catch phrase used by ecologists and hydrologists to describe everything from variability in measured stream characteristics (e.g. standard deviation in D_{50} (Cardinale et al. 2002); variation in spatial location of sampling (Torgersen and Close 2004)) to the size, shape, configuration and distribution of habitat patches in space (Palmer et al. 2000; Boyero 2003; Brown 2003). The enthusiasm for use of newly developed indices that measure various aspects of spatial heterogeneity has lead prominent landscape ecologists to publish cautionary papers clarifying operational definitions, elucidating common problems in applying various indices and offering suggestions for proper interpretation and conclusions from the results (Li and Wu 2004). Information from these papers and the few recent studies that have incorporated analyses of the spatial configuration of channel habitat structure helped to guide the analysis of *R. boylii* habitat for this study.

Defined specifically as “the complexity and/or variability of a system property in space and/or time”, spatial heterogeneity can be quantified for categorical data (measurements of ‘complexity’) or numerical data (measurements of ‘variability’) (Li and Reynolds 1995). In reference to in-stream habitats, terms such as ‘landscape’ and ‘patch’, which are usually scaled to the organism of interest, can be defined at smaller scales such as the stream segment and microhabitat, respectively. Several studies on habitat preferences of macroinvertebrates have incorporated landscape indices, defining substrate patches at the sub-meter scale and landscapes at the riffle-pool or stream segment scales (Beisel et al. 2000; Palmer et al. 2000; Boyero 2003).

In this study, the landscape was defined as the study reach, and a patch was a geomorphic unit. Shown not only to generally reflect geomorphic and ecologic processes (Montgomery and Buffington 1997; Montgomery et al. 1999; Thomson et al. 2001), the reach-scale and geomorphic unit scale were particularly appropriate for assessing *R. boylii*, which have been shown to respond to mesohabitats such as pools and riffles (Van Wagner 1996; Yarnell 2000) as well as specific reach types (concurrent microhabitat study, Yarnell 2004). Therefore, this study defined ‘habitat heterogeneity’ as the spatial complexity of geomorphic units within a stream reach.

The habitat heterogeneity of each study reach was quantified after the methods proposed by Li and Reynolds (1995). To evaluate categorical maps, they suggested assessing the relative complexity of the patches within the map, specifically the composition and configuration of the patches. A previous Li and Reynolds (1994) study showed four indices in particular were effective in quantifying the various aspects of patch composition and configuration: diversity, contagion, fractal dimension and patchiness. These indices represent the number and proportions of patch types, spatial arrangement of patches, patch shape, and contrast between neighboring patches, respectively. In order to fully explore how the various aspects of habitat heterogeneity relate to *R. boylii* abundance, these four landscape-level indices were evaluated as well as a variety of class-level indices that focus on specific geomorphic units, such as pools and bars, shown to be relevant to *R. boylii*.

Methods

Study Area

A large number of small to moderate sized populations of *R. boylii* currently exist across the northern Sierra Nevada range, the majority of which are located between the Stanislaus River watershed to the south and the Feather River watershed to the north (Jennings and Hayes 1994). The Yuba River Drainage is located just south of the Feather River Basin in Nevada County. Four tributaries within the Yuba River watershed were selected for study, each known to sustain small sub-populations of *R. boylii*: Shady Creek, Rush Creek and Humbug Creek on the South Yuba River and Oregon Creek on the Middle Yuba River (figure 2.1). These creeks vary both in terms of stream habitat availability and occupation by *R. boylii*. Chapter 1 provides additional details on the *R. boylii* populations in these creeks.

The four study creeks are similar to most mid-elevation Sierran drainages having moderate to steep slopes, confined valleys with occasional bedrock outcrops, narrow disconnected riparian zones, coarse substrates, and steep channel morphologies including cascades, steps, riffles and pools. All four creeks have been subject to various land uses including mining (in-stream, hydraulic and high banking), logging and development, but the degree of impact varies between each creek resulting in varied habitat complexity between and within each watershed. Shady Creek differs from the other study creeks in that it continues to recover from extensive past aggradation of hydraulic mining debris. Some reaches with steeper slopes have recovered to the original bedrock surfaces, but the majority of reaches continue to degrade through vast piles of tailings leaving remnant terraces behind. These four creeks represent common stream habitats that are known to support *R. boylii* populations elsewhere in the northern Sierra Nevada, such as the Bear River and its tributaries (pers. comm. A.Carlson, U.S. Forest Service), and Clear Creek (Van Wagner 1996). Table 2.1 summarizes the main geomorphic characteristics of each creek.

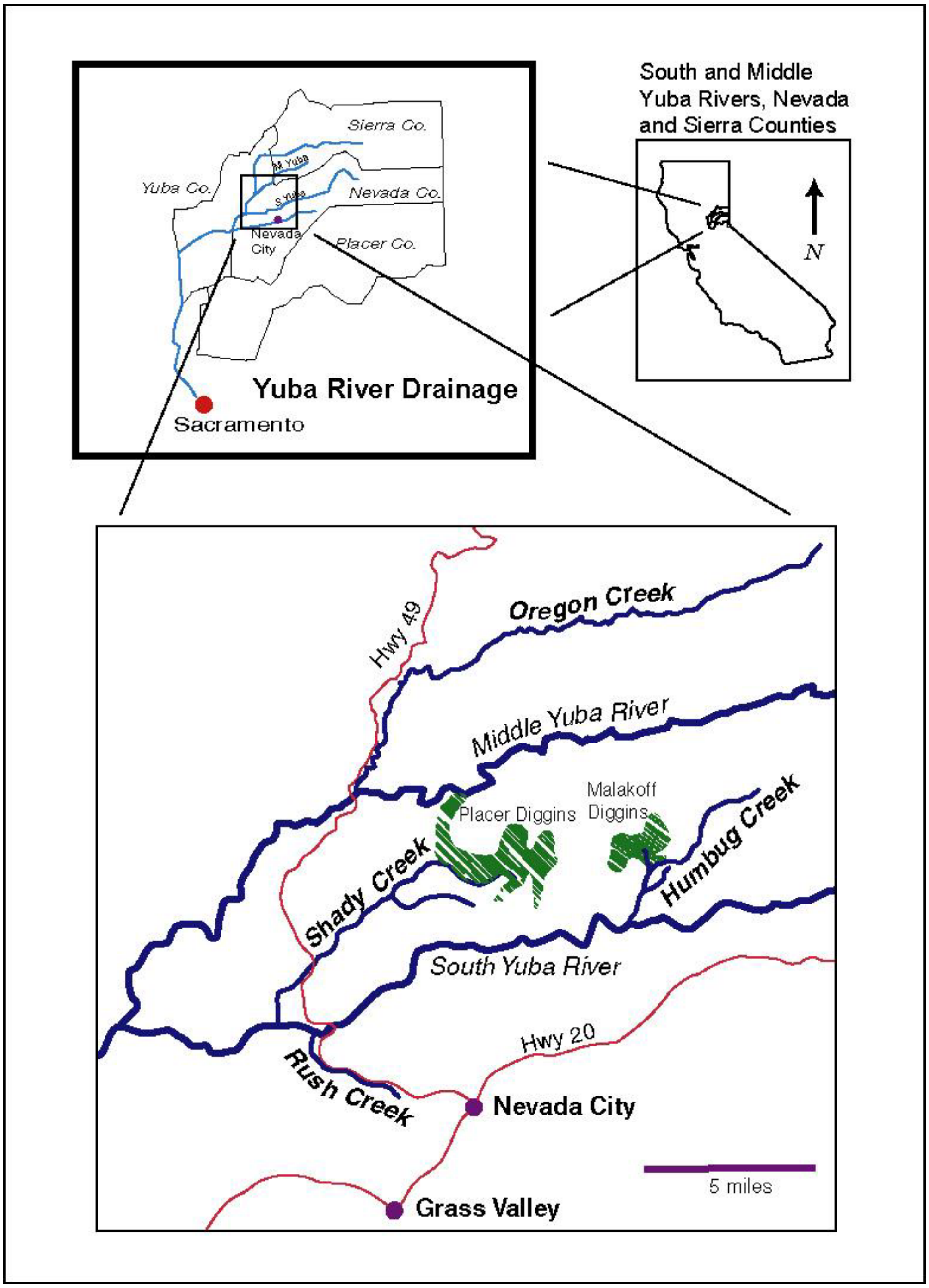


Figure 2.1. Location of study creeks.

Creek	Total Drainage Area (km^2)	Total Elevation Range (m)	Estimated Mean Annual Discharge (cfs)	Dominant Channel Morphology	Dominant Substrate Types
Humbug	27.75	660 - 1470	25	Plunge Pools, Boulder Steps, Coarse Bars, High Gradient Riffles	Cobble, Boulder, Bedrock
Oregon	91.08	450 - 1400	35	Plunge Pools, Boulder Steps, Cascades	Boulder, Bedrock, Cobble
Rush	14.56	340 - 940	10	Plunge Pools, Boulder Steps, Cascades, Coarse Bars	Boulder, Bedrock, Cobble
Shady	37.58	310 - 890	15	Riffles, Runs, Gravel Bars, Shallow Pools	Cobble, Gravel, Sand

Table 2.1. Geomorphic characteristics of each study creek.

Geomorphic Mapping

Twelve study reaches were selected, three on each of the four study tributaries, each representing one of the three dominant reach types (as defined by Montgomery and Buffington 1997) occurring on that tributary. Table 2.2 summarizes the characteristics of each study reach, and figure 2.2 shows the locations of each reach within the study creek.

Each study reach was topographically mapped using a total station (Topcon) such that a complete 3-dimensional surface was created and the dominant geomorphic units in each reach were delineated. Geomorphic units were defined based on common definitions provided in the literature (table 2.3). The field survey data from each reach was imported into ArcGIS v.8.3 (ESRI 2002) and digitized into a polygon-based feature file representing a planform map of the geomorphic units comprising that reach (figure 2.3). A total of twelve reach-scale maps were created in ArcGIS each representing one of the three dominant reach types occurring on each of the four study creeks.

Creek	Study Reach	Reach Type	Reach Length (m)	Drainage Area Upstream (km2)	Dominant Geomorphic Features	Dominant Substrate Size
Humbug	Blair Pond	Step-Pool	58	10.4	Boulder Steps, Plunge Pools, Coarse Bar	Boulder, Cobble
Humbug	Gage Site	Riffle-Pool	81	20.9	Coarse Bars, High Gradient Riffles, Shallow Pools	Cobble
Humbug	Picnic Bar	Plane Bed	45	21.25	Low Gradient Riffle, Coarse Shallow Bar	Cobble
Oregon	Oregon Creek Road	Cascade	65	27.7	Boulders, Coarse Bars, High Gradient Rapids	Boulder, Cobble
Oregon	Gage Pools	Bedrock	99	56.5	Bedrock Chutes, Plunge Pools	Bedrock
Oregon	Celestial Pools	Step-Pool	88	85.4	Boulder Steps, Plunge Pools	Boulder
Rush	Bare Rock	Bedrock	69	12.8	Bedrock Chutes, Plunge Pools	Bedrock
Rush	Aaron's Pools	Step-Pool	57	14.6	Boulder Steps, Plunge Pools, Coarse Bars	Cobble
Rush	Road Jumble	Cascade	80	14.6	Boulders, Coarse Bars, High Gradient Rapids	Boulder
Shady	Dead Tree Scape	Braided	92	1.7	Low Gradient Riffles, Many Fine/Coarse Bars, Shallow Pools	Gravel
Shady	Rust Pit	Plane Bed	81	14	Low Gradient Riffles, Few Fine/Coarse Bars	Gravel
Shady	Shady Road	Riffle-Pool	97	22.7	Low Gradient Riffles, Shallow Pools, Coarse Bars	Gravel

Table 2.2. Geomorphic characteristics of each study reach

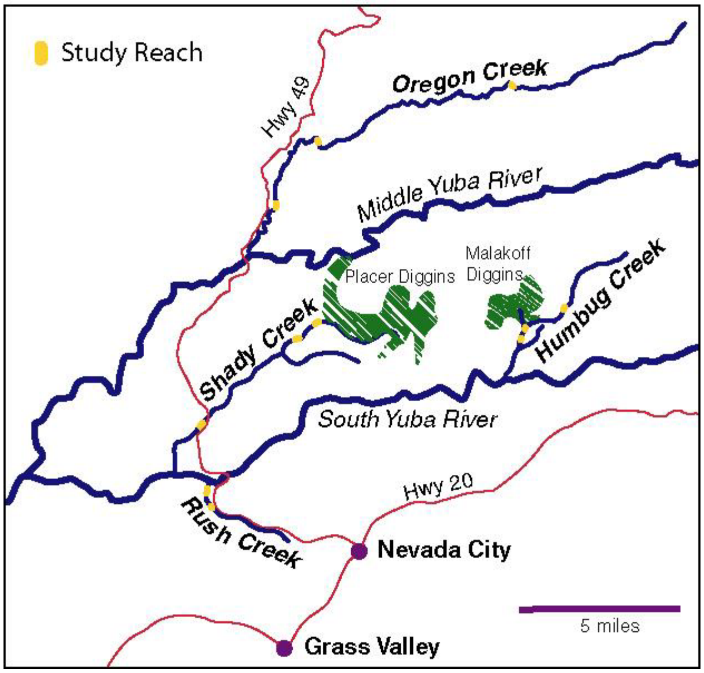


Figure 2.2. Location of study reaches within each study creek.

Geomorphic Unit	Observational Definittion
Pool	Region of deeper than average, slower-moving water with fine bed materials and low water surface slope (Gordon et al)
Run	Non-turbulent, low velocity flowing water with uniform depth and velocity and low water surface slope. Shallower and faster than a pool, but deeper and slower than a riffle (Hawkins et al. 1993).
Riffle	Region of shallower than average, fast-moving water with coarse bed material and moderate to high water surface slope (Gordon et al)
Rapid/ Cascade	Turbulent high-velocity flow including chutes and hydraulic jumps swirling around exposed boulders and over larger than average particles with high water surface slope (Hawkins et al. 1993).
Step	A group of boulders arranged in a straight or curved line across the channel (Wohl 2000)
Side Channel	Stream channel branching off of and re-connecting to main channel that is inundated during high flow, but is reduced or dry during low flow due to higher than average channel elevation
Bar	Dynamic unvegetated bedform feature created by sediment deposition (Gordon et al) that is submerged at bankfull flow (Wohl 2000)
Floodplain	Occasionally inundated depositional surface next to the active channel (Wohl 2000)
Log Jam	Logs or woody debris (>10 cm diameter) piled in or next to the channel resulting in obstruction of flow (Wohl 2000)
Boulder	Larger than average (usually > 1m diameter) grain size in or next to the channel resulting in obstruction of flow
Terrace	Former floodplain accessed only in extreme floods that may relate to past debris flows in high gradient channels (Wohl 2000)
Bedrock	Exposed bedrock surface influencing channel dynamics

Table 2.3. Operational definitions of geomorphic units.

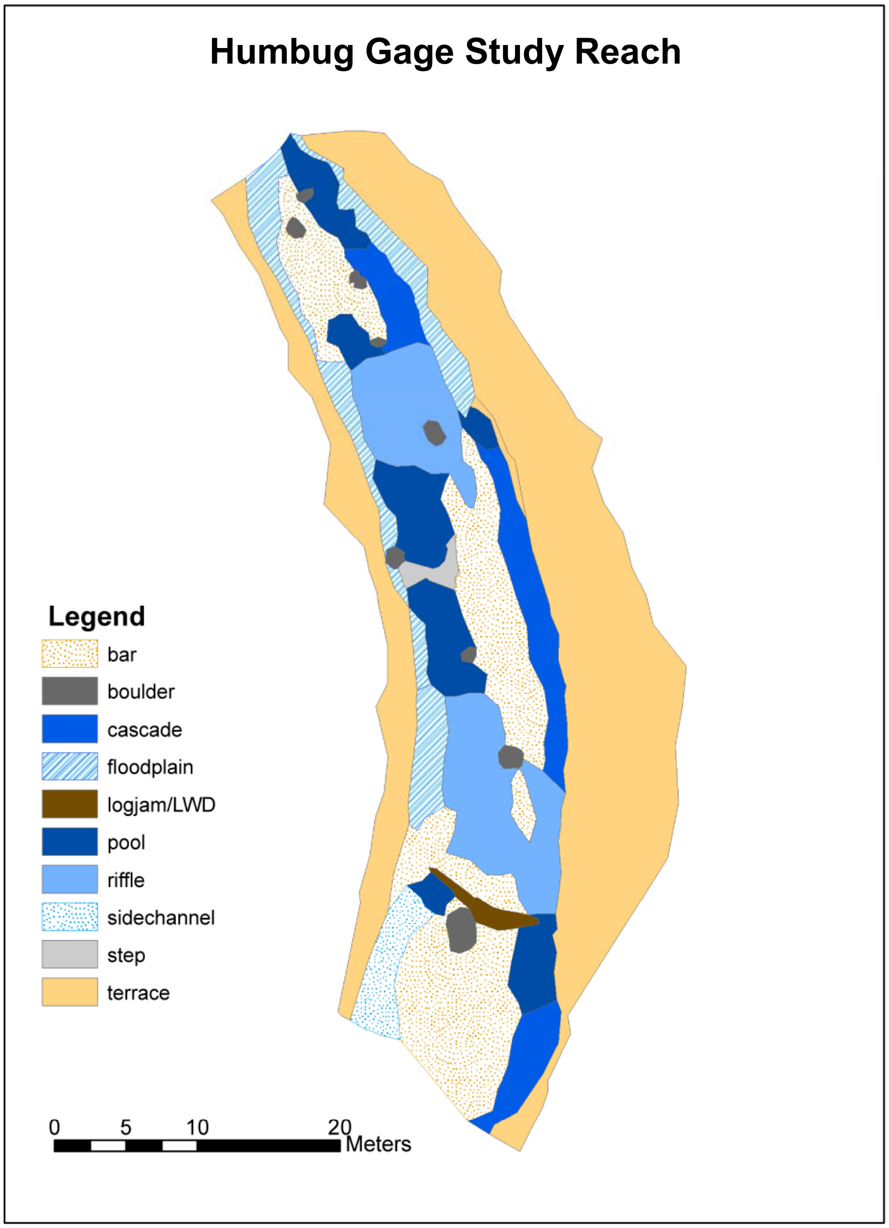


Figure 2.3. Example of digitized reach-scale planform map delineating geomorphic units.

Habitat Heterogeneity Indices

The habitat heterogeneity of each study reach was evaluated using metrics in FRAGSTATS v.3.3 (McGarigal et al. 2002). This program has been shown to be useful in analyzing categorical maps (Raines 2002), and can directly evaluate raster-based grids exported from ArcGIS. To create the input for FRAGSTATS, each planform map generated in ArcGIS was converted from a polygon-based feature file to a raster format using the spatial analyst functions in ArcGIS. When comparing landscapes, potential problems relating to scale can arise depending both on the total area of the landscape and the cell size used in creating the raster grid (Wiens 2002). In order to limit problems with comparing reaches of different areas, excess areas beyond the active channel boundary were trimmed. During the topographic mapping in the field, each reach was surveyed laterally to the base of the valley slope or to the farthest terraces as applicable. This resulted in some reaches having a greater mapped area beyond their bankfull boundaries than others. *R. boylii* are rarely seen more than a few meters from the water's edge, so a 2m buffer was created around the bankfull channel boundaries using the geoprocessing tools in ArcGIS and all areas beyond this buffer were not evaluated. To eliminate any potential bias due to cell size, each grid cell was set to 0.25m. The drainage area and mean annual discharge of each study creek is within an order of magnitude of the other study creeks (table 2.1), so the relative size of geomorphic features and channel dimensions are reasonably similar ranging from 5-20 m^2 in size. A 0.25m grid cell was appropriate for accurately representing the size and shape of typical geomorphic units, and it encompassed the resolution of the geomorphic surveying completed in the field. Once these adjustments were made in ArcGIS, the raster datasets were exported to FRAGSTATS for analysis.

FRAGSTATS includes a wide variety of metrics that can be calculated at three different scales of analysis: the patch-level, the class-level and the landscape-level. In this study, patches equate to individual geomorphic units, classes represent each geomorphic unit type and the landscape is the study reach. The four primary indices recommended by Li and Reynolds (1994) (diversity, contagion, fractal dimension and patchiness) were evaluated at the landscape-level in FRAGSTATS. The following metrics were chosen to represent the first three indices respectively: Shannon's Diversity Index (SHDI), Contagion (CONTAG), and Perimeter-Area Fractal Dimension (PAFRAC). FRAGSTATS has two metrics that measure aspects of patchiness, Similarity Index (SIMI) and Total Edge Contrast Index (TECI). Both these metrics require quantifications of the contrast or similarity between varying patch types. However, there is no literature that discusses how aquatic species like *R. boylii* respond to contrasting geomorphic features such as pools and riffles in a manner conducive to assigning contrast values. As it was beyond the scope of this study to define and test various contrast weights specific to *R. boylii*, this index was excluded from the analysis.

Several other FRAGSTATS metrics were evaluated for each study reach in an effort to further explore the heterogeneity of geomorphic units within each study reach. At the landscape level, Simpson's Evenness Index (SIEI), Relative Patch Richness (RPR) and Interspersion and Juxtapositon Index (IJI) were also calculated. SHDI incorporates both evenness (distribution of areas between patch types) and richness (number of patch types) to determine the overall diversity in patch types. Comparisons among SIEI, RPR and SHDI can provide information on which aspect of patch composition a dependent variable might respond to. Contagion incorporates measures of interspersion, aggradation and dispersion, reflecting multiple components of how patches are configured across a landscape. As a result, Contagion is highly correlated with patch type diversity and dominance (Ritters et al 1995) and therefore may not be useful in multiple regression modeling due to problems of collinearity. IJI is a component of CONTAG, measuring only the degree to which patches are interspersed across the landscape. As a result, IJI is not affected by the number and size of patches, contiguity between patches or dispersion of patches across the landscape. Comparisons between these two metrics can likewise provide information on which aspects of patch configuration a dependent variable might respond to.

The three diversity metrics (SHDI, SIEI and RPR) are calculated by employing the area of each patch and the proportion of the landscape that each patch type occupies (McGarigal and Marks 1995). The calculation is similar to the traditional methods of calculating diversity associated with species richness, but patch area or number of patch types is used rather than species number or number of species types in the equations.

Conceptually, contagion measures the degree to which patches occur in aggregated or ‘contagious’ distributions (McGarigal and Marks 1995). It is based on the extent to which cells of the same patch type are clumped or aggregated. Interspersion, on the other hand, measures the degree to which patches, not cells, are intermixed. Differing from dispersion, which measures the degree to which patches of the same type are positioned relative to each other based on a nearest neighbor calculation, interspersion is calculated from an adjacency matrix composed of the proportions of edges in each pairwise patch type. The result is that dispersion measures how clustered patches of each type are across the landscape, while interspersion measures the degree to which all patch types are intermixed. IJI is calculated from an adjacency matrix composed of the proportions of edges in each pairwise patch type and ranges from 0 to 100, where 100 is maximum interspersion when all patch types are equally adjacent to all other patch types (McGarigal and Marks 1995). CONTAG subsumes both dispersion and interspersion in that it is based on the probability of finding a cell of type i next to a cell of type j (Li and Reynolds 1993). CONTAG ranges from 0 to 100, approaching 100 when all patch types (based on cell adjacencies) are maximally aggregated or the landscape consists of a single patch.

In order to evaluate whether the composition or configuration of specific geomorphic units, such as pools or bars, were relevant to *R. boylii*, several metrics were analyzed at the class-level: Percentage of the Landscape (PLAND), Patch Density (PD), Mean Patch Area (AREA) and IJI. PLAND measures the proportion of the total landscape that each patch type occupies, PD is the number of patches divided by the total landscape area, and AREA is the average area for each patch type. IJI at the class-level represents the same aspects of spatial configuration as at the landscape-level, however the interspersion of each patch type relative to adjacent patch types is measured rather than the interspersion of all patch types.

Frog Abundance

Frog abundance was determined based on *R. boylii* survey results from the microhabitat study detailed in chapter 1. In the microhabitat study, frog population distributions were determined from visual encounter surveys (Heyer et al. 1994) during the 2003 breeding and foraging season (May – October). Frog survey segments varied in length from 1.2 – 3.2 km and included the range of reach types observed within each tributary. As part of a reach-scale analysis of habitat associations, the total number of individuals observed annually in each reach type was compared with the number of individuals expected to occur given an even distribution of individuals throughout the survey segment (refer to methods in chapter 1). Results from the microhabitat study showed a positive correlation between frog density and reach type, such that frogs were observed more often than expected in certain reach types and less than expected in others.

For this study, relative frog abundance within each study reach was calculated as the ratio of observed to expected number of individuals in the associated reach type using the observed and expected frog density data presented in chapter 1. The ratio between observed and expected number of frogs provided a single number that could be compared with the landscape metrics calculated within each study reach. Like most biological species distribution data, the ratio of observed to expected number of frogs was not normally distributed, so a log transformation of the data was calculated and used in the statistical analysis.

Statistical Analysis

Bivariate correlation analysis and multiple linear regression were used to assess the relationship between the habitat heterogeneity metrics and relative frog abundance. Specifically, cross-correlation analysis was used to assess all pairwise correlations between class-level and landscape-level metrics, while multiple regression was used to determine which metrics were significant predictors of relative frog abundance.

Linear regression is sensitive to multicollinearity among predictor variables (Tabachnick and Fidell 2001). Therefore, a non-parametric cross-correlation analysis was completed to assess all pairwise correlations between the landscape metric variables. Any pair of variables with a significant correlation value (Spearman's Rho > $|0.500|$; $p < 0.05$)

was assessed and the least biologically descriptive variable of the pair was excluded from the regression analysis. The linear regresssion model was applied using the SPSS v 12.0 software package (SPSS 2003) and run using the enter model-building algorithm so that each potential predictor could be evaluated for significance within the context of the other predictors. The goal was to determine which combination of the potential landscape metrics explained the greatest variance in observed frog abundance. Each regression model was checked for problems with multicollinearity using standard tolerance values of less than 0.2 as indicators of collinear variables. Selection of a best-fit model was based on maximizing the adjusted R^2, including only predictors with t-statistics greater than 2.0, and an examination of the residuals and partial residual plots for normality (Belsley et al. 1980).

Results

Frog Abundance

The ratio of observed to expected number of frogs in each reach varied from zero to greater than four (table 2.4). Frogs were not observed in any step-pool reaches on Humbug and Oregon creeks. The absence of frogs in a study reach cannot be attributed solely to the degree of physical habitat heterogeneity in the reach. Other physical or biological factors, such as limited food availability, non-native predators or limited hours of sunlight, may create unsuitable habitat conditions that would preclude frog presence. Therefore, a log (n+1) transformation, commonly used for zero data values, was considered an inaccurate representation of the data. Only standard log transformed data from reaches where frogs were present (10 of 12 study reaches) were included in the data analysis.

Creek	Reach Type	Observed (#)	Expected (#)	Ratio Observed to Expected	Log Transformed Ratio
Humbug	Step-Pool	0	2.0	0.00	NA
Humbug	Riffle-Pool	11	6.0	1.82	0.26
Humbug	Plane Bed	2	1.4	1.44	0.16
Oregon	Cascade	5	3.1	1.63	0.21
Oregon	Bedrock	1	2.6	0.38	-0.42
Oregon	Step-Pool	0	1.5	0.00	NA
Rush	Bedrock	2	5.4	0.37	-0.43
Rush	Step-Pool	3	0.6	4.76	0.68
Rush	Cascade	8	6.9	1.15	0.06
Shady	Braided	436	290.4	1.50	0.18
Shady	Plane Bed	303	410.9	0.74	-0.13
Shady	Riffle-Pool	12	16.9	0.71	-0.15

Table 2.4. Frog abundance for each study reach. Observed and expected data are from the microhabitat study and reflect the total number of individuals observed or expected in all reaches of that type on that creek.

Landscape-level Metrics

A summary of the landscape-level metrics calculated for each study reach is provided in table 2.5. The bivariate correlation analysis revealed that over half of the landscape metrics were moderately to significantly correlated within the study reaches (table 2.6). Four pairs were highly correlated; therefore only one metric of the pair was included in any linear regression model at a time.

Creek	Reach Type	PAFRAC	CONTAG	IJI	RPR	SHDI	SIEI
Humbug	Plane Bed	1.42	54.73	68.95	46.15	1.31	0.80
Humbug	Riffle Pool	1.37	48.97	77.90	76.92	1.94	0.92
Humbug	Step Pool	1.58	44.79	69.06	61.54	1.83	0.93
Oregon	Bedrock	1.48	62.35	72.50	30.77	0.87	0.63
Oregon	Cascade	1.26	52.49	76.97	61.54	1.66	0.90
Oregon	Step Pool	1.36	52.89	74.76	53.85	1.61	0.88
Rush	Bedrock	1.31	68.78	56.35	38.46	0.79	0.51
Rush	Cascade	1.54	43.21	71.34	46.15	1.57	0.90
Rush	Step Pool	1.49	46.62	83.81	76.92	2.02	0.93
Shady	Braided	1.62	50.93	67.58	46.15	1.46	0.86
Shady	Plane Bed	1.49	54.61	46.71	46.15	1.33	0.85
Shady	Riffle Pool	1.40	49.80	82.92	46.15	1.57	0.89

Table 2.5. Calculated landscape-level metrics for each study reach.

Bivariate Pair	Pearson's Bivariate Correlation	p-value	Significance
CONTAG – SHDI	-0.874	< 0.001	**
CONTAG – RPR	-0.604	0.038	*
CONTAG – SIEI	-0.936	< 0.001	**
CONTAG – IJI	-0.467	0.125	
CONTAG – PAFRAC	- 0.464	0.128	
IJI – SHDI	0.572	0.052	*
IJI – RPR	0.488	0.108	
IJI – SIEI	0.451	0.141	
IJI – PAFRAC	- 0.139	0.667	
SHDI – RPR	0.897	< 0.001	**
SHDI – SIEI	0.924	< 0.001	**
SHDI – PAFRAC	0.150	0.642	
RPR – SIEI	0.691	0.013	*
RPR – PAFRAC	- 0.093	0.774	
SIEI – PAFRAC	0.287	0.366	

Table 2.6. Results of bivariate correlation analysis of landscape-level metrics. Correlations are shown as significant at the 0.05 level (*) and the 0.01 level (**).

The linear regression model that explained the greatest variance in frog abundance included only Shannon's Diversity Index (SHDI) as a predictor (table 2.7). The results from other models generated are also shown in table 2.7. In general, when some measure of diversity (SHDI, RPR or SIEI) was included in the model, the model had high significance ($p < 0.05$) and explained greater than 60% of the variance within the data. Four of the ten models generated were robust with significance values less than 0.01, of which three included one of the diversity measures. Of the three diversity measures, SHDI was most significant and explained the highest variance, followed by RPR and SIEI, respectively. Models that included either a measure of patch shape (PAFRAC) or measure of interspersion (IJI) generally did not perform as well as models where only a measure of diversity was included. However, the model including PAFRAC and RPR was almost as robust as the SHDI model, with a greater R^2 value, but a slightly lower overall significance. The model including SHDI and PAFRAC had a high model significance and high R^2 value, but PAFRAC had a low t-value and was not a significant predictor within the model. Figure 2.4 shows the linear relationship between frog abundance and SHDI.

Variables included In model	**Standardized Coefficients**	**t-value**	**p-value**	**F-statistic**	**R^2**
SHDI	0.877	3.706	0.010		
PAFRAC	0.102	0.536	0.611		
IJI	0.001	0.005	0.996		
Model summary			*0.018*	*7.687*	*0.794*
SHDI	0.877	5.094	0.001		
PAFRAC	0.101	0.589	0.574		
Model summary			*0.004*	*13.452*	*0.794*
SHDI	0.885	5.378	0.001		
Model summary			***0.001***	*28.918*	*0.783*
RPR	0.751	2.736	0.041		
SIEI	0.149	0.527	0.621		
IJI	0.100	0.487	0.647		
PAFRAC	0.279	1.344	0.237		
Model summary			*0.026*	*7.276*	*0.853*
RPR	0.913	5.819	0.001		
PAFRAC	0.336	2.142	0.069		
Model summary			***0.002***	*17.519*	*0.833*
RPR	0.851	4.585	0.002		
Model summary			***0.002***	*21.018*	*0.724*
SIEI	0.676	2.265	0.064		
PAFRAC	0.016	0.061	0.953		
IJI	0.205	0.707	0.506		
Model summary			*0.091*	*3.464*	*0.634*
SIEI	0.682	2.636	0.034		
IJI	0.200	0.774	0.464		
Model summary			*0.030*	*6.055*	*0.634*
SIEI	0.776	3.481	0.008		
Model summary			***0.008***	*12.118*	*0.602*
CONTAG	- 0.697	- 1.903	0.106		
PAFRAC	- 0.091	- 0.290	0.782		
IJI	0.150	0.443	0.673		
Model summary			*0.137*	*2.723*	*0.577*

Table 2.7. Results of linear regression modeling. Student's t tests the significance of each variable within the model, and ANOVA (F-statistic) tests the significance of the resulting final model. Robust models, where all predictors are significant and the model significance is less than 0.01, are indicated with bold font in the p-value column.

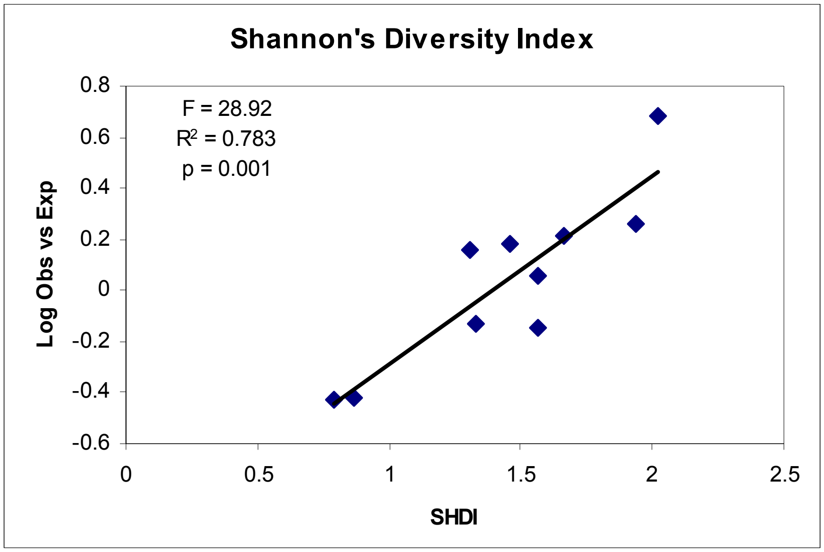


Figure 2.4. Relationship between frog abundance (log of the ratio between observed and expected number of frogs) and Shannon's Diversity Index (SHDI) within the study reaches.

Class-level Metrics

Four patch types common to most of the study reaches were selected for further analysis at the class level: bars, pools, riffles and side channels. A bivariate correlation analysis was completed comparing all pairwise combinations of each of the four class-level metrics (PLAND, AREA, PD and IJI) with each of the four patch types. A total of 240 pairwise combinations were evaluated, of which 27 pairs were moderately correlated with Pearson's correlation values greater than 0.600 and 8 pairs were significantly correlated with p-values less than 0.05. Table 2.8 lists the class-level metrics that were significantly correlated. The AREA metrics were moderately correlated with most other metrics, and the riffle and side channel patch types were often correlated with other metrics and patch types. As a result, the AREA metrics, IJI of riffles and side channels and PD of riffles were excluded from further statistical analysis because they were the least biologically descriptive of the correlated pairs.

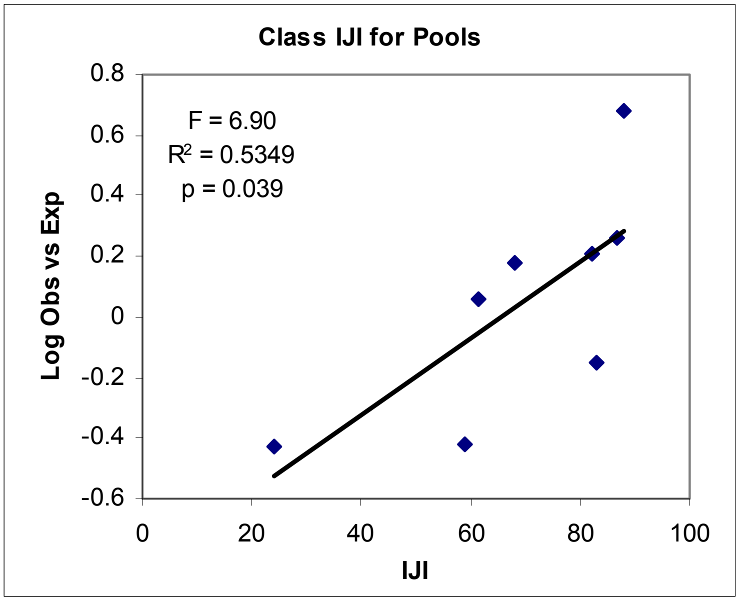
Bivariate Pair	Pearson's Value	p-value	Significance
IJI side channels – IJI bars	-0.924	0.025	*
IJI side channels – IJI pools	-0.916	0.029	*
AREA bars – PLND bars	0.665	0.036	*
AREA bars – IJI riffles	0.858	0.029	*
PD bars – PLND bars	0.640	0.046	*
PD riffles – PLND side channels	-0.934	0.020	*
PD side channels – IJI riffles	-0.987	0.002	**
PD side channels – AREA bars	-0.905	0.035	*

Table 2.8. The most significant results of bivariate correlation analysis of class-level metrics. Correlations are shown as significant at the 0.05 level (*) and the 0.01 level (**).

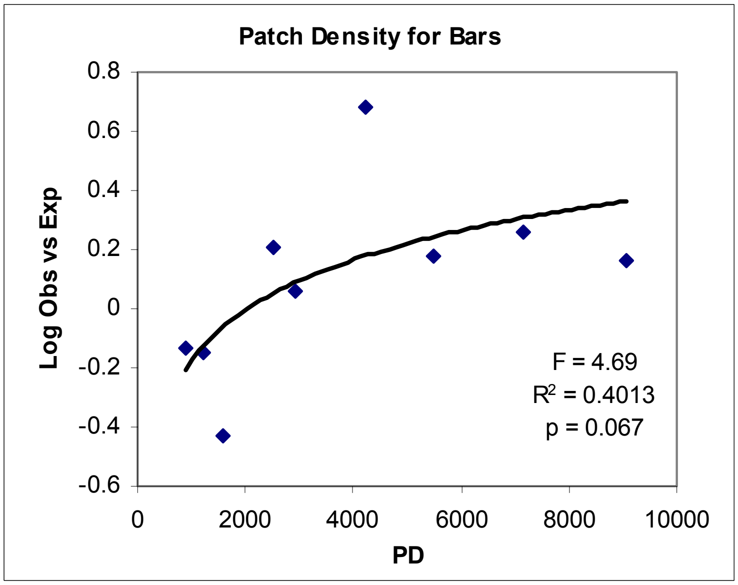
Although the four patch types chosen for additional analysis were the most common of the possible patches, they were not equally present in all study reaches. Therefore, multiple linear regression was not suitable to determine whether the class-level metrics could be used as possible predictors of frog abundance. However, associations between each metric and frog abundance were evaluated using standard curve fitting algorithms in SPSS. Of the 8 relationships tested, only the interspersion of pools was significant at the 0.05 level, while the patch density of bars was moderately significant at p = 0.067 (table 2.9). As the interspersion of pools increased, frog abundance increased linearly, and as the patch density of bars increased, frog abundance increased logarithmically (figure 2.5).

Frog Abundance versus	Type of Curve Fit	R^2	p-value	Significance
IJI of bars	linear	0.041	0.601	
IJI of pools	linear	0.5349	0.039	*
PD of bars	logrithmic	0.4013	0.067	
PD of pools	linear	0.187	0.28	
PLAND of bars	logrithmic	0.284	0.14	
PLAND of pools	linear	0.026	0.705	
PLAND of riffles	linear	0.007	0.897	
PLAND of side channels	linear	0.2654	0.374	

Table 2.9. Analysis of the relationship between frog abundance and class-level metrics. Correlations are shown as significant at the 0.05 level (*).



5a)

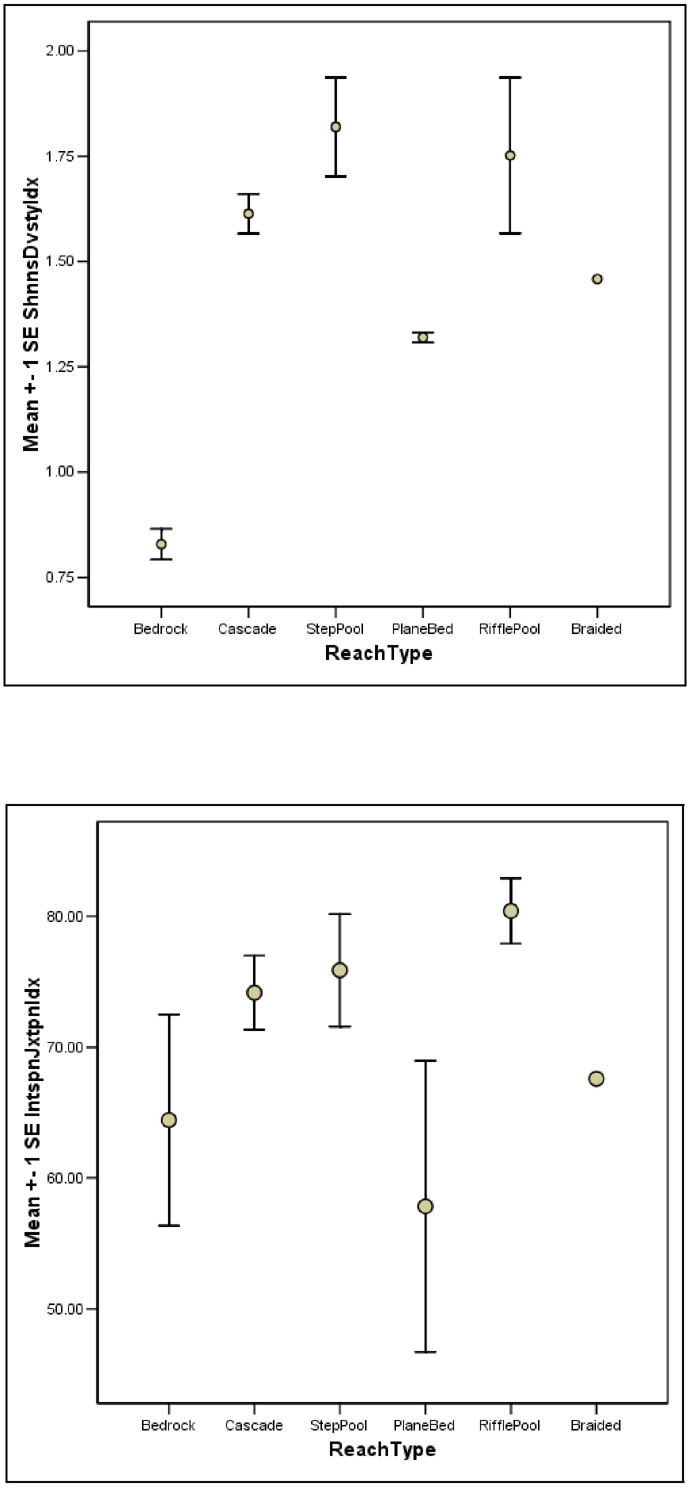


5b)

Figure 2.5. Curve fit of frog abundance to a) interspersion (IJI) of pools, and b) patch density (PD) of bars.

Heterogeneity and Reach Type

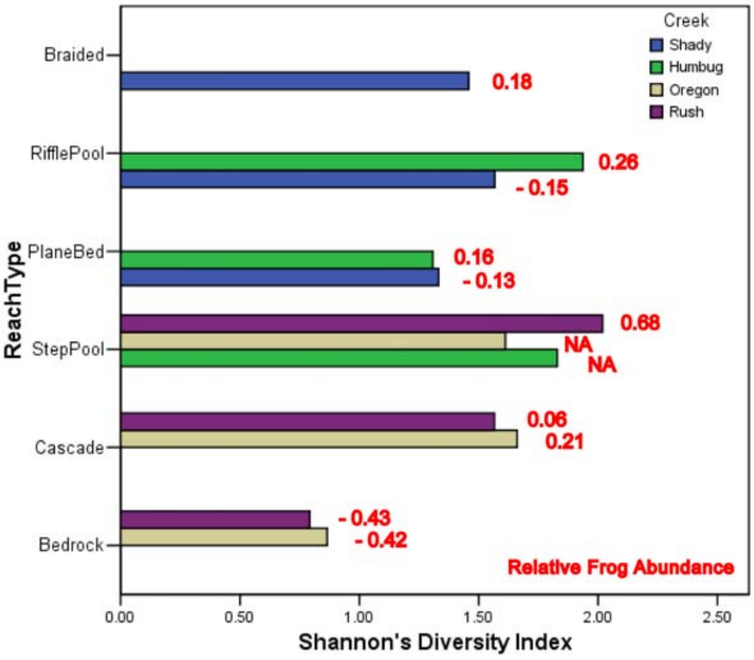
A strong association between *R. boylii* lifestage and reach type was shown to occur the *R. boylii* microhabitat study presented in chapter 1, and provided the basis for the relative frog abundance calculations in this study. To determine if this association related to the degree of habitat heterogeneity associated with each reach type, the landscape metrics were compared with reach type across creeks. Figure 2.6 shows the relationships between reach type and two independent landscape metrics representing patch composition (SHDI) and patch configuration (IJI). The data do not show a clear distinction of heterogeneity between reach types, with the exception that bedrock reaches are significantly less heterogeneous than other reach types. However, a comparison of heterogeneity between reach types occurring within a single creek, rather than across creeks, reveals that reaches with higher heterogeneity are associated with greater relative frog abundance (figure 2.7). Of the reach types present on each creek, the reach types with greater heterogeneity, especially in terms of diversity of geomorphic unit type (SHDI), have the highest relative frog abundance.



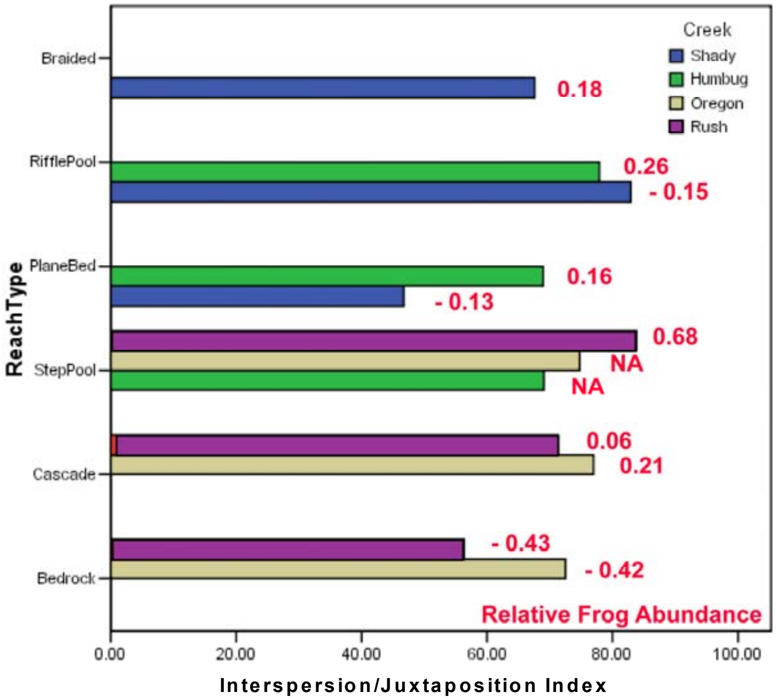
6a)

6b)

Figure 2.6. Relationship between general reach type and a) SHDI and b) IJI. Points indicate the mean value; error bars indicate +/- 1 standard deviation.



7a)



7b)

Figure 2.7. Relationship between reach type and a) SHDI and b) IJI sorted by creek. Red text indicates relative frog abundance (log transformed ratio of observed to expected number of frogs).

Discussion

Frog abundance was more strongly associated with the spatial composition components of habitat heterogeneity than with the spatial configuration components. Heterogeneity indices that quantified the relative diversity of geomorphic units within a reach had the highest correlations with relative frog abundance. Of the several FRAGSTATS metrics tested, Shannon's Diversity Index (SHDI) was the best predictor of frog abundance such that as the diversity in geomorphic units throughout the reach increased, relative frog abundance increased. This finding agreed well with results from the microhabitat study presented in chapter 1. Individuals were shown to have distinct, disparate habitat associations depending on lifestage and season. As a result, reaches with increased habitat complexity may potentially provide a larger number of habitats suitable to each lifestage, a greater variety of habitats with multiple functions (e.g. cover, forage, basking and breeding) and a greater variety of refugia as flows fluctuate throughout the season. In addition, reaches where multiple microhabitats exist that are suitable for several lifestages throughout the year may help to limit the movement of frogs between preferred habitats, thus decreasing energy expenditure and reducing the risk of exposure to predators. Reaches with a greater diversity of geomorphic units, as quantified by metrics like SHDI, may provide a selective advantage for *R. boylii* by increasing survival rates at all lifestages.

The weak association between *R. boylii* and the spatial composition components of habitat heterogeneity, especially the interspersion of all geomorphic unit types (IJI), was contrary to findings in other benthological studies where spatial composition was a key component in habitat preference (Beisel et al. 2000; Palmer et al. 2000). *R. boylii* are routinely observed basking on bars or boulders adjacent to pools or riffles where they can quickly jump into deep or swift water to gain cover from predators (personal observation). A reasonable assumption is that the greater the interspersion of all geomorphic units, the greater the probability of finding a basking location immediately adjacent to a cover location. However, the data did not support this assumption.

The lack of association between frog abundance and habitat interspersion may be attributed to the scale of study. At the reach scale river processes are such that geomorphic units are inherently interspersed due to repeating sequences of bar-pool-riffle or step-pool units. In addition, as the diversity of geomorphic units increases, the confined elongate nature of streams may simply force greater interspersion of all habitats. A macroinvertebrate study by Palmer et al (2000) found that individuals responded to both diversity in substrate composition and the spatial arrangement of the substrate; as contagion decreased, species diversity decreased. However, the scale of this study was smaller than the stream reach; specifically, microhabitat patches were sub-meter in size and the landscape was at the geomorphic unit scale. As a result, their landscapes for analyses were generally less restricted and unconfined. Most terrestrial watershed and landscape-scale studies encompass areas that are larger and less confined where clumping and aggradation of patches is more likely to occur. Therefore, *R. boylii* response to levels of interspersion of all geomorphic units at the stream reach scale may be masked by the inherent nature of stream habitats to intersperse at the reach-scale.

At the class-level however, the abundance of *R. boylii* did show a significant correlation with the interspersion of pools and a moderate association with the patch density of bars (table 2.9). These associations are interpreted to reflect an affiliation with specific geomorphic units shown to be important microhabitats for individual lifestages, rather than general habitat interspersion across the stream reach. Pools are key microhabitats for adults in particular, and as pools become more intermixed with other habitat types, presumably the probability of basking sites adjacent to pools increases. Similarly, as the number of bars in a reach increases, the availability of oviposition sites, shallow water edge habitat and basking sites increases. Although not conclusive, these data suggest the spatial configuration of specific geomorphic units important to various lifestages may be more important to *R. boylii* than the general interspersion and configuration of all geomorphic units at the reach scale.

The association between various lifestages and reach type observed in the microhabitat study (chapter 1) potentially suggested that certain reach types inherently have a greater diversity of geomorphic units than others. For example, riffle-pool reaches might consistently have greater habitat diversity than step-pool reaches due to a higher occurrence of bars, and thus also have greater relative frog abundance than step-pool reaches. However, data from this study showed step-pool reaches have varying degrees of habitat heterogeneity across creeks, often with SHDI values comparable or higher than riffle-pool reaches. Frog abundance in step-pool reaches was equally as variable across creeks. As a result, there was no trend between reach type and habitat diversity or reach type and total frog abundance across creeks. Rather, frogs were observed in the highest numbers in whichever reach type had the highest habitat diversity of the reach types available on that creek.

The observed association between habitat heterogeneity and frog abundance has several implications for conservation of *R. boylii*. Stream reaches with greater diversity in geomorphic features not only provide greater suitability for multiple lifestages in a shorter stream section, but when combined with natural high variability in flows, increase the likelihood that in any given flow conditions the required habitat characteristics will exist for multiple lifestages. This is especially true for the more vulnerable and less mobile lifestages of eggs and tadpoles, where specific velocity, depth and substrate conditions are required for survival. For example, in higher diversity reaches, channel bars and side margins with varying elevations are more likely to provide suitable oviposition sites in both drier low flow years and wetter high flow years. Lower diversity reaches with little variation in geomorphology are more likely to provide suitable egg-laying sites only when flow conditions are just right to inundate the channel substrate at depths appropriate for oviposition. Restoration practices that seek to increase reach-scale geomorphic diversity will not only provide increased habitat for oviposition and tadpole rearing, but provide greater options for refugia from high winter flows or seasonal pulse flows for juveniles and adults.

Works Cited

Beisel, J. N., P. Usseglio-Polatera and J. C. Moreteau (2000). The spatial heterogeneity of a river bottom: a key factor determining macroinvertebrate communities. *Hydrobiologia* 422: 163-171.

Belsley, D. A., E. Kuh and R. E. Welsch (1980). Regression Diagnostics: Identifying Influencial Data and Sources of Collinearity. New York, John Wiley & Sons.

Boyero, L. (2003). The quantification of local substrate heterogeneity in streams and its significance for macroinvertebrate assemblages. *Hydrobiologia* 499(1-3): 161-168.

Brown, B. L. (2003). Spatial heterogeneity reduces temporal variability in stream insect communities. *Ecology Letters* 6(4): 316-325.

Cardinale, B. J., M. A. Palmer, C. M. Swan, S. Brooks and N. L. Poff (2002). The influence of substrate heterogeneity on biofilm metabolism in a stream ecosystem. *Ecology* 83(2): 412-422.

Downes, B. J., P. S. Lake, E. S. G. Schreiber and A. Glaister (2000). Habitat structure, resources and diversity: the separate effects of surface roughness and macroalgae on stream invertebrates. *Oecologia* 123(4): 569-581.

ESRI, Inc. (2002). ESRI ArcGIS ver.8.3. www.esri.com, ESRI Inc.

Frissell, C. A., W. J. Liss, C. E. Warren and M. D. Hurley (1986). A Hierarchical Framework For Stream Habitat Classification - Viewing Streams in a Watershed Context. *Environmental Management* 10(2): 199-214.

Hawkins, C. P., J. L. Kershner, P. A. Bisson, M. D. Bryant, L. M. Decker, S. V. Gregory, D. A. McCullough, C. K. Overton, G. H. Reeves, R. J. Steedman and M. K. Young (1993). A Hierarchical Approach to Classifying Stream Habitat Features. *Fisheries* 18(6): 3-12.

Heyer, W. R., M. A. Donnelly, R. W. McDiarmid, L. C. Hayek and M. S. Foster, Eds. (1994). Measuring and monitoring biological diversity: Standard methods for amphibians. Biological Diversity Handbook Series. Washington D.C., Smithsonian Institution Press.

Jennings, M. R. and M. P. Hayes (1994). Amphibian and reptile species of special concern in California. Final Report. Rancho Cordova, California Department of Fish and Game Inland Fisheries Division.

Kupferberg, S. J. (1996). Hydrologic and geomorphic factors affecting conservation of a river-breeding frog (*Rana boylii*). *Ecological Applications* 6(4): 1332-1344.

Li, H. and J. F. Reynolds (1995). On Definition and Quantification of Heterogeneity. *Oikos* 73(2): 280-284.

Li, H. B. and J. F. Reynolds (1993). A New Contagion Index to Quantify Spatial Patterns of Landscapes. *Landscape Ecology* 8(3): 155-162.

Li, H. B. and J. G. Wu (2004). Use and misuse of landscape indices. *Landscape Ecology* 19(4): 389-399.

Lind, A. J., H. H. Welsh and R. A. Wilson (1996). The effects of a dam on breeding habitat and egg survival of the foothill yellow-legged frog (*Rana boylii*) in northwestern California. *Herpetological Review* 27(2): 62-67.

McGarigal, K., S. A. Cushman, M. C. Neel and E. Ene (2002). FRAGSTATS: Spatial Pattern Analysis Program for Categorical Maps. www.umass.edu/landeco/research/fragstats/fragstats.html, Authors at University of Massachusetts, Amherst.

McGarigal, K. and B. J. Marks (1995). FRAGSTATS: spatial pattern analysis program for quantifying landscape structure, U.S. Forest Service, General Technical Report PNW-351.

Minshall, G. W. and C. T. Robinson (1998). Macroinvertebrate community structure in relation to measures of lotic habitat heterogeneity. *Archiv Fur Hydrobiologie* 141(2): 129-151.

Montgomery, D. R. (1999). Process domains and the river continuum. *Journal of the American Water Resources Association* 35(2): 397-410.

Montgomery, D. R., T. B. Abbe, J. M. Buffington, N. P. Peterson, K. M. Schmidt and J. D. Stock (1996). Distribution of bedrock and alluvial channels in forested mountain drainage basins. *Nature* 381(6583): 587-589.

Montgomery, D. R., E. M. Beamer, G. R. Pess and T. P. Quinn (1999). Channel type and salmonid spawning distribution and abundance. *Canadian Journal of Fisheries and Aquatic Sciences* 56(3): 377-387.

Montgomery, D. R. and J. M. Buffington (1997). Channel-reach morphology in mountain drainage basins. *Geological Society of America Bulletin* 109(5): 596-611.

Newson, M. D. and C. L. Newson (2000). Geomorphology, ecology and river channel habitat: mesoscale approaches to basin-scale challenges. *Progress in Physical Geography* 24(2): 195-217.

Palmer, M. A., P. Arensburger, A. P. Martin and D. W. Denman (1996). Disturbance and patch specific responses: The interactive effects of woody debris and floods on lotic invertebrates. *Oecologia* 105(2): 247-257.

Palmer, M. A., C. M. Swan, K. Nelson, P. Silver and R. Alvestad (2000). Streambed landscapes: evidence that stream invertebrates respond to the type and spatial arrangement of patches. *Landscape Ecology* 15(6): 563-576.

Poole, G. C. (2002). Fluvial landscape ecology: addressing uniqueness within the river discontinuum. *Freshwater Biology* 47(4): 641-660.

Power, M. E. (1992). Habitat Heterogeneity and the Functional-Significance of Fish in River Food Webs. *Ecology* 73(5): 1675-1688.

Raines, G. L. (2002). Description and comparison of geologic maps with FRAGSTATS - a spatial statistics program. *Computers & Geosciences* 28(2): 169-177.

Resh, V. H., A. V. Brown, A. P. Covich, M. E. Gurtz, H. W. Li, G. W. Minshall, S. R. Reice, A. L. Sheldon, J. B. Wallace and R. C. Wissmar (1988). The Role of Disturbance in Stream Ecology. *Journal of the North American Benthological Society* 7(4): 433-455.

SPSS, Inc. (2003). SPSS 12.0 for Windows: Base, Regression Models and Advanced Models. Chicago, IL, SPSS Inc.

Strayer, D. L. (1999). Use of flow refuges by unionid mussels in rivers. *Journal of the North American Benthological Society* 18(4): 468-476.

Tabachnick, B. G. and L. S. Fidell (2001). Using Multivariate Statistics. Boston, MA, Allyn and Bacon.

Thomson, J. R., M. P. Taylor, K. A. Fryirs and G. J. Brierley (2001). A geomorphological framework for river characterization and habitat assessment. *Aquatic Conservation-Marine and Freshwater Ecosystems* 11(5): 373-389.

Torgersen, C. E. and D. A. Close (2004). Influence of habitat heterogeneity on the distribution of larval Pacific lamprey (*Lampetra tridentata*) at two spatial scales. Freshwater Biology 49(5): 614-630.

Townsend, C. R., M. R. Scarsbrook and S. Doledec (1997). The intermediate disturbance hypothesis, refugia, and biodiversity in streams. *Limnology and Oceanography* 42(5): 938-949.

Turner, M. G., W. W. Hargrove, R. H. Gardner and W. H. Romme (1994). Effects of Fire On Landscape Heterogeneity in Yellowstone- National-Park, Wyoming. *Journal of Vegetation Science* 5(5): 731-742.

Van Wagner, T. J. (1996). Selected life-history and ecological aspects of a population of foothill yellow-legged frogs (*Rana boylii*) from Clear Creek, Nevada County, California. Master's Thesis. Department of Biological Sciences. Chico, California State University, Chico: 143.

Ward, J. V., F. Malard and K. Tockner (2001). Landscape ecology: a framework for integrating pattern and process in river corridors. *Landscape Ecology* 17: 35-45.

Ward, J. V., K. Tockner, D. B. Arscott and C. Claret (2002). Riverine landscape diversity. *Freshwater Biology* 47(4): 517-539.

Wiens, J. A. (2002). Riverine landscapes: taking landscape ecology into the water. *Freshwater Biology* 47(4): 501-515.

Wohl, E. (2000). Mountain Rivers. Washington D.C., American Geophysical Union.

Wootton, J. T. (1998). Effects of disturbance on species diversity: A multitrophic perspective. *American Naturalist* 152(6): 803-825.

Yarnell, S. M. (2000). The influence of sediment supply and transport capacity on Foothill Yellow-legged Frog habitat, South Yuba River, California. Master's Thesis. Geology. Davis, CA, University of California, Davis: 241.

CHAPTER 3: The Influence of Relative Sediment Supply on Riverine Habitat Heterogeneity

Abstract

The inherent diversity of aquatic habitats throughout a stream environment and associated biological responses are linked to physical processes that act at various length and time scales within a watershed. A fundamental driver of stream geomorphology that integrates multi-scale processes is the relationship between sediment supply and transport capacity. The sediment supply/transport capacity ratio dictates not only the aggradational or degradational state of a system, but controls channel morphology and substrate textures, perhaps the two most important characteristics of physical habitat. This study explored the complex interactions between riverine habitat heterogeneity and the geomorphic and hydraulic processes governing channel conditions by testing the hypothesis that maximum habitat heterogeneity occurs in stream reaches with a moderate relative local sediment supply, as measured by the supply/capacity ratio. Habitat heterogeneity was quantified using spatial heterogeneity measures from the field of landscape ecology, and relative sediment supply was quantified using a dimensionless bedload transport rate, q^*.

Data from previously published flume and field studies and a new field study on several tributaries to the South Yuba River in Nevada County, California were evaluated to test the hypothesis. Calculated q^* values were plotted against an ecologically meaningful heterogeneity index, Shannon's Diversity Index (SHDI), measured for each study reach. Results showed that in alluvial reaches where flow and sediment interacted freely without obstruction, moderate relative sediment supplies correlated with the highest SHDI values;

however, in reaches where less mobile structural elements, such as large woody debris and boulders, were present, SHDI increased as the percentage of structural elements increased. The results indicate two potential mechanisms for how relative sediment supply may drive geomorphic diversity in natural river systems at the reach scale. When less mobile structural elements are not a large proportion of the reach landscape, the supply/capacity ratio dictates the range of sediment textures and geomorphic features observed within the reach such that channels with a moderate relative sediment supply exhibit a high diversity of geomorphic features and surface textures in support of the study hypothesis. In contrast, when boulders and large woody debris are a large proportion of a channel reach, increased local scour and deposition creates a greater variety of geomorphic features and sorted sediment textures, thereby increasing the heterogeneity in physical habitat types observed. For both mechanisms, it is the combination of variable sediment influx and variable flow magnitude and frequency that creates the variations in sediment mobility required to maximize geomorphic diversity.

Introduction

Geomorphology and hydrology serve as the physical foundation for stream ecosystems. Channel morphology provides the structural basis of the aquatic environment, while discharge and hydraulic characteristics govern the size and quality of the aquatic environment (Maddock 1999). The interaction between hydrology, geomorphology and aquatic species habitat across multiple spatio-temporal scales is often discussed in the literature, yet remains poorly understood (Imhof et al. 1996; Naiman et al. 1999; Petts 2000).

In particular, there has been great difficulty in linking aquatic habitat characteristics to the physical processes that drive change within a watershed (Imhof et al. 1996).

Riverine habitat heterogeneity – the inherent diversity of aquatic habitats throughout a stream environment – has become recognized as a key attribute of river ecosystems (Power 1992). Studies have shown that greater heterogeneity in stream habitat increases aquatic species diversity (Beisel et al. 2000; Brown 2003). Diversity in stream habitat provides not only a greater number of niches for species to occupy, but provides a greater variety of habitats available to species for breeding, foraging and refugia in the highly dynamic and variable environment of a river system (Townsend et al. 1997; Ward et al. 1999; Ward and Tockner 2001). Despite the widespread recognition that habitat heterogeneity is important to aquatic ecosystems, few studies address the processes responsible for the creation and maintenance of heterogeneity.

Stream habitat heterogeneity and associated biological response at the reach scale are linked to physical processes that act at various length and time scales within a watershed (Poole, 2002). A key linkage is with the balance between the sediment supply and transport capacity of a stream system (Pitlick and Wilcock 2001). As a fundamental driver of stream geomorphology, the relationship between sediment supply and transport capacity dictates not only the aggradational or degradational state of a system, but controls channel morphology and substrate textures (Dietrich et al. 1989; Lisle et al. 1993), perhaps the two most important characteristics of physical habitat. This study explores the complex interactions between riverine habitat heterogeneity and the geomorphic and hydraulic processes governing channel conditions by testing the hypothesis that maximum habitat heterogeneity occurs in stream reaches with a moderate relative local sediment supply, as measured by the sediment supply/transport capacity ratio. Habitat heterogeneity is quantified using spatial heterogeneity measures from the field of landscape ecology (Li and Reynolds 1995), and relative sediment supply is quantified using a dimensionless bedload transport rate, q* (Dietrich et al. 1989). Comparisons between flume and field studies reveal two potential mechanisms for how geomorphic diversity and variability in surface textures occur in streams. While the influence of structural channel features such as large woody debris increases habitat diversity as observed in previous studies (Buffington and Montgomery 1999a), variability in sediment influx and flow may maximize geomorphic heterogeneity.

Background

The processes creating physical habitat complexity are often alluded to in the literature, but discussed only generally in qualitative terms that relate increased channel dynamism to increased channel diversity (for example see Madej 1999; McKenney 2001). Studies have indicated that channel features increasing local scour and deposition, such as the presence of large woody debris, increase pool depth and frequency thereby increasing channel diversity (Ralph et al. 1994; Montgomery et al. 1995; Abbe and Montgomery 1996). Similarly, changes in land use that result in bed degradation or loss of woody debris result in channel simplification (Horan et al. 2000; Buffington et al. 2002). Yet, detailed quantitative studies on how varying degrees of habitat complexity relate to physical geomorphic and hydrologic processes are generally lacking.

Spatial aspects of morphological channel change are driven by discharge and sediment supply fluctuations, but modified by spatial feedbacks associated with internal channel morphology (Lane et al. 1996). Studies have shown that varying rates of sediment supply produce fundamentally different substrate textures (Buffington and Montgomery 1999b; Lisle et al. 2000), while variations in both discharge and sediment supply control channel morphology (Dietrich et al. 1989; Lane et al. 1996; Massong and Montgomery 2000). Stream reaches with a high relative sediment supply, where the volume of sediment overwhelms the capacity of the stream to transport the material, generally exhibit bed aggradation with unsorted, fine surface textures (Dietrich et al. 1989; Lisle et al. 1993), simple channel morphologies (Andrews 1984; Madej 1999), limited scour depth (Lisle 1982; Buffington et al. 2002) and loss of usable habitat (Pitlick and Van Steeter 1998).

Reaches with a low relative sediment supply on the other hand, have the ability to transport most of the sediment supplied to the stream with nominal transient storage of sediment, leaving behind only the least mobile particles. The lack of sediment deposition creates bed degradation and results in simple featureless channels dominated by uniformly large coarse sediments. These conditions have been observed in flume studies at low sediment feed rates (Dietrich et al. 1989; Lisle et al. 1993) as well as in natural streams below dams (Power et al. 1996; Buffington and Montgomery 1999a; Pitlick and Wilcock 2001) and in high gradient mountain reaches where sediment deposition is associated only with debris flows (Benda and Cundy 1990) and large woody debris (Montgomery et al. 1996).

Reaches with a moderate relative sediment supply therefore, may exhibit the greatest geomorphic diversity by creating channel conditions with both a variety in geomorphic features, such as scour pools and depositional bars, and a variety of surface textures due to differential sorting of sediments at variable flows. This study attempts to address this question with the hypothesis that a moderate relative sediment supply creates maximum spatial heterogeneity in morphology and surface texture (figure 3.1).

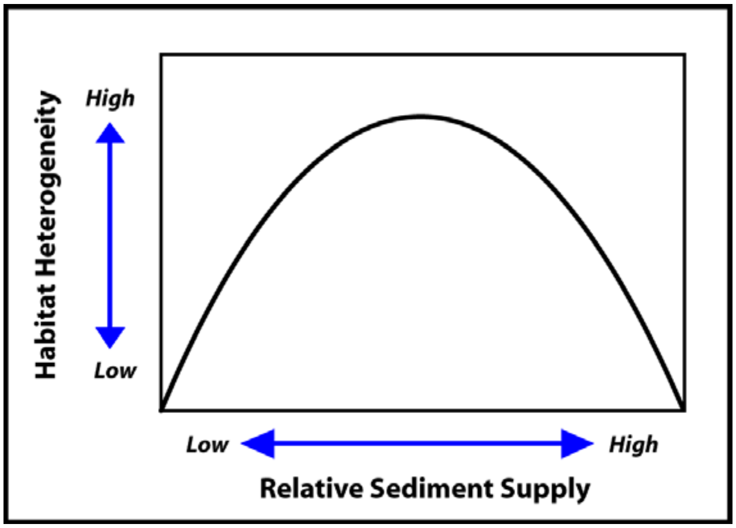


Figure 3.1. Hypothesized theoretical relationship between physical habitat heterogeneity and relative sediment supply.

For this study, physical habitat heterogeneity is quantified using an ecologically meaningful spatial heterogeneity index, Shannon's Diversity Index (SHDI), and relative sediment supply is quantified using a dimensionless bedload transport rate, q*. Although many spatial heterogeneity indices exist that quantify different aspects of physical habitat heterogeneity, SHDI was shown to be an ecologically meaningful metric for *Rana boylii*, a sensitive aquatic species occupying many tributaries in the South Yuba River drainage (chapter 2). In order to determine if relative sediment supply is correlated with varying degrees of habitat heterogeneity, use of a heterogeneity metric that is known to relate to biological patterns allows for not only indirect comparisons between physical and ecological patterns, but for an applied interpretation of potential relationships as well.

The dimensionless bedload transport rate, q*, is a quantitative metric based on hydraulic characteristics and surface texture that correlates with the amount of sediment supplied to the channel versus the ability of the stream to transport the sediment (Dietrich et al. 1989). It has shown to be useful not only in quantifying relative sediment supply in the field (Kinerson 1990), but also for measuring sedimentation impacts on channel morphology and surface texture (Rutten 1998; Lisle et al. 2000; Yarnell 2000). q* is calculated from bedload transport equations that use field measured parameters as inputs:

$$q^* = \frac{q_s}{q_l} = \left(\frac{(\tau_b - \tau_{cs})}{(\tau_b - \tau_{cl})} \right)^{1.5} \quad (1)$$

where q_s is the sediment transport rate of surface bed material, q_l is the sediment transport rate of bedload, τ_b is the bed shear stress imposed by a flow, and τ_{cs} and τ_{cl} are the critical bed shear stresses required to initiate motion of the surface and bedload material, respectively. Although not widely used in evaluations of stream habitat conditions specifically, q* has been shown in a previous study to have some ecological relevance for Foothill Yellow-legged Frog (*Rana boylii*) (Yarnell 2000), and therefore is also appropriate for comparisons between physical and ecological patterns.

Methods

Data from previously published studies and a new field study on several tributaries to the South Yuba River in Nevada County, California were used to test the hypothesis. In all cases, calculated q* values were plotted against the Shannon's Diversity Index (SHDI) measured for each study reach in order to assess the relationship between spatial habitat heterogeneity and relative sediment supply. SHDI was calculated for each study reach using the spatial analysis program FRAGSTATS v.3.3 (McGarigal et al. 2002). Details on the methods for using the program and calculating SHDI are discussed in detail in chapter 2.

Previously Published Studies

Two flume studies and one field study were found in the literature to contain appropriate data on calculated q* values as well as published maps or figures of the sediment texture and geomorphic characteristics of each study reach. The two flume studies (Dietrich et al. 1989; Lisle et al. 1993) included figures depicting surface texture distributions from a series of flume runs where sediment supply was varied as discharge remained constant. These figures were scanned, and each surface texture patch was delineated digitally in ArcGIS taking into account any additional information on the location of specific features such as bars, pools and riffles. Once a planform map of each flume run was created, the data was input into FRAGSTATS for analysis. SHDI was calculated for each flume run or study reach and plotted against the published q* values.

The methods for calculating q* for each flume study varied slightly due to the choice of bed shear stress equations used in the q* equation. Both studies incorporated the Shields' stress relation to calculate the critical shear stress required to initiate particle movement (equation 2); however, Dietrich et al. (1989) calculated boundary shear stress using flow depth and the energy slope (equation 3), while Lisle et al. (1993) computed boundary shear stress from mean variables for the channel as a whole, specifically incorporating both barform and grain resistances (equation 4):

$$\tau_c = \tau_* g(\rho_s - \rho)(D_{50}) \tag{2}$$

where τ_c is the critical bed shear stress, τ_* is the empirically derived Shields' constant, $g(\rho_s - \rho)$ is the submerged specific gravity of sediment and (D_{50}) is the median particle size of the bedload or surface material as applicable;

$$\tau_b = \rho g h s \tag{3}$$

where τ_b is the bed shear stress, ρ is the density of water, g is gravity, h is the height of water at bankfull and s is the water surface slope; and

$$Q^* = \left(\frac{(\tau_G + \tau_B) - \tau_{cs}}{(\tau_G + \tau_B) - \tau_{cl}} \right)^{1.5} \tag{4}$$

where Q* is used in place of q* to denote a value that is computed from mean variables from the channel as a whole, τ_B is bar resistance, τ_B is grain resistance, and τ_{cl} and , τ_{cs} are the critical shear stress of the bedload and surface material, respectively.

The addition of bar resistance in the Lisle et al. (1993) calculations may explain the variability in range of values between the two studies. Q* values calculated at high sediment feed rates in the Lisle et al. (1993) study were postulated to have been lower than expected due to the coarseness of bar heads where large particles accumulated as the bars were formed. Increased grain diameter in the local surface material would result in a lower average Q* value. However, within each flume study, the q* values provided a qualitative assessment of low, moderate and high relative sediment supplies.

The field study by Kinerson (1990) was evaluated in a similar fashion to the flume studies. Maps of each study reach were scanned, digitized in ArcGIS to delineate varying surface textures and geomorphic features, and input into FRAGSTATS to determine SHDI. Due to the added complexity of features observed in the field versus the simplicity of the flume, the percent area of each feature was also calculated in FRAGSTATS. The percent area of less mobile structural elements such as large woody debris and boulders may relate to the diversity and sediment transport within each reach in a different manner than more mobile alluvial sediments.

Although Kinerson (1990) calculated q* using the same sediment transport equation as Dietrich et al. (1989), several assumptions were made to account for complexities inherent to natural field conditions. Unlike the flume studies, where the controlled environment allowed for exact measurements of the bedload supply material, the grain size distribution of the bedload could not be obtained directly in the field. As a result, the subsurface material was used as a proxy for the bedload material. Similarly, use of equation 3 to calculate the bed shear stress is a rough approximation of actual shear stresses occurring in a natural stream. It is only applicable in channels with simple geometry where grain roughness dominates over bedform roughness. Therefore, to account for wide variations in surface texture and local shear stresses, several local q* values were calculated throughout each field study reach and then averaged to obtain a Q* value reflecting the overall relative sediment supply for the reach. Similar to the Lisle et al (1993) study, use of Q* in place of q* denotes a dimensionless bedload transport rate for the channel as a whole. The reach-averaged Q* values were then qualitatively compared with visual and observational assessments of the relative sediment supply within each study reach. Similar to conclusions from the flume studies, Kinerson (1990) concluded that the quantitative Q* values adequately depicted low, moderate and high relative sediment supplies.

South Yuba River Field Study

The South Yuba River field study sites were the same representative reaches as those selected for the heterogeneity study described in chapter 2, with the exception that bedrock-dominated sites where q* measurements would not be valid were excluded (table 3.1). The geomorphic features in each reach were mapped and digitized in ArcGIS to create detailed planform maps that could be imported into FRAGSTATS for analysis. Detailed methods of the field mapping, ArcGIS conversion and FRASTATS analysis are described in chapter 2. As with the analysis of the Kinerson (1990) field study, both SHDI and the percent area of each geomorphic feature were calculated using FRAGSTATS for comparison with field determined q* values.

Creek	Study Reach	Reach Type	Reach Length (m)	Drainage Area Upstream (km2)	Dominant Geomorphic Features	Dominant Substrate Size
Humbug	Blair Pond	Step-Pool	58	10.4	Boulder Steps, Plunge Pools, Coarse Bar	Boulder, Cobble
Humbug	Gage Site	Riffle-Pool	81	20.9	Coarse Bars, High Gradient Riffles, Shallow Pools	Cobble
Oregon	Oregon Creek Road	Cascade	65	27.7	Boulders, Coarse Bars, High Gradient Rapids	Boulder, Cobble
Oregon	Celestial Pools	Step-Pool	88	85.4	Boulder Steps, Plunge Pools	Boulder
Rush	Aaron's Pools	Step-Pool	57	14.6	Boulder Steps, Plunge Pools, Coarse Bars	Cobble
Rush	Road Jumble	Cascade	80	14.6	Boulders, Coarse Bars, High Gradient Rapids	Boulder
Shady	Dead Tree Scape	Braided	92	1.7	Low Gradient Riffles, Many Fine/Coarse Bars, Shallow Pools	Gravel
Shady	Rust Pit	Plane Bed	81	14	Low Gradient Riffles, Few Fine/Coarse Bars	Gravel
Shady	Shady Road	Riffle-Pool	97	22.7	Low Gradient Riffles, Shallow Pools, Coarse Bars	Gravel

Table 3.1. Geomorphic characteristics of each study reach.

The relative sediment supply for each study reach was determined using the same methods as described by Kinerson (1990). The same sediment transport relation was used to calculate q* (equation 1), and critical shear stress values were based on grain roughness using the Shields stress relation (equation 2). Bedload measurements obtained during high flows on Shady Creek were used to verify equation 1 as a reasonable estimate of observed bedload transport and to calculate a Shield's constant that was appropriate for the specific channel conditions. A critical entrainment value of 0.045 was calculated for the Shady Creek study reaches and used in equation 2. Unfortunately, during the study period (WY 2001 – 2002) winter flows were not high enough to initiate bedload transport on the remaining three study creeks. Therefore, a critical entrainment value of 0.03 was used to approximate the shields stress reflecting the coarser, more stable nature of the remaining study reaches (Andrews 1983; Lisle et al. 2000). Lastly, local calculations of q* were averaged throughout each study reach to obtain a Q* value representing the dimensionless bedload transport rate of the channel as a whole.

Results

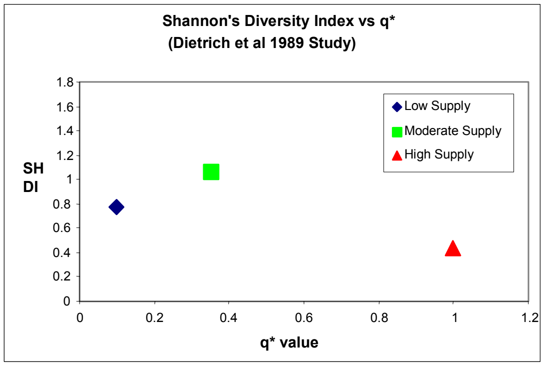
Within each of the flume studies, the flume run with the moderate relative sediment supply had the highest SHDI value (table 3.2; figure 3.2). Data from the two field studies however, showed a linearly increasing trend such that as relative sediment supply increased, SHDI increased (figure 3.3).

The primary geomorphic difference between the field and flume conditions was the presence of less mobile structural elements, such as large woody debris and boulders, in the field reaches. To determine if geomorphic diversity was related to the presence of the structural elements, SHDI was plotted against the percent area of large woody debris and boulders (figure 3.4). For both field studies, SHDI linearly increased as the percent structure within the study reach increased.

Study	Site/Reach	Relative Supply	q* or Q*	SHDI
Dietrich et al (1989)	flume	Low	0.1	0.77
	flume	moderate	0.35	1.06
	flume	High	1	0.44
Lisle et al (1993)	flume	low	0.00	1.23
	flume	moderate	0.27	1.27
	flume	High	0.41	0.93
Kinerson (1990)	Lagunitas	Low	0.05	0.82
	Sagehen	Low	0.61	0.64
	Caspar	moderate	0.96	1.49
	Jacoby	moderate	0.89	1.24
	Prairie	High	0.95	0.94
	Wildcat	High	1.01	1.53
South Yuba River	Dead Tree Scape	NA	0.37	1.46
	Rust Pit	NA	0.17	1.33
	Shady Rd	NA	0.28	1.57
	Aarons Pools	NA	0.27	2.02
	Road Jumble	NA	0.36	1.57
	Celestial Pools	NA	0.36	1.61
	Oregon Ck Rd	NA	0.49	1.66
	Blair Pond	NA	0.50	1.83

Table 3.2. Summary of calculated q* values and Shannon's Diversity Index values for each study.

a)



b)

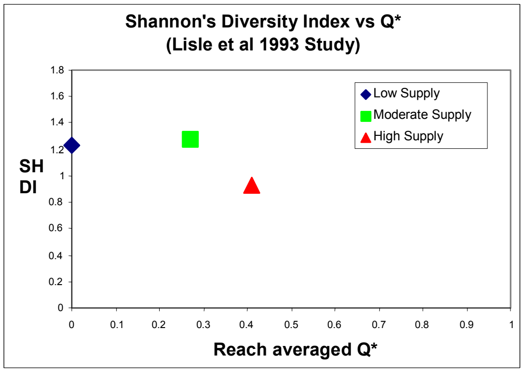


Figure 3.2. Relationship between relative sediment supply (q* or Q*) and geomorphic diversity (SHDI) for a) Dietrich et al. (1989) flume study and b) Lisle et al. (1993) flume study.

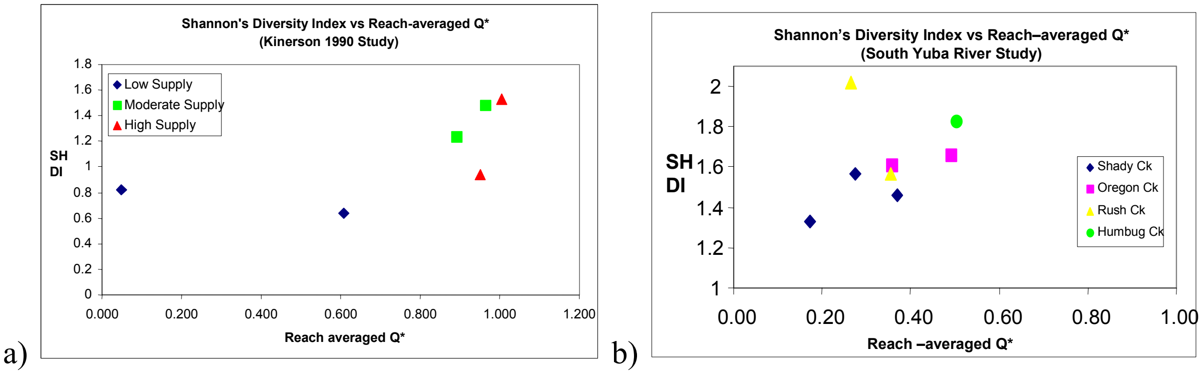


Figure 3.3. Relationship between relative sediment supply (Q*) and geomorphic diversity (SHDI) for a) Kinerson (1990) field study and b) South Yuba River field study.

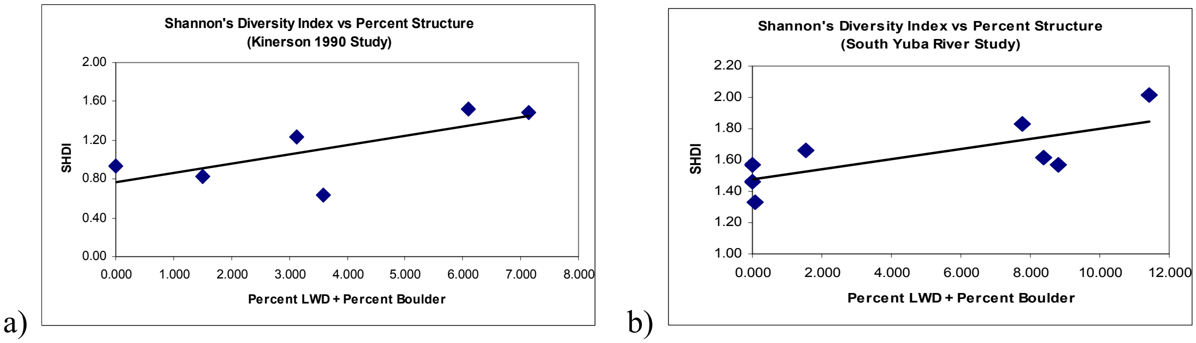
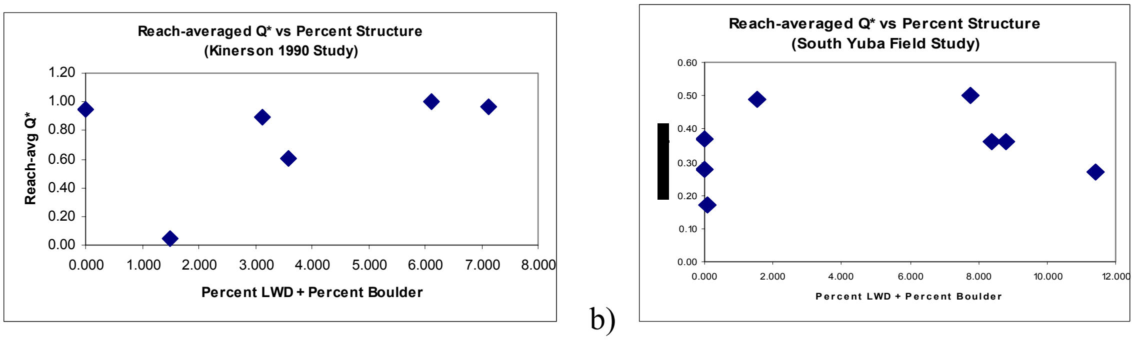


Figure 3.4. Plot of Shannon's Diversity Index versus Percent area of structural elements for a) Kinerson (1990) field study ($R^2 = 0.519$; $F = 4.32$; $p = 0.106$) and b) South Yuba River field study ($R^2 = 0.544$; $F = 7.16$; $p = 0.037$).

Considering that SHDI was positively related to both the calculated Q* values and the percent area of structural elements, Q* was plotted against the percent structural elements for each study reach (figure 3.5). A best-fit curve to each relationship was roughly logarithmic, though not significant statistically. Reach-averaged Q* increased rapidly with increasing percent structure, but remained consistently high once the percent structure was greater than approximately 3% of the total area. In reaches were the percent structure was low (less than approximately 3%), a full range of Q* values occurred.



a)

b)

Figure 3.5. Relationship between reach-averaged Q* and percent area of structural elements for a) Kinerson (1990) field study and b) South Yuba River field study.

In order to examine the relationship between SHDI and Q* without the overriding influence of a high degree of structural elements, only those field reaches where large woody debris and boulders comprised less than 3% of the total area were plotted (figure 3.6). Without the presence of less mobile elements, those reaches with moderate relative sediment supplies and moderate values of Q* had the highest SHDI values, similar to the results observed in each of the flume studies.

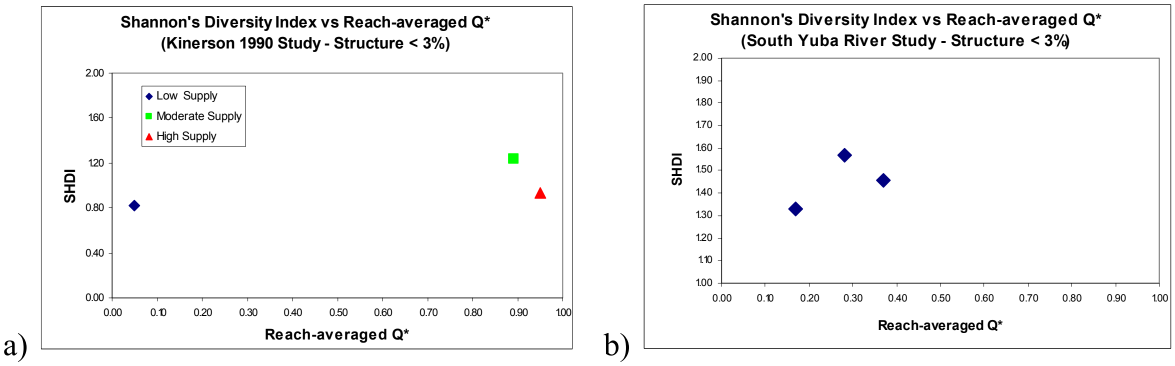


Figure 3.6. Relationship between relative sediment supply (Q*) and geomorphic diversity (SHDI) in reaches with less than 3% structural elements for a) Kinerson (1990) field study and b) South Yuba River field study.

When the data from all four studies was combined, excluding those field reaches where structural elements comprise greater than 3% of the total reach area, a broad unimodal trend was observed (figure 3.7). Reaches with a moderate relative sediment supply as measured by Q* had the highest geomorphic diversity as measured by SHDI.

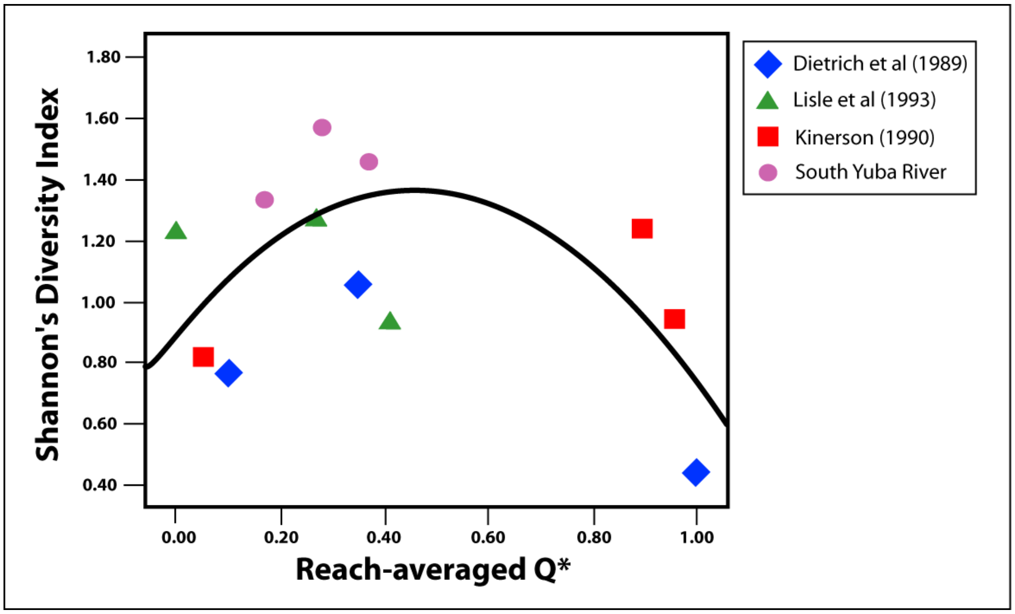


Figure 3.7. Plot of relative sediment supply (Q*) versus geomorphic diversity (SHDI) for reaches from all four studies where percent area of structural elements was less than 3% (quadratic curve, $R^2 = 0.401$, $F = 3.34$, $p = 0.077$).

Discussion

The results indicate two potential mechanisms for how relative sediment supply may be driving geomorphic diversity in natural river systems at the reach scale. When less mobile structural elements, such as large woody debris and boulders, are not a large proportion of the reach landscape, the relationship between sediment supply and transport capacity dictates the range of sediment textures and geomorphic features observed within the reach. Moderate relative sediment supplies create channel conditions where differential scour and deposition result in pools, riffles and bars, each with varying sorted surface textures. These features are mobilized, scoured and deposited at different temporal and spatial scales depending on variability in the flow regime. Unlike channels with high relative sediment supplies where the bed material is continually in motion and highly unsorted, or reaches with low relative sediment supplies where the substrate rarely mobilizes, channels with a moderate relative sediment supply exhibit a high diversity of geomorphic features, a high diversity of surface textures and thus a high overall heterogeneity in physical habitat types available at any given flow.

In contrast, when boulders and large woody debris become an increasingly larger proportion of a channel reach, habitat heterogeneity is “forced” by interactions between the less mobile structural elements, flow, and bedload. The structural elements constrict and alter local flow paths creating greater variations in local flow velocities. As the structure diverts flow, higher velocities are forced to the outer edges of the structure promoting local scour. The scoured sediments are often deposited just downstream as velocities decrease in the wake of the structure (Buffington and Montgomery 1999a; Manga and Kirchner 2000).

As a result, the increase in local scour and deposition caused by the structural elements creates a greater variety of geomorphic features and sorted sediment textures, thereby increasing the heterogeneity in physical habitat types observed.

The data indicate that, regardless of the mechanism, processes that increase differential scour and deposition create an increased variety of geomorphic features and surface textures resulting in greater physical habitat diversity. These processes may either be related to the relationship between transport capacity and sediment supply as suggested by the study hypothesis or to local hydraulic processes influenced by less mobile structural elements such as large woody debris and boulders. The study results indicate both mechanisms may occur, with the influence of structural elements overriding the relative sediment supply once some threshold is passed (e.g. when structural elements comprise greater than approximately 3% of the total reach landscape as observed in this study).

In general however, physical habitat complexity is likely maximized through a combination of a locally moderate sediment supply and a varied flow regime. It is the combination of variable sediment influx and variable flow magnitude and frequency that creates the variations in sediment mobility required to maximize geomorphic diversity. In stream reaches where sediment supply is low, such as downstream of dams, high flow variability may have little impact on stream geomorphology as there is no sediment to sort and redistribute. In these types of reaches, a higher percentage of structural elements may promote deposition of what little sediment moves through the system thereby slightly increasing geomorphic diversity, but overall geomorphic heterogeneity will remain limited. In streams with high sediment supply but low flow variability, geomorphic diversity will also be low as the hydraulic processes required to sort sediment are limited. Unlike low sediment supply reaches however, high supply reaches may exhibit increased diversity with a more varied flow regime. An increase in flow variability would promote differential sediment mobility increasing textural sorting, in essence transitioning a reach with high relative sediment supply to a moderate relative sediment supply. In this case, an increased percentage of structural elements would further encourage local scour and deposition resulting in a greater overall geomorphic diversity. The resulting conclusion is that while increased structural elements do promote greater habitat heterogeneity in many instances, maximum geomorphic diversity is likely achieved when both the sediment influx and flow regime are varied.

These conclusions support the generally accepted notion in the literature that additions of large woody debris to a stream channel increase habitat heterogeneity (Abbe and Montgomery 1996; Buffington and Montgomery 1999a). However, in order to maximize geomorphic diversity in a stream reach, the degree of variability in both sediment supply and flow must be considered. Additions of structural elements to channels in an effort to increase habitat diversity may have little impact in reaches with a low sediment supply. In these reaches, techniques designed to increase local sediment supplies, such as gravel augmentation or increasing access to sediment stored in banks, may have a larger effect. If a stream reach has been severely impacted by excess sediment on the other hand, introduction of structural elements to promote local scour and deposition may greatly increase geomorphic diversity along with techniques designed to reduce sediment inputs to the channel.

For aquatic species known to key off geomorphic conditions in a stream reach, such as the Foothill Yellow-legged frog (*Rana boylii)* and many salmonid species, additional insight to how geomorphic diversity is created and maintained is beneficial for conservation efforts. High gradient streams where these species often reside generally exhibit physical conditions indicative of moderate to low relative sediment supplies (Montgomery and Buffington 1997). Boulder substrates, limited depositional features and lack of scour pools may limit habitat suitability. High gradient reaches near increased sediment inputs therefore are more likely to exhibit greater habitat diversity. Reaches near tributary confluences for example, where debris inputs are high and flow is more variable, have been suggested to be 'biodiversity hotspots' with high habitat heterogeneity (Benda et al. 2003). Increased input of large woody debris and sediment from the tributary would increase the local sediment supply in an otherwise low supply reach increasing local scour and deposition and textural sorting resulting in increased geomorphic diversity. Similarly, wide valley segments have a greater potential for large woody debris input from floodplains and coarse sediment input from terraces and banks. The resulting increase in local scour and deposition from these inputs may also create greater geomorphic diversity within associated stream reaches. Conservation efforts should therefore focus on these areas where natural processes act to create local habitat diversity.

For species like *R. boylii* that show preferences for stream reaches with greater habitat heterogeneity (chapter 2), reaches where local sediment mobility is high may be preferentially selected. Data from the microhabitat study (chapter 1) showed individuals were often observed closer to tributary confluences than expected and in wider valley segments than expected. Stream reaches in these locations would not only provide an increased diversity in habitat as discussed above, but may also be subject to a greater disturbance regime than high gradient reaches with low sediment mobility. Certain geomorphic features such as unvegetated cobble bars and scour pools are common habitats for various lifestages of *R. boylii* (Kupferberg 1996; Van Wagner 1996) and must be periodically disturbed to be maintained. The increased local scour and deposition that occurs in stream reaches with greater variability in flow and sediment flux creates just such a higher disturbance rate. As a result, conservation efforts for many aquatic organisms and *R. boylii* in particular are best directed towards stream segments where sediment inputs are variable, large woody debris and other structural inputs are high and flow variability is high.

Works Cited

Abbe, T. B. and D. R. Montgomery (1996). Large woody debris jams, channel hydraulics and habitat formation in large rivers. *Regulated Rivers-Research & Management* 12(2-3): 201-221.

Andrews, E. D. (1983). Entrainment of Gravel From Naturally Sorted Riverbed Material. *Geological Society of America Bulletin* 94(10): 1225-1231.

Andrews, E. D. (1984). Bed-Material Entrainment and Hydraulic Geometry of Gravel-Bed Rivers in Colorado. *Geological Society of America Bulletin* 95(3): 371-378.

Beisel, J. N., P. Usseglio-Polatera and J. C. Moreteau (2000). The spatial heterogeneity of a river bottom: a key factor determining macroinvertebrate communities. *Hydrobiologia* 422: 163-171.

Benda, L., C. Veldhuisen and J. Black (2003). Debris flows as agents of morphological heterogeneity at low-order confluences, Olympic Mountains, Washington. *Geological Society of America Bulletin* 115(9): 1110-1121.

Benda, L. E. and T. W. Cundy (1990). Predicting deposition of debris flows in mountain channels. *Canadian Geotechnical Journal* 27: 409–417.

Brown, B. L. (2003). Spatial heterogeneity reduces temporal variability in stream insect communities. *Ecology Letters* 6(4): 316-325.

Buffington, J. M., T. E. Lisle, R. D. Woodsmith and S. Hilton (2002). Controls on the size and occurrence of pools in coarse-grained forect rivers. *River Research and Applications* 18: 507-531.

Buffington, J. M. and D. R. Montgomery (1999a). Effects of hydraulic roughness on surface textures of gravel- bed rivers. *Water Resources Research* 35(11): 3507-3521.

Buffington, J. M. and D. R. Montgomery (1999b). Effects of sediment supply on surface textures of gravel-bed rivers. *Water Resources Research* 35(11): 3523-3530.

Dietrich, W. E., J. W. Kirchner, H. Ikeda and F. Iseya (1989). Sediment Supply and the Development of the Coarse Surface Layer in Gravel-Bedded Rivers. *Nature* 340(6230): 215-217.

Horan, D. L., J. L. Kershner, C. P. Hawkins and T. A. Crowl (2000). Effects of habitat area and complexity on Colorado River cutthroat trout density in Uinta Mountain streams. *Transactions of the American Fisheries Society* 129(6): 1250-1263.

Imhof, J. G., J. Fitzgibbon and W. K. Annable (1996). A hierarchical evaluation system for characterizing watershed ecosystems for fish habitat. *Canadian Journal of Fisheries and Aquatic Sciences* 53: 312-326.

Kinerson, D. (1990). Bed surface response to sediment supply. Master's Thesis. Geology. Berkeley, University of California, Berkeley.

Kupferberg, S. J. (1996). Hydrologic and geomorphic factors affecting conservation of a river-breeding frog (*Rana boylii*). *Ecological Applications* 6(4): 1332-1344.

Lane, S. N., K. S. Richards and J. H. Chandler (1996). Discharge and sediment supply controls on erosion and deposition in a dynamic alluvial channel. *Geomorphology* 15(1): 1-15.

Li, H. and J. F. Reynolds (1995). On Definition and Quantification of Heterogeneity. *Oikos* 73(2): 280-284.

Lisle, T. E. (1982). Effects of Aggradation and Degradation On Riffle-Pool Morphology in Natural Gravel Channels, Northwestern California. *Water Resources Research* 18(6): 1643-1651.

Lisle, T. E., F. Iseya and H. Ikeda (1993). Response of a Channel With Alternate Bars to a Decrease in Supply of Mixed-Size Bed-Load - a Flume Experiment. *Water Resources Research* 29(11): 3623-3629.

Lisle, T. E., J. M. Nelson, J. Pitlick, M. A. Madej and B. L. Barkett (2000). Variability of bed mobility in natural, gravel-bed channels and adjustments to sediment load at local and reach scales. *Water Resources Research* 36(12): 3743-3755.

Maddock, I. (1999). The importance of physical habitat assessment for evaluating river health. *Freshwater Biology* 41(2): 373-391.

Madej, M. A. (1999). Temporal and spatial variability in thalweg profiles of a gravel-bed river. *Earth Surface Processes and Landforms* 24(12): 1153-1169.

Manga, M. and J. W. Kirchner (2000). Stress partitioning in streams by large woody debris. *Water Resources Research* 36(8): 2373-2379.

Massong, T. M. and D. R. Montgomery (2000). Influence of sediment supply, lithology, and wood debris on the distribution of bedrock and alluvial channels. *Geological Society of America Bulletin* 112(4): 591-599.

McGarigal, K., S. A. Cushman, M. C. Neel and E. Ene (2002). FRAGSTATS: Spatial Pattern Analysis Program for Categorical Maps. www.umass.edu/landeco/research/fragstats/fragstats.html, Authors at University of Massachusetts, Amherst.

McKenney, R., Ed. (2001). Channel changes and habitat diversity in a warm-water, gravel-bed stream. Geomorphic Processes and Riverine Habitat. Washington D.C., American Geophysical Union.

Montgomery, D. R., T. B. Abbe, J. M. Buffington, N. P. Peterson, K. M. Schmidt and J. D. Stock (1996). Distribution of bedrock and alluvial channels in forested mountain drainage basins. *Nature* 381(6583): 587-589.

Montgomery, D. R. and J. M. Buffington (1997). Channel-reach morphology in mountain drainage basins. *Geological Society of America Bulletin* 109(5): 596-611.

Montgomery, D. R., J. M. Buffington, R. D. Smith, K. M. Schmidt and G. Pess (1995). Pool Spacing in Forest Channels. *Water Resources Research* 31(4): 1097-1105.

Naiman, R. J., S. R. Elliott, J. M. Helfield and T. C. O'Keefe (1999). Biophysical interactions and the structure and dynamics of riverine ecosystems: the importance of biotic feedbacks. *Hydrobiologia* 410: 79-86.

Petts, G. E. (2000). A perspective on the abiotic processes sustaining the ecological integrity of running waters. *Hydrobiologia* 422: 15-27.

Pitlick, J. and M. M. Van Steeter (1998). Geomorphology and endangered fish habitats of the upper Colorado River 2. Linking sediment transport to habitat maintenance. *Water Resources Research* 34(2): 303-316.

Pitlick, J. and P. R. Wilcock, Eds. (2001). Relations between streamflow, sediment transport and aquatic habitat in regulated rivers. Geomorphic Processes and Riverine Habitat. Washington D.C., American Geophysical Union.

Power, M. E. (1992). Habitat Heterogeneity and the Functional-Significance of Fish in River Food Webs. *Ecology* 73(5): 1675-1688.

Power, M. E., W. E. Dietrich and J. C. Finlay (1996). Dams and downstream aquatic biodiversity: Potential food web consequences of hydrologic and geomorphic change. *Environmental Management* 20(6): 887-895.

Ralph, S. C., G. C. Poole, L. L. Conquest and R. J. Naiman (1994). Stream Channel Morphology and Woody Debris in Logged and Unlogged Basins of Western Washington. *Canadian Journal of Fisheries and Aquatic Sciences* 51(1): 37-51.

Rutten, L. T. (1998). Quantitative Assessment of the response to changing sediment supply, North Fork American River, CA. Master's Thesis. Geology. Davis, University of California, Davis: 39.

Townsend, C. R., M. R. Scarsbrook and S. Doledec (1997). The intermediate disturbance hypothesis, refugia, and biodiversity in streams. *Limnology and Oceanography* 42(5): 938-949.

Van Wagner, T. J. (1996). Selected life-history and ecological aspects of a population of foothill yellow-legged frogs (*Rana boylii*) from Clear Creek, Nevada County, California. Master's Thesis. Department of Biological Sciences. Chico, California State University, Chico: 143.

Ward, J. V. and K. Tockner (2001). Biodiversity: towards a unifying theme for river ecology. *Freshwater Biology* 46(6): 807-819.

Ward, J. V., K. Tockner and F. Schiemer (1999). Biodiversity of floodplain river ecosystems: Ecotones and connectivity. *Regulated Rivers-Research & Management* 15(1-3): 125-139.

Yarnell, S. M. (2000). The influence of sediment supply and transport capacity on Foothill Yellow-legged Frog habitat, South Yuba River, California. Master's Thesis. Geology. Davis, CA, University of California, Davis: 241.