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A “TAIL” OF TWO STREAMS: FACTORS INFLUENCING ROCKY MOUNTAIN TAILED FROG (*Ascaphus montanus*) TADPOLE DISTRIBUTION AND ABUNDANCE IN IDAHO AND MONTANA

by
Jason Leon Jones

A thesis
submitted in partial fulfillment
of the requirements for the degree of
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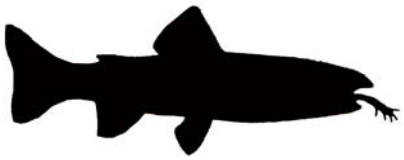
ABSTRACT

The ecology of stream organisms can vary with ontogeny, spatial scale, and network context, especially if the species' range encompasses strong biogeoclimatic gradients. The goal of this thesis was to evaluate the influence of abiotic and biotic factors on Rocky Mountain tailed frog (*Ascaphus montanus*) tadpole densities across a nested hierarchy of spatial scales in two biogeoclimatically distinct stream networks. In order to achieve this goal, I sampled Mica Creek in Idaho and Youngs Creek in Montana, from the origin of the stream to the stream's confluence with a major river. I provided a justification for comparing distribution and abundance of tadpoles using two different sampling techniques (Chapter 1), illustrated that distribution and abundance patterns may differ within and between two different stream networks (Chapter 2), and examined abiotic and biotic factors influencing tadpoles across spatial scales and between life stages within and between the two stream networks (Chapter 3).

To my family and friends, you are one in the same…



FROG ON!

PREFACE

The overarching goal of this thesis was to examine the factors influencing the distribution and abundance of Rocky Mountain tailed frog (*Ascaphus montanus*) tadpoles in two biologically, geologically, and climatically (biogeoclimatically) distinct stream networks. In order to achieve this goal, I composed three chapters, which 1) provided a justification for comparing the distribution and abundance of tadpoles using two different sampling techniques, 2) illustrated that distribution and abundance patterns may differ within and between two different stream networks, and 3) examined abiotic and biotic factors influencing tadpoles across spatial scales and between life stages within and between the two stream networks. In order to achieve the goal, I sampled two biogeoclimatically distinct streams, Mica Creek in Idaho and Youngs Creek in Montana, from the origin of the stream to the stream's confluence with a major river.

In Chapter 1, I used two sampling techniques, kick sampling and snorkeling, and compared the two techniques for estimating tadpole occurrence and abundance in the two stream networks. Because most studies on stream amphibians have investigated the patterns of distribution and abundance only in headwater streams, the knowledge of amphibian ecology and use of sampling techniques have been largely limited to small stream reaches. Although the common sampling approaches are similar in overall technique and are relatively labor intense, they generally result in a high probability of capturing most of the individuals. However, because the typical sampling techniques are so labor intense and amphibians are commonly found in high densities in the headwaters, sampling is seldom applied to larger downstream reaches. In Chapter 1, I addressed this

problem by comparing the detectability, occupancy, and abundance estimates from two sampling techniques, kick sampling (common method) and snorkeling (new method).

As another step to achieving the goal, I sampled two stream networks that were known to have high tadpole densities, but were biogeoclimatically distinct. In Chapter 2, I addressed yet another problem common with many stream amphibian studies, which is that most studies have occurred in small tributaries within the same region. Thus, the distribution and abundance patterns and factors influencing these patterns may not appear to change, which may result in a "one size fits all" management approach that may not be appropriate for a species whose range spans a variety of biogeoclimatically different regions. In Chapter 2, I addressed this problem by investigating the variation in occurrence, abundance, and tadpole age class aggregation within and between stream systems.

Finally, using the methods employed in Chapter 1 and the patterns observed in Chapter 2, I evaluated the factors associated with tadpole occurrence and abundance across spatial scales, within and between stream networks, and throughout larval ontogeny (Chapter 3). This final chapter touches on a fundamental problem in science: what we know is largely limited by how we sample. Because many studies on stream amphibians have focused on the factors influencing distribution and abundance at one spatial scale within a region and have largely disregarded the ecological implication of ontogenetic change, the understanding of what factors influence their ecology may also be limited. I use Chapter 3 to describe an example of how abiotic and biotic factors influencing tadpole distribution and abundance can change with spatial scale, regional context, and ontogeny.

Chapter 1: Comparisons of kick-sampling and snorkeling for estimating

Rocky Mountain Tailed Frog (*Ascaphus montanus*) tadpole presence and abundance

INTRODUCTION

Rocky Mountain tailed frog tadpoles are long-lived (Metter, 1964, 1967; Daugherty and Sheldon, 1982; Brown, 1990), cold-water stream obligates, which are locally abundant in appropriate habitats (Bury, 1988; Hawkins et al., 1988; Corn and Bury, 1989) and are sensitive to environmental perturbation (Hawkins et al., 1988; Corn and Bury, 1989; Welsh and Olliver, 1998; Diller and Wallace, 1999; Dupuis and Steventon, 1999). Because tadpoles reside in relatively complex stream systems, which are difficult to sample and result in low detection probabilities, for two to five years, are abundant and conspicuous, and are regarded as bio-indicators, they are model organisms to evaluate alternative sampling techniques, particularly if the technique increases detection probabilities and reduces environmental disturbance. As with any technique that is used to estimate occupancy and abundance of an organism with multiple cohorts, age class and the associated detection and capture probability should be taken into consideration.

For several decades, biologists have used kick sampling (or modified versions thereof) as a primary method for surveying stream-dwelling amphibians (Svihla, 1959: Franz and Lee, 1970; Daugherty and Sheldon, 1982; Hawkins et al., 1988; Bury and Corn, 1991; Welsh et al., 1997; Lohman, 2002; Stoddard and Hayes 2005; Dupuis and Friele, 2006). Kick sampling has been commonly used in amphibian inventories to monitor basin-wide distribution (Franz and Lee, 1970; Bull and Carter, 1996; Stoddard and Hayes, 2005; Dupuis and Friele, 2006), model site-level occupancy (Adams and Frissell, 2001; Stoddard and Hayes, 2005), estimate abundance (Hawkins et al., 1988; Welsh et al., 1997; Lohman, 2002; Lowe and Bolger, 2002), evaluate amphibian habitat-

use (Hawkins et al., 1988; Adams and Frissell, 2001; Adams and Bury, 2002; Wahbe and Bunnell, 2003), and monitor species movement patterns (Adams and Frissell, 2001; Wahbe and Bunnell, 2001; Lowe et al., 2006). Kick sampling is a useful technique particularly in small, shallow streams, where complex habitat may result in low detection probabilities (see Bury and Corn, 1991). The gear required to kick sample is modest, lightweight, and relatively inexpensive. Although the associated cost is relatively low, the technique can require substantial physical effort and time (Bury and Corn, 1991; Hayes et al., 2002).

Despite kick sampling's wide spread use and advantages, there are several limitations and a few potential ethical concerns associated with this technique. Kick sampling in deep environments, where stream depth exceeds net height, may limit capture probability, because mobile animals may avoid capture in slow moving water (Heyer et al., 1994). In addition, as stream channels get larger, the amount of effort required to adequately survey a channel unit increases dramatically, making it problematic in the largest streams occupied by stream dwelling amphibians (Bury and Corn, 1991). In addition to such limitations, biologists' attention has recently been drawn to several concerns regarding the habitat disturbance that results from kick sample surveys (L. Diller *pers. comm.*; M. Hayes *pers. comm.*; D. Pilliod *pers. comm.*). In streams where seasonal flow regimes do not mobilize the entire streambed, habitat alterations resulting from kick sampling, which does involve movement of entire stream bed, may affect future amphibian monitoring efforts (L. Bailey *pers. comm.*; L. Diller *pers. comm.*) in addition to inventorying and monitoring efforts for other stream dwelling organisms in the same basin (G. Minshall *pers. comm.*). In addition, kick sampling may

cause relatively high mortality (≤ 3%) among tadpoles (Jones, unpublished data), which may also have implications for monitoring amphibian populations, particularly species of concern.

Implementing an alternative to kick sampling for stream dwelling amphibians would require that the technique is comparable across habitats for estimating occupancy and density. Though other techniques have been evaluated, few have resulted in comparable, or better, occupancy and density estimates, particularly across a broad range of habitat (e.g., deep and slow water), while appearing to decrease habitat alteration (Hayes et al., 2002; Quinn et al., 2007); none have allowed for extensive *in situ* behavioral observations (e.g., Heyer et al., 1994).

Here, I evaluate underwater visual surveys via mask and snorkel as an alternative, or perhaps complementary, method to kick sampling for estimating Rocky Mountain tailed frog (*Ascaphus montanus*) tadpole occurrence and abundance. My specific objectives were to: (1) compare tadpole occupancy and detection probabilities at the channel unit and reach scale obtained when day and night snorkeling versus kick sampling; (2) compare tadpole density estimates obtained via day and night snorkeling versus kick sampling; (3) use baseline estimates of tadpole abundance obtained from three-pass kick sampling catch data, which is adjusted for capture efficiency, to understand how capture probabilities vary for each age class by substrate composition; and (4) examine the influence of stream habitat characteristics on tadpole occupancy estimates by these two techniques.

MATERIALS AND METHODS

Study Sites.—I conducted my study in Youngs Creek, on the Flathead National Forest in northwestern Montana, and Mica Creek, in northern Idaho, managed by Potlatch Corporation. The study streams were located within the South Fork Flathead River and St. Joe River drainages respectively (Figure 1). Elevation of the study areas overlapped slightly, with Youngs Creek ranging from 1380 to 2200 m and Mica Creek from 975 to 1450 m above sea level. The forest of the Montana study site was characterized by ponderosa pine (*Pinus ponderosa*) and Douglas-fir (*Pseudotsuga menziesii*), whereas the Idaho study site consisted of western red cedar (*Thuja plicata*), western hemlock (*Tsuga heterophylla*), and grand fir (*Abies grandis*). Mean annual precipitation varied slightly between my study sites; Montana received 100 cm and Idaho received 140 cm (Western Regional Climate Center, 2002).

I conducted day surveys of tadpole occurrence and abundance in 9 study reaches, including 46 sampled channel units, between July and August 2006. I also conducted nighttime snorkeling surveys 33% of these sites. I expected there would be differences in snorkeling efficiency for tadpoles in daytime versus nighttime, based on previous research regarding cryptic, benthic dwelling organisms (Thurow and Shill, 1996) and input from tailed frog biologists (C. Hawkins *pers. comm.*). Study reaches were located in first to third-order stream segments and the number of study reaches per segment was weighted by the length of each segment (modified from Bury and Corn, 1991; Bury et al., 2002). Each study reach measured 250 m in length. Five randomly selected channel units (1-5 m in length) were sampled in each study reach. Based on previous studies concerning *Ascaphus* spp. ecology (e.g., Hawkins et al., 1988), I randomly selected

channel units located in riffle habitat. I located each channel unit by unrolling a tape measure from the downstream edge of a designated reach starting point to the downstream edge of the next randomly placed, upstream unit.

Tadpole Surveys.—I surveyed channel units for tadpoles using two-divers and a two-person kick sampling team during the day between the hours 0900 and 1900, and performed nighttime snorkel surveys between the hours of 2300 and 0300 during the same 24-hour period. After each daytime snorkel survey, I measured stream-wetted width, depth, and velocity. During each snorkel survey, I measured substrate heterogeneity (embeddedness and size). For safety and logistical reasons, daytime snorkel surveys were conducted first at all sites (Thurow and Schill, 1996). To insure that I nighttime snorkeled and kick sampled in the same 5 m channel unit, I marked the beginning and end of each channel unit with flagging tape, which I removed after kick sampling surveys. Single-pass snorkeling surveys were timed and began at the downstream end of each channel unit (Thurow et al., 2006). During each survey, both divers, who were equipped with dry suits, masks, and snorkels, crawled slowly upstream in a zigzag pattern, using the middle of the channel as a reference point to avoid double counting tadpoles. All tadpoles were counted and classified into one of three age classes based on limb morphology (Metter, 1967): first-year (1y), second-year (2y), and third-year (3y). Divers paused at the end of each channel unit to relay information to a data recorder on the streambank. Snorkeling effort was recorded as the time (mm:ss) required survey each channel unit (m^2). During nighttime surveys, each diver used hand-held underwater flashlights (Tuff Lite®, Garrity Industries, Madison, Connecticut, USA).

After daytime surveys, channel units were left undisturbed for an average of 8 h prior to nighttime surveys and 17 h prior to kick sampling surveys.

Within each channel unit surveyed via snorkeling, a transect 1 m in length was sampled via single-pass kick sampling. This 1 m transect was located directly in the center of the 5 m snorkeling unit. While one person stabilized two hand-held D-frame nets (0.8 mm mesh) on the downstream edge of the site, the other person lifted all large cover items (stone and wood) immediately situated above the nets and kicked through the substrate to facilitate the capture of tadpoles in the nets (Corn and Bury, 1991; Bury et al., 2002). The nets were periodically searched for tadpoles and any tadpole encountered was placed into a collapsible nylon bucket on the stream bank; tadpoles were then segregated by age class. I recorded the kick sampling effort as the time required to kick through an entire channel unit, plus the time spent searching through nets at each channel unit.

Statistical Analyses.—I compared tadpole occupancy at the channel unit and reach scales, and detection probabilities at the reach scale for each technique. Although channel units surveyed via snorkeling were larger than those surveyed via kick sampling, I compared tadpole occupancy and detection probabilities for each age class and technique. At the channel unit scale I compared tadpole occupancy by technique using a simple logistic regression. Logistic regression allowed me to evaluate which technique, if either, underestimated occupancy through a type-2 error (false negative). To estimate occupancy and detection probabilities at the reach scale, I used the program *PRESENCE* v. 2.0 (Patuxent Wildlife Research Center, Laurel, Maryland, USA; McKenzie et al., 2006). Reach scale detection probabilities were based on the occupancy estimates

obtained from the five channel units snorkeled and kick sampled; *Presence* was then used to estimate the probability of detecting a tadpole in a single channel unit within the sampled reaches.

Prior to comparing kick sample and snorkeling capture probabilities, I estimated a single-pass capture probability by using three-pass kick sample removal surveys for 22 channel units in the microcomputer program designed for estimating fish population size and associated variance based on multi-pass removal data (Seber, 1982; Kwak, 1992). The three-pass kick sample removal tadpole densities were estimated using the three-pass kick sampling removals, and were compared to single-pass estimates using a linear regression model. Standard removal methods for fish are biased by fish size (Peterson et al., 2004); given that tailed frog tadpoles have three distinct larval stages that vary in morphology and size (≤1y and ≥2y), I estimated the capture probability for a single-pass kick sample for each age class. I then compared density estimates obtained via single-pass snorkeling to those from single-pass kick sampling using a linear regression model. For single-pass kick samples, I also used a regression model to determine if stream depth, flow velocity, substrate heterogeneity, and tadpole age composition influenced my capture probability. I used a multiple-regression model to evaluate which variables accounted for the largest amount of variation in the model for capture probability.

Using the mean sampling effort required to kick sample a 1m² transect, I estimated the sample area that would correspond to a comparable amount of effort via snorkeling. Based on my preliminary comparisons, snorkeling a single 5 m belt was comparable in unit effort to kick sampling a 1 m channel unit. I used a student's *t*-test to compare the mean sampling effort required for my two techniques.

RESULTS

Tadpole occupancy estimates and detection probabilities were comparable between techniques at the channel unit and reach scales (Tables 1 and 2), but varied by tadpole age class (Table 3). Overall, in Youngs Creek and Mica Creek, tadpoles were present in 96% of the channel units and all of the reaches surveyed. The 1y age class comprised the bulk of the estimated tadpole density (58%). The 2y and 3y age classes consisted of 25% and 17%, respectively, of the total tadpole density. At the channel unit scale, daytime snorkeling surveys when compared to the other techniques provided an equal, if not slightly greater, chance of detecting tadpoles (nighttime snorkeling: $\chi^2_{1, 30}$ = 2.14, r^2 = 0.05, P = 0.14; kick sampling surveys: $\chi^2_{1, 92}$ = 3.01, r^2 = 0.06, P = 0.08). However, nighttime snorkeling and kick sampling appeared to underestimate occupancy (type-2 error) in 13% and 5% of the channel units, respectively. When segregated by age class (1-3y), tadpole occupancy varied by technique and between the streams. Tadpoles of age 1, 2, and 3 were present in 85, 88, 76% of the channel units, respectively; all age classes were present in the reaches surveyed. The proportion of channel units within reaches that were found to be occupied via snorkeling was 100% for all age classes. However, the proportion of channel units found to be occupied via kick sampling varied by age class, ranging from 79% (2y) to 90% (1y and 3y; Table 3). In Mica Creek, kick sampling surveys commonly underestimated occupancy for each age class when compared with daytime snorkeling surveys (1y: $\chi^2_{1, 50}$ = 3.95, r^2 = 0.07, P = 0.05; 2y: $\chi^2_{1,50}$ = 12.50, r^2 = 0.20, P < 0.01; 3y: $\chi^2_{1,50}$ = 2.92, r^2 = 0.04, P = 0.09).

The probability of detecting tadpoles by each technique was similar, but varied by age class (Table 3). Tadpoles were detected in all of the occupied units during day

snorkeling surveys, 89% of the 15 units surveyed by night snorkeling, and 88% during kick sampling surveys. At the reach scale, the probability of detecting a tadpole using a single channel unit decreased for both day snorkeling and kick sampling; detection probabilities, on average, were 96% (SE ± 0.04) for day snorkeling and 85% (SE ± 0.07) for kick sampling a single 5 m or 1 m channel unit, respectively (Table 1). When segregated by age class (1-3y), the probability that a tadpole would be detected in a single channel unit of a reach varied by tadpole age and sampling technique. Detection probabilities were higher for snorkeling than kick sampling surveys; snorkeling surveys detected 85, 85, and 79% of 1y, 2y, and 3y tadpoles, respectively, at the reach scale, whereas kick sampling detected 80, 62, and 57% of 1y, 2y, and 3y tadpoles.

Snorkeling and kick sampling were comparable for estimating tadpole density at the channel unit and reach scales. At the channel unit scale tadpole density estimates were positively correlated for all techniques, but higher for daytime surveys, for daytime and nighttime snorkeling surveys ($n = 15$, $r^2 = 0.70$, $P < 0.01$, $d_{day} = 0.36 + 0.74*d_{night}$) and for day snorkeling and kick sampling surveys (Figure 2; $n = 46$, $r^2 = 0.63$, $P < 0.01$, $d_{day} = 0.094 + 0.90*d_{kick}$). At the reach scale tadpole densities were positively correlated for day and night snorkeling ($n = 3$, $r^2 = 1.00$, $P = 0.01$, $d_{day} = 0.0742 + 0.8785*d_{night}$) and for day snorkeling and kick sampling ($n = 9$, $r^2 = 0.93$, $P < 0.01$, $d_{day} = -0.42 + 1.20*d_{kick}$).

Snorkeling and kick sampling density estimates were comparable for all age classes, but capture probability varied for kick sampling for all age classes and by substrate composition. On average, older tadpoles (2-3y) had significantly higher capture probabilities via single-pass kick sample surveys when compared to 1y tadpoles ($F_{1,28}$ =

5.54, $P = 0.03$). Tadpole capture probabilities decreased with increasing stream depth (n = 14, $r^2 = 0.30$, $P = 0.04$). Although depth negatively influenced single-pass kick sample capture probabilities, very little variation associated with capture probability was described by depth. Variation in capture probability increased with an increasing proportion of cobble (65-256 mm) and 1y tadpoles (n = 14, $r^2 = 0.72$, $P = 0.02$). The variation associated with single-pass capture probability was significantly different for sites with more cobble and 1y tadpoles ($F_{1,14} = 14.01$, $P < 0.01$).

Sampling effort at the channel unit scale was comparable for snorkeling 5 m units and kick sampling 1 m units. However per sample area, kick sampling required 4.8-times more sampling effort than day snorkeling (Table 1; $F_{1,84} = 45.99$, $P < 0.01$). Although day snorkeling was more efficient than kick sampling per sample area in both streams, Youngs Creek required, on average, 59% less sampling effort per area to survey than Mica Creek ($F_{1,84} = 5.26$, $P = 0.02$).

DISCUSSION

Snorkeling provided comparable estimates of Rocky Mountain tailed frog tadpole occupancy (and associated detection probabilities) and comparable estimates of density for all age classes when compared to kick sampling. On average, snorkeling required one-forth of the sampling effort required by kick sampling and provided a means of sampling amphibian populations in slow-flowing, wider, and deeper channel units. The gear requirements for snorkeling are few, lightweight, and moderately inexpensive. Similar to kick sampling, the technique requires few personnel and the associated cost is relatively low for its efficiency. While few personnel are required, it is highly

recommended that divers do not attempt surveys without additional support. Table 4 summarizes the advantages and limitations observed for each technique when sampling for tailed frog tadpoles.

Detection probabilities were comparable between the techniques for 1y tadpoles, but were surprisingly higher for older age classes when snorkeling. I cannot make any conclusive statement regarding the importance of the covariates (e.g., cobble, flow, depth) on overall detection probabilities; but when each tadpole age class was fit to the same models, there was some suggestion that for all age-classes, particularly 3y tadpoles, detection probabilities may increase with increasing proportions of cobble (Table 3). I may have detected fewer 2-3y year tadpoles when kick sampling because of tadpoles' tendency to aggregate, their comparatively low densities, and the smaller area I sampled when kick sampling compared to snorkeling. Based on *in situ* observations, older age classes were patchier in their distribution, commonly aggregating within a channel unit (e.g., under or on a single rock); 1y tadpoles were commonly scattered. The decreased likelihood of detecting older age classes when kick sampling for tadpoles may have implications when estimating biomass for this species, which can weigh up to five-times more than 1y tadpoles.

Although kick sampling required more time per unit effort to sample, kick sampling resulted in comparable tadpole density estimates. Despite the potential for missing small patches of older age class tadpoles, three-pass removal estimates confirmed that the first pass of kick sampling generally captured most of the older age class individuals. Additionally, channel units with increasing proportions of cobble and 1y tadpoles explained the most variation in capture probability. Though depth explained

little regarding the variation in single-pass capture probabilities, increasing stream depth was associated with decreased probabilities of tadpole capture. While stream depth appeared to negatively influence single-pass kick sampling results, it did not appear to influence estimates for snorkeling. The increase in cobble as a substrate presumably resulted in increased interstitial space for tadpole refugia and, coupled with an increasing proportion of 1y tadpoles (the smallest bodied cohort sampled), may have limited the capture probability of both sampling techniques.

Although snorkeling was comparable to kick sampling for estimating tadpole distribution and abundance, snorkeling is generally limited by water clarity (Gardiner, 1984; Griffith et al., 1984; Helfman, 1992). Although most streams occupied by tailed frogs tadpoles are relatively clear, seasonal run-off events and storms can greatly reduce underwater visibility, which can directly influence occupancy and density estimates. Small, shallow streams (first-order) may require more effort to snorkel than kick sample, particularly if copious amounts of large woody debris and other in-stream obstructions impede the diver from crawling upstream. Additionally, snorkeling is limited by the ability of the observer to submerge their mask underwater; streams that are exceptionally shallow (≤ 20 cm) may require kick sampling or an alternate method.

While kick sampling remains a standard technique for measuring tadpole occupancy and density in stream ecosystems, snorkeling may provide additional insights and benefits. Underwater observation may allow observers an opportunity to monitor newly hatched tadpoles and adult behavior. For example, I conducted a pilot investigation of tadpole feeding by comparing substrate selected by tadpoles versus those randomly selected from the same channel unit. Additionally, snorkeling caused no

observed mortality, which appears substantially less than the 3% tadpole mortality rate associated with kick sampling (Jones, unpublished data). This is of importance when considering which technique to employ for sampling populations of Coastal and Rocky Mountain tailed frogs that are species of concern. Thus, for a suite of reasons snorkeling may be a worthwhile consideration as an alternative to traditional sampling techniques.

TABLES

Table 1. Comparison of daytime snorkeling and kick sampling estimates of Rocky Mountain tailed frog (*Ascaphus montanus*) tadpoles by occupancy (Ψ), detection probability (p), estimated density (D: measured in tadpoles/meter²), and sampling effort (UE: measured in mm:ss/m²). Surveys conducted in Youngs Creek and Mica Creek in 2007. Values are means with standard errors (SE).

Technique	**Ψ (±SE)**	***p* (±SE)**	**D (±SE)**	**UE (±SE)**
Day	1.00	0.96	1.60	00:54
Snorkeling	(0.00)	(0.03)	(0.46)	(00:37)
Kick	1.00	0.85	1.68	04:18
Sampling	(0.00)	(0.05)	(0.41)	(00:35)

Table 2. Comparison of daytime snorkeling and kick sampling estimates of Rocky Mountain tailed frog tadpoles as ranked by AIC (ΔAIC), AIC model weights (*wi*), overall estimate of the fraction of sample reaches occupied (Ψ), and associated standard error (SE(Ψ)).

Model, by technique	**ΔAIC**	w_i	**Ψ**	**SE(Ψ)**
Day Snorkeling				
Ψ(.), *p*(.)	0.00	0.73	1.00	0.00
Ψ(.), *p*(Cobble)	1.96	0.27	1.00	0.00
Kick Sampling				
Ψ(.), *p*(.)	0.00	0.63	1.00	0.00
Ψ(.), *p*(Cobble)	1.08	0.36	1.00	0.00

Table 3. Comparison of daytime snorkeling and kick sampling estimates of Rocky Mountain tailed frog tadpoles by age class as ranked by AIC (ΔAIC), AIC model weights (*wi*), overall estimate of the fraction of sample reaches occupied (Ψ), and associated standard error (SE(Ψ)).

Model, by technique & age-class		**ΔAIC**	w_i	**Ψ**	**SE(Ψ)**
Day Snorkeling					
1y	Ψ(.), *p*(Cobble)	0.00	0.57	1.00	0.00
	Ψ(.), *p*(.)	0.57	0.43	1.00	0.00
2y	Ψ(.), *p*(.)	0.00	0.53	1.00	0.00
	Ψ(.), *p*(Cobble)	0.25	0.46	1.00	0.00
3y	Ψ(.), *p*(Cobble)	0.00	0.91	1.00	0.00
	Ψ(.), *p*(.)	4.80	0.08	1.00	0.00
Kick Sampling					
1y	Ψ(.), *p*(Cobble)	0.00	0.55	0.89	0.10
	Ψ(.), *p*(.)	0.77	0.38	0.89	0.10
	Ψ(.), *p*(Depth)	5.56	0.03	0.89	0.10
2y	Ψ(.), *p*(Cobble)	0.00	0.34	0.79	0.14
	Ψ(.), *p*(.)	0.96	0.21	0.78	0.14
	Ψ(.), *p*(Flow)	1.29	0.18	0.79	0.14
	Ψ(.), *p*(Depth)	2.23	0.11	0.79	0.14
3y	Ψ(.), *p*(Cobble)	0.00	0.45	0.90	0.11
	Ψ(.), *p*(Flow)	1.19	0.25	0.92	0.11
	Ψ(.), *p*(.)	2.04	0.16	0.90	0.11
	Ψ(.), *p*(Depth)	2.57	0.12	0.91	0.11

Table 4. Comparisons between day snorkeling and kick sampling for inventorying and monitoring Rocky Mountain tailed frog tadpoles in first- to third-order streams.

Technique	**Stream Order**	**Stream Depth**	**Habitat**	**Habitat Alteration**	**Population Estimates**	**Tadpole Mortality**
Day Snorkeling	≥ 1st Order	≥ 20 cm	Riffles & Pools	N/A	Occupancy, density, behavior	N/A
Kick Sampling	1st-2nd Order	≤ 40 cm	Riffles	Variable	Occupancy, density, biomass	3% (±1)

FIGURE CAPTIONS

Figure 1. Study sites (from upper right to lower right): Youngs Creek, headwater of the South Fork of the Flathead River, Bob Marshall Wilderness Area, Montana and Mica Creek, tributary of the St. Joe River, Idaho.

Figure 2. Rocky Mountain tailed frog (*Ascaphus montanus*) tadpoles captured in the Mica and Youngs creek watershed in 2007. Age classes of *A. montanus* tadpoles are categorized into three age classes based on ontogeny (from left to right): First year (1y) tadpoles have no limb buds and are significantly smaller than older age classes; second year (2y) tadpoles have non-functional limb buds; third year (3y) tadpoles vary in their ontogeny, but have at least 2 functional limbs and are generally comparable in size to 2y tadpoles.

Figure 3. Rocky Mountain tailed frog tadpole densities estimates in the Youngs Creek and Mica Creek watershed in 2007. Tadpole densities at the channel unit and, consequently, reach scale were positively correlated for kick sampling and snorkeling. Dashed line is the identity line y = x. Regression line for data was not statistically different from y = x.

FIGURES

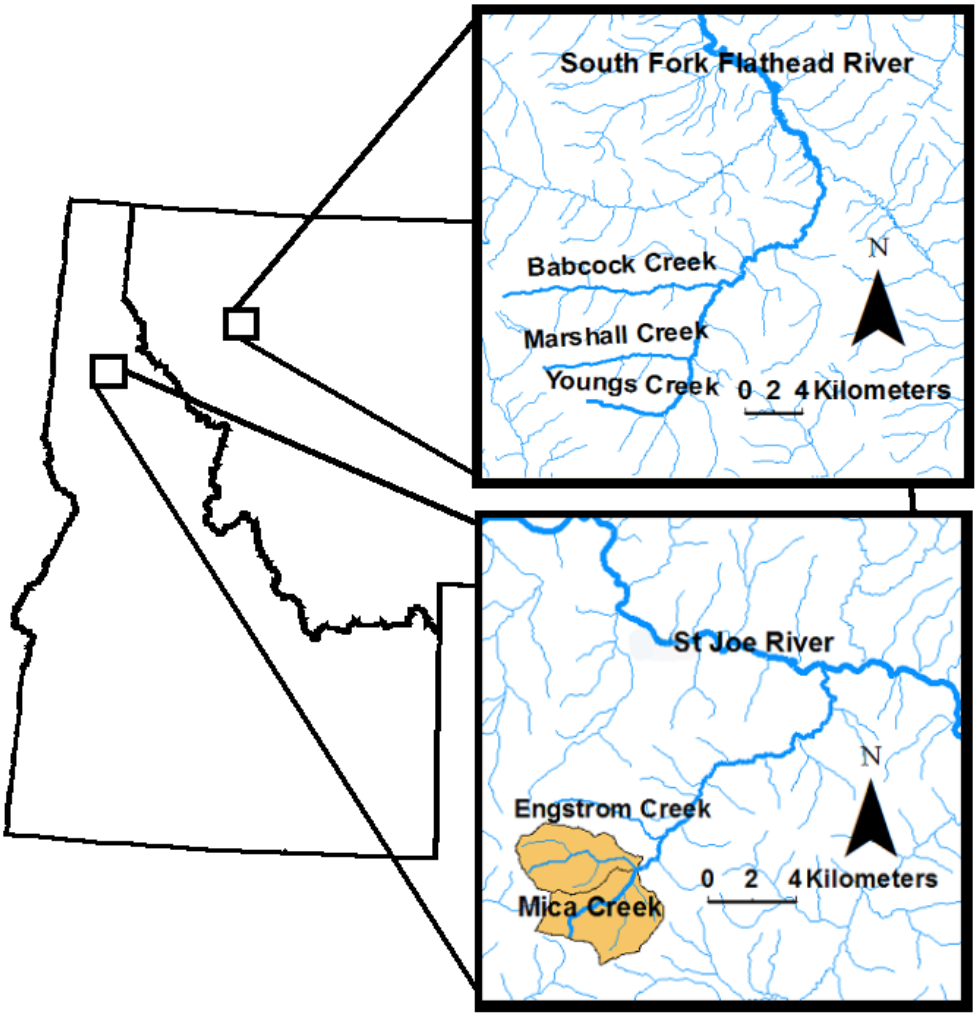


Figure 1.

Figure 2.

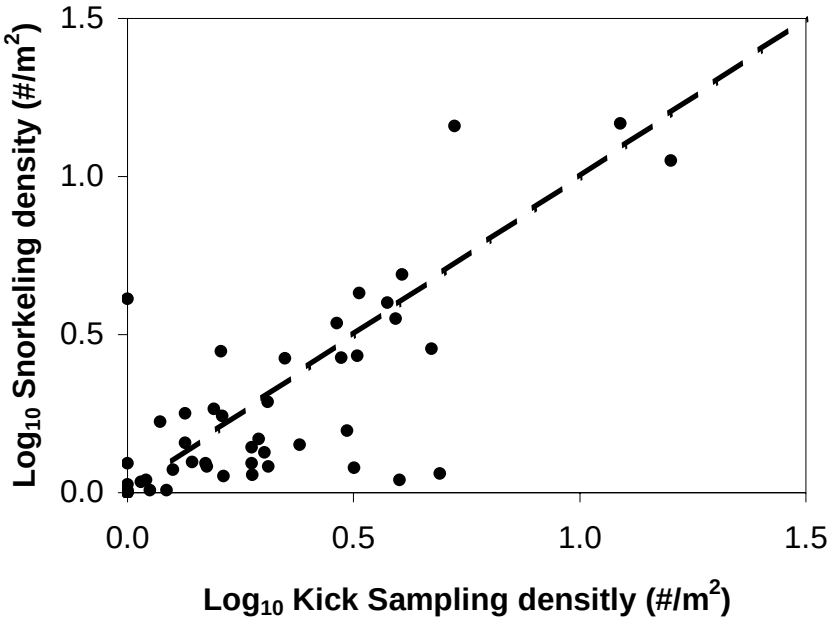

1.5
1.0
0.5
0.0
0.0
0.5
1.0
1.5
Log10 Snorkeling density (#/m2)
Log10 Kick Sampling densitly (#/m2)

Figure 3.

Chapter 2: *Ascaphus montanus* tadpole distribution and abundance patterns vary by regional context and age class

INTRODUCTION

Distribution and abundance patterns can vary significantly across a species range, especially if their range encompasses strong biogeoclimatic gradients. This may be especially true for organisms like amphibians and reptiles, which are mobile and sensitive to environmental gradients (see review Morrison and Hero, 2003). Though several studies have investigated the influence of geographic context on the ecology, specifically the distribution and abundance, of reptiles (Fitch 1970, 1985; Niewiarowski 1994), few have investigated geographical variation in the ecology of amphibians (see reviews by Morrison and Hero, 2003; Rosso et al., 2004). While the understanding of amphibian ecology is increasing, so is the need for awareness of variation among populations (e.g., intraspecific variation in distribution and abundance patterns and life history traits). Understanding intraspecific variation among populations is important particularly when management practices rely on generalized models that attempt to explain patterns in species ecology. Though inherent differences in the distribution and abundance patterns from one stream to the next might be disregarded as noise, such heterogeneity includes information fundamental to the ecology of the species and may confound the results of general models for that species.

Distribution and abundance patterns for a species can also vary with ontogeny. Most amphibians have complex life cycles involving abrupt changes in morphology, physiology, behavior, and ecology (Wilbur, 1980). Some amphibians may experience additional ontogenetic shifts due to prolonged (>2 years) larval development, during which time they may exhibit additional shifts in ecology (DeVlaming and Bury, 1970). This may be especially true for some stream dwelling amphibians, which inhabit dynamic

stream networks and require multiple years to complete metamorphosis (Metter, 1964; DeVlaming and Bury, 1970; Hairston, 1973; Welsh and Ollivier, 1998). Though regional context and ontogeny can independently influence the distribution and abundance patterns of a species, the differences observed with ontogeny may be regionally dependent (Berven et al., 1979; Berven, 1983; Merilä et al. 2000). Investigation of the influence of ontogeny on stream dwelling amphibian ecology in biogeoclimatically distinct watersheds is a requisite for improved understanding of species distribution and abundance, as well as defining what constitutes habitat suitability across their range.

The connectivity and configuration of habitat can strongly affect species distribution and abundance patterns (see review in Moilanen and Nieminen, 2002), particularly in branched stream networks (Ganio et al., 2005; Grant et al., 2007). The elements of habitat in stream networks are largely linear, and thus the spatial structure of a species' ecology may be a function of distances imposed by the network's configuration and connectivity (Grant et al., 2007). The use of geostatistics has allowed ecologists to graphically and quantitatively describe how connectivity and configuration of network branches affect spatial patterns of factors such as stream nutrient concentrations (Dent and Grimm, 1999), as well as "patchiness" in the distribution of such organisms as stream fish (Torgersen et al., 2004: Ganio et al., 2005). In fact, Torgersen et al. (2004) showed patch size for stream fish varied with watershed characteristics. Here I use the term patchiness, or patch size, to indicate the spatial distance over which a species abundance is spatially correlated, specifically a patch represents an aggregation of values (e.g., densities) that differs from its surroundings (Rossi et al., 1992; Dent and Grimm, 1999; Ettema and Wardle, 2002). Though the

understanding of amphibian patchiness (particularly amphibian habitat patchiness) has advanced beyond the classic metapopulation "pond-as-patch" concept for pond breeding amphibians (Semlitsch, 1998; Marsh and Trenham, 2001; Pilliod et al., 2002; Bartelt et al., 2004), no such investigations have occurred for stream dwelling amphibians. Quantifying the spatial structure of amphibian aggregations in stream networks is important for understanding the basic ecology of that species. In particular, there may be variation in species patch size by region and/or age class, which could be important in identifying appropriate spatial scales for sampling these organisms and their habitat.

The stream dwelling tailed frog, *Ascaphus* spp. (Anura; Ascaphidae), is well suited for study of the effect of regional context and ontogeny on species distribution and abundance patterns. Tailed frogs are considered cold water stream obligates that inhabit fast flowing, mountain streams (Nussbaum et al., 1983). Because of their prolonged larval development (> 2 years) and sensitivity to environmental conditions (e.g., temperature, sediment), tailed frog tadpole densities have been commonly used indicators for headwater stream ecosystem "health" (Corn and Bury, 1989; Welsh, 1990; Welsh and Ollivier, 1998). Understanding whether tadpoles inhabiting geographically distinct areas are sensitive to a similar suite of variables is needed, especially since many studies of tailed frog natural history suggest that geographic variation exists in tadpole size, age class structure, and growth rates among and within *Ascaphus* spp. (Metter, 1964, 1967; Daugherty and Sheldon, 1982; Wallace and Diller, 1998; Hayes et al., 2006; Burkholder and Diller, 2007). Comparing tailed frog tadpole distribution and abundance patterns in biogeoclimatically distinct streams will provide a foundation for understanding the differences geographic and ontogenetic variation may impart on their ecology, and will

have important implications for the management of this amphibian throughout their range.

Because Rocky Mountain tailed frogs (*A. montanus*) occupy a wide range of stream habitats, ranging from semi-arid environments to temperate rainforests (Metter and Pauken, 1969), i expected the distribution and abundance patterns for geographically distinct populations to change by region. Though few studies on tailed frog tadpoles have considered differences in distribution and abundance patterns between larval age classes (Pilliod, 2004; Lohman, 2005; Hayes, et al., 2006), it has been suggested that older tadpoles may readily move downstream (Hunter, 1998). Because tadpole age classes differ significantly in body size (Metter, 1967) and older tadpoles may move downstream, I expected tadpole age classes to differ in their distribution and abundance within stream networks. Because geographic variation exists in tadpole size, age class structure, and growth rates in *Ascaphus* sp., I expected that region and ontogeny would interact, causing tadpole age class distribution and abundance patterns to vary between geographically distinct networks. Finally, I also expected that tadpole patch size between watersheds would also differ in part because of differences in stream network configuration.

In this study I investigated: (1) how distribution and abundance patterns of Rocky Mountain tailed frog (*A. montanus*) tadpoles may vary in two biogeoclimatically distinct watersheds, (2) how these patterns may also vary with ontogeny, and (3) how tadpole patchiness may vary by region and by age class. The approach consisted of (1) intensively sampling throughout two watersheds (herein referred to as stream networks), from the stream's origin to the largest reach I observed tadpoles occupying, (2)

categorizing tadpoles into three age class based on development, and (3) using a geostatistical modeling approach to assess the spatial structure of tadpole aggregations within reaches in both networks. By sampling tailed frog tadpoles throughout two biogeoclimatically distinct stream networks, I will be able to better address how variation in distribution and abundance patterns relates to geographic and/or ontogenetic variation and to what extent ecological variation indicates stream health, or habitat quality.

MATERIALS AND METHODS

Study Area.—During the summers of 2005 and 2006, I conducted my study in two third-order stream networks (Strahler, 1964): Youngs Creek (302 km²), in the South Fork of the Flathead basin, Montana, and Mica Creek (103 km²), in the St. Joe River basin, Idaho (Figure 1, Chapter 1). Elevation between the study areas overlap (Youngs Creek 1380 to 2200 m; Mica Creek 975 to 1450 m) and moderate to steep forested slopes surround both stream networks. The Montana study site is characterized by ponderosa pine (*Pinus ponderosa*) and Douglas-fir (*Pseudotsuga menziesii*) forest, whereas the Idaho study site consists of western red cedar (*Thuja plicata*), western hemlock (*Tsuga heterophylla*), and grand fir (*Abies grandis*) forest. Mean annual precipitation varies between the study sites; Youngs Creek receives an average of 100 cm and Mica Creek receives an average of 140 cm (Western Regional Climate Center, 2007). Additionally, mean maximum and minimum air temperatures taken from 1895 to 2007 varied between the counties in which the stream networks occurred; Youngs Creek (Flathead County) ranged from –23.5 to 28.7°C and Mica Creek (Shoshone County) ranged from –18.1 to 29.7°C (Western Regional Climate Center, 2007).

Study Design.—I distributed my samples throughout each network, including the mainstem, beginning at the confluence with the larger river (i.e., South Fork Flathead and St. Joe) and continued, throughout a subset of third, second, and first-order tributaries, to the mainstem's headwater reaches. I located my sample reaches in first to third-order stream segments and, stratifying each stream segment by order and length, randomly placed a number of sample reaches within each segment (modified from Bury and Corn, 1991; Bury et al., 2002). Based on hypothesized tadpole drift of 4 m per day (see Wahbe and Bunnell, 2001), geomorphic valley segment types, and logistic constraints, I placed my sample reaches 200-1000 m apart to ensure sampling independence (Dupuis and Friele, 2006). Each study reach measured 250 m in length, within which I sampled five randomly selected channel units (1 to 5 m in length). I located each channel unit by unrolling a tape measure from the downstream edge of a designated reach starting point to the downstream edge of the next randomly placed, upstream unit. Based on previous studies concerning *Ascaphus* spp. ecology (e.g., Hawkins et al., 1988), I randomly selected channel units located in low to high-grade riffle habitat. Although some of the reaches were surveyed both of the two sampling years, the channel units sampled within each reach varied with year.

Tadpole Sampling.— I conducted my surveys between late-June and early-August in 2005 and 2006. My sampling occurred during the descending limb of the hydrograph for each stream. I surveyed channel units for tadpoles with a two-person kick sampling team or two-snorkelers during the day between the hours 0900 and 1900. Kick sampling consisted of one person who stabilized two hand-held D-frame nets (0.8 mm mesh) on the downstream edge of the site and another person who lifted large cover items

immediately situated above the nets and kicked through the substrate to facilitate the capture of tadpoles in the nets (Corn and Bury, 1991; Bury et al., 2002). Based on the stream size, I periodically searched the nets for tadpoles, placing any tadpole encountered into a collapsible nylon bucket on the stream bank. I visually categorized tadpoles by age classes based on morphology (Figure 2, Chapter 1; Metter, 1964, 1967) and determined total density and biomass of each age class. Kick sampling worked well in small and intermediate sized streams (first to second-order), but the limitations of this technique were evident in big, swift water. In the larger stream reaches, I snorkeled five randomly selected five m long channel units in each reach (Chapter 1). I increased the size of my channel unit to keep my sample length proportional to my sample width. Because snorkeling is a fairly new and low impact method for estimating stream amphibian density, I overlapped kick sampling and snorkeling in a subset of my channel units and used my estimates to compare the effectiveness of snorkeling for estimating occurrence and abundance of tadpoles; my snorkeling estimates were highly correlated with those obtained from kick sampling at the reach and channel unit scales (Chapter 1). I used age class specific density and length measurements to estimate biomass for the reaches I snorkeled.

Data Analyses.—In both networks, I calculated mean tadpole density and biomass for each stream reach. Based on hypothesized movement patterns (Wahbe and Bunnell, 2001), I located the sampling sites far enough apart to ensure that tadpoles would not move between my sampling reaches during the duration of each season. Though the stream networks were comparable by stream order, they were different in overall size and shape (e.g., bifurcation ratio). Because the stream networks were different I used width

as a surrogate for stream order and compared the mean density and biomass estimates (age specific and combined) with stream width. I compared the differences in tadpole occupancy between and within stream networks using a modified Chi-square test, the Cochran-Mantel-Haenszel (CMH) test, which compares two groups on a binary response by adjusting for additional control variables (e.g., year), thus increasing the power of the test to detect association. Tadpole density and biomass estimates were not normally distributed, and thus did not meet the assumptions of analysis of variance; as a result, I compared my density and biomass estimates between the two streams using nonparametric Mann Whitney-U tests and within my streams the nonparametric Kruskal-Wallis test for 3 or more groups (Mann and Whitney, 1947; Kruskal and Wallis, 1952). To determine if the variation associated with tadpole density and biomass was similar between the two stream networks and sampling years, I compared the coefficient of variation (CV) for each stream and year using non-parametric Mann Whitney-U tests. To determine how individual tadpoles were distributed in space (e.g., clustered, dispersed, or randomly spaced) at the channel unit and reach scale, I estimated an index of dispersion, the coefficient of dispersion (CD):

$$CD = \sigma^2(n - 1)/Y$$

where σ^2 represents the sample variance, n is the sample size, and Y is the sample mean (Southwood, 1978). I compared my CD test statistic for each scale by stream and year in a chi-square test to determine the significance of the distribution at an alpha of 0.05. All analyses were conducted in SAS 9.1 software (SAS, 2003).

Geostatistical Analysis.—I used geostatistical analysis to describe the spatial dependence of tadpole densities within reaches in the two stream networks. Using

ArcGIS 9.2 (ESRI, 2007), I generated distances between channel units within each reach (Dussault and Brochu, 2003) to create a distance matrix of all possible network distances between all channel units within each reach for both streams. I performed logarithmic transformations to all density estimates to meet the assumptions of normality. I generated empirical semivariograms for reaches by calculating the semivariance statistic (γ) for a range of distance intervals (h):

$$\gamma(h) = (1/(2N(h)))*\Sigma[z(s_i)-z(s_i+h)]^2$$

where $N(h)$ represents the number of observation pairs separated by distance h, $z(s_i)$ is the log transformed density of tadpoles at location s_i, and $z(s_i+h)$ is the log transformed tadpole density at distance h from s_i. To meet the geostatistical guideline that each lag distance class was represented by a minimum average of 30 pairs, I combined my distance matrices for the two sampling seasons and used distance intervals of 6.5 m for within reach models. Using an S-PLUS statistical software script (Ganio et al., 2006), I fit a spherical model to the semivariograms to obtain estimates of the range, sill, and nugget (S-PLUS, 2002). The value at which the semivariance levels off to an asymptote is referred to as the "sill," whereas the corresponding lag distance of the sill is referred to as the "range." The sill provides an estimate of total population variance, whereas the range value indicates the distance over which values are spatially correlated, which I interpreted as a patch size, beyond which data (e.g., tadpole densities) are stochastically independent (Rossi et al., 1992; Dent and Grimm, 1999; Ettema and Wardle, 2002). The "nugget" represents the unaccounted-for spatial variance imparted by sampling error or spatial dependence at smaller scales than sampled (Rossi et al., 1992). The difference between the sill and the nugget indicates the proportion of the variance that can be

modeled as spatially dependent (i.e., spatially structured variance) (Rossi et al. 1992). If a sill and range were not apparent and the variogram revealed no spatial structure, I assumed the patterns in tadpole densities within reaches were random (Ettema and Wardle, 2002; Gresswell et al., 2006).

RESULTS

Tailed frog tadpoles were relatively abundant and ubiquitous in both stream networks. I captured 4,471 tailed frog tadpoles in 485 channel units (100 sample reaches) distributed over 124 kilometers of stream in the two networks (Table 1). Tadpoles occupied a similar proportion of channel units in Youngs and Mica for the two seasons (Mean proportions: Mica Creek = 0.725; Youngs Creek = 0.742; CMH $\chi^2 = 0.164$, DF = 1, P = 0.686). Surprisingly, tadpoles in both networks were observed in some of the largest stream reaches (Mica Creek: 13 m width; Youngs Creek: 18 m). Tadpoles did not occupy reaches exceeding 13 m width in Mica Creek or 18 m width in Youngs Creek. Though tadpoles were relatively abundant and ubiquitous in both networks, tadpole abundance and biomass differed in the two streams. Mica Creek, the smaller network (mean width = 3.69 m; SE = ±0.17), had significantly higher tadpole density (3.05/m² ±0.31) and biomass (1.84g/m² ±0.18) estimates than Youngs Creek (mean width = 7.55 m ±0.30; density = 1.33/m² ±0.14; biomass = 1.11g/m² ±0.20; Kruskal-Wallis$_{\text{Density}}$ H = 12.09, DF = 3; P = 0.0071; Kruskal-Wallis$_{Biomass}$ H = 11.80, DF = 3, P = 0.008; Table 1). However, because Youngs Creek's was significantly larger in overall stream width (Kruskal-Wallis$_{Width}$ H = 121.19, DF = 3, P < 0.001), total tadpole abundance was similar in Youngs Creek and Mica Creek (Kruskal-Wallis H = 3.460, DF = 3, P = 0.326). The

coefficient of variation in tadpole density was also similar throughout both networks for both seasons (Kruskal-Wallis H = 0.098, DF = 3, P = 0.992). Additionally, indices of dispersion among channel units showed that tadpole density estimates were highly aggregated or clumped in space for both streams during the two sampling periods (Table 1). When indices of dispersion were compared between reaches, tadpole densities were clumped in both streams, except for Youngs Creek in 2005.

Though tadpole density and biomass exhibited an overall downstream decrease in the networks, patterns in tadpole distribution, density, and biomass were different between the two networks (Figure 1). Tadpole density estimates were strongly correlated with tadpole biomass estimates (log_{10} transformed Linear Regression: $r^2 = 0.783$, DF = 357, P < 0.001). In the headwater branches of Youngs Creek, all reaches near the stream's origin were occupied and had the highest tadpole density (Kruskal-Wallis H = 22.72, DF = 8, P = 0.004). Tadpole density decreased immediately downstream of the Youngs Creek headwater branches, as width exceeded approximately 2 m, but then maintained comparable densities into reaches measuring as wide as 15 m (Kruskal-Wallis H = 12.01, DF = 6, P = 0.062). Interestingly, when tadpole raw abundance was compared across stream widths, no significant difference occurred (Kruskal-Wallis H = 14.85, DF = 8, P = 0.062). In contrast, the Mica Creek headwater branches were not all occupied (Figure 2). Tadpole density increased as stream width approached 4 m, then decreased significantly as stream width increased (Kruskal-Wallis H = 25.48, DF = 4, P < 0.001). Unlike Youngs Creek, tadpole raw abundance significantly decreased with stream width in Mica Creek (Kruskal-Wallis H = 14.34, DF = 4, P = 0.006).

Though both watersheds had three distinguishable tadpole age classes (1-3y) that occupied a similar proportion of channel units, the overall distribution and abundance patterns were significantly different between the two networks. The proportion of occupied channel units occupied by each age class did not differ between networks or seasons (1y: CMH $\chi^2 = 1.697$, DF = 1, P = 0.193; 2y: CMH $\chi^2 = 0.190$, DF = 1, P = 0.6633; 3y: CMH $\chi^2 = 1.494$, DF = 1, P = 0.222). Older tadpoles (2-3y) comprised significantly lower overall densities than the 1y age class in both sampling years (2y: Kruskal-Wallis H = 10.028, DF = 3, P = 0.018; 3y: Kruskal-Wallis H = 9.851, DF = 3, P = 0.020). In addition, tadpoles of the 1y age class in Youngs, along with all age classes in Mica, did not change in their density and biomass estimates between the two sampling years (Table 1). Despite the differences observed between the years for 2y and 3y tadpoles in Youngs Creek, 1y tadpoles on average comprised the highest proportion of the estimated density in both stream networks (Kruskal-Wallis H = 9.270, DF = 2, P = 0.010). No difference was observed between the three age classes in the proportion of biomass they occupied in each channel unit. Although 1y tadpoles were on average twice as abundant as 3y tadpoles, 3y tadpoles were at least twice as massive as 1y tadpoles (Kruskal-Wallis H = 601.049, DF = 2, P < 0.001) and thus comprised a comparable proportion of the biomass in both networks.

The age class distribution patterns differed between and within the two networks. In Youngs Creek, 1y tadpoles appeared to aggregate in headwater reaches that were nearest to the origin of the stream and decreased dramatically with increasing stream size (Figure 2), whereas 3y tadpoles peaked in relative abundance further downstream. In Mica Creek, 1y tadpoles aggregated further upstream, attaining maximum densities 1-2

km downstream of the smallest reaches sampled, whereas 3y appeared to occupy larger reaches further downstream (Figure 2). Comparisons between 1y and 3y tadpoles revealed that, although densities of both age classes decreased with increasing distance downstream, 1y tadpoles decreased significantly more than 3y in both stream networks (ANCOVA). Indices of dispersion at the channel unit scale showed that individuals in all tadpole age classes commonly aggregated within a stream reach (Table 1). However, indices of dispersion between stream reaches revealed that as tadpoles increased in age they became less aggregated and more randomly dispersed throughout both stream networks.

Geostatistical Analysis.— Tailed frog tadpole densities differed in their patchiness between the two stream networks and for different age classes. Although a high degree of spatial variation existed in tailed frog tadpole densities within reaches, moderate to high proportions of the variance contained spatial structure in Youngs Creek. In Youngs Creek, tadpole density values were correlated with separation distance and fitted a spherical theoretical model. The proportion of spatially structured variance within reaches in Youngs Creek was moderate (59%) with tadpole densities exhibiting a patch size of spatial autocorrelation below 82.6 m (Table 2, Figure 3). In contrast, Mica Creek tadpole densities were not correlated to a separation distance and therefore no spherical model parameters were obtained (Table 2, Figure 4). In Youngs Creek, tadpole densities varied in their proportion of spatially structured variance and patch sizes by age class. First year tadpole densities had a high proportion of spatially structured variance (84%) and the smallest patch size (17.2 m), whereas 2y tadpoles had less variance (25%)

and a similar sized patch (18.4 m) and 3y had relatively high proportions of variance (64%) and the largest patches (51.2 m).

DISCUSSION

Rocky Mountain tailed frog tadpoles were abundant in both stream networks. In both networks, tadpole densities exceeded those previously reported in the literature, with maximum densities exceeding 45 tadpoles/m² in both headwaters (Bury, 1988; Hawkins et al., 1988, Corn and Bury, 1989). Although tadpole densities were highly variable, tadpoles occurred throughout both 5th order stream networks. The high relative densities, biomass estimates, and extensive distribution of tadpoles within both networks appears to be attributed to a suite of physical habitat variables across multiple spatial scales, ranging from geology and temperature at the network scale, to cobble size, embeddedness, and food availability at the transect scale (Chapter 3).

Although tadpoles were similar in their density metrics at the scale of the stream network, tadpoles varied in the spatial distribution and abundance patterns between the two stream networks. Tadpoles occurred in higher densities in headwater stream reaches, but peak densities did not occur at the same longitudinal position in the two networks, which may be attributed to network scale differences such as the network structure (connectivity and juxtaposition of stream branches), or the flood disturbance and temperature regimes. Tadpoles in Youngs Creek, a glacial and lake fed stream system, peaked in density closer to the stream's origin, whereas tadpoles in Mica Creek, a spring fed stream network, peaked in density further downstream. This difference in the stream origins may affect the quality of headwater habitat for tadpoles, as well as for juveniles

and adults. Hunter (1998) and Wahbe et al. (2004) hypothesized that tailed frogs may exhibit a colonization cycle similar to that observed with stream invertebrates (Müller, 1974), with peak tadpole densities occurring downstream of peak post-metamorph densities due to downstream tadpole drift and post-metamorph and adult recolonization in headwater reaches. Although I did not target juvenile (n = 18) and adult tailed frogs (n = 143), I did observe a higher concentration of both age classes throughout the upper reaches of the headwaters in Mica Creek; I observed no juveniles and few adults (n = 17) in Youngs Creek, and those were located primarily in headwaters (Jones, unpublished data). A higher proportion of reproductively mature adults in the headwaters should directly result in a higher proportion of egg deposition sites in those headwater stream reaches. Because 1y tadpoles over-winter and experience peak annual discharge before my sampling periods, it is likely that 1y tadpoles peak in density immediately downstream from high quality adult habitat. To evaluate this relationship, future studies on *Ascaphus* spp. movement patterns should consider using drift sampling techniques to asses tadpole movement during peak run-off periods.

Network structure may also influence tadpole distribution and abundance patterns, particularly downstream. Network structure and flood disturbance regimes are largely dependent upon topography, geology, and climate. Although the overall elevation relief within the two drainages is similar, Youngs Creek has a steeper gradient in the headwater reaches than Mica Creek. This steep gradient, coupled with differences in parent geology and snowmelt regime in Youngs Creek results in higher magnitude, shorter duration, flood pulses, which pushes floods through the network more rapidly than in Mica Creek, which experiences frequent rain on snow events and thus lower magnitude, longer

duration flood pulses (Chapter 3). The higher magnitude and shorter duration flood pulses can remove smaller barriers to amphibian dispersal (e.g., large woody debris; Hauer et al., 1999), which may increase passive movement of tadpoles into larger stream reaches, further downstream (Wahbe and Bunnell, 2001). Although the surrounding landscapes of both networks consisted largely of metamorphic rock (e.g., quartzite and argillite), they differed in the geological composition of the stream channel. The unembedded glacial alluvium deposited along Youngs Creek may provide adequate tadpole refugia from the headwater to >15 m wide stream reaches, located over 30 km downstream. Whereas, the more embedded meta-sedimentary substrate and the occurrence of bedrock exposed in the downstream reaches of Mica Creek may provide less refugia for tadpoles inhabiting lower gradient, downstream riffles. Finally, higher mean stream temperatures observed in Mica Creek may further restrict tadpole distribution and abundance patterns; however, recent evidence supports Rocky Mountain tailed frog tadpoles may have a higher thermal tolerance than previously thought (Dunham et al., 2007).

Tadpole distribution and abundance patterns varied with ontogeny. The fundamental differences in the hydrologic and temperature regimes of the two streams may explain some variation observed between tadpole age classes. I observed first year tadpoles aggregating more in the headwaters, whereas 3y were found further downstream, particularly in Youngs Creek. Although tadpoles experienced substantial mortality with ontogeny, biomass increased with age. Thus, larger bodied animals that comprise higher proportions of downstream-reach densities may undergo niche shifts (i.e., physiological, ecological), which are driven by ontogeny and drift. DeVlaming and

Bury (1970) observed that *in vitro*, older *A. truei* tadpoles selected habitat at higher temperatures than 1y tadpoles. Ecologically, the larger stream reaches may provide important habitat (e.g., less competition, more forage) for larger tadpoles, which play important roles as colonizers upon completing metamorphosis (Daugherty and Sheldon, 1982; Matsuda and Richardson, 2000; Matsuda and Richardson, 2005).

Tailed frogs tadpoles are patchy in their abundance within and between stream networks. Because tailed frogs disperse among streams, aggregations of frogs may not represent distinct populations (Wahbe et al., 2004), but instead may represent spatially correlated patches, which may function as important metapopulations that are prone to local extinction and recolonization events (Hanski and Simberloff, 1997). In Youngs Creek, moderate to high proportions of the variance observed between riffle-pool sequences contained spatial structure. Variance became spatially independent, or stochastic, within the scale of a sample reach (125 m). Additionally, 3y tadpoles were spatially correlated at three times the patch size of younger tadpoles age classes, supporting the notion that 3y tadpoles may drift greater distances and exhibit larger-scale movements in general. In Mica Creek, tadpole densities lacked spatial structure within stream reaches. One explanation may be that because Youngs Creek maintains a higher annual flood pulse, tadpoles, particularly 3y, may drift more and exhibit less site fidelity than in Mica Creek.

Because I did not sample tadpoles in a spatially continuous fashion, it is possible that I unknowingly missed the scale (or scales) at which tadpoles were spatially structured. Although I rigorously sampled throughout each stream network, my hierarchically nested sampling design (channel units, reaches, segments, stream orders,

networks) ensured that all spatial scales were far enough apart to ensure that tadpoles would not move between the sampling units during the duration of my sampling, thus at the reach scale and beyond I successfully minimized spatial autocorrelation. However, the nugget effect observed in both Youngs and Mica creeks indicates that either experimental error added additional variance or additional spatial variability existed below the minimum lag distance (6.5 m; Rossi et al., 1992). Field observations were made that suggested spatial variability existed below my minimum lag distance. Through the snorkeling surveys, tadpoles were confirmed to exhibit a high degree of patchiness within riffles (at scales < 5 m) throughout both stream networks, where they were commonly observed aggregating under one single rock or group of rocks (Jones, unpublished data).

In this study I found that patterns in tadpole distribution and abundance vary between drainages that are not separated by much geographic distance, as well as between tadpole age classes. Although both streams I studied had relatively high tadpole densities, my observations suggest generalized models that attempt to explain tadpole distribution and abundance may not always be adequate for predicting occurrence or abundance from one drainage to the next, or even from one age class to the next. Studies modeling habitat variables across biogeoclimatically different streams should consider that inherent differences in the distribution and abundance pattern from one stream to the next might confound the results of general habitat models for a particular species. Additionally, tadpoles occurred throughout the stream networks; larger streams that appear on the periphery of distribution may be ecologically important for development of older age classes and the dispersal of postmetamorphs within and between stream

networks. Future studies could benefit from expanding the spatial extent of sampling beyond headwater streams, particularly when drift, and presumably niche shifts, may occur with ontogeny. If studies continually focus on headwater streams and regard the larger branches where species may occur as noise, I may fail to detect the influence that the larger networks has on a species ecology. Finally, because *A. montanus* tadpoles abundances are a commonly used index for measuring stream quality, and management practices vary across their range, resource managers interested in conserving tailed frog populations should understand that intraspecific variation can exist and that geography and ontogeny influence patch size.

TABLES

Table 1. Sites sampled and proportion of sites occupied for *Ascaphus montanus* tadpoles by age class in Mica Creek, Idaho, and Youngs Creek, Montana for 2005-2006.

Stream	Year	Metric	N	1Y	2Y	3Y	All Tadpoles
Mica	2005	Raw Abundance	100	319	165	148	632
	2006	Raw Abundance	144	1038	386	198	1622
	2005	Mean Abundance	100	3.19 (±0.65)	1.65 (±0.24)	1.48 (±0.38)	6.32 (±0.87)
	2006	Mean Abundance	144	7.21 (±1.47)	2.68 (±0.45)	1.38 (±0.31)	11.26 (±2.05)
	2005	Occupied Channel Units	100	49 (49%)	56 (56%)	41 (41%)	72 (72%)
	2006	Occupied Channel Units	144	84 (58.3%)	75 (52%)	57 (39%)	105 (72.9%)
	2005	Mean Density	100	1.74 (±0.40)	0.76 (±0.11)	0.54 (±0.12)	3.04 (±0.47)
	2006	Mean Density	144	2.06 (±0.38)	0.68 (±0.12)	0.42 (±0.09)	3.16 (±0.53)
	2005	Proportion of Density	100	42.1% (±4.3)	36.5% (±3.6)	21.4% (±3.2)	
	2006	Proportion of Density	144	54.0% (±3.5)	29.2% (±3.0)	16.8% (±2.4)	
	2005	Mean Biomass	100	0.45 (±0.09)	0.65 (±0.09)	0.96 (±0.25)	2.07 (±0.31)
	2006	Mean Biomass	144	0.64(±0.11)	0.57 (±0.10)	0.69 (±0.15)	1.90 (±0.30)
	2005	Proportion of Biomass	100	29.5% (±4.2)	40.5% (±4.0)	30.0% (±4.1)	
	2006	Proportion of Biomass	144	37.8% (±3.3)	33.3% (±3.0)	28.9% (±3.1)	
	2005	Coefficient of Variation	21	1.10 (±0.10)	1.24 (±0.12)	1.38 (±0.11)	1.58 (±0.10)
	2006	Coefficient of Variation	30	1.01 (±0.06)	1.08 (±0.07)	1.20(±0.08)	1.53 (±0.10)
	2005	Co. of Disp.-Channel	100	8.99 (P<0.01)	1.6 (P<0.01)	2.57 (P<0.01)	7.35 (P<0.01)
	2006	Co. of Disp.-Channel	144	9.82 (P<0.01)	2.91 (P<0.01)	1.13 (P=0.15)	9.76 (P<0.01)
	2005	Co. of Disp.-Reach	21	3.06 (P<0.01)	1.18 (P=0.33)	1.17 (P=0.33)	3.62 (P<0.01)
	2006	Co. of Disp.-Reach	30	1.96 (P<0.01)	1.30 (P=0.18)	0.59 (P=0.05)	2.72 (P<0.01)
Youngs	2005	Raw Abundance	130	481	552	366	1399
	2006	Raw Abundance	111	415	249	154	818
	2005	Mean Abundance	130	3.70 (±0.74)	4.25 (±0.84)	2.82 (±0.51)	10.76 (±1.75)
	2006	Mean Abundance	111	3.74 (±0.64)	2.24 (±0.50)	1.39 (±0.32)	7.37 (±1.17)
	2005	Occupied channel units	130	75 (57.7%)	76 (58.5%)	72 (55.4%)	100 (76.9%)
	2006	Occupied channel units	111	65 (58.6%)	62 (55.9%)	46 (41.4%)	81 (73.0%)
	2005	Mean Density	130	0.91 (±0.17)	0.87 (±0.14)	0.57 (±0.12)	2.34 (±0.32)
	2006	Mean Density	111	1.02 (±0.39)	0.26 (±0.04)	0.13 (±0.03)	1.41 (±0.40)
	2005	Proportion of Density	130	36.4% (±3.2)	35.5% (±3.1)	28.1% (±3.5)	
	2006	Proportion of Density	111	49.9% (±3.8)	28.7% (±3.4)	21.5% (±3.9)	
	2005	Mean Biomass	130	0.24 (±0.06)	0.55 (±0.09)	0.88 (±0.17)	1.67 (±0.24)
	2006	Mean Biomass	111	0.27 (±0.10)	0.25 (±0.04)	0.25 (±0.05)	0.77 (±0.13)
	2005	Proportion of Biomass	130	22.3% (±3.2)	35.1% (±3.1)	42.1 (±3.5)	
	2006	Proportion of Biomass	111	31.2% (±3.9)	34.6% (±3.4)	33.3 (±3.9)	
	2005	Coefficient of Variation	26	1.023 (±0.09)	1.27 (±0.10)	1.21 (±0.12)	1.22 (±0.12)
	2006	Coefficient of Variation	23	1.24 (±0.09)	1.47 (±0.11)	1.44 (±0.12)	1.64 (±0.10)
	2005	Coefficient of Dispersal	130	1.12 (P=0.19)	0.63 (P<0.01)	3.64 (P<0.01)	2.69 (P<0.01)
	2006	Coefficient of Dispersal	111	14.9 (P<0.01)	3.35 (P<0.01)	3.74 (P<0.01)	16.7 (P<0.01)
	2005	Coefficient of Dispersal	26	0.58 (P=0.04)	0.46 (P<0.01)	0.98 (P=0.55)	1.23 (P=0.23)
	2006	Coefficient of Dispersal	23	3.80 (P<0.01)	1.04 (P=0.47)	1.17 (P=0.05)	4.80 (P<0.01)

Table 2. Spatial structure of tadpoles in Youngs Creek and Mica Creek. For all models, the nugget variance, sill variance, structural variance, and range (patch size) are given. Mica Creek tadpoles did not fit any model (---).

Youngs Creek Tadpoles	All tadpoles	1y	2y	3y
Range (m)	84.124	17.206	18.376	51.180
Sill (C_o + C)	0.609	0.668	0.401	0.307
Nugget (C_o)	0.591	0.103	0.302	0.111
Structural Variance (C/C_o + C)	0.588	0.867	0.570	0.734
Fitted Model	Spherical	Spherical	Spherical	Spherical
Mica Creek Tadpoles				
Range (m)	> 125.00	31.311	0.941	0.249
Sill (C_o + C)	41.029	0.000	0.133	0.025
Nugget (C_o)	0.984	0.887	0.454	0.416
Structural Variance (C/C_o + C)	0.998	0.000	0.226	0.057
Fitted Model	---	---	---	---

FIGURE CAPTIONS

Figure 1. The longitudinal distribution of Rocky Mountain tailed frog (*Ascaphus montanus*) tadpole density along varying sizes of stream branches in the Youngs Creek and Mica Creek networks. Each point represents the mean density or biomass at each stream width. The error bars surrounding each mean represent the standard error.

Figure 2. The proportion of 1y and 3y Rocky Mountain tailed frog tadpoles distributed across Youngs Creek. With increasing stream width, 1y tadpoles decreased dramatically in the proportion of the total density they occupied. The proportion of 3y tadpoles increased with increasing stream width, whereas their actual densities remained comparable throughout the network (Figure 1).

Figure 3. Empirical variograms of Rocky Mountain tailed frog tadpole densities in Youngs Creek for all age classes of tadpoles (a), 1y (b), 2y (c), and 3y (d) tadpoles. Variograms show the semivariance (γ) as a function of the separation distance (m).

Figure 4. Empirical variograms of Rocky Mountain tailed frog tadpole densities in Mica Creek for all age classes of tadpoles (a), 1y (b), 2y (c), and 3y (d) tadpoles. Variograms show the semivariance (γ) as a function of the separation distance (m).

FIGURES

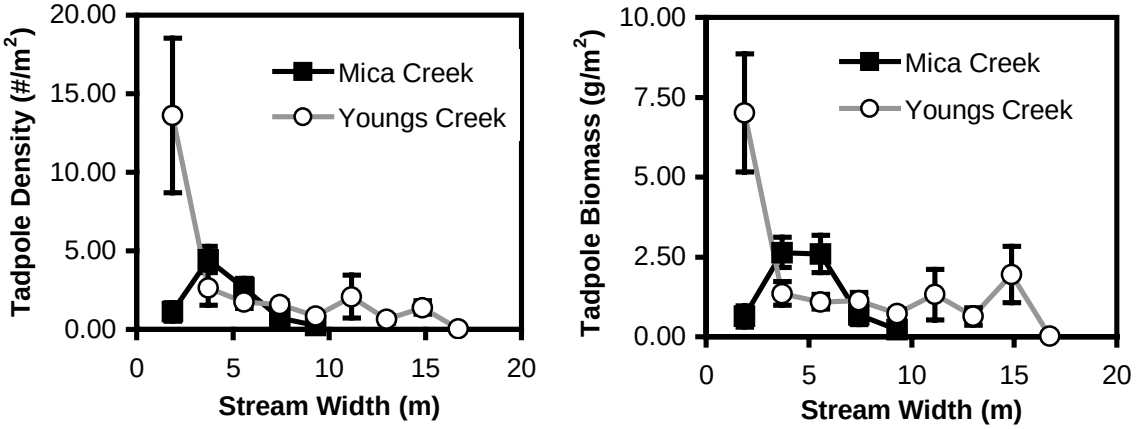


Figure 1.

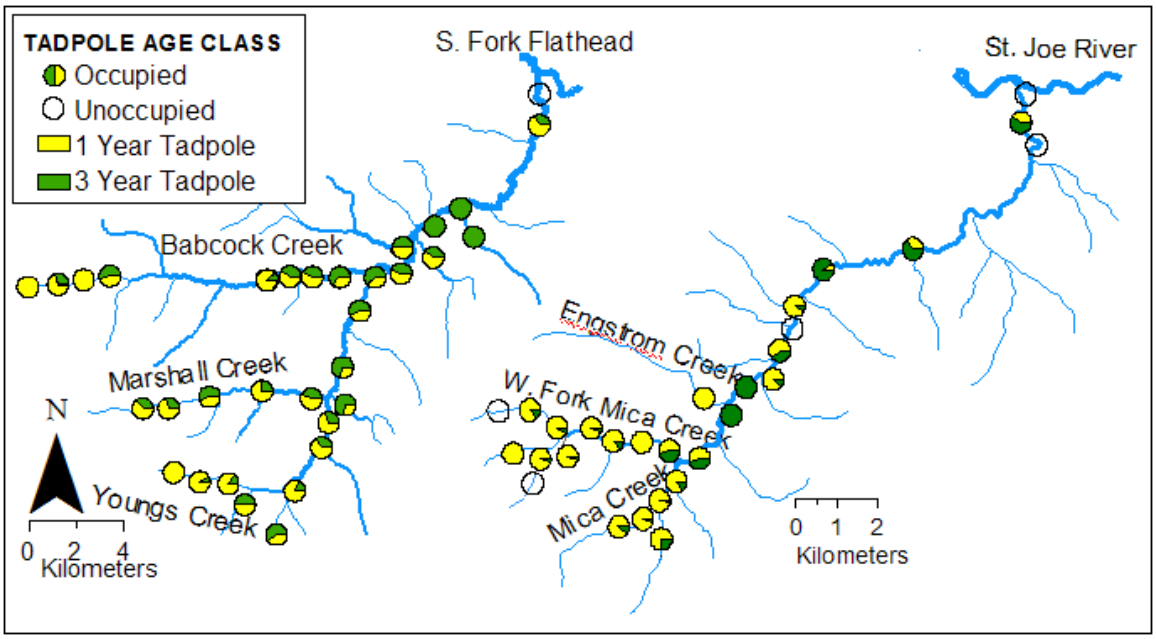

TADPOLE AGE CLASS
Occupied
Unoccupied
1 Year Tadpole
3 Year Tadpole
S. Fork Flathead
St. Joe River
Babcock Creek
Engstrom Creek
Marshall Creek
W. Fork Mica Creek
Mica Creek
Youngs Creek
N
0 2 4
Kilometers
0 1 2
Kilometers

Figure 2.

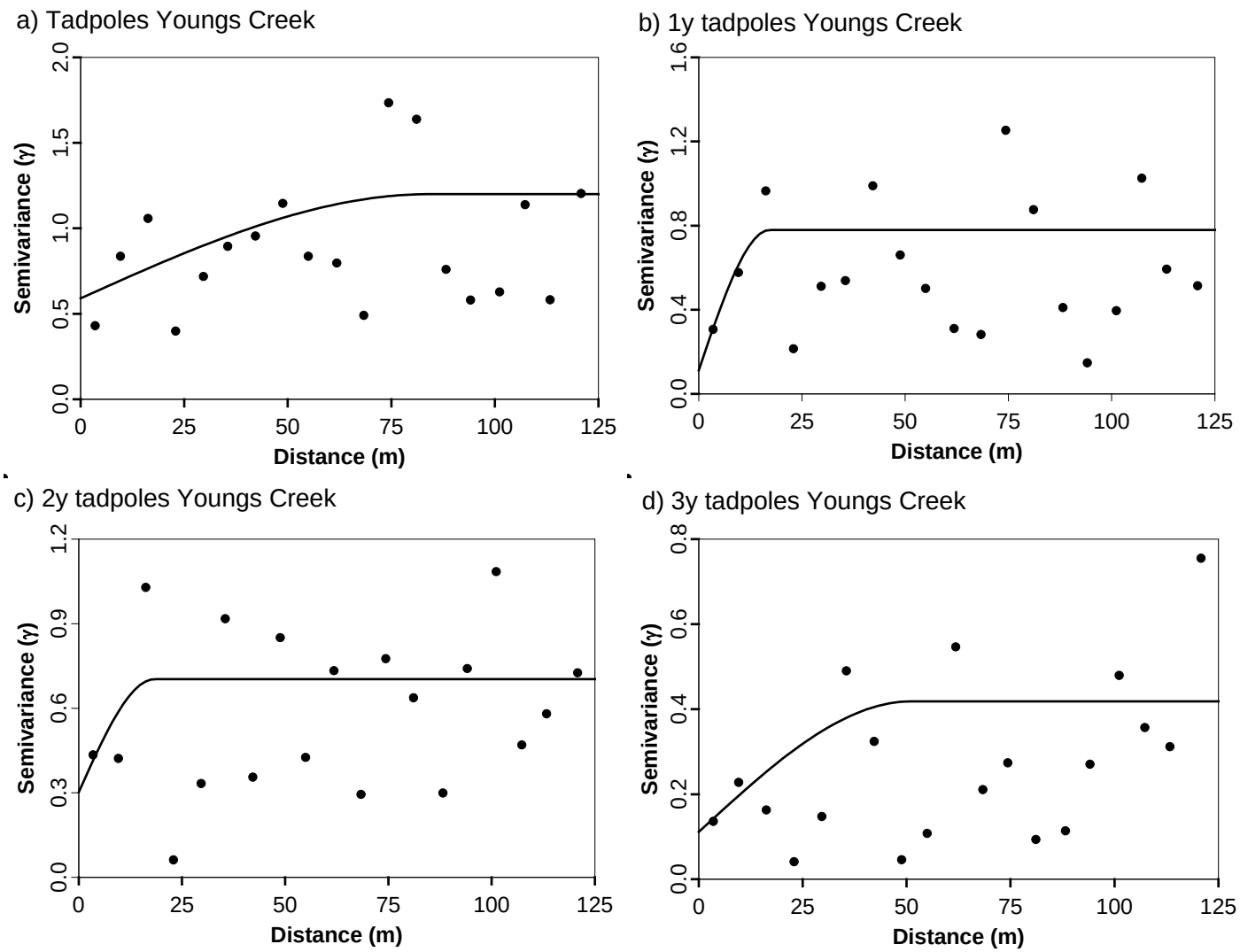

a) Tadpoles Youngs Creek
b) 1y tadpoles Youngs Creek
c) 2y tadpoles Youngs Creek
d) 3y tadpoles Youngs Creek
Semivariance (γ)
Distance (m)
0.0
0.5
1.0
1.5
2.0
0.4
0.8
1.2
1.6
0.3
0.6
0.9
0.2
0
25
50
75
100
125

Figure 3.

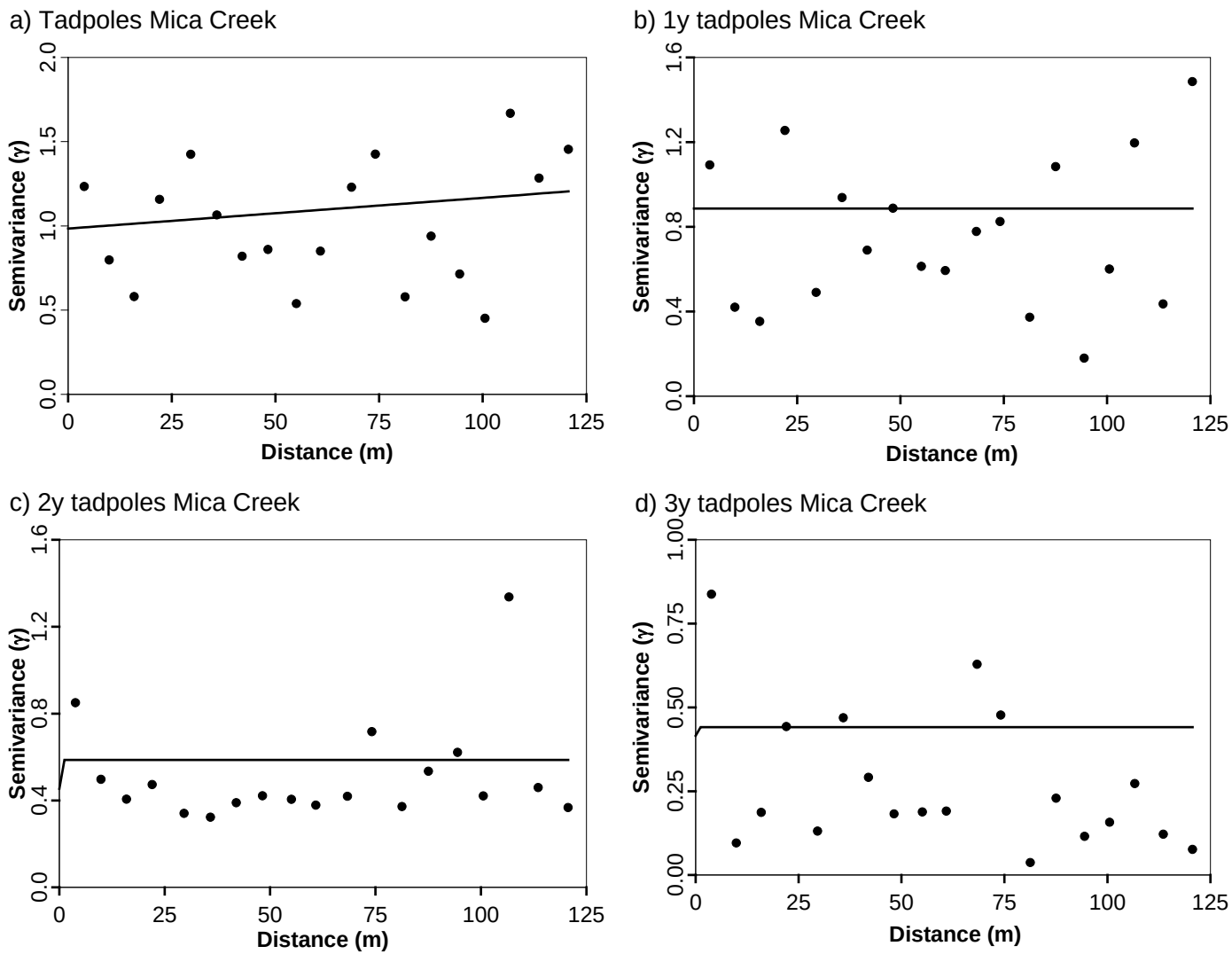

a) Tadpoles Mica Creek
b) 1y tadpoles Mica Creek
c) 2y tadpoles Mica Creek
d) 3y tadpoles Mica Creek
Semivariance (γ)
Distance (m)
0.0
0.5
1.0
1.5
2.0
0.4
0.8
1.2
1.6
0.00
0.25
0.50
0.75
1.00
0
25
50
75
100
125

Figure 4.

Chapter 3: Rocks to regions: Factors influencing *Ascaphus montanus* tadpole abundance at multiple spatial scales

INTRODUCTION

Ecologists now recognize the importance of studies that encompass multiple spatial scales in order to evaluate factors affecting the distribution and abundance of organisms (Weins, 1989; Levins, 1992; Bissonette, 1997), and this trend is increasingly more evident in studies of vertebrate taxa in stream ecosystems (c.f., Torgersen and Close, 2004; Dupuis and Friele, 2006). Though recent investigations regarding the ecology of stream dwelling amphibians have applied multi-scale approaches (Diller and Wallace, 1996; Welsh and Lind, 2002; Russell et al., 2004; Stoddard and Hayes, 2005; Dupuis and Friele, 2006), the scope of these and most other studies have focused on identifying physical habitat associations in headwater stream basins where they are known to be abundant (Burton and Likens, 1975; Hawkins et al., 1983; Nussbaum et al., 1983; Bury and Corn, 1989; Leonard et al., 1993). Thus, present understanding of the ecology of these taxa in stream ecosystems may be constrained by the scope of past sampling efforts (for review see Chapter 2), and therefore an understanding of how factors may affect amphibian distribution and abundance across multiple spatial scales in stream networks is needed.

Although the Rocky Mountain (RM) tailed frog (*Ascaphus montanus*) is an abundant and widely distributed stream amphibian (Nussbaum et al., 1983), the understanding of physical habitat characteristics influencing their abundance has been based primarily on single, relatively small, scale studies (for a review see Dupuis and Friele, 2006). Studies investigating the relationships between habitat factors and tadpole abundance of both the RM and the closely related coastal tailed frog (*A. truei*) have been limited to headwater streams (1st – 3rd order) and conducted at the scale of the channel

unit (0.1-2 m), the reach (10-100 m), or both (Noble and Putnam, 1931; Metter, 1964; Hawkins et al., 1988; Bury and Corn, 1991; Welsh and Ollivier, 1998; Adams and Frissell, 2001). Within the past decade, several studies have investigated the abiotic factors influencing coastal tailed frog tadpoles at broader spatial scales (e.g., stream, sub-basin, and watershed scales; Diller and Wallace, 1999; Welsh and Lind, 2002; Stoddard and Hayes, 2005), but only one has applied this to RM tailed frog (Dupuis and Friele, 2006). However, no studies have compared the factors influencing tailed frog tadpole abundance across multiple scales throughout relatively large, intact stream networks.

Although most research has focused on the relationships between the physical habitat factors and tadpole abundance, there have been few investigations of the influence of biotic factors on tadpole abundance, particularly for the RM tailed frog. The RM tailed frog tadpole, like the coastal tailed frog, is thought to feed primarily on the benthic biofilm, or the biomass of chlorophyll-*a* (Metter, 1964; Franz, 1970), which includes a diverse community of algae and diatoms along with heterotrophic microbes and detritus (Weitzel, 1979). The understanding of the relationship between RM tailed frog tadpoles and food has been largely based on coastal tailed frog gut content analysis (Metter, 1964, Franz, 1970) and small-scale studies of coastal tailed frogs (Kiffney and Richardson, 2001; Kim and Richardson, 2000). Additionally, a broad taxonomic range of aquatic predators may influence, through direct consumption or chemical cues, tailed frog tadpole distribution and abundance (Feminella and Hawkins, 1994). Although it is not known whether RM tailed frog tadpoles are as strongly influenced by predatory taxa, their occurrence throughout fish bearing streams suggests that predation may not play a major role on their distribution and abundance. Understanding how and at what spatial

scale tadpoles are influenced by the biomass of chlorophyll-*a* and predation, and how this may vary with habitat context, would ultimately assist in identifying the importance of biotic interactions on tadpole distribution and abundance and may reveal the trophic role(s) this abundant grazer is playing in stream ecosystems.

Few studies regarding stream amphibians have considered the differences in habitat use or biotic interactions that may occur with stages of larval development. Although most stream tadpoles appear to require less than one year to complete metamorphosis, tailed frogs experience prolonged larval development (≥2 years; Metter, 1964), which can result in pronounced changes in distribution and abundance (c.f., Chapter 2). Changes in an organism's distribution and abundance, coupled with significant increases in body size can result in ecological niche shifts (Wilbur, 1980). For instance, through *in vitro* investigations DeVlaming and Bury (1970) illustrated that coastal tailed frog tadpoles exhibited significant shifts in habitat selection with development. Likewise, as tadpoles grow they may exhibit shifts in diet (see Kupferberg, 1997) and may change in vulnerability to predation (Blair and Wasserberg 2000; Relyea, 2003). Because RM tailed frog tadpoles experience prolonged larval development with significant changes in size (Metter, 1964), factors affecting the distribution and abundance of first year tadpoles (1y) may differ from those influencing tadpoles nearing metamorphosis, but this has not been investigated.

Although regional variation in distribution and abundance patterns exist for RM tailed frog tadpoles (Chapter 2), understanding of whether abiotic and biotic factors change in their influence on tadpoles across biogeoclimatically distinct stream networks is lacking. As an example, in British Columbia, coastal tailed frog tadpoles appeared to

be limited by nutrients, thus an increase in basal nutrients (nitrogen and phosphorus) resulted in higher tadpole biomass, with no apparent corresponding decrease in the biomass of chlorophyll-*a* biomass (Kiffney and Richardson, 2001). However, variation exists in stream systems within and between regions, with some streams exhibiting higher tadpole densities with decreased the biomass of chlorophyll-*a* growth (Kim and Richardson, 2000; Mallory and Richardson, 2005). Understanding the resources that may limit the distribution and abundance of a species, and how these resources may change between regions, is important for understanding broad ecosystem processes and will assist managers in species and ecosystem based conservation strategies, particularly for those species who's range encompasses strong biogeoclimatic gradients.

The goal of the study was to evaluate the influence of abiotic and biotic factors on RM tailed frog tadpole densities across a nested hierarchy of spatial scales across two large, biogeoclimatically distinct stream networks. Specifically, the objectives were to use an information-theoretic (IT) modeling approach (Burnham and Anderson, 1998) to (1) examine habitat relationships at the channel unit, reach, and sub-basin scales, (2) examine the importance of the biomass of chlorophyll-*a* and predation versus abiotic models for explaining RM tailed frog tadpole abundance at the channel unit and reach scales respectively, (3) determine whether abiotic and biotic relationships shift for older tadpole age classes, and (4) evaluate the differences observed in tadpole ecology between the two biogeoclimatically different stream networks based on the model outputs.

MATERIALS AND METHODS

Study Area.—I conducted the study in two third-order stream networks (Strahler, 1964): Youngs Creek (302 km²), in the South Fork of the Flathead basin of northwestern Montana, and Mica Creek (103 km²), in the St. Joe basin of northern Idaho (Figure 1, Chapter 1). Because both networks were known to have relatively high and comparable densities of tailed frog tadpoles (Lohman, 2002; *G. Grisak pers. comm.*; Chapter 2), any differences in tadpole densities appeared to not obscure the findings, but instead allowed for comparisons between the biogeoclimatic distinct networks. Comparisons of the factors influencing tadpole density between the study streams represented the broadest spatial scale of the investigation. Although elevation ranges of the study areas overlap (Youngs Creek 1380 to 2200 m; Mica Creek 975 to 1450 m) and both have moderate to steep forested slopes, the networks occupied two biogeoclimatically distinct regions. The Montana study site is characterized by ponderosa pine (*Pinus ponderosa*) and Douglas-fir (*Pseudotsuga menziesii*) forest, whereas the Idaho study site consists of western red cedar (*Thuja plicata*), western hemlock (*Tsuga heterophylla*), and grand fir (*Abies grandis*) forest. The geology of the Youngs Creek watershed consists primarily of quartzite, with deposits of alluvium from glacial drift lining the bottom of the mainstem drainage (Taylor et al., 1985). Whereas that of the Mica Creek watershed consists of layers of the Wallace Formation (quartzite, siltite, and argillite) and belts of igneous (gabbro and basalt) and sedimentary rocks on downstream segments (Lewis et al., 2000). Mean annual precipitation varies between the study sites; Youngs Creek receives an average of 100 cm and Mica Creek receives an average of 140 cm (Western Regional Climate Center, 2007). Additionally, mean maximum and minimum air temperatures taken from

1895 to 2007 varied between the counties in which the stream networks occurred; Youngs Creek (Flathead County) ranged from –23.5 to 28.7°C and Mica Creek (Shoshone County) ranged from –18.1 to 29.7°C (Western Regional Climate Center, 2007).

Sampling Design.—Within each network, I distributed study reaches along the mainstem, beginning at the confluence with the larger river (i.e., South Fork Flathead and St. Joe rivers) and continued, throughout a subset of third, second, and first-order tributaries, to the mainstem's headwaters. Sampling reaches represented the intermediate spatial scale of the investigation. All sampling reaches were located in perennial streams. I randomly placed up to four study reaches within each segment of a given stream order, depending on the length of the segment (modified from Bury and Corn, 1991; Bury et al., 2002). I located the 250 m study reaches 250-1000 m apart to ensure sampling independence (Wahbe and Bunnell, 2001). Within each reach, I randomly selected five channel units (1 to 5 m in length) for sampling. I located these channel units by unrolling a tape measure from the downstream starting point of a designated reach to the downstream edge of the next randomly placed, upstream channel unit. Following previous studies of *Ascaphus* spp. ecology (e.g., Hawkins et al., 1988), I stratified the sampling by channel unit type, then focused on randomly sampling channel units located in low to high-gradient riffle habitat because of (1) methodological constraints, and (2) the correlation of tadpoles to such riffle habitats (Nussbaum et al., 1983). To maintain a high detection probability for tadpoles when kick sampling (Chapter 1), I relocated channel units that were located in pools or deep riffles to the nearest upstream channel unit of appropriate depth (≤ 40 cm).

Animal Sampling.— I conducted surveys between late-June and early-August in 2005 and 2006. Sampling occurred during the descending limb of the hydrograph for each stream. Although some of the study reaches were sampled in both years, the channel units selected within each reach varied by year. Channel units were surveyed for tadpoles using a two-person kick sampling team or two-snorkelers during the day between the hours 0900 and 1900. Kick sampling consisted of one person who stabilized two hand-held D-frame nets (0.8 mm mesh) on the downstream edge of the site and another person who lifted large cover items immediately situated above the nets and kicked through the substrate to facilitate the capture of tadpoles in the nets (Corn and Bury, 1991; Bury et al., 2002). Based on the stream size, the workers periodically searched the nets for tadpoles, placing any tadpole encountered into a collapsible nylon bucket on the streambank, workers segregated tadpoles by age classes (1-3 year; Metter, 1964, 1967). Kick sampling worked well in small and intermediate sized streams (first to third-order), but the limitations of this technique were evident in larger, swifter water. In the larger stream reaches, workers snorkeled five randomly selected 5 m long channel units in each reach. When snorkeling in larger study reaches, I increased the size of sampling units to keep sample unit length proportional to width. Because snorkeling is a fairly new and low impact method for estimating stream amphibian density, I conducted both kick sampling and snorkeling in a subset of sample units and compared estimates of tadpole occurrence and abundance; snorkeling estimates were highly correlated with those obtained via kick sampling at the reach and channel unit scales (Chapter 1).

Habitat Variables.—I used the results from more than 30 studies concerning *Ascaphus* spp. tadpole ecology, and my own preliminary observations to guide selection

of environmental variables that I measured in the field. The habitat variables I used were obtained in the field or from geographic information system (GIS) data layers (Table 1, Appendix 1). Though many habitat variables were measured at the channel unit scale, I used means, maximums, and binomial values for a sub-set of these variables to analyze tadpole density-habitat associations at larger spatial scales. At the channel unit scale, six habitat variable categories were measured, two of which contained sub-categories, for a total of 15 possible variables: substrate (six categories), embeddedness (five categories), water velocity, stream width, large woody debris, and gradient. A modified Wolman's pebble count was used for estimating the percentage of six substrate size categories and 5 substrate embeddedness categories at the downstream end of each channel unit before sampling for tadpoles (Appendix 1). I visually estimated the percentage of large woody debris and canopy cover in and over each channel unit, respectively. I also measured the stream's wetted width and calculated a mean laminar water velocity across each channel unit by averaging the time required for a bobber to move one meter over three runs (Diller and Wallace, 1999) (Appendix 1). Gradient for each sampled channel unit was derived from digital elevation models (DEMs) by obtaining the maximum percent change in slope from one 10m cell to the next.

To obtain the biomass of chlorophyll-*a* standing crop biomass, I randomly selected from a uniform distribution a minimum of 12 study reaches throughout each network. In an attempt to sample over a two-week window during the period of peak primary production, and also to facilitate comparisons between the streams, I sampled the biomass of chlorophyll-*a* in both streams between July 21 and August 4, 2006. Within each reach, I randomly selected three channel units to sample for the biomass of

chlorophyll-*a*; in each channel unit I sampled a known area of five rocks, which were randomly selected from the thalweg, but had a flat and large enough surface area to obtain a sample of the biomass of chlorophyll-*a* (Davis et al., 2001). I labeled and froze samples immediately in dry ice until they were processed in the laboratory using standard protocols (APHA, 1995). I estimated the mean biomass of chlorophyll-*a*, a widely accepted index of the biomass of primary producers (Steinmann, et al., 2006), for each channel unit that I sampled.

At the reach scale, I considered seven predictor variables influencing tadpole abundance: heat load index, elevation, temperature, substrate size, substrate embeddedness, fish presence, and basin context (e.g., headwater sub-basin or mainstem). Because six habitat variables were measured at the channel unit scale, but were considered in the literature to be important predictor variables at the reach scale, I used mean (heat load index, elevation, gradient, substrate embeddedness and size), maximum (point water temperature), and binomial (fish presence) estimates in the analysis (see below). I measured aspect at each channel unit using a hand held compass, and transformed stream aspect in degrees (θ) into a unitless heat load index, with a maximum value (1) when aspect was SW and minimum (0) when aspect was NE, using the equation: heat load index = $(1 - \cos(\theta - 45))/2$ (Equation 1) (Beers et al., 1966; Stoddard and Hayes, 2005). The mean heat load index was then calculated for each reach. I also measured stream temperature in the thalweg of each channel unit with a hand held thermometer (±0.5°C). Because water temperature varies temporally, the maximum temperatures were calculated for each stream segment, thus stream reaches within a segment were assigned the maximum water temperature obtained within their

corresponding segment. Using 10 m DEMs in ArcGIS, I calculated the mean elevation and gradient at each reach. Because barriers to fish movement were rarely present within a reach, I documented the presence and species composition of all fish observed during and between the sampling of channel units. At the sub-basin scale, I evaluated two habitat variables that I expected might influence tadpole abundance: mean basin aspect and basin elevation range. I classified sub-basins into 3rd order basins or mainstem ($\geq$ 3rd order); I considered smaller tributaries ($\leq$ 2nd order) occurring along the mainstem, but adjacent to a sub-basin, as part of the sub-basin.

Data Analyses.—I used an AIC based approach to rank the importance of each linear models and the habitat variables at each spatial scale in explaining tadpole abundance. In both networks, I calculated and used tadpole density at the channel unit as the response variable. At subsequent spatial scales, I estimated and used the mean tadpole density as the response variable. Based on the distribution of the tadpole density residuals, I performed a logarithmic transformation to meet the assumption of normal distribution for parametric analysis. I used PROC MIXED linear models (SAS, 2003) to evaluate and draw inference regarding factors influencing tadpole density at each spatial scale. Additionally, PROC MIXED models also allowed me to control for stochastic (RANDOM), nested effects at each scale (i.e., region, sub-basin, segment, reach), and constrain analysis to the variation associated with each of the spatial scales of interest. I pooled data for each field season and treated year as a RANDOM effect in the PROC MIXED model, as I was not attempting to address patterns in annual variation across the two stream networks.

To determine what factors influenced tadpoles across a hierarchy of spatial scales, I used the information-theoretic Akaike's information criterion (AIC) approach. AIC is based on the Kullback-Leibler information, which represents the relationship between the maximum likelihood and the information lost when a model attempts to approximate reality (Anderson et al., 2000). AIC requires careful consideration in determining the set of candidate *a priori* models to use, and these are based on previous investigations. To avoid spurious correlations and increase the number of variables, and thus the number of candidate models, I modified the three step-process used by Stoddard (2001) for stream amphibians and developed a four-step approach for constructing the most parsimonious models with the most biologically relevant information. First, I reviewed 30 ecological studies on *Ascaphus* spp., noting the study area, the top-ranking variables that influenced occurrence, density, or biomass, the spatial scale(s) of study, and any observations or discussion points regarding potentially important, but unmeasured, habitat variables (Table 1). Second, I considered the relevance of each variable to the Youngs Creek and Mica Creek study systems and my overall objectives, and thus measured only those variables that I thought would result in the most meaningful data (e.g., I disregarded forest type, geology, and climate because I nested the multi-scale approach in two biogeoclimatically distinct streams). Third, I designed a ranking system to determine which model variables ranked the highest at each spatial scale (Appendix 2). Fourth, I then used this ranking system in the AIC model building exercise for each spatial scale.

To examine habitat relationships at the channel unit, reach, and sub-basin scales I ranked all candidate models at each scale according to their AIC_c values, an approach that corrected for small sample sizes but is also appropriate for large sample sizes (Burnham

and Anderson, 1998). The best model (i.e., most parsimonious) was the model with the smallest AIC_c value. To compare models, I calculated ΔAIC_c by subtracting each model's AIC_c value from the best model. I drew inference from models within 2 units of the top AIC_c value ($\Delta AIC_c \leq 2$) at the channel unit scale and 4 units for the the biomass of chlorophyll-*a* and broader scale models ($\Delta AIC_c \leq 4$). Akaike weights (w_i) were calculated to determine the strength of evidence favoring each model in a set. I used multimodel inference, or model averaging, to estimate the relative importance of individual parameters in the top-ranking or best fitting set of models (Burnham and Anderson, 1998; Burnham and Anderson, 2004). I calculated 95% confidence intervals for each variable in the top-model sets and, if the confidence interval did not overlap with zero, regarded the variable as having a "significant" effect on tadpole density (Mazerolle, 2006). All analyses were conducted in SAS 9.1 software (SAS, 2003).

As a means of making models parsimonious and maintaining meaningful variables for predicting tadpole density, I constrained the analysis to ≤ 5 variables per model at each spatial scale and excluded, from analysis, variables that were highly correlated (Spearman's $r^2 \geq 0.70$). At the channel unit, I reduced the six cobble categories to three to avoid redundancy and maintain ecological relevance: 16-33 mm (P25), 34-56 mm (P50), and 57-164 mm (P100). Because several studies on *Ascaphus* have used more coarse estimates of substrate size in the analysis, I allowed two neighboring substrate categories to be present in a model. Similar to substrate, the embeddedness categories were reduced from five to two: 0-10% (EM1) and 10-25% (EM2). Because these embeddedness categories both approximate "loosely" embedded substrates, both categories were used in any one model. Because substrate size and

embeddedness have been identified as important predictor variables of tadpole abundance at the reach scale, I used the mean percentages for the top-ranking substrate and embeddedness categories in the models. To minimize the number of predictor variables in the reach scale analyses, substrate and embeddedness were used together during the reach scale analyses. Although some overlap did occur at the sub-basin scale for annual precipitation between the two regions, precipitation was highly correlated with elevation ($r^2 = 0.88$) and thus precipitation was eliminated from the analysis.

I used the top-ranking abiotic variables at the channel unit and reach scale to determine the relative importance of the biomass of chlorophyll-*a* and predation, respectively, on RM tailed frog tadpole abundance. Because I used a subset of the observations and I compared and eventually reduced the number of abiotic variables in the biomass of chlorophyll-*a* model, I standardized the abiotic variable estimates using Z-scores. The Z-score, a dimensionless quantity estimated by subtracting the population mean from the individual score and dividing the difference by the standard deviation, removed the effect of scale for each variable in the top-ranking models (T. Peterson, pers. comm.). I used only the top-ranking substrate and embeddedness category in the evaluation of the biomass of chlorophyll-*a* at the channel unit scale.

RESULTS

I detected 3,890 tailed frog tadpoles in 451 channel units (93 study reaches), which were distributed in 5 sub-basins and two mainstem sections of the two stream networks. I sampled tadpoles across a range of stream widths, spanning from the headwater to the confluence of a major river (Youngs: 0.3-22.4 m; Mica: 0.5-13.0 m). I

observed tadpoles across a slightly smaller range of stream widths (Youngs: 1.0-18.0 m; Mica: 0.7-13.0 m). 1y tadpoles represented the largest proportion of the captures (48%), followed by 2y (31%), and 3y tadpoles (21%). Tadpoles occurred in all sub-basins, 86 of 93 (92%) reaches, and 330 of 451 (73%) channel units.

Channel Unit Scale.—The physical habitat factors influencing tailed frog tadpoles at the channel unit scale differed between the two stream networks. In Youngs Creek the best fitting model included moderate to large sized cobble (P50 and P100), loosely embedded (EM1 and EM2) substrates, and fast moving water (FLOW) (Table 2). The weight of evidence ratio favoring the model was only 1.3 times greater than that of the second-best model, which included only cobble and embeddedness, indicating some uncertainty in the selection of the best candidate model. Tadpole abundance significantly increased with cobble and loosely embedded substrate (EM1), and decreased with slower water velocity. Cobble had the greatest effect among predictor variables for tadpole density (Table 3). Although moderately-loose embedded substrate (EM2) was an important predictor variable in top-ranking models, the positive relationship was not significant. Interestingly, the biomass of chlorophyll-*a* (CHLORO-a) was negatively associated with tadpole density at the channel unit scale in Youngs Creek and influenced tadpoles to a greater extent than did water velocity, but the relationship was not significant (Table 3).

In Mica Creek, the best model for tailed frog tadpole densities at the channel unit was the all-inclusive global model (P25, P50, P100, EM1, EM2, FLOW, WET, LWD, GRAD, CANOPY) (Table 2). Although the second-best model received some empirical support ($\Delta AIC_c = 1.80$), it contained all variables but P100. Of the ten variables present

in the top models, only large cobble and loosely embedded substrate were not significant in their influence on tadpole densities (Table 3). Overall, tadpole densities significantly increased with small to moderate sized cobble (P25 and P50), followed by moderately-loose embedded substrates, and decreased with slow moving water, large woody debris, open over-story canopies, channel width, and stream gradient. The biomass of chlorophyll-*a* had an overall negative association with tadpole density in Mica Creek (Table 3). Similar to Youngs Creek, the biomass of chlorophyll-*a* influenced tadpole densities to a greater extent than did water velocity, large woody debris, canopy cover, channel width, and stream gradient.

Reach Scale.— The factors influencing tailed frog tadpoles at the reach scale also differed between the two stream networks. In Youngs Creek the best fitting model included heat load (HEAT), water temperature (TEMP), loosely embedded substrate (EM1), cobble (P50), and sub-basin (BASIN) (Table 4). Tadpole abundance significantly decreased with an increasing heat load index (e.g., SW flowing streams), but increased with measured water temperature. Additionally, tadpole densities significantly decreased in sub-basins located further downstream and along the mainstem (Table 5). The weight of evidence ratio favoring the top model was only 1.7 times greater than that of the second-best model, which lacked water temperature and indicated that some uncertainty existed in the selection of the best model. Heat load had the greatest effect as a predictor variable for tadpole density (Table 5). Although, cobble and embeddedness were important predictor variables in top-ranking models, their influence was not significant. The presence of fish (FISH) appeared to have a negative effect on tadpole density in Youngs Creek, but the relationship was not significant (Table 5). Additionally,

the best combined biotic-abiotic model for tadpole densities was the global model, but the weight of evidence favoring this model over the second-best model that lacked fish was 1.42, indicating model uncertainty (Table 4).

In Mica Creek, the best fitting model for tadpole densities at the reach scale included heat load, moderately-loose embeddedness, and cobble (Table 4). Although the best model contained sub-basin context and water temperature, only cobble and embeddedness had significantly positive effects on tadpole densities in Mica Creek (Table 5). The second-best model received little empirical support ($\Delta AIC_c > 2$), but contained only cobble and embeddedness. Surprisingly, fish presence was significantly and positively associated with tadpole density in Mica Creek (Table 5). Although the weight of evidence in favor of the best candidate model was low (1.3), all models within $\Delta AIC_c > 4$ contained cobble, embeddedness, and fish (Table 4).

Sub-basin.—The best fitting model for tadpole densities at the sub-basin scale also differed between the two stream networks. Of the two variables used, mean basin heat load and change in basin elevation, heat load was the only variable to occur in the best fitting model for tadpole densities in Youngs Creek (Table 6). A decrease in heat load index (e.g., NE flowing streams) positively influenced tadpole densities; however this relationship was not significant (Table 6). The weight of evidence in favor of heat load was relatively strong when compared with the global model (2.5) and the model containing elevation (63.4). In contrast, Mica Creek tadpoles did not appear to be influenced by elevation or heat load, as the null model was the best fitting model (Table 6). These results complement the results at the finer, reach scale, where heat load significantly influenced Youngs Creek tadpoles.

Age Class: Channel unit.—In Youngs Creek, the best fitting models for each age class contained cobble and embeddedness (Table 7). Models containing water velocity were among the best fitting models for older tadpoles (2 – 3y), particularly for 3y tadpoles where an increase in water velocity significantly increased 3y tadpole abundance. Additionally, tadpole's response to cobble size shifted with increasing age, with moderate sized cobble having the greatest effect on 1y tadpoles and larger cobble having the greatest effect on older tadpoles, specifically 3y (Table 8). In contrast to the grouped analysis of tadpoles, embeddedness weakly influenced all three age classes in Youngs Creek. The biomass of chlorophyll-*a* appeared in the top model for 1y and 2y in Youngs Creek, but not for 3y tadpoles (Table 7).

In Mica Creek, the best fitting models for each age class contained cobble, embeddedness, and water velocity (Table 7). However, the best fitting model for 1y tadpoles was the global model, whereas the best-fitting models for older tadpoles contained a smaller number of variables. Loosely embedded cobble became more important with increasing age in Mica Creek (Table 8). Although moderate sized cobble appeared to positively influence all age classes, age classes responded to substrate size differently, with smaller cobble having a greatest effect on 1y tadpoles and larger cobble having the greatest effect on older tadpoles, specifically 3y. Finally, in Mica Creek the biomass of chlorophyll-*a* appeared to be less important for 3y tadpoles than it was for 1y tadpoles, with flow replacing the biomass of chlorophyll-*a* in the top-ranking 3y tadpole model (Table 7).

Age Class: Reach.— In Youngs Creek, the best fitting reach scale model for each age class contained moderate sized cobble, embeddedness, and heat load (Table 9).

Models contained fewer variables with increasing age. Models containing water temperature and sub-basin context were among the best fitting for 1y and 2y tadpoles. Although water temperature did not appear to influence 3y tadpoles, sub-basin context did weakly influence 3y densities (Table 10). Additionally, the negative effect of southwest flowing streams increased with increasing age (Table 9 and 10). Although fish presence did appear in the best fitting model for all age classes (Table 9), fish did not significantly decrease the density of any age class (Table 10).

In Mica Creek, the best fitting model for each age class contained small cobble, embeddedness, and heat load (Table 9). Similar to Youngs Creek, models contained fewer variables with increasing age. The best fitting model for 1y tadpoles included sub-basin context, which along with embeddedness became less important with age, whereas cobble became more important with age (Table 10). Finally, fish presence was positively and significantly correlated to tadpole abundance across all age classes (Table 10), and thus occurred in the best fitting model for each age class (Table 9).

DISCUSSION

Although tadpoles were widely distributed and observed in great abundance throughout both networks (Chapter 2), the factors influencing tadpole abundance differed across spatial-scales, between networks, and between tadpole age classes. Biotic variables improved the habitat models, but appeared to differ in their importance and/or sign depending on the interaction. The influence of the predictor variables at the finest spatial scales (e.g., channel unit) appeared to be mediated, in a hierarchical way, by the variables influencing tadpoles at broader scales (e.g., region). Because AIC cannot

directly compare the two streams (Burnham and Anderson, 1998), I cautiously discuss the similarities and differences between the networks for the abundance data.

The factors influencing tadpoles may not be confined to one spatial scale, particularly if the mosaic of disturbance patches and refuges created in a system differs between regions. Although the results of this study confirm that substrate and swift moving riffles are important variables for predicting tadpole abundance at the channel unit scale, the variables predicting tadpole abundance at broader spatial scales differed between the two streams. In Mica Creek, the habitat variables at the channel unit scale (e.g., substrate size and embeddedness) greatly influenced the patterns observed at the reach scale. In Youngs Creek, broader scale variables (e.g., heat load and basin context) influenced tadpoles at the reach scale. Because tadpoles in Mica Creek did not exhibit discrete patch sizes at the reach scale (Chapter 2), tadpoles may be limited by the same habitat features across spatial scales, thereby relegating the effects of seemingly broader scale variables on tadpole abundance. Interestingly, at the sub-basin scale I observed that changes in heat load continued to influence tadpole densities, particularly in the Youngs Creek network. However, I caution that the comparisons at the sub-basin scale consisted of small sample sizes; thus, the biological significance may be obscured. The differences I observed in tadpole patch sizes between the two streams (Chapter 2) supports the notion that tadpoles can be influenced by factors that extend beyond the spatial scale imposed by the sampling design, and that habitat patches and refuges may change in size, and importance, between regions.

Although the biotic variables explained additional variation from the habitat models, the effect fish had on tadpole abundance at the reach scale differed between the

two regions. In Youngs Creek, tadpole abundance was not strongly influenced by the presence of fish. However in Mica Creek, tadpole abundance was positively associated with the presence of fish, which primarily consisted of the benthic dwelling mottled sculpin (*Cottus beldingi*) that are known to associate with substrate characteristics similar to those observed for tadpoles (Swanson et al., 1998; Jones, unpublished data). Although trout were present throughout both drainages, estimates of trout presence and abundance may have been less accurate than those obtained for sculpin, particularly for kick sampled reaches. Therefore, the positive association observed between fish and tadpoles may only represent the relationship observed for sculpin and not for non-native trout species.

Although differences and similarities were observed in the factors influencing tadpoles between the two streams, tadpole age classes exhibited similar trends in the factors that influenced abundance in both streams. At the channel unit, increases in water velocity and cobble size became more important for 3y tadpoles than 1y tadpoles. Because of their size, older tadpoles appear to require larger surfaces, for which to adhere. Larger substrates move less frequently, but accumulate more sediment; thus, older tadpoles may need to inhabit swifter water to mediate these effects because 1) fast moving riffles flush sediment from large cobble and provide protection from predation (e.g., trout) and/or 2) an increased dissolved oxygen supply may be required during metamorphosis. Although the standing crop biomass of chlorophyll-*a* increases in quantity with substrate stability (related to size) and quality with frequent scouring events, it is unlikely that 3y tadpoles associate with larger cobble and higher velocity waters because of food subsidies. In both streams the biomass of chlorophyll-*a* became less important with increasing age in both streams, which may be attributed to

morphological and dietary changes induced by metamorphosis. At the reach scale, heat load became more important with increasing age. Although younger tadpoles appeared to be less influenced by heat load, the high density and widespread distribution of 1y tadpoles may dilute the effect that direct solar exposure may have on tadpoles. Additionally, sub-basin context had more effect on younger tadpoles, such that headwater basins appeared to be more important for 1y tadpoles than older tadpoles. Although these results support that headwater sub-basins provide important habitat for younger tadpoles, tadpoles occurred throughout both networks and exceeded the largest sized basin thought to maintain tadpole aggregations (Hunter, 1998; Dupuis and Friele, 2006). Because tadpoles frequently inhabit downstream reaches (Chapter 2) and exhibit habitat shifts with ontogeny, there exists a greater need for understanding how habitat interactions influence population dynamics (e.g., recruitment, colonization, extinction, etc.), particularly in larger stream networks.

The changes that occurred in the substrate characteristics and the number of predictor variables influencing tadpoles between the two streams appeared to be mediated by the differences in the flood disturbance regime experienced by the two drainages. Although these changes in habitat associations appear to be linked to regional differences in seasonal flood pulses, they may also be attributed to tadpole morphological adaptations. Because tadpoles seldom swim freely, they commonly associate with substrates large enough to accommodate foraging and provide adequate refuge (Gradwell, 1970; Altig and Broadie, 1972; Feminella and Hawkins, 1994). Therefore, tadpoles inhabiting environments that undergo higher magnitude disturbances (e.g., scouring events, release of fine sediment), like Youngs Creek (Parrett and Johnson,

2004), may associate with larger cobble, which offers a higher proportion of stable refugia during high flow events and more interstices (Death and Winterbourne, 1995; Duncan et al., 1999). However, in streams with lower magnitude disturbances like Mica Creek, the less mobile, larger cobble may be more highly embedded, which may drive tadpoles to occupy smaller sized cobble that still provides stable refugia, while offering adequate interstitial space from high currents and predation (Altig and Brodie, 1972). Additionally, lower magnitude disturbances may result in a greater accumulation of LWD, thus impeding tadpole movement (Wahbe and Bunnell, 2001) and decreasing water velocity (Hauer et al., 1999), which can result in tadpoles negatively associating with LWD. Finally, because species inhabiting highly dynamic (e.g., high magnitude flood pulse) systems may be influenced by fewer factors at fine spatial scales, less dynamic systems may require a more complex suite of habitat variables to adequately affect a species distribution and abundance. Although the two drainages were biogeoclimatically distinct, they also differed in overall basin area, thus tadpoles inhabiting the two drainages experienced dramatically different flood disturbance regimes that appeared to have influenced the distribution and abundance patterns.

The findings here support previous research on tailed frog habitat, but also provide evidence that larval amphibian distribution and abundance patterns may change with spatial-scale, regional context, and ontogeny. My findings support the notion that amphibian responses at fine scales are mediated by broad scales (Stoddard and Hayes, 2005). Thus an understanding of the geophysical, climatic, ontogenetic, and ecological characteristics, as well as measures of stream habitat, are important to consider when modeling tadpole distribution and abundance patterns and when developing species and

ecosystem based conservation strategies.

TABLES

Table 1. Ranking system used to determine the model variables used at the spatial scales sampled (channel unit, reach, basin). Top variables were given the highest rank value of 1; whereas variables that were slightly important in their contribution or merely additive to other top-ranking variables were given a lower ranking of 0.75; variables that were not measured, but were hypothesized as being important factors to consider in future studies, were given the lowest rank of 0.25. Rank values were summed and the variables were assigned an overall rank in order of their "importance" as predictor variables for *Ascaphus* spp. tadpole density. Top variables, and their values, used at the corresponding spatial scale are noted in italics. Variables used in models of different spatial scales are noted with asterics (***); variables not used (*) or that were not considered important at a spatial scale are noted with dashes (--). The ranking system was used in the AIC model building exercise at each spatial scale.

	Channel-Unit				**Reach**			**Basin**		
Variable	**1**	**0.75**	**0.25**	**Total**	**1**	**0.75**	**Total**	**1**	**Total**	**Literature Reference**
Cobble [a]	9	1	0	9.75	1	0	1.00	--	--	2,3,5,8,10,13,15,26,27,28,30
Fines [b]	5	0	0	5.00	2	0	2.00	--	--	5,10,11,15,26,27
Discharge [c]	4	1	0	4.75	--	--	--	--	--	11,15,26,28
Temp.	3	1	2	4.25	2	0	2.00	--	--	1,2,4,7,10,11,13,25
Gradient	3	1	0	3.75	1	1	1.75	--	--	2,10,11,13,27,28
Food [d]	3	0	2	3.50	--	--	--	--	--	4,7,18,19,20
Width	2	0	0	2.00	--	--	--	--	--	8,28
Canopy	1	1	0	1.75	--	--	--	--	--	2,13
LWD	0	2	0	1.50	--	--	--	--	--	1,14
Fish	1	0	1	1.25	***	***	***	--	--	21
Year*	1	0	0	1.00	--	--	--	--	--	2,28
Elevation	0	1	0	0.75	3	0	3.00	1	1.00	2,11,31
Heat Load	--	--	--	--	3	1	3.75	1	1.00	8,11,28,30
Forest*	--	--	--	--	2	0	2.00	3	3.00	2,8,15 ("Not important" 22)
Basin Size	--	--	--	--	2	0	2.00	1	1.00	11,16
Geology*	--	--	--	--	1	0	1.00	1	1.00	2
Ruggedness*	--	--	--	--	0	1	0.75	--	--	11
Precipitation*	--	--	--	--	0	1	0.75	--	--	2
Slope	--	--	--	--	--	--	--	2	2.00	8,28

[a] I considered "Cobble" as substrate ranging from large pebbles (≥ 16 mm) to large cobble (≤ 256 mm).
[b] I considered percent "Fines" (≤ 3 mm) synonymous with percent of substrate embedded.
[c] I considered "Discharge" (m^3/s) a function of water velocity (s/m) multiplied by area (m^2), because I used width in the channel unit analysis, I used the raw estimates of water velocity.
[d] I considered "Food" to be the biomass of chlorophyll-*a*, specifically standing crop biomass of chlorophyll-*a*.

Table 2. Channel unit scale mixed models explaining influence of abiotic and biotic habitat variables on total tadpole abundance in two stream networks (Youngs and Mica creeks). Model rankings were based on AIC_c and only best fitting models were used in comparisons (Abiotic: $\Delta AIC_c \leq 2$; Biotic: $\Delta AIC_c \leq 4$).

Stream	Model	AIC	AIC_c	ΔAIC_c	w_i	Evidence Ratio
Youngs Creek						
Abiotic	P50, P100, EM1, EM2, FLOW	745.50	745.60	0.00	0.31	1.00
	P50, P100, EM1, EM2	746.00	746.20	0.60	0.23	1.35
	P50, P100, EM1, EM2, FLOW, CANOPY	747.00	747.20	1.60	0.14	2.23
	P50, P100, EM1, FLOW, WET	747.40	747.60	2.00	0.11	2.72
	P50, P100, EM1, EM2, FLOW, WET, LWD	748.60	748.80	3.20	0.06	4.95
	P50, P100, EM1, FLOW, WET	748.90	749.10	3.50	0.05	5.75
	P50, P100, EM2, FLOW	749.30	749.50	3.90	0.04	7.03
Biotic	P50, EM1, CHLORO-a	111.60	112.50	0.00	0.29	1.00
	P50, EM1, CHLORO-a, FLOW	112.00	113.00	0.50	0.23	1.28
	P50, EM1	112.40	113.30	0.80	0.20	1.49
	P50, EM1, FLOW	113.20	114.10	1.60	0.13	2.23
	P50, CHLORO-a	114.70	115.60	3.10	0.06	4.71
	P50, CHLORO-a, FLOW	115.10	116.00	3.50	0.05	5.75
	P50	115.60	116.50	4.00	0.04	7.39
Mica Creek						
Abiotic	GLOBAL	752.80	752.80	0.00	0.71	1.00
	P25, P50, EM1, EM2, FLOW, WET, CANOPY, LWD, GRADIENT	754.50	754.60	1.80	0.29	2.46
	P25, P50, EM2, FLOW, WET, CANOPY, LWD, GRADIENT	756.80	756.80	4.00	0.08	8.87
Biotic	P50, EM2	177.30	177.40	0.00	0.45	1.00
	P50, EM2, CHLORO-a	177.40	177.50	0.10	0.43	1.05
	P50, EM2, CHLORO-a, FLOW	179.80	180.10	2.70	0.12	3.67

Table 3. Channel unit scale habitat variables (abiotic and biotic) explaining total tadpole abundance in two stream networks (Youngs and Mica creeks). Model rankings were based on AIC_c and only variables in the best fitting models were used in comparisons (Abiotic: $\Delta AIC_c \leq 2$; Biotic: $\Delta AIC_c \leq 4$). Variables that were significant in their influence on tadpole abundance are noted by asterisks (*), as is the sign of the relationship (- or +).

Stream	Variable	Estimate	S.E.	Upper 95% CI	Lower 95% CI	Relationship
Youngs Creek						
Abiotic	P50	2.59	0.33	3.24	1.95	*/+
	P100	2.16	0.31	2.76	1.56	*/+
	EM1	0.96	0.26	1.47	0.45	*/+
	EM2	0.53	0.80	2.10	-1.04	
	FLOW	-0.16	0.01	-0.14	-0.17	*/-
Biotic	P50	2.34	1.16	4.62	0.06	*/+
	EM1	1.10	0.76	2.60	-0.40	
	CHLORO-*a*	-0.23	0.63	1.01	-1.46	
	FLOW	-0.12	0.28	0.42	-0.66	
Mica Creek						
Abiotic	P50	2.66	0.77	4.17	1.15	*/+
	P25	1.73	0.85	3.39	0.07	*/+
	EM2	1.71	0.67	3.02	0.40	*/+
	EM1	0.69	0.45	1.58	-0.20	
	FLOW	-0.43	0.12	-0.19	-0.66	*/-
	P100	0.38	0.87	2.08	-1.32	
	LWD	-0.26	0.11	-0.04	-0.48	*/-
	CANOPY	-0.21	0.05	-0.11	-0.31	*/-
	WET	-0.14	0.06	-0.02	-0.25	*/-
	GRADIENT	-0.03	0.01	-0.01	-0.04	*/-
Biotic	P50	4.33	1.43	7.14	1.53	*/+
	EM2	1.94	1.50	4.88	-0.99	
	FLOW	-0.19	0.27	0.34	-0.72	
	CHLORO-*a*	-0.14	0.36	0.56	-0.84	

Table 4. Reach scale mixed models explaining influence of abiotic and biotic habitat variables on total tadpole abundance in two stream networks (Youngs and Mica creeks). Model rankings were based on AIC_c and only best fitting models were used in comparisons ($\Delta AIC_c \leq 4$).

Stream	Model	AIC	AIC_c	ΔAIC_c	w_i	Evidence Ratio
Youngs Creek						
Abiotic	HEAT, TEMP, EM1, P50, BASIN	127.50	127.60	0.00	0.56	1.00
	HEAT, EM1, P50, BASIN	128.60	128.70	1.10	0.32	1.73
	HEAT, ELEVATION, EM1, P50	130.50	130.70	3.10	0.12	4.71
Biotic	GLOBAL	126.80	126.90	0.00	0.40	1.00
	HEAT, TEMP, EM1, P50, BASIN	127.50	127.60	0.70	0.28	1.42
	HEAT, EM1, P50, BASIN	128.60	128.70	1.80	0.16	2.46
	HEAT, FISH, EM1, P50, BASIN	128.70	128.80	1.90	0.15	2.59
	HEAT, FISH, EM1, P50, BASIN	128.70	128.80	1.90	0.15	2.59
Mica Creek						
Abiotic	HEAT, EM2, P50	142.70	142.80	0.00	0.61	1.00
	EM2, P50	144.90	145.00	2.20	0.20	3.00
	HEAT, TEMP, EM2, P50	146.50	146.60	3.80	0.09	6.69
	HEAT, EM2, P50, BASIN	146.50	146.60	3.80	0.09	6.69
Biotic	HEAT, FISH, EM2, P50	133.40	133.50	0.00	0.46	1.00
	HEAT, FISH, EM2, P50, BASIN	134.00	134.10	0.60	0.34	1.35
	FISH, EM2, P50	136.20	136.30	2.80	0.11	4.06
	FISH, EM2, P50, BASIN	137.00	137.10	3.60	0.08	6.05

Table 5. Reach scale habitat variables (abiotic and biotic) explaining total tadpole abundance in two stream networks (Youngs and Mica creeks). Model rankings were based on AIC_c and only variables in the best fitting models were used in comparisons ($\Delta AIC_c \leq 4$). Variables that are significant in their influence on tadpole abundance are noted by asterisks (*), as is the sign of the relationship (- or +).

Stream	Variable	Estimate	S.E.	Upper 95% C.I.	Lower 95% C.I.	Relationship
Youngs Creek						
Abiotic	HEAT	-2.30	0.92	-0.48	-4.11	*/-
	P50	1.53	1.35	4.18	-1.12	
	EM1	-0.36	0.86	1.32	-2.05	
	BASIN	-0.26	0.07	-0.12	-0.40	*/-
	TEMP	0.15	0.07	0.29	0.02	*/+
	ELEVATION	0.00	0.00	0.01	0.00	
Biotic	HEAT	-2.26	0.93	-0.43	-4.09	*/-
	P50	1.53	1.34	4.16	-1.10	
	EM1	-0.33	0.85	1.34	-1.99	
	FISH	-0.30	0.31	0.31	-0.91	
	BASIN	-0.26	0.07	-0.12	-0.40	*/-
	TEMP	0.16	0.07	0.30	0.02	*/+
Mica Creek						
Abiotic	P50	6.62	2.16	10.85	2.39	*/+
	EM2	4.88	1.96	8.72	1.04	*/+
	HEAT	-0.46	1.15	1.80	-2.72	
	TEMP	-0.02	0.06	0.10	-0.13	
	BASIN	-0.02	0.05	0.09	-0.12	
Biotic	P50	6.98	1.99	10.89	3.07	*/+
	EM2	3.76	1.91	7.51	0.00	*/+
	FISH	1.45	0.46	2.34	0.55	*/+
	HEAT	-1.04	1.05	1.01	-3.09	
	BASIN	-1.04	0.94	0.81	-2.89	

Table 6. Basin scale mixed models explaining influence of biotic and abiotic habitat variables on tadpole age class abundance in two stream networks (Youngs and Mica creeks). Model rankings were based on AIC_c and only best fitting models were used in comparisons ($\Delta AIC_c \leq 4$). Variables that are significant in their influence on tadpole abundance are noted by asterisks (*), as is the sign of the relationship (- or +).

Stream	Model	AIC	AIC_c	ΔAIC_c	w_i	Evidence Ratio
Youngs Cr.	HEAT	16.80	17.80	0.00	0.70	1.00
	HEAT, ELEVATION (GLOBAL)	18.30	19.60	1.80	0.28	2.46
	ELEVATION	25.10	26.10	8.30	0.01	63.43
	NULL	25.20	28.20	10.40	0.00	181.27
Mica Cr.	NULL	12.80	14.80	0.00	0.52	1.00
	HEAT	3.00	15.00	0.20	0.47	4.01
	HEAT, ELEVATION (GLOBAL)	14.00	26.00	11.20	0.00	981.90
	ELEVATION	22.80	26.80	12.00	0.00	1464.82

Stream	Variable	Estimate	S.E.	Upper 95% C.I.	Lower 95% C.I.	Relationship
Youngs Cr.	HEAT	-4.79	3.16	1.40	-10.97	
	ELEVATION	0.01	0.00	0.01	0.00	
Mica Cr.	HEAT	24.00	4.85	33.50	14.49	*/+
	ELEVATION	0.00	0.00	0.00	0.00	

Table 7. Channel unit scale mixed models explaining influence of biotic and abiotic habitat variables on tadpole age class abundance in two stream networks (Youngs and Mica creeks). Model rankings were based on AIC_c and only best fitting models were used in comparisons ($\Delta AIC_c \leq 4$).

Stream-Age Class	Model	AIC	AIC_c	ΔAIC_c	w_i	Evidence Ratio
Youngs Creek						
Abiotic-1y	P50, P100, EM1, EM2	718.80	718.90	63.10	1.00	1.00
Abiotic-2y	P50, P100, EM1, EM2	672.80	673.00	0.00	0.55	1.00
	P50, P100, EM1, FLOW	674.60	674.80	1.80	0.22	2.46
	P50, P100, EM2, FLOW	674.70	674.80	1.80	0.22	2.46
Abiotic-3y	P50, P100, EM1, EM2, FLOW	622.20	622.40	0.00	0.34	1.00
	P50, P100, EM2, FLOW	622.60	622.80	0.40	0.28	1.22
	P50, P100, EM1, FLOW	624.00	624.20	1.80	0.14	2.46
	P50, P100, EM1, FLOW, WET	624.30	624.40	2.00	0.12	2.72
	P50, P100, EM1, EM2, FLOW, WET, LWD	624.30	624.40	2.00	0.12	2.72
Biotic-1y	PERI, P50, EM1	111.10	112.10	0.00	0.33	1.00
	PERI, P50, EM1, FLOW	111.60	112.60	0.50	0.26	1.28
	P50, EM1	112.30	113.20	1.10	0.19	1.73
	P50, EM1, FLOW	113.10	114.10	2.00	0.12	2.72
	PERI, P50	115.10	116.00	3.90	0.05	7.03
	PERI, EM1	115.20	116.10	4.00	0.05	7.39
Biotic-2y	PERI, P50, EM1	97.00	97.40	0.00	0.27	1.00
	P50, EM1	97.60	98.00	0.60	0.20	1.35
	PERI, P50, EM1, FLOW	97.90	98.40	1.00	0.16	1.65
	PERI, P50	98.70	99.10	1.70	0.11	2.34
	P50, EM1, FLOW	98.80	99.30	1.90	0.10	2.59
	P50	99.30	99.70	2.30	0.08	3.16
	PERI, P50, FLOW	99.60	100.00	2.60	0.07	3.67
Biotic-3y	P50, EM1	72.90	73.40	0.00	0.27	1.00
	PERI, P50, EM1	73.20	73.60	0.20	0.25	1.11
	P50	74.10	74.50	1.10	0.16	1.73
	P50, EM1, FLOW	74.40	74.90	1.50	0.13	2.12
	PERI, P50, FLOW	75.40	75.90	2.50	0.08	3.49
	P50, FLOW	75.70	76.10	2.70	0.07	3.86
	EM1	76.40	76.80	3.40	0.05	5.47
Mica Creek						
Abiotic-1y	P25, P50, EM1, EM2, FLOW, CANOPY, LWD, GRADIENT	759.40	759.50	0.00	0.68	1.00
	GLOBAL	760.90	761.00	1.50	0.32	2.12
Abiotic-2y	P25, P50, EM1, EM2, FLOW	702.20	702.30	0.00	0.54	1.00
	P25, P50, EM2, FLOW	703.60	703.70	1.40	0.27	2.01
	P50, P100, EM1, EM2, FLOW	704.30	704.40	2.10	0.19	2.86
Abiotic-3y	P25, P50, EM1, EM2, FLOW, WET, CANOPY, LWD	655.70	655.80	0.00	0.68	1.00
	P50, P100, EM1, EM2, FLOW, WET, LWD	657.20	657.30	1.50	0.32	2.12
Biotic-1y	PERI, P50, EM2, FLOW	176.70	176.90	0.00	0.38	1.00

	PERI, P50, EM2	177.00	177.30	0.40	0.31	1.22
	P50, EM2	177.60	177.90	1.00	0.23	1.65
	P50, EM2, FLOW	179.30	179.90	3.00	0.08	4.48
Biotic-2y	P50, EM2	161.60	161.80	0.00	0.32	1.00
	PERI, P50, EM2	162.00	162.30	0.50	0.25	1.28
	P50, EM2, FLOW	162.80	163.10	1.30	0.17	1.92
	PERI, P50, EM2, FLOW	163.20	163.50	1.70	0.14	2.34
	PERI, P50	164.40	164.70	2.90	0.08	4.26
	P50, FLOW	165.20	165.50	3.70	0.05	6.36
Biotic-3y	P50, EM2, FLOW	143.90	144.10	0.00	0.36	1.00
	PERI, P50, EM2	144.60	144.80	0.70	0.25	1.42
	P50, EM2	144.70	145.00	0.90	0.23	1.57
	PERI, P50, EM2, FLOW	146.10	146.70	2.60	0.10	3.67
	EM2	147.10	147.30	3.20	0.07	4.95

Table 8. Channel unit scale habitat variables (abiotic and biotic) explaining tadpole age class abundance in two stream networks (Youngs and Mica creeks). Model rankings were based on AIC_c and only variables in the best fitting models were used in comparisons (Abiotic: $\Delta AIC_c \leq 2$; Biotic: $\Delta AIC_c \leq 4$). Variables that are significant in their influence on tadpole abundance are noted by asterisks (*), as is the sign of the relationship (- or +).

Stream-Age	Variable	Estimate	S.E.	Upper 95% C.I.	Lower 95% C.I.	Relationship
Youngs Creek						
Abiotic-1y	P50	1.84	0.55	2.93	0.76	*/+
	P100	1.21	0.53	2.25	0.17	*/+
	EM1	0.48	0.48	1.42	-0.47	
	EM2	0.45	0.86	2.14	-1.24	
Abiotic-2y	P100	1.93	0.48	2.86	1.00	*/+
	P50	1.43	0.49	2.39	0.48	*/+
	EM1	0.56	0.44	1.43	-0.30	
	EM2	0.38	0.79	1.92	-1.17	
	FLOW	-0.13	0.07	0.00	-0.27	
Abiotic-3y	P100	1.58	0.42	2.40	0.76	*/+
	P50	0.71	0.42	1.53	-0.11	
	EM2	-0.67	0.65	0.61	-1.94	
	EM1	0.33	0.38	1.08	-0.42	
	FLOW	-0.19	0.06	-0.06	-0.31	*/-
	LWD	-0.10	0.09	0.08	-0.28	
	WET	-0.03	0.02	0.00	-0.07	
Biotic-1y	P50	1.72	1.19	4.05	-0.61	
	EM1	1.39	0.77	2.91	-0.12	
	PERI	-0.39	0.63	0.85	-1.63	
	FLOW	-0.11	0.28	0.44	-0.66	
Biotic-2y	P50	1.71	0.96	3.59	-0.17	
	EM1	0.58	0.63	1.83	-0.66	
	PERI	-0.27	0.51	0.72	-1.27	
	FLOW	-0.07	0.23	0.38	-0.53	
Biotic-3y	P50	1.04	0.62	2.26	-0.18	
	EM1	-0.42	0.45	0.47	-1.31	
	PERI	-0.16	0.33	0.49	-0.82	
	FLOW	-0.10	0.17	0.23	-0.43	
Mica Creek						
Abiotic-1y	P50	2.52	0.78	4.06	0.99	*/+
	EM2	1.62	0.73	3.04	0.20	*/+
	P25	1.44	0.78	2.98	-0.09	
	P100	0.30	0.88	2.02	-1.42	
	EM1	-0.29	0.53	0.75	-1.33	
	LWD	-0.27	0.11	-0.04	-0.49	*/-
	FLOW	-0.26	0.12	-0.02	-0.49	*/-
	CANOPY	-0.23	0.07	-0.10	-0.37	*/-
	WET	-0.05	0.07	0.08	-0.18	
	GRADIENT	-0.03	0.01	-0.01	-0.04	*/-

Abiotic-2y	P50	2.62	0.68	3.95	1.29	*/+
	P25	1.08	0.62	2.30	-0.14	
	EM2	1.03	0.66	2.32	-0.25	
	P100	-0.51	0.62	0.70	-1.72	
	EM1	0.51	0.49	1.46	-0.45	
	FLOW	-0.26	0.11	-0.04	-0.47	*/-
Abiotic-3y	EM1	1.43	0.43	2.27	0.59	*/+
	P50	0.66	0.60	1.83	-0.52	
	EM2	0.62	0.59	1.77	-0.53	
	P100	0.58	0.59	1.73	-0.57	
	LWD	-0.29	0.09	-0.10	-0.47	*/-
	FLOW	-0.24	0.10	-0.04	-0.43	*/-
	CANOPY	-0.14	0.06	-0.03	-0.25	*/-
	P25	-0.12	0.60	1.05	-1.29	
	WET	-0.08	0.04	0.01	-0.16	
Biotic-1y	EM2	2.42	1.62	5.59	-0.74	
	P50	2.33	1.52	5.30	-0.64	
	PERI	-0.35	0.34	0.32	-1.02	
	FLOW	-0.29	0.25	0.21	-0.79	
Biotic-2y	P50	3.16	1.21	5.53	0.79	*/+
	PERI	0.13	0.29	0.70	-0.44	
	FLOW	-0.03	0.22	0.39	-0.46	
	EM2	0.02	1.35	2.66	-2.62	
Biotic-3y	P50	0.74	1.07	2.85	-1.36	
	EM2	-0.32	1.12	1.88	-2.53	
	FLOW	-0.28	0.18	0.07	-0.63	
	PERI	0.25	0.24	0.73	-0.23	

Table 9. Reach scale mixed models explaining influence of biotic and abiotic habitat variables on tadpole age class abundance in two stream networks (Youngs and Mica creeks). Model rankings were based on AIC_c and only best fitting models were used in comparisons (Abiotic: $\Delta AIC_c \leq 2$; Biotic: $\Delta AIC_c \leq 4$).

Stream-Age Class	Model	AIC	AIC_c	ΔAIC_c	w_i	Evidence Ratio
Youngs Creek						
Abiotic-1y	HEAT, TEMP, EM1, P50, BASIN	115.30	115.40	0.00	0.83	1.00
	HEAT, EM1, P50, BASIN	118.50	118.60	3.20	0.17	4.95
Abiotic-2y	HEAT, EM1, P50, BASIN	114.90	115.20	0.00	0.61	1.00
	HEAT, TEMP, EM1, P50, BASIN	116.50	116.90	1.70	0.26	2.34
	HEAT, EM1, P50	118.10	118.40	3.20	0.12	4.95
Abiotic-3y	HEAT, EM1, P50	108.20	108.50	0.00	0.87	1.00
	HEAT, EM1, P50, BASIN	112.00	112.30	3.80	0.13	6.69
Biotic-1y	HEAT, TEMP, EM1, P50, BASIN	115.30	115.40	0.00	0.45	1.00
	HEAT, FISH, TEMP, EM1, P50, BASIN	115.90	116.00	0.60	0.33	1.35
	HEAT, EM1, P50, BASIN	118.50	118.60	3.20	0.09	4.95
	FISH, TEMP, EM1, P50, BASIN	119.10	119.20	3.80	0.07	6.69
	HEAT, FISH, EM1, P50, BASIN	119.20	119.30	3.90	0.06	7.03
Biotic-2y	HEAT, EM1, P50, BASIN	114.90	115.20	0.00	0.40	1.00
	HEAT, FISH, EM1, P50, BASIN	115.70	116.10	0.90	0.26	1.57
	HEAT, TEMP, EM1, P50, BASIN	116.50	116.90	1.70	0.17	2.34
	HEAT, FISH, TEMP, EM1, P50, BASIN	117.40	117.80	2.60	0.11	3.67
	HEAT, FISH, EM1, P50	118.70	119.00	3.80	0.06	6.69
Biotic-3y	HEAT, FISH, EM1, P50	107.60	107.90	0.00	0.57	1.00
	HEAT, EM1, P50	108.20	108.50	0.60	0.43	1.35
Mica Creek						
Abiotic-1y	HEAT, EM2, P50, BASIN	149.1	149.4	0.0	0.59	1.00
	EM2, P50, BASIN	151.3	151.6	2.2	0.2	3.00
	HEAT, EM2, P50	152.5	152.8	3.4	0.11	5.47
	HEAT, TEMP, EM2, P50, BASIN	152.6	152.9	3.5	0.1	5.75
Abiotic-2y	HEAT, EM2, P50	120.1	120.2	0.0	0.7	1.00
	EM2, P50	121.8	121.9	1.7	0.3	2.34
Abiotic-3y	HEAT, EM2, P50	119.5	119.6	0.0	0.61	1.00
	HEAT, EM2, P50, BASIN	121.7	121.8	2.2	0.2	3.00
	EM2, P50	121.8	121.9	2.3	0.19	3.16
Biotic-1y	HEAT, FISH, EM2, P50, BASIN	141.5	141.9	0.0	0.77	1.00
	FISH, EM2, P50, BASIN	144	144.3	2.4	0.23	3.32
Biotic-2y	HEAT, FISH, EM2, P50	113.9	114	0.0	0.66	1.00
	FISH, EM2, P50	115.9	116	2.0	0.24	2.72
	HEAT, FISH, EM2, P50, BASIN	117.8	117.9	3.9	0.09	7.03
Biotic-3y	HEAT, FISH, EM2, P50	108.3	108.4	0.0	0.86	1.00
	FISH, EM2, P50	111.9	112	3.6	0.14	6.05

Table 10. Reach scale habitat variables (abiotic and biotic) explaining tadpole age class abundance in two stream networks (Youngs and Mica creeks). Model rankings were based on AIC_c and only variables in the best fitting models were used in comparisons ($AIC_c \leq 4$). Variables that are significant in their influence on tadpole abundance are noted by asterisks (*), as is the sign of the relationship (- or +).

Stream-Age Class	Variable	Estimate	S.E.	Upper 95% C.I.	Lower 95% C.I.	Relationship
Youngs Creek						
Abiotic-1y	HEAT	-1.15	0.80	0.41	-2.72	
	EM1	-0.82	0.73	0.60	-2.24	
	P50	0.58	1.14	2.82	-1.67	
	BASIN	-0.33	0.06	-0.21	-0.44	*/-
	TEMP	0.16	0.06	0.28	0.05	*/+
Abiotic-2y	P50	1.49	1.13	3.71	-0.73	
	HEAT	-1.30	0.78	0.23	-2.82	
	EM1	-0.46	0.84	1.19	-2.11	
	BASIN	-0.14	0.05	-0.04	-0.23	*/-
	TEMP	0.09	0.06	0.20	-0.03	
Abiotic-3y	HEAT	-1.97	0.73	-0.53	-3.40	*/-
	P50	0.93	1.07	3.02	-1.16	
	EM1	-0.56	0.82	1.05	-2.16	
	BASIN	-0.04	0.04	0.04	-0.11	
Biotic-1y	HEAT	-1.14	0.80	0.43	-2.71	
	EM1	-0.81	0.73	0.62	-2.25	
	P50	0.60	1.15	2.86	-1.66	
	BASIN	-0.33	0.06	-0.21	-0.44	
	TEMP	0.17	0.06	0.29	0.05	*/+
	FISH	-0.12	0.27	0.41	-0.64	
Biotic-2y	P50	1.51	1.13	3.73	-0.72	
	HEAT	-1.30	0.78	0.23	-2.82	
	EM1	-0.46	0.84	1.20	-2.11	
	BASIN	-0.14	0.05	-0.04	-0.23	*/-
	FISH	0.00	0.26	0.52	-0.52	
	TEMP	0.09	0.06	0.20	-0.03	
Biotic-3y	HEAT	-1.95	0.73	-0.52	-3.38	*/-
	P50	1.05	1.08	3.15	-1.06	
	EM1	-0.55	0.81	1.04	-2.15	
	FISH	-0.30	0.23	0.16	-0.76	
Mica Creek						
Abiotic-1y	EM2	6.32	2.13	10.50	2.14	*/+
	P50	1.82	2.28	6.29	-2.66	
	HEAT	-0.23	1.18	2.09	-2.54	
	BASIN	-0.15	0.06	-0.04	-0.26	*/-
	TEMP	0.00	0.07	0.14	-0.15	
Abiotic-2y	P50	4.93	1.65	8.16	1.70	*/+
	EM2	2.44	1.49	5.36	-0.48	
	HEAT	-0.24	0.88	1.49	-1.98	

Abiotic-3y	P50	5.51	1.67	8.78	2.24	*/+
	HEAT	-0.72	0.87	0.99	-2.43	
	EM2	-0.36	1.52	2.61	-3.34	
	BASIN	0.06	0.04	0.14	-0.02	
Biotic-1y	EM2	4.78	1.97	8.64	0.93	*/+
	P50	1.85	2.07	5.92	-2.21	
	FISH	1.30	0.47	2.22	0.38	*/+
	HEAT	-0.76	1.09	1.38	-2.90	
	BASIN	-0.21	0.06	-0.11	-0.32	
Biotic-2y	P50	5.33	1.56	8.39	2.27	*/+
	EM2	1.98	1.43	4.77	-0.81	
	FISH	0.88	0.33	1.53	0.22	*/+
	HEAT	-0.60	0.84	1.04	-2.25	
	BASIN	-0.03	0.04	0.05	-0.12	
Biotic-3y	P50	5.96	1.47	8.85	3.08	*/+
	HEAT	-1.17	0.79	0.37	-2.71	
	FISH	1.11	0.31	1.72	0.51	*/+
	EM2	-1.05	1.33	1.55	-3.65	

APPENDICES

Appendix 1. List of variables with the unit in which each variable was measured and a brief description of the variable and how it was measured.

Variable	Unit	Description
Heat load		Record the direction of water flow at downstream edge of transect using a magnetic compass, in relation to true north, not magnetic. Using the equation: Heat load index = $(1 - \cos(\theta - 45))/2$, where θ is aspect in degrees, a unitless number is obtained. The heat index is a number between 0 and 1, with the maximum value being obtained when aspect is SW and minimum when aspect is NE.
Water temperature	° C	Record the thalweg temperature at downstream edge of transect.
Gradient	%	Stream gradient will be measured using digital elevation models (DEM) in a GIS.
Wetted width	cm	Width of the stream transect to be surveyed; this is generally the wetted width with few exceptions (wetted depth will be recorded in those instances). Width will be used in calculation of the density and biomass of amphibians captured.
Water velocity	m/s	Using submersible fishing bobber and line, bobber is filled until buoyant and placed in the thalweg. Record the time it takes to travel 1m from upstream edge to downstream edge of transect (repeated three times).
Pebble counts	%	A Wolman pebble count will be conducted at each transect. Using the substrate classification system, pebbles (>8mm) will be measured along the intermediate axis. The stream will be visually divided into thirds, moving from left to right, ten pebbles will be measured in each third.
Substrate embeddedness	%	Estimation of embeddedness occurs during the pebble count. The degree of embeddedness is recorded as the percent of the pebble covered in fine sediment (<2mm); percentages are divided into categories: 0-5%, 5-25%, 25-50%, 50-75%, 75-100%.
Large woody debris (LWD)	%	Estimate the entire transect covered by in-stream large woody debris (woody debris measuring >5mm diameter) using categorical percentages: 0-5%, 5-25%, 25-50%, 50-75%, 75-100%.
Chlorophyll-*a* biomass	g/m^2	Standing crop biomass of chlorophyll-*a* taken from 3.12 cm^2 area sample. Five rocks were sampled at each channel unit and the mean biomass was estimated for each channel unit.
Canopy	%	Estimates of overhanging vegetation or other shading cover providing cover across the the entire channel unit area will be determined through visual observation, a Solar Pathfinder will be used to truth these observations on a subset of the transects sampled.
Fish presence	+/-	Visual observations across the length of the reach.
Annual precipitation	mm	Annual precipitation will be determined using GIS layers.
Parent geology	type	Parent geology will be determined using GIS layers.
Elevation	m	Stream elevation will be measured using DEMs in a GIS.

Appendix 2. Ranking system used to determine the relative importance of each variable used in the literature for each spatial scale.

1- Each variable was assigned one numeric value (rank) for each instance in which the variable occurred, and significantly improved, a model predicting tadpole distribution and abundance (Table 1).

2- Top variables were given the highest rank value of 1; whereas variables that were slightly important in their contribution or merely additive to other top-ranking variables were given a lower ranking of 0.75; variables that were not measured, but were hypothesized as being important factors to consider in future studies, were given the lowest rank of 0.25.

3- Values from each were summed and the variables were assigned an overall rank in order of their importance as predictor variables for *Ascaphus* tadpole density.

FUTURE DIRECTIONS

The three chapters of this thesis either lent support to the examination of or examined the factors influencing the distribution and abundance of Rocky Mountain tailed frog (*Ascaphus montanus*) tadpoles in two biogeoclimatically distinct stream networks. Throughout the composition of this thesis, it became evident that future investigations would add clarity to the ideas investigated in this thesis. In the following paragraphs I suggest directions for future research on the Rocky Mountain tailed frog. I believe that investigating these questions would have allowed me to better understand the factors influencing Rocky Mountain tailed frog ecology throughout their range.

Although this thesis provided evidence that tadpoles are positively correlated with fish species (Chapter 3), it did not provide further insight as to how fish species, particularly native and non-native trout, and tadpoles interact in these systems. Based on our findings, the two streams networks I surveyed contained the highest *Ascaphus* spp. tadpole densities reported in the literature (Chapter 2). Interestingly, these streams were also densely occupied by char (Youngs) and sculpin (Mica). Additionally, the native Westslope cutthroat (Youngs) and non-native Brook trout (Mica) were found in high densities throughout both stream networks. Although the dominant fish species did not appear to negatively influence tadpoles at the reach scale, a regional comparison on the effects of native and non-native trout species on frog distribution and abundance in biogeoclimatically different systems might reveal whether non-native trout have greater effects than native trout on tadpoles.

Initially, I had anticipated working on the effects of timber harvest on tailed frog tadpoles. Because sample sizes were small and temporal comparisons were difficult to make between the two different sampling designs, rigorous assessment of the effects of timber harvest was not possible. Based on previous research I suspected tailed frog tadpoles and adults would be negatively influenced by timber harvest and associated activities in headwater streams (e.g., Bury and Corn, 1988), but no research has investigated network scale response, particularly in downstream reaches inhabited by tadpoles. To remedy this problem, I suggest continued sampling of the entire stream network, which would allow for before and after comparisons in the landscape level response of tadpoles to timber harvest within the same network. Because Mica Creek and Youngs Creek are managed differently for timber resources and future plans exist for large-scale timber harvests across the entire Mica Creek drainage and no plans for harvest in Youngs Creek, before and after comparisons could further reveal the broad scale effects of timber harvest on tailed frogs. Additionally, I suggest that comparisons of the landscape level response be made between two biogeoclimatically similar stream networks, and if possible between biogeoclimatically distinct regions. Coupling the understanding that factors influencing tadpoles change within and between streams with the understanding of the landscape level response to timber harvest in different regions would help managers in determining what factors change within and between biogeoclimatically distinct networks and how to best determine critical habitat for frogs at various life stages.

Differences in the flood disturbance regime between two regions appeared to mediate the response of the tadpoles within the two stream networks (Chapter 2 and 3).

However, long term monitoring of the entire network may reveal how the two populations respond to flood disturbances temporally. The stream networks experiencing rain on snow events (e.g., Mica Creek) may have an overall lower magnitude flood disturbance on average, but may experience an overall higher amount of variability in the flood's magnitude. Therefore, the snapshot taken during these relatively low magnitude flood years may not adequately represent the importance of flood disturbance variability on tadpole distribution, particularly in lower magnitude flood streams like Mica Creek. Additionally, Youngs Creek may have a higher frequency of high magnitude flood disturbances that facilitates an annual movement of tadpoles throughout the stream network, whereas the episodic high magnitude flood disturbances in Mica Creek may result in dramatic changes in the distribution and abundance patterns of tadpoles every ten years, and may be a less frequent but important driver for amphibian recolonization.

Although this thesis did not investigate distribution and abundance patterns for adult tailed frogs and, consequently, did not address how adults influence tadpole patterns, I think it is important to acknowledge that adults directly influence tadpole patterns. Future research investigating tadpole ecology should consider sampling and integrating adult distribution and abundance into the analysis of the factors influencing tadpole ecology. Additionally, there exists a need for describing the factors that influence adults and metamorphs, and whether these factors change within and between stream networks. Moreover, I argue that these changes could reveal important insights as to how adults and metamorph frogs may also mediate the differences in the patterns I observed in tadpole ecology within and between the two streams.

Although chapter three revealed that a periphyton influences tadpoles, it is not clear as to whether the interaction is driven by the tadpoles (top-down) or by the periphyton (bottom-up). Although it was not reported in this thesis, I conducted some pilot sampling at a finer spatial scale (i.e., the rock) to verify my preliminary findings that tadpoles interact with chlorophyll-*a* standing crop biomass differently in the two systems. Results from this work suggested that at finer spatial scales than most studies investigate, tadpoles appear to be associating with a low standing crop biomass in both stream networks. Interestingly, the standing crop biomass is comparable in both streams, but the overall relationship appears to change when resource availability is considered, as some streams have higher standing crop biomass of chlorophyll-*a* than others (Jones, unpublished data). Thus, the understanding of how tadpoles interact with food requires further analysis at multiple spatial scales, including expansion of the sampling scope to include an even smaller spatial scale that may assist in explaining how food resources influence tadpoles within and between streams.

Tadpole patch size appeared to vary within the reaches for the two stream networks. However, patch sizes between stream basins and between the headwater and downstream reaches could not be compared due to the spacing of the sampling channel units and reaches and the low number of observations per drainage. To remedy this problem, I suggest more spatially continuous sampling of tadpoles using the snorkeling technique developed here (see Torgersen et al., 2004). Because snorkeling is relatively fast and effective, continuous snorkeling from the headwater to the downstream reaches and within a variety of sub-basins could be accomplished, particularly in streams where barriers to movement were infrequent. More spatially continuous data would have

provided me the opportunity to compare patch sizes between basins and between headwater and downstream reaches, and would have added further power to evaluate the hypothesis that flood disturbance regime mediates tadpole distribution and abundance patterns.

Although the suggestions I pose here represent only a fraction of the possibilities awaiting tailed frog researchers, they may also be applicable to a variety of stream amphibians throughout the world. Because there are many amphibians that commonly associate with stream systems and amphibians, particularly stream obligates, are experiencing unprecedented declines, understanding how the patterns of distribution and abundance change with spatial and temporal scale, ontogeny, and regional context will provide an ecological foundation for future studies, including those investigating the role amphibians play in stream and terrestrial food webs.

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