The distribution of the Rocky Mountain tailed frog (Ascaphus montanus) in relation to the fluvial system: Implications for management and conservation

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ORIGINAL ARTICLE

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The distribution of the Rocky Mountain tailed frog (*Ascaphus montanus*) in relation to the fluvial system: implications for management and conservation

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Abstract The mating, egg-laying, and larval development of tailed frogs occur in dynamic mountain streams. During the lengthy (up to 5 years) aquatic residency these species are vulnerable to channel disturbances that can be exacerbated by land uses. Researchers have highlighted specific tailed frog habitat associations but never in the context of fluvial system processes. Based on an extensive regional study with a watershed-wide sampling strategy, we demonstrate that the Rocky Mountain tailed frog (*Ascaphus montanus*) is limited to contributing basins of roughly 0.3–100 km^2 in size, with peak numbers in basins up to 35 km^2. We conclude that the primary determinant of tailed frog distribution patterns in a watershed is basin area, a proximate variable for channel process domain and regional stream discharge: tailed frogs are adapted to cascade and step-pool channel morphologies that characterize these small basins, presumably because they afford more bedform stability and pore-space refugia than do smaller, colluvial headwaters, or larger, floodplain-forming plane bed and pool-riffle bedforms of mainstem rivers. Secondarily, climate and physiography interact to influence occurrence and abundance at the watershed level by controlling such variables as runoff, water temperature, and sedimentation regime. This point has important management implications because it forces us to recognize that in complex ecosystems, wildlife habitat associations are contingent on site-specific interactions amongst fluvial system control variables: significance levels of any one variable to tailed frog distribution will not necessarily be consistent among basins. The study clearly shows that case studies can produce conflicting results when they lack a process-based understanding of ecological response.

Keywords Tailed frog · Stream · Habitat associations · Watershed processes · Landscape influences

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Introduction

Knowledge of biotic and abiotic factors, over a range of spatial and temporal scales, is required to manage or restore ecosystems (Franklin 1993). Lack of this knowledge can lead to complex problems involving ecology, biogeography, population genetics, and evolution (Brown 1989). The stream environment carries its own set of complex interactions that drive ecological response (Scheuerlein 1999; Naiman et al. 2000; Gomi et al. 2002), with feedback mechanisms that can vary in space and time, and with disturbance.

The fluvial system is hierarchical, with regional controls shaping local conditions (Knighton 1984; Fig. 1). Climate is first in the hierarchy; along the Cordillera regional climate varies from maritime to continental. Local physiographic (landscape) parameters such as stream base-level elevation, and valley-bottom to ridge-top relief modify regional climate to produce a mosaic of ecological zones (Meidinger and Pojar 1991; Demarchi 1993). At the watershed level, geomorphologists have long recognized that basin morphometric variables (e.g., basin area, ruggedness, relief) can be correlated to geomorphic processes like rate of sediment supply (Schumm 1956), that in turn are reflected in site-level characteristics, such as bank stability, bedload movement, and bedform type (Fig. 1).

Tailed frogs (*Ascaphus* sp.) reside in and next to perennial mountain streams. Mating, egg-laying, and larval development occur in stream: adult female frogs deposit egg masses beneath large relatively stable cobbles

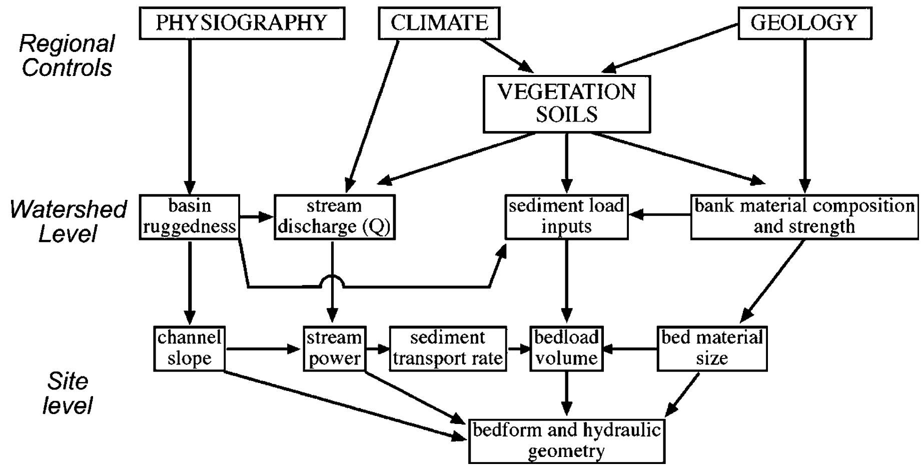

Fig. 1 Regional and watershed controls on fluvial processes (after Knighton 1984)

or boulders in the summer, and hatchlings emerge the following spring. At northern latitudes it takes up to four additional summers for tadpoles to metamorphose and begin a life of both lotic and terrestrial activity (Daugherty and Sheldon 1982a; Brown 1990). Thus, the larval life stages are particularly vulnerable to extreme flood events that cause channel disturbance (Metter 1968), and they survive and thrive only because they are highly adapted to this physiographic niche (see Scheuerlein 1999). When land use alters channel condition (e.g., Wood-Smith and Buffington 1996) tailed frogs can be affected, though reports have shown variable results (e.g., see Corn and Bury 1989; Hawkins et al. 1988; Dupuis and Steventon 1999; Wahbe et al. 2003).

Some researchers have demonstrated the significance of specific habitat controls to the occurrence and abundance of tailed frogs: geology (Diller and Wallace 1999; Wilkins and Peterson 2000); land use (Gaige 1920; Noble and Putnam 1931; Bury 1983; Corn and Bury 1989; Aubry 2000; Kelsey 1995; Bull and Carter 1996; Dupuis and Steventon 1999; Welsh and Lind 2002); and fine sediment (Welsh and Ollivier 1998). Hunter (1998) was the first to describe landscape-level tailed frog distribution patterns (in a single watershed) but did not interpret the results in terms of watershed-level controls. Stoddard (2002) examined watershed-level forestry impacts on coastal tailed frog (*Ascaphus truei*) distribution, but similarly focused her discussion on micro-scale habitat variables (e.g., sedimentation, temperature regime).

As proposed by Dupuis et al. (2000), this study elaborates on existing knowledge of tailed frog ecology by exploring the macro and site-level controls that drive occurrence and abundance of the Rocky Mountain tailed frog (*Ascaphus montanus*). Recognition of the hierarchical structure and interactive character of fluvial system parameters has guided data collection and analyses, and the interpretation of tailed frog distribution and abundance patterns. The work thus provides an example of process-based ecological research, and in this way has application beyond tailed frog science and management.

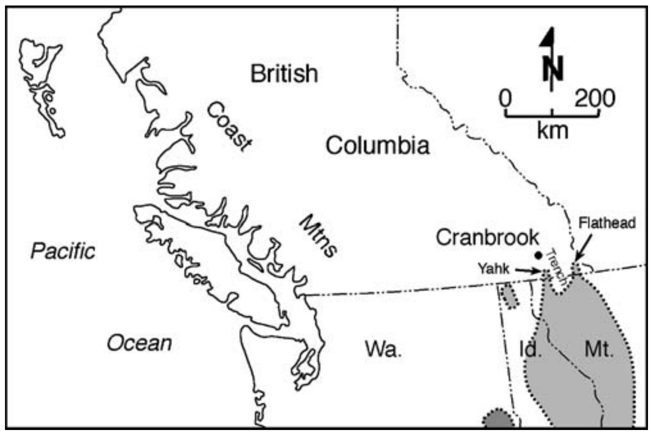

Fig. 2 Study area in southeastern British Columbia, showing disjunct populations. *Wa.* Washington, *Id.* Idaho, *Mt.* Montana

Materials and methods

Study area description

The Rocky Mountain tailed frog (*A. montanus*) forms two disjunct populations in southeastern British Columbia (Fig. 2). The range limits of the populations were described during extensive regional sampling programs conducted between 1997 and 2004 (Dupuis and Bunnell 1997; Dupuis and Wilson 1999; Dupuis and Friele 2002, 2004). Both populations extend only about 20–25 km north of the Canada/US border from source areas in the US (Montana): one is found in the Yahk River headwaters (Fig. 3) within the Columbia Mountains and Highlands Ecoregion; the second is found in Cabin and Couldrey Creeks (Fig. 4), which are western sub-basins to the upper Flathead River, within the Western Continental Ranges Ecoregion (see Demarchi 1993). The populations are separated geographically, with the Yahk lying to the west and the Flathead to the east of the Rocky Mountain trench.

Climate in the study area is continental. At Cranbrook (Fig. 2; elevation 940 m), mean annual

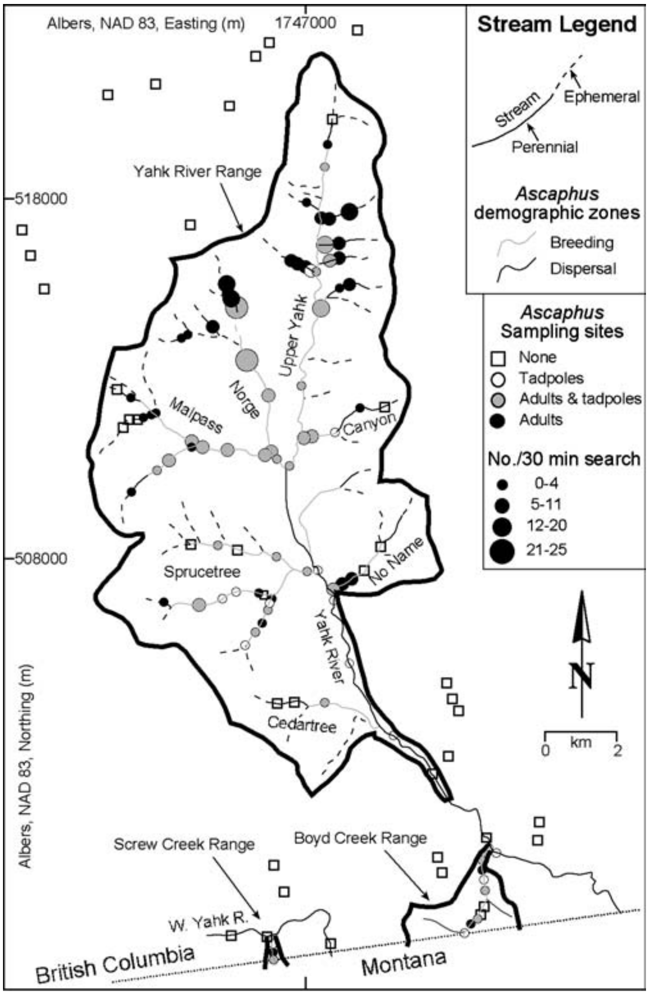

Fig. 3 Tadpole and adult distribution in the Yahk River watershed

precipitation is about 400 mm/year, with about 30% falling as snow between the months of September and April (Environment Canada 2004). Maximum precipitation occurs as rain from May to July inclusive as a result of convective storms. A secondary precipitation peak occurs from November to January. Winter precipitation results in the accumulation of a thin snow pack. Mean annual temperature is about 5.5°C (Environment Canada 2004). Freezing temperatures occur from November to March inclusive. April, September, and October are cool, with average daily temperature of 0–10°C; average daily temperatures exceeding 10°C occur from May to August inclusive. July is the hottest month of the year, with an average daily temperature of 18°C.

Stream runoff (based on gauges near the mouths of Cabin and Couldrey creeks: Fig. 4) reflects the continental climate, with an annual runoff peak in May and June resulting from a combination of snowmelt and rain-on-snow. There is a secondary, but very small runoff peak in fall derived from storms. This peak is subdued because temperatures are generally cold, and most precipitation falls as snow. Most instantaneous discharge peaks occur in May, as a consequence of rain-on-snow events. Very rarely, a fall storm may result in a severe flood (Environment Canada 2004). Low flow periods occur from August to September, and in January and February.

Physiographic differences between the Yahk and Flathead cause differences in local climate. Timberline in the region is situated at about 2,000 m elevation. The Yahk River mainstem flows at 1,200 m elevation, and valley-bottom to drainage divide relief is a maximum of 600 m. Thus, its tributaries drain entirely forested catchments. Local climate results in predominantly moist–warm interior cedar hemlock (ICHmw) and Engelmann spruce–subalpine fir (ESSFwm) biogeoclimatic forest variants (Meidinger and Pojar 1991). Late summer headwater stream temperatures are typically cool (8–16°C), and within the range of the tailed frog. In the Flathead, the base level of the Cabin and Couldrey mainstems is about 1,500 m elevation. With a local relief of up to 600–700 m, some drainage basins reach into the alpine. Alpine ridges form the northern (29-mile Leslie Ridge) and western (Couldrey Ridge) boundaries of the mapped range, and Inverted Ridge separates the Cabin and Couldrey drainages (Fig. 4). This local climate supports primarily dry–cool ESSF (ESSFdk) and montane spruce (MSdk) biogeoclimatic forest variants (Meidinger and Pojar 1991). In this setting, late summer temperatures of creeks range from 5 to 17°C, with some being colder than optimal for tailed frog.

Both regions contain sedimentary rock (e.g., argillite, siltstone, and quartzite; refer to Leech 1960; Holland 1976; Journeay et al. 2000) that range from reasonably hard but brittle, to poorly consolidated and very soft.

Sampling

Data were collected in 2001 (Yahk) and 2003 (Flathead). All sampling occurred in late summer, during the low flow period following the snowmelt freshet, and during a period of drought (i.e., sustained low relative humidity). In these conditions, encounters of all life stages are optimized because creeks are easier to search and frogs are confined to creeks or seepages to maintain moist skin for breathing (see Claussen 1973). All fieldwork was coordinated and led by the authors, lending consistency to the search results.

Within the defined range of each population, samples were distributed at intervals along mainstems, and up all tributaries (Figs. 3, 4) to the highest limits of perennial first-order reaches, yielding complete coverage of the perennial stream segments within the whole range area. As much as possible, given time and access constraints, samples were located just upstream of confluences, on both contributing stream segments. Samples were located far enough apart (minimum 200 m) to ensure sample independence both from the frog's perspective, considering the amount of tadpole drift (see Wahbe and Bunnell 2001; maximum 4 m/day) and site fidelity (see Daugherty and Sheldon

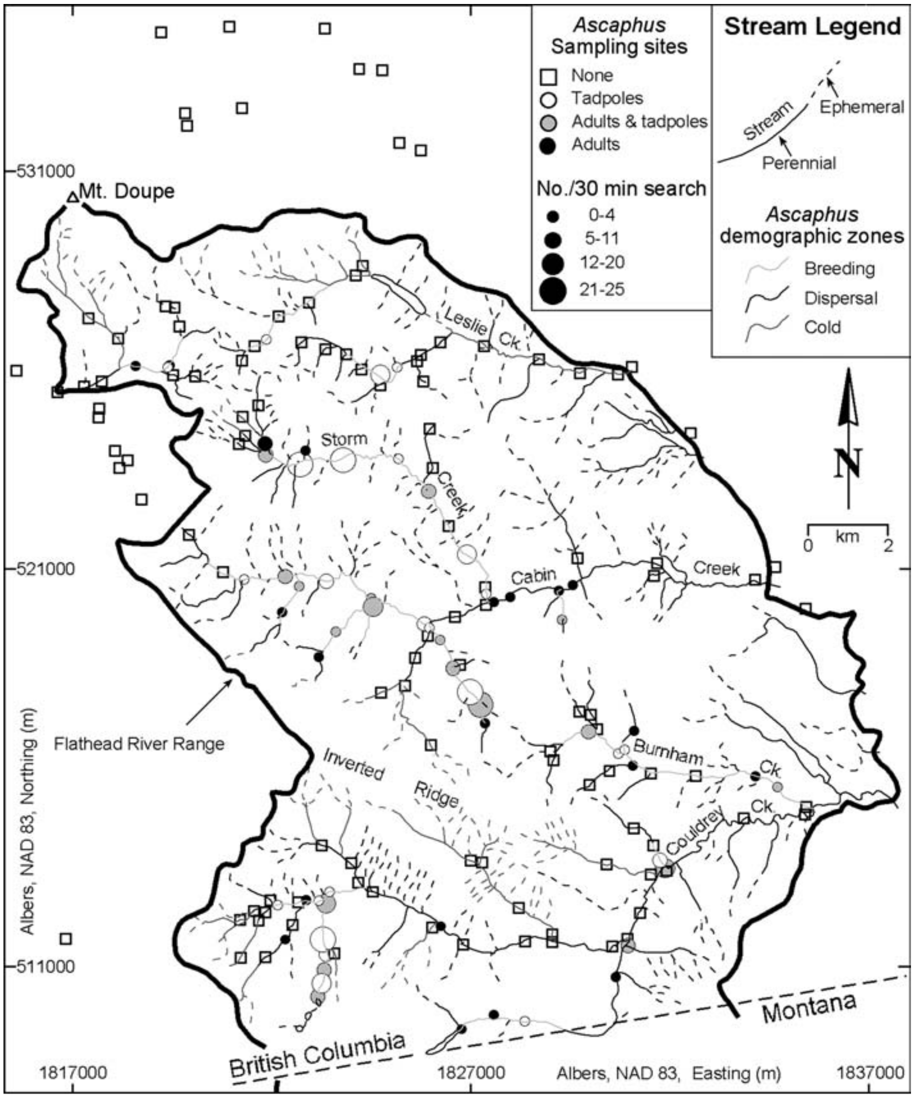

Fig. 4 Tadpole and adult distribution in the Flathead River watershed

1982b; mean adult territory of 20 m), and geomorphically, given that parameters such as bedform, hydraulic geometry, discharge, and stream temperature, vary widely over short distances along the stream length (Knighton 1984).

Parameters measured or estimated at each sample site are listed in Table 1. Site descriptions were completed prior to each tailed frog survey. For the sake of efficiency (obtaining a large number of samples), timed channel-simplifying searches were conducted: searchers spent 30 min looking for tadpoles and frogs, by lifting and removing all loose boulder and cobble substrate from the channel bed, hand-raking loose pebble substrate, and examining channel banks (for a maximum channel length of about 25 m). Larger stones removed from the channel were examined for adhering tadpoles before placement on the bank. A net was held downstream of the search location as substrate was removed or hand-raked. Removing refuge space (i.e., simplifying the habitat) in this way allowed for encounters/captures to be optimized regardless of habitat complexity. After sample completion, substrate was returned to the channel.

Stream temperature was measured at the time of sampling using a calibrated scientific thermometer. Stream discharge is the product of channel width, depth, and flow velocity: stream width and depth were measured from the high water mark, or vegetation trimline along the channel banks, using a tape measure. The velocity of regular floods (V_{HW}; those producing the high water mark) was estimated using Costa's (1983) equation, $V_{HW} = 0.18(D^{90})^{0.487}$, where D^{90} is a measure of the coarsest substrate moved by the flow. With an interest in regular flooding rather than channel disturbing threshold peak discharge (see Chin 1998), the largest substrates were measured from pools instead of stable steps. At each site the intermediate, or *b*-axis of the ten largest stones moved regularly by the flow (i.e., the largest imbricate clasts with bright surfaces) was measured to estimate D^{90}.

Table 1 Landscape (map-derived) and habitat (field-derived) variables measured at each Rocky Mountain tailed frog sample site (see text for details of field and analytical methods). *BGC* Biogeoclimatic, A_{HW} high water cross-sectional area, Q_{HW} high water discharge index, V_{HW} velocity of regular floods producing high water mark, D^{90} measure of coarsest substrate moved by the flow

Map (landscape)	Field (site or habitat)	Derivation/description of values (units)
Basin area		Digitized map area (km^2) above sample point
Elevation		GIS-queried (m)
Relief		GIS-queried (m); height above sample
Ruggedness		[Vertical height (m) above sample/length above sample (m)]; expressed as a percentage
BGC zone		BGC subzone; GIS-queried
Aspect		Expressed as degrees
	H_2O temp	Water temperature (°C)
	Reach slope	Reach slope (%) over a distance of 50 m
	Channel geometry	High water depth and width; wet width and depth
	Channel condition	Evidence of floods, sediment pulses, debris flows, braiding, etc.
	Substrate embeddedness	0 = none; 1 = low (no matrix sediment around the first layer of cobbles); 2 = moderate (first layer of cobbles are up to 50% buried); 3 = high (first layer of cobbles > 50% buried)
	Discharge	Q_{HW} (high water; m^3/s) = cross-sectional area (A_{HW})×velocity (V_{HW}), where $V_{HW} = 0.18(D^{90})^{0.487}$ (see Materials and methods)

The biogeoclimatic zone and elevation of each sample site were compiled by GIS query using digital databases provided by the British Columbia Ministry of Water Land and Air Protection. For each site, the contributing basin area was manually digitized and calculated by GIS. Basin ruggedness (Melton 1958) refers to the overall basin slope, and was calculated as relief above the sample site divided by the square root of basin area ($H/A_b^{1/2}$), where A_b is basin area. An index of high water discharge (Q_{HW}) affecting the sample site was estimated using the high water cross-sectional area (A_{HW}) measured at the site, multiplied by the velocity (V_{HW}) estimate (see above). For site-level statistical analyses, predicted discharge (Q_P) was calculated as a proximate of basin area (A_b) by log–log regression with field estimated discharge (Q_{HW}), for all sample points (see Knighton 1984). The area/discharge regression is $Q_P = 0.41A_b^{0.81}$ ($r^2 = 0.71$).

Analytical techniques

For statistical tests, variables were grouped into two categories: (1) regional/landscape level, which are also variables that can be map-derived; and (2) site level, which are variables that tailed frogs would directly respond to, such as stream temperature. The entire data set was originally lumped to examine the significance of regional controls, and then data were split into Yahk and Flathead regions to test effects of watershed-level variables.

For the analysis of tailed frog occurrence (i.e., present/not detected), all life stages were combined for a general understanding of the species distribution, and then aquatic (tadpole) and terrestrial (adult and juvenile) life stages were explored separately. Where abundance is concerned, tadpoles and frogs were treated separately, since they have different, albeit overlapping ecological niches (Hunter 1998).

Principle component analyses

Principle component analysis (PCA) was initially employed to investigate the relationship of tailed frogs to regional/landscape and site-level parameters. PCA tests are beneficial because they: (1) do not require normality; (2) can handle categorical and ordinal variables; (3) permit simultaneous exploration of multiple variables; and (4) integrate the many related measurements into summary components (Environmental Protection Agency 2002). Principle components were defined by the variables with the highest loadings (≥0.55). Components with an Eigenvalue > 1 were examined for their influence on tailed frog detection rate and abundance.

As with ecological counts in general, all life stages show a negative binomial distribution with numerous zeros (see White and Bennetts 1996). This skewness necessitates the separation of the data into two categories: (1) detected/not-detected data to be tested through logistic regressions; and (2) abundance data (zeros excluded) to be tested through linear regressions. All life stages were combined to explore detectability patterns. Whereas, tadpoles and frogs were treated separately to investigate abundance, given their differing (though overlapping) ecological needs and habits.

All data were log-transformed to meet the assumptions of normality and variance homogeneity (Krebs 1989). An alpha level of $P < 0.1$ was deemed appropriate in testing for significance of habitat variables, as it provides a more sensitive test for the detection of ecological trends (Toft and Shea 1983; Toft 1991).

Classification and regression tree-based analyses

To know the direction of influence parameters have on dependent variables, tailed frog habitat associations were further explored using classification and regression tree-based (C&RT) methods. Originally proposed for detecting non-linear interactions among variables (Denison et al. 2002), tree-fitting methods are akin to classical cluster analysis but are easier to interpret when both continuous and categorical predictor variables are used. Moreover, they assume no specific multiplicative relationship between predictor variables so that resulting models are robust to both the shapes of frequency distributions of predictor variables, and the presence of outliers (Verbyla 1987).

C&RT models create hierarchical trees by recursive partitioning of habitat predictor variable sets into mutually exclusive subsets which are most homogeneous with respect to the biological response variable of interest (i.e., species occurrence or abundance; Brieman et al. 1984). The top node of the tree contains the entire sample. The classification algorithm for splitting assumes the response variable follows a multinomial distribution. Each step in splitting the sample finds the variable most important in reducing remaining variation in the response variable of the subset. Thus, the length of each branch reflects the proportion of explained deviance in the model. The goodness-of-split criterion used was least squares deviation.

The output tree diagram represents a nested set of ecological dependencies among habitat factors, exposing how key environmental variables can act to constrain the ranges of other variables, given the observed species response. By treating the pathway through the tree nodes from the initial node to the terminal node for each site as a set of site classification rules, one can infer how different environmental factors may combine to determine observed patterns in the response variable of interest.

Results

A total of 236 surveys were conducted. The species was present in 39% of the Flathead region creeks ($n = 156$) and 80% of the Yahk region creeks ($n = 80$). In the Flathead, 309 individuals were captured, comprising primarily tadpoles (323 including new metamorphs); frogs made up 17% of the encounters (25 juveniles and 42 adults). Conversely, we encountered 482 individuals in the Yahk area of which 52% were frogs (206 adults and 42 juveniles), not including 28 newly metamorphosed tadpoles.

Although tailed frogs were found in basins up to 100 km^2 (Fig. 5), they were largely concentrated in the headwaters, particularly in the Yahk River watershed (Figs. 3, 4). Tadpoles were generally found in greater numbers (occurrence and abundance), primarily in basins ranging from roughly 0.5 to 35 km^2 (Fig. 5). There were three tadpole records in larger basins (in the Yahk River mainstem); these were all situated near tributary confluences. The adult abundance peak is upstream of the tadpole abundance peak (Fig. 5).

Important regional and landscape level variables

Tailed frog occurrence

Based on a PCA of all data combined, certain landscape level parameters (PC1—basin size, relief, elevation, and BGC zone, which explained 50.4% of the variation in the data) interacted together to significantly influence tailed frog occurrence (logistic regression: Wald = 14.66; $P < 0.001$; $n = 236$ complete cases). C&RT analyses shed light on how regional and watershed-level parameters influence occurrence. In a C&RT tree of the Yahk and Flathead areas combined (Fig. 6), the species was detected far more often (85%) in warm and moist, valley-bottom forest variants of ESSFwm and ICHmw than in cooler forest variants upslope (41% in ESSFdk, MSdk, ICHmk). Further, there were fewer detections in south-facing basins of the drier biogeoclimatic zones, and none in south-facing basins if they were smaller than 1.1 km^2. This C&RT analysis explained 34% (r^2 equivalent) of the total deviance in the data; biogeoclimatic zone accounted for the majority (38.9%) of the explained deviance in the data, basin area explained 30.8%, and aspect explained 16%.

Given that the warmer, wetter biogeographic zones were all situated in the Yahk River watershed, separate analyses were done for each region under study to explore the watershed-level parameters of importance with respect to differences in physiography. PCA yielded similar results for the Yahk and Flathead regions (Table 2) as those for the areas combined, but C&RT analyses shed new light on watershed-level controls. In the Yahk River area, tailed frogs were primarily detected where relief was relatively high (Fig. 7), though they were found in areas of low relief (< 350 m) when basin size was > 1 km^2. Within the higher relief (> 350 m) watersheds, tailed frogs were most frequently found in the warm, moist forests of the valley bottom and least frequently found in the south-facing drainages of higher elevation (montane spruce) forests. This C&RT tree explained 41% of the total deviance in tailed frog occurrence data. The proportion of explained deviance was as follows: relief (45.9%), aspect (16.5%), sample elevation (14.4%), BGC zone (12.2%), and basin size (11%). In the Flathead region, tailed frogs were not detected where relief was > 575 m. (Fig. 8). Where relief was < 575 m, tadpoles were seen 3 times more often in larger tributary basins (> 1.8 km^2), particularly those that were not south-facing (Fig. 8). The Flathead macro-scale C&RT analysis explained 38% of the total deviance in the data; relief accounted for 43.9% of the explained deviance, followed by basin area (37%), and aspect (10.7%).

Separate PCAs for tadpole and frog occurrence in the Yahk confirm the importance of the landscape parameters (basin size, relief, elevation, and BGC zone) to tadpoles (PC1; Table 2), and aspect and ruggedness (PC2; Table 2) to both life stages. PCA of each life stage in the Flathead confirm the importance of basin

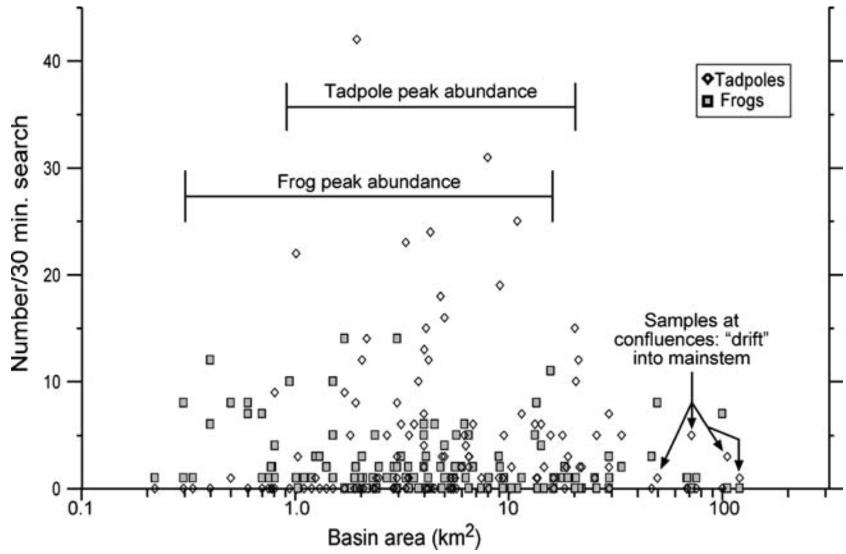

Fig. 5 Tailed frog abundance in relation to the size of the contributing basin

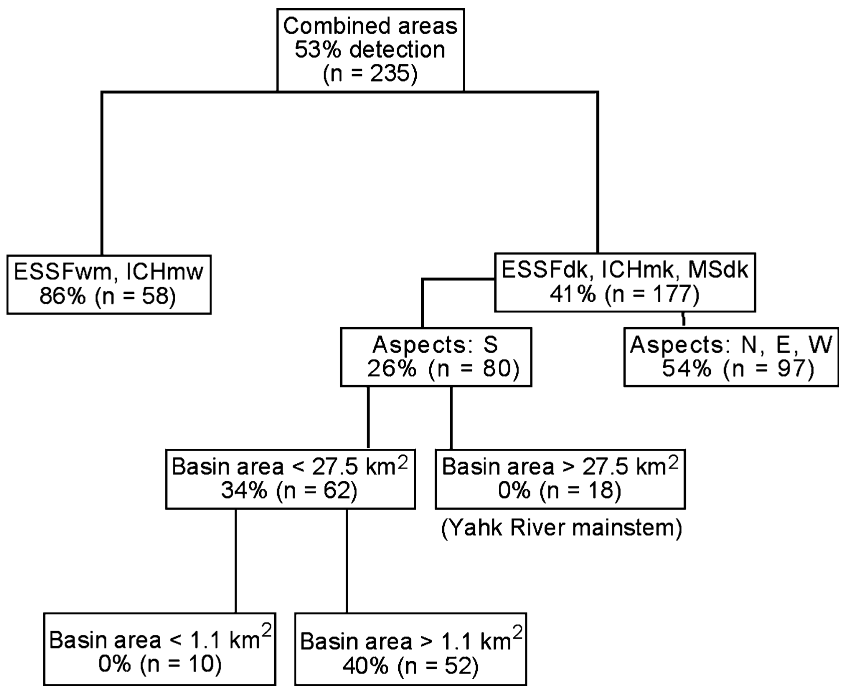

Fig. 6 Classification and regression tree-based (C&RT) analysis: macro-scale influences on the Rocky Mountain tailed frog; the *length of the branches* reflects the proportion of explained deviance in the model (tree). *ESSFwm* Warm–moist Engelmann spruce–subalpine fir, *ICHmw* moist–warm interior cedar hemlock, *ESSFdk* dry–cool ESSF, *ICHmk* moist–cool ICH, *MSdk* dry–cool montane spruce

morphometry to tadpoles, but there are insufficient data to explore frog occurrence patterns.

Frog and tadpole abundance

A PCA of the combined (Yahk plus Flathead) data for tadpole-bearing sites revealed that elevation, relief, and biogeoclimatic zone (PC1, which explains 48.5% of the variability in this dataset) also interacted to significantly influence tadpole abundance (linear regression: $t = -2.954$; $P = 0.004$; $n = 78$ complete cases). C&RT analyses hinted at similar broad-scale influences, but were unclear. Frogs (adults and juveniles) had very different abundance patterns in the two areas, with unusually large numbers in the headwaters of the Yahk River watershed (see Figs. 3 4). For this reason, analyses were not done on frog numbers for the combined areas.

When the areas were treated separately, there were no apparent links between tadpole or adult abundance and macro-scale parameters in the Yahk area based on PCA analyses. C&RT results hinted at the importance of relief and contributing basin area to both the aquatic and terrestrial life stages, but there is no clear pattern of association. In PCAs of the Flathead area, there were no

Table 2 Principle Component (*PC*) analysis summary of landscape and site variables influencing Rocky Mountain tailed frog occurrence. *Tads* Tadpoles

Scale	Region	Principle components with eigenvalues >1	Life stage	Logistic regression (Wald statistic; *W*)
Landscape	Flathead ($n=171$ complete cases)	PC1: basin size, relief, elevation, ruggedness, BGC (explains 56% of variation)	Both	$W=4.20$; $P=0.04$
			Frogs	$W=1.25$; $P=0.26$
			Tads	$W=3.80$; $P=0.05$
		PC2: aspect (explains 18% of variation)	Both	$W=0.00$; $P=0.59$
			Frogs	$W=1.01$; $P=0.31$
			Tads	$W=0.39$; $P=0.53$
	Yahk ($n=65$ complete cases)	PC1: relief, elevation, basin size, BGC (explains 48% of variation)	Both	$W=4.98$; $P=0.03$
			Frogs	$W=0.28$; $P=0.59$
			Tads	$W=9.38$; $P=0.002$
		PC2: ruggedness and aspect (explains 21% of variation)	Both	$W=0.70$; $P=0.40$
			Frogs	$W=3.25$; $P=0.07$
			Tads	$W=5.27$; $P=0.02$
Habitat (site)	Flathead ($n=153$ complete cases)	PC1: discharge, reach slope, embeddedness (explains 47% of variation)	Both	$W=0.43$; $P=0.51$
			Frogs	$W=0.26$; $P=0.61$
			Tads	$W=4.01$; $P=0.05$
		PC2: water temperature (explains 26% of variation)	Both	$W=7.45$; $P=0.006$
			Frogs	$W=5.12$; $P=0.02$
			Tads	$W=3.05$; $P=0.08$
	Yahk ($n=79$ complete cases)	PC1: discharge, water temperature, reach slope (explains 54% of variation)	Both	$W=1.46$; $P=0.23$
			Frogs	$W=6.97$; $P=0.01$
			Tads	$W=7.36$; $P=0.007$
		PC2: embeddedness (explains 22% of variation)	Both	$W=12.21$; $P=0.0005$
			Frogs	$W=6.00$; $P=0.008$
			Tads	$W=10.61$; $P=0.001$

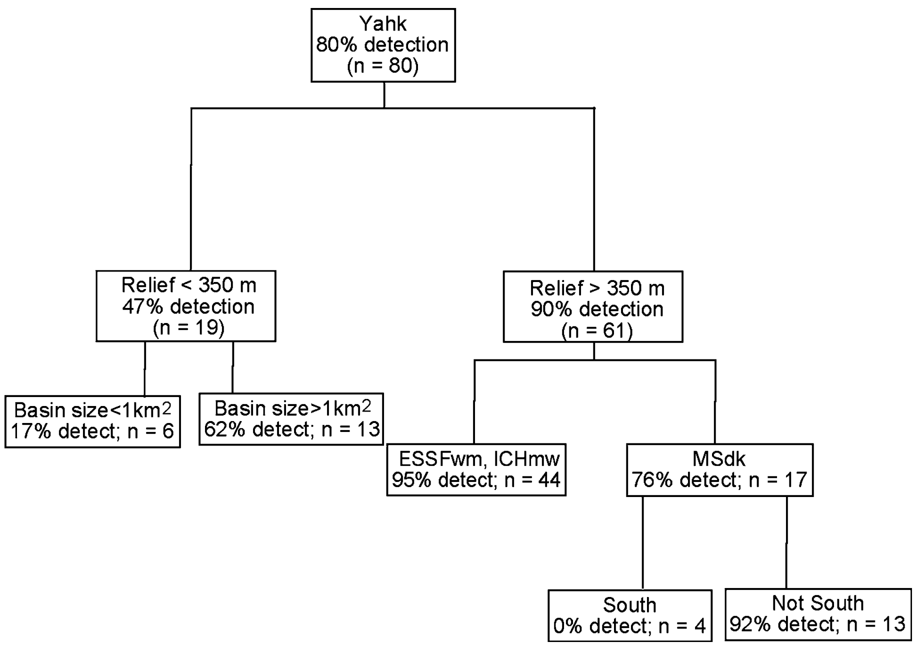

Fig. 7 C&RT analysis: watershed parameters of significance to tailed frogs in the Yahk region. For abbreviations, see Fig. 6

evident large-scale parameters associated with frog abundance but elevation, relief, basin size and BGC zone together (PC1, explaining 46.7% of the variability in the dataset) were significantly correlated with tadpole abundance (linear regression: $t=-2.45$, $P=0.018$, $n=51$ complete cases with tadpoles). In the Flathead C&RT trees, there were no straightforward patterns driving tadpole and/or frog abundance, although elevation, basin area and relief figured prominently.

Important site-level parameters

Tailed frog occurrence

When all data are combined, PCAs indicate that tailed frog occurrence (based on detection rates) is governed by embeddedness and high water discharge (PC1), as well as reach slope and water temperature (PC2; Table 2). When the Yahk and Flathead areas are analyzed separately substrate embeddedness had a significant effect on occurrence in the Yahk, whereas, water temperature had a significant influence in the Flathead (Table 2).

A C&RT analysis of all data combined drew no straightforward patterns of site-level tailed frog associations. However, based on a C&RT analysis of the Yahk area, detection rate dropped from 95% in creeks with no to low embeddedness, to 55% in creeks with moderate to high embeddedness. In these latter streams, the species was more often detected if the high water discharge was > 0.5 m^3/s, or the slope was steep (Fig. 9). Tailed frogs were found in one of five warm streams (≥13°C) and in 75% of cooler streams (< 13°C). In this analysis, which explained 47% of the total deviance in the data, embeddedness accounted for 48.3% of the explained deviance in tailed frog detection rate, predicted discharge accounted for 23%, water temperature explained 16%, and reach slope explained 12.5%.

A C&RT tree of the Flathead illustrates that water temperature is the primary governing factor in tailed frog distribution at the site level; the species was generally not detected in streams colder than 8°C in late summer (Fig. 10). Within warmer streams (> 8°C), tailed frogs were frequently detected (55% of the time) in contributing basins with predicted high water

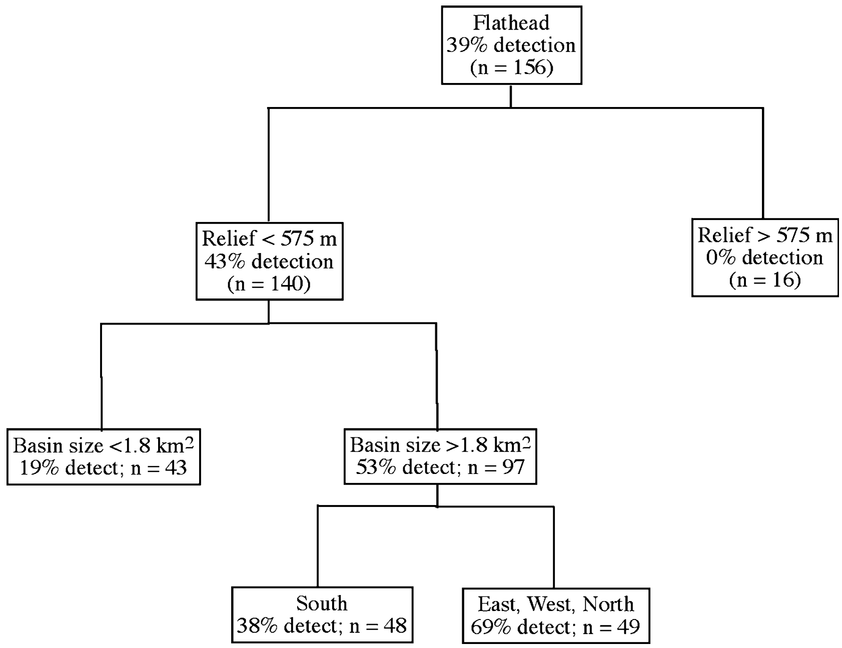

Fig. 8 C&RT analysis: watershed parameters of significance to tailed frogs in the Flathead region

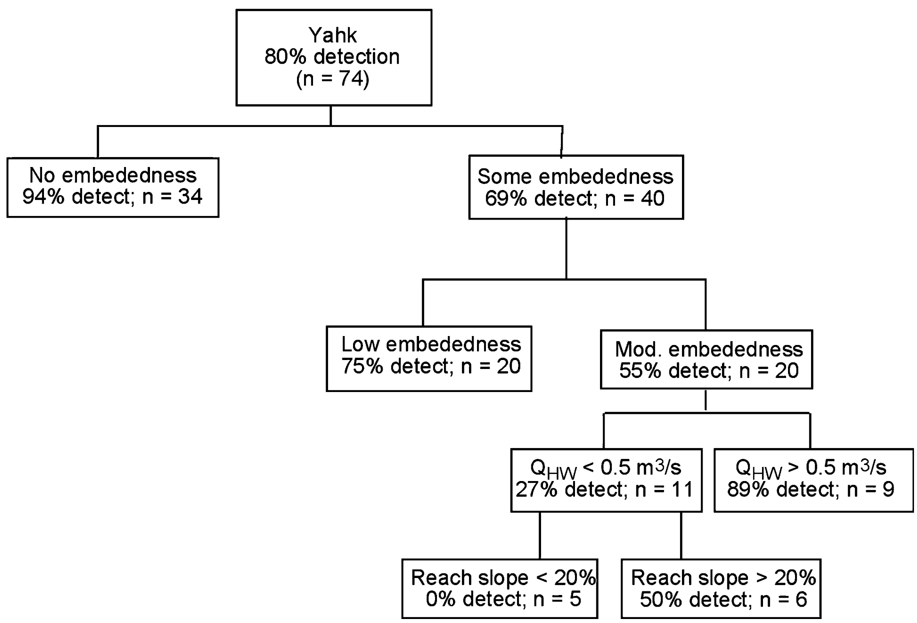

Fig. 9 C&RT analysis: site-level variables of significance to tailed frogs in the Yahk region. Q_{HW} High water discharge index

discharges of 0.7–14 m^3/s; the species was uncommonly found (22% of the time) in creeks with smaller discharges, and then, only if reach slope was low (Fig. 10). This C&RT analysis explained 30% of the total deviance; predicted discharge accounted for 44.1% of the explained deviance, water temperature accounted for 25.4%, and reach slope explained 16.9%.

Frog and tadpole abundance

Based on a PCA, tadpole abundance was not significantly associated with site-level parameters ($n = 59$ complete tadpole records), though a C&RT analysis suggests that embeddedness plays an important role [it accounted for 24% of explained deviance in a model that explained 55% (r^2 equivalent) of the total deviance]: there was a mean of 1.2 tadpoles/min ± 32 SD in creeks with low to no embeddedness compared to 0.19 tadpoles/min ± 0.8 SD, where embeddedness was moderate to high. In creeks with higher embeddedness values, tadpoles faired better if reach slope was also moderate (between 6 and 12%). Analyses of fluvial interactions were limited to the fully aquatic life stages (tadpoles) because distribution patterns of the semi-aquatic post-metamorphs are more complex (e.g., there were unusually high abundances in the Yahk, especially in the headwaters; numbers were low throughout the Flathead).

When each area was treated separately, there was no obvious correlation between tadpole abundance and site characteristics for the Yahk River watershed ($n = 34$ records with tadpoles) in either PCA or C&RT tests. A PCA suggests frog abundance was strongly correlated with discharge and reach slope in the Yahk (PC1—linear regression: $t = -2.919$, $P = 0.005$, $n = 34$ complete cases with frogs) while a C&RT test pointed to reach slope and embeddedness as important interactive factors (together these variables accounted for 59% of the explained deviance). In a model that explained 35% (r^2 equivalent) of the total deviance: adults and juveniles were more abundant (0.25 individuals/min ± 0.14 SD) in steep areas (> 25%), where embeddedness is invariably low, than in places with gentler grades (0.12 individuals/min ± 0.51 SD). In creeks with < 25% gradient, frog abundance was more than twice as high when embeddedness was low or nil (0.14 individuals/min ± 0.43 SD compared to 0.06 individuals/min ± 0.04 SD in creeks with moderate to high levels of embeddedness). There were no discernable tadpole or frog abundance patterns in the C&RT and PCA analyses for the Flathead region, though discharge and water temperature figured prominently in the C&RT trees.

Discussion

Occurrence versus abundance data: statistical considerations

Given the complexity of ecosystem interactions, regional studies that hope to tease out significance of habitat associations require large sample sizes, particularly when dealing with species abundance data. Occurrence data optimize sample size and, as with this study, can provide a relatively clear picture of distribution patterns. Conversely, measures of relative abundance have higher variability, and they are often negatively skewed (White and Bennetts 1996), requiring truncation of zero data for standard statistical analyses, or successive partitioning for multinomial analyses such as C&RT. This increased variance and reduced sample size results in a loss of statistical power. Obtaining absolute abundance data reduces variance, but it can be very time consuming and costly, and such constraints usually do not permit extensive sampling. In this study, relative abundance estimates were more realistic and feasible for addressing the broad scale distribution patterns of tailed frogs (see Figs. 3, 4).

Relative abundance estimates must be used with caution because they can reflect differences in habitat

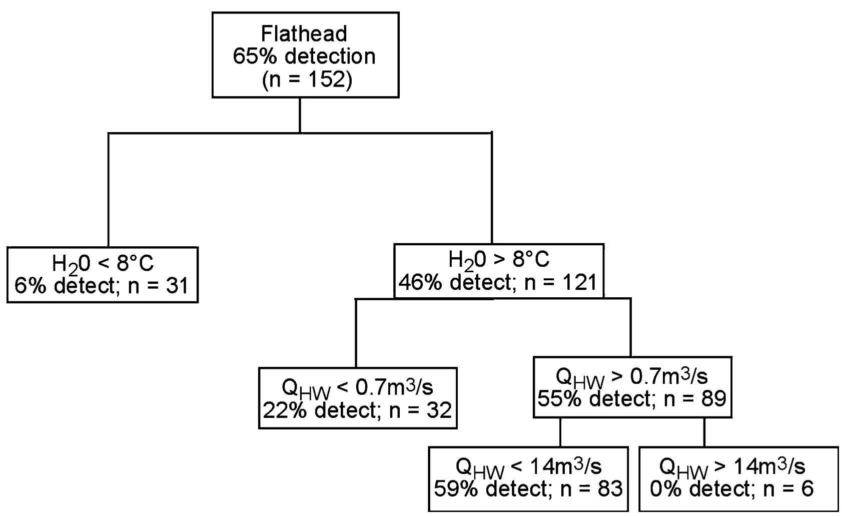

Fig. 10 C&RT analysis: site-level variables of significance to tailed frogs in the Flathead region. For abbreviations, see Figs. 6 and 9

complexity rather than true abundances. In this study, accuracy of relative abundance estimates (i.e., number of tailed frogs/min) was increased by simplifying all microhabitats (pools, steps, etc.) to pebble and sand substrates, thereby minimizing biases in detectability. Also, surveyors focused on areas that could be searched effectively (e.g., avoiding deep pools and log jams)—even larger creeks have habitat that can be thoroughly searched at low water levels. Indeed, a comparison between area and timed searches in the Yahk River watershed suggests that true and relative abundance estimates are correlated: 1.4 versus 0.8 tadpoles/min in Sprucetree Creek; 0.6 versus 0.4 tadpoles/min in Boyd Creek; 1.7 versus 1.4 tadpoles/min in Norge Creek (L. A. Dupuis and P. A. Friele, unpublished data). Based on more than a decade of tailed frog research in coastal and continental climates, the authors believe that relative abundance data from timed channel-simplifying surveys reflect real ecological trends, given sufficient sample sizes.

Distribution patterns

Site level

That tailed frog tadpole numbers are inversely correlated with embeddedness, or high levels of fine sediment (Welsh and Ollivier 1998; Diller and Wallace 1999; Wilkins and Peterson 2000), is supported by this study. It is likely that sand and pebbles fill the interstitial matrix of coarser channel substrate, thereby reducing the availability of foraging surfaces and refuge space.

Tailed frogs (all life stages) have the narrowest range of temperature tolerance of any North American frog (Brown 1975). Many authors have documented an upper stream temperature threshold of roughly 19°C (e.g., Brown 1975; Hawkins et al. 1988); warm creeks can be particularly limiting at the species southern range limit (Welsh 1990). This study demonstrates that cold creek temperatures can be equally limiting to tailed frogs, in the northern portion of their range. Creeks draining steep, high elevation ridges in the Flathead River watershed ranged in water temperature from 6 to 8.5°C depending on the time of day sampled, and contained no tadpoles. The implication is that creeks that only reach 8.5°C by the afternoon in late summer have too short a growing season to support viable breeding (this does not preclude movement and dispersal of individuals). In support of this, Brown (1975) showed that tailed frog tadpole growth and development ceases at 5°C in a laboratory setting.

Watershed level

In this study, tailed frogs were found in channels draining basin areas of up to 120 km^2. This is essentially identical to that reported by Hunter (1998) in his habitat modeling for the Blue River watershed of Oregon. Although there are anecdotal records for tadpoles in rivers and large streams, numbers are never high in large watercourses regardless of the survey technique employed (electro-shocking, seining, timed searches along the margins, area searches with downstream collection nets; L. Dupuis and P. Friele, personal observation). In this study there were three tadpole records from mainstem sites, but these were located near the mouths of tributaries, and may be there as a result of drift.

Watershed relief and predicted discharge, which were also significant to tailed frog distribution, are proximate variables to basin area. Samples with high relief for example, are generally of low elevation, and therefore have larger contributing drainage areas. In the Flathead, high relief sites (> 575 m) were located along the (fourth-order) mainstem rivers—Cabin and Couldrey Creeks (Fig. 4); they contained no tailed frogs. Although there were few high relief (mainstem) samples in the Yahk River watershed, relief still points to the importance of basin area as a key variable in this region. Moderately high relief sites (> 350 m), representing second- and third-order tributaries, had the greatest rate of occurrence and only lower relief areas (i.e., smaller basins) with sufficient discharge had relatively high occurrence. In summary, contributing basins cannot be too small or large. Optimum regular flood flows are 0.5–25 m^3/s in the Yahk and 0.7–14 m^3/s in the Flathead, which corresponds to contributing basins of roughly 1.5–40 km^2 (Fig. 11). In support of our findings, Hunter (1998) found this ‘‘middle’’ realm to have the highest probability of tailed frog occurrence in his modeling exercises.

Montgomery and Buffington (1997) and other researchers cited therein, demonstrate that channel morphology is correlated to reach slope. Since reach slope increases as basin size decreases, there is a progressive shift in channel morphology, or process domain (Montgomery 1999), as one moves headward in a drainage basin. Reach morphologies shift from pool-riffle and plane-bed bedforms along the mainstem, floodplain-forming rivers (i.e., fourth- and fifth-order channels), to step-pool and cascade bedforms in the middle reaches (second and third order), to colluvial reaches in the smallest headwaters (first order). In our study, our highest encounter rates and abundances (Fig. 5) of tailed frog tadpoles are associated with the step-pool and cascade reach morphologies (Fig. 11). We thus identify this realm as the natal zone for tailed frogs in the fluvial network.

Scheuerlein (1999) discusses the ecological implications of the physical conditions imposed by step-pool (and cascade) morphologies. Tailed frog’s egg-laying, hatchling survival, and larval growth periods are favored by the sediment-supply limited nature of these reaches (see Montgomery and Buffington 1997); and the attendant geomorphic conditions characterized by armored beds, stable bedforms, clean, coarse refuge space, and reduced tractive forces as a result of tumbling flow.

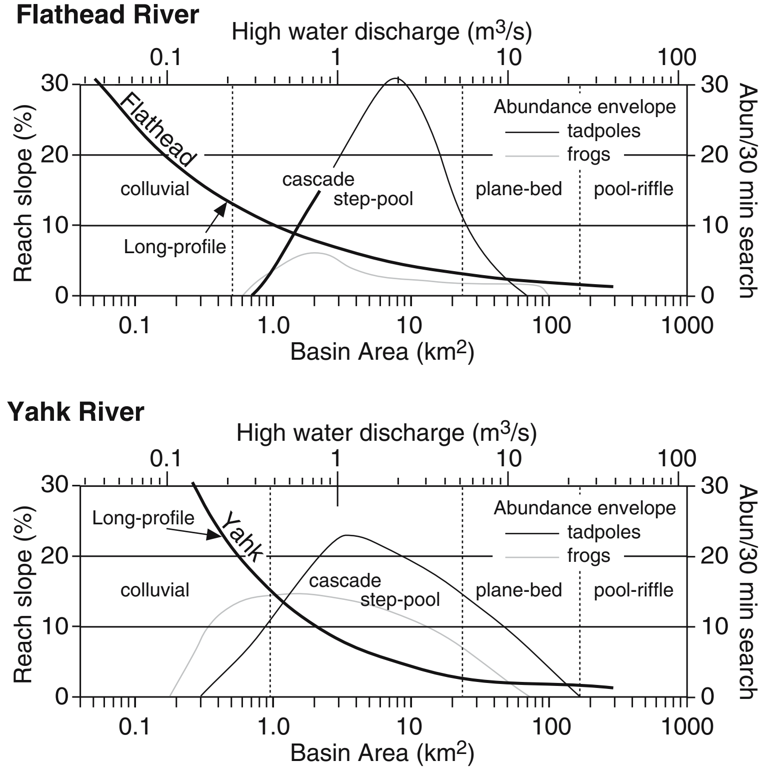

Fig. 11 Physiographic niche of the tailed frog in southeastern British Columbia. Note the relation of basin area (*bottom axis*) with high water discharge (*top axis*), derived from predicted discharge, as described in the Materials and methods. The channel long profile is an exponential fit. Channel process domains after Montgomery and Buffington (1997). The tailed frog abundance envelopes encompass the data shown in Fig. 5. Occurrence rates are highest where abundance is highest

We conclude that tailed frogs are adapted to cascade and step-pool stream domains, because farther downstream, in pool/riffle and meandering reaches, discharges are greater and bedforms more unstable (see Montgomery and Buffington 1997); one would expect egg mass survival to be lower and tadpole mortality to be higher. Upstream in the colluvial reaches, risk of channel drying during low runoff years is higher, channel substrates are loose, and more fines are present. Hence these areas also probably suffer higher tadpole mortality. Thus, we conclude that geomorphic thresholds define the ecological/physiographic niche of the tailed frog (Fig. 11).

As Hunter (1998) and Stoddard (2002) have noted in their watershed-level studies of tailed frog distribution, frog (adults and juveniles) abundance peaks are situated slightly upstream of tadpole abundance peaks. This tendency for segregation was also noted in our study (Fig. 11). Certainly, adults are less vulnerable to potential channel instability, stream impermanence, and colder temperatures of headwaters, than are the water-bound tadpoles. Kelsey (1995) suggests that adults congregate upstream to mate since they cannot rely on vocal cues to find one another. Alternatively, or in addition, frogs may have an innate tendency to move upstream for dispersal purposes, by migrating over divides (where drainage density is high) into adjacent watersheds. This tendency would also counteract the tadpole tendency to drift downstream (e.g., Wahbe and Bunnell 2001), often into reaches with less favorable geomorphic conditions (i.e., sediment transport-limited, floodplain-forming; Montgomery and Buffington 1997).

Regional level

That the fluvial system is complex, with site-level conditions driven by regional and landscape level controls, is illustrated by our results. The Yahk and Flathead tailed frog populations, found west and east of the Rocky Mountain trench, exist in contrasting environments. Although subject to a similar continental climate, differences in valley base-level elevation cause differences in local climate and stream thermal regime. For example, the ESSFwm forest variant, which is predominant in the Yahk, has a mean annual precipitation of 1,525 mm and a mean annual temperature of 2.8°C; whereas the ESSFdk variant, which is predominant in the Flathead, has a mean annual precipitation of 860 mm and a mean annual temperature is 0.4°C (Meidinger and Reynolds 1997). As a result of a higher valley base level, many of the Flathead streams drain basins with alpine headwaters, and consequently have cold (<8.5°C) late summer temperatures. The existence of cold creeks limits potential occupancy and leads to a marked decline in the tailed frog occurrence rate in the Flathead as compared to the Yahk. In the Yahk, where base-level elevation and relief do not result in cold stream conditions, embeddedness significantly affects animal distribution. Embeddedness of cobble substrates is caused by relatively high sediment supply (with respect to transport capacity). Generally, substrate in step-pool streams is armored and clean, but in certain Yahk sub-basins sediment supply seems to be relatively high, reducing channel condition and leading to lower abundance.

Conclusion

We conclude that the primary determinant of tailed frog distribution patterns in a watershed is basin area, a proximate variable for channel process domain and regional stream discharge. Tailed frogs are adapted to cascade and step-pool channel morphologies that characterize these small basins, presumably because they afford more bedform stability and pore-space refugia than do smaller, colluvial headwaters, or larger, floodplain-forming plane-bed and pool-riffle reaches of mainstem rivers. Climate and physiography interact to influence occurrence and abundance at the watershed level by controlling such variables as runoff, water temperature and sedimentation regime. This point has important management implications because it forces us to recognize that in complex ecosystems, wildlife habitat associations are contingent on site-specific interactions amongst fluvial system control variables: significance levels of any one variable to tailed frog distribution will not necessarily be consistent among basins. The study clearly shows that case studies can produce conflicting results when they lack a process-based understanding of ecological response.

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