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Ascaphus truei Stejneger 1899
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Ascaphus montanus (Mittleman and Myers) 1949:

A Pilot Meta-Analysis
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Executive Summary

We present a preliminary synthesis of results derived from five datasets on the habitat associations for tailed frogs (*Ascaphus* spp.) in headwater stream ecosystems in the Pacific Northwest region of North America. After outlining our understanding of how management of riparian ecosystems may affect tailed frog populations, we summarize:

(1) important functional relationships between physical and biological (including tailed frogs) components of headwater stream ecosystems; and

(2) present hypotheses related to the effects of forest management on tailed frog habitats and populations.

We then describe the analytical approach we used to examine the relationship between tailed frogs (occurrence and abundance) and physical factors operating at landscape, watershed, and stream-reach levels. Using four datasets across the range of the Olympic tailed frog (*A. truei*: 685 sampled sites ranging from 46° N in southwestern Washington State to 54° N latitude in northwestern British Columbia [BC]) and one within the range of the Rocky Mountain tailed frog (*A. montanus*: 250 sampled sites in southeastern BC), we extracted a subset of 223 sites with enough habitat data to apply Classification and Regression Tree (CART) analysis to identify habitat association patterns within and among study areas. Within this set, Olympic tailed frog was recorded at 107 of 223 (48%) sites and the Rocky Mountain tailed frog was found at 26 of 115 (23%) sites.

Bedrock geology consistently emerged as a important landscape determinant of tailed frog occurrence while substrate composition and morphology of stream channels and streambeds were important local scale factors in determining tailed frog abundance patterns. Despite some inconsistencies in habitat data among studies, our results suggested that increasing watershed disturbance decreased probability of tailed frog occurrence and reduced tailed frog abundance across the range of both species. Numerous complex, non-linear relationships between tailed frogs and various environmental factors that operate at different spatial scales may explain the inconsistent interpretations among studies. These complexities present the greatest challenge to development of general, predictive models.

The pilot meta-analysis combined with our understanding of headwater stream ecology suggested the following:

(1) Tailed frog populations appear to respond to environmental factors operating at multiple spatial scales. The effects of local disturbance on tailed frog populations is best understood by understanding how those environmental factors interact with each other. While bedrock geology may be the most important single determinant of tailed frog occurrence; watershed topography, history of disturbance, and climate all interact with bedrock geology to determine habitat suitability for tailed frogs.

(2) Not all tailed frog populations are equally susceptible to disturbance. Tailed frogs are likely to be less resilient to disturbance (e.g., forest management) in streams with geologies that produce fine-grained stream sediments or in low-gradient streams that store fine sediments. Developing riparian management strategies that maintain a channel's natural substrate dynamics may be important

in designing conservation strategies for species like tailed frogs, which appear to be sensitive to changes in stream substrate composition.

(3) We found interactions among habitat factors (and processes) that appear to influence occurrence and abundance of tailed frogs. These interactions result in geographic variability that makes it difficult to predict how forest management will affect tailed frogs unless all important environmental factors (at all scales) are considered. If the environmental factors that govern tailed frog's response to disturbance are region-specific, then habitat protection strategies for tailed frogs may also need to be region-specific.

(4) Additional analysis with the inclusion of specific data elements missing from our pilot analysis (e.g., distributions of different age and sex classes; stream productivity; time since last disturbance) should be used to supplement the analysis presented here. More complete data should lead to better understanding of processes governing tailed frog occurrence and abundance.

This study was unique in the sense that we assembled a large set of sample streams over a large geographic area. Analysis using CART seemed to be particularly appropriate for drawing inferences from such diverse studies. However, we recognize several limitations of this study, which should be addressed in subsequent meta-analysis. These include:

1) obtaining reliable ages for stands adjacent to the sampled sites in BC;
2) obtaining more refined road data for coastal BC;
3) refining the geological classifications used in this study;
4) developing a reliable method of characterizing stream morphology from available data (substrate composition, presence/absence of large wood in streams); and
5) using other sources of data (cohort distributions, estimates of primary productivity) that might help us better predict the effects of disturbance on tailed frogs.

We propose to extend our meta-analysis techniques to include maximum likelihood and Bayesian model evaluation using a hierarchical statistical approach, i.e., hypotheses regarding the effects of individual habitat features on population structure may be tested while controlling for conditional effects of other habitat factors. We also plan to compare conclusions from these analyses with those derived from empirical models constructed using information theoretical approaches.

1.0 Introduction

Background

In temperate forests of western North America, many resident vertebrates are associated with riparian habitats during their breeding season (Bunnell *et al.* 1997, Bunnell *et al.* 1999). For example, in British Columbia, 90 of 156 (57.7%) of breeding terrestrial vertebrate species (including 7 of 10 amphibian species) show close relationships with riparian habitat during the breeding season (Bunnell *et al.* 2001*a*). While the effect of timber harvest on riparian associated species is the subject of much research, Bunnell *et al.* (2001a) suggested that modification of riparian habitat influences the long-term success of many riparian-associated species.

Scientists have studied the effects of riparian timber harvest on stream drainage networks (Figure 1) and their associated ecosystems in the Pacific Northwest (PNW) for nearly half a century (Chapman 1962). Early research focused on the short-term effects of timber harvest on water temperature and sediment loads (Bisson *et al.* 1992). As data accumulated, new hypotheses were developed and tested, perspectives broadened, and our understanding of forest-stream interactions matured alongside advances in ecosystem theory (Sousa 1984, Chapin *et al.* 1996). In recent years, a two-part consensus has emerged regarding the effects of forestry in general, and riparian harvests in particular, on stream ecosystems in the PNW. First, the effects of riparian forest harvest on stream ecosystems is linked across spatial scales (stream to basin) and over time (years to centuries) (Vannote *et al.* 1980, Frissell *et al.* 1986, Naiman 1992, Swanson and Franklin 1992, Williams and Williams 1997, Naiman *et al.* 2000). Second, the physical and biological components of stream ecosystems vary widely through time and space. As a result, the effects of riparian forest management on stream ecosystems will vary depending on geology, climate, channel size and gradient, natural disturbance history, and community composition (Gregory *et al.* 1987, Niemi *et al.* 1990, Poff and Ward 1990, Reeves *et al.* 1995).
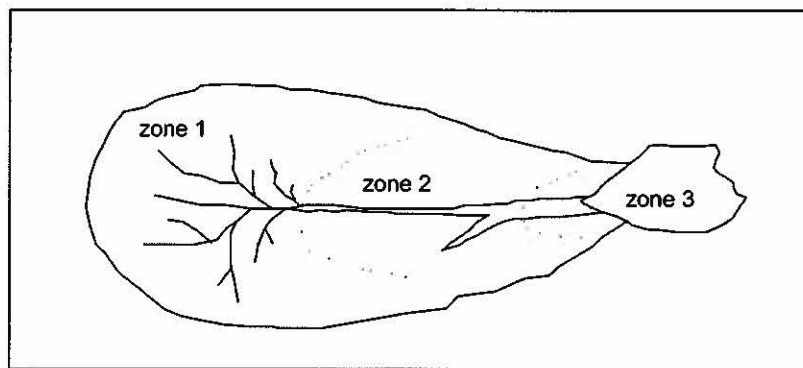
Figure 1. Schematic representation of the different zones of a drainage basin. Zone 1 is the origin zone (headwaters), zone 2 the transport zone (major valleys), and zone 3 the deposition zone. Terminology and schematic adapted from Church (1992).

Problem Statement

Fundamental information gaps exist in our current understanding of the relationships between forest management and stream-associated amphibians. These gaps exist in part because of the diverse biophysical conditions in montane landscapes of the PNW, which make it difficult to replicate environmental conditions within studies. Uncertainties also arise because while general habitat use patterns are known for most amphibians, the spatial scales at which these species use habitat are poorly understood. These uncertainties challenge our ability to construct generalized and reliable habitat models. Conducting a meta-analysis is one way of gaining a broad geographic perspective that is absent in local data sets. This study was designed to use that perspective to help address two of five priority wildlife research and monitoring tasks outlined in Schedule L-2 of the Forest and Fish (FFR) report.

1. *Verification of models that address stream-associated amphibians* (G4)

    We need to better understand the habitat factors upon which stream-associated amphibians depend, and how those habitat factors are influenced by forest management practices. This meta-analysis can clarify fundamental ambiguities in models that address stream-associated amphibians in general, and tailed frogs in particular, and may be critical to developing strategies that are relatively sensitive to detecting changes in tailed frog occupancy over time. Detecting changes in occupancy in an efficient manner is a crucial part of the process leading to a second priority wildlife research and monitoring task: G7.

2. *Testing the effectiveness of buffer patches for amphibians in westside Type N (non-fish bearing) streams.* (G7)

    Determining whether the patch buffer prescription is effective for amphibians in Type N streams, including the tailed frog, is a fundamental goal of FFR.

Study Species

Tailed frogs (*Ascaphus truei* and *A. montanus)* may be more susceptible to forest management than other stream associated amphibians because of their life history characteristics. Tailed frogs have relatively low fecundity, slow rates of development, and require a relatively narrow range of physical conditions, e.g., cool, swift-flowing streams with riparian vegetation and substrates that provide adequate interstitial space (Richardson and Neill 1998; Dupuis and Steventon 1999). These notions of susceptibility have often resulted in heightened conservation status: *A. truei* is considered Threatened in British Columbia, and is listed as a Species of Special Concern in Oregon and California, whereas *A. montanus* is listed as Endangered in British Columbia (Wahbe *et al.* 2001).

Current evidence suggests that populations of *Ascaphus* in unmanaged habitats may be relatively persistent, but direct demographic evidence of this is lacking. It is also unclear how tailed frog populations respond to forest management as studies have often yielded contradictory results (Wahbe *et al.* 2001 for a review and studies cited therein). While local stream characteristics (e.g., substrate composition, water temperatures and distribution of woody debris) are related to tadpole densities (Dupuis *et al.* 2000), the nature of these relationships is poorly understood. Moreover, it is unclear how other

local- and landscape-scale factors affect tailed frogs (Sutherland and Bunnell 2001). Unambiguous understanding of tailed frog-habitat relationships is crucial both because conservation efforts can be risky where we do not fully understand the species' habitat requirements and because harvest opportunities may be unnecessarily restricted.

These ambiguities led us to pose three key questions that a meta-analysis of tailed frogs should address:

1) What local- and landscape-scale characteristics are related to the occurrence and abundance of tailed frogs?
2) How do these local and landscape-scale characteristics change in space and time as a function of natural and human-caused disturbance?
3) Which factors best explain how tailed frogs respond to forest management across their ranges?

Objectives

The goal of this study was to develop species-habitat relationship models using existing survey data that would help explain tailed frog population dynamics in managed forests. This pilot study was intended to define the parameters and test methods that might be used in a more comprehensive meta-analysis.

We had three specific objectives for the overall study:

1) Determine the suite of habitat characteristics needed for a tailed frog meta-analysis;
2) Explore available tailed frog data sets using commonly applied statistical approaches. Then, conduct a preliminary meta-analysis, using Classification and Regression Trees (CART), to define the set of habitat factors that most strongly influence tailed frogs occurrence and abundance; and
3) Begin to assemble available data sets and potential co-operators for a more complete meta-analysis.

We addressed objectives 1 and 2 in this report, and began to assemble co-operators for a more complete meta-analysis.

Primary Processes of Interest

Considerable background literature documents the general effects of forest management on physical and biological components of aquatic ecosystems in the PNW (see Young 2001 for a recent summary; also see Gregory *et al.* 1987 and other studies in the same volume; Niemi *et al.* 1990, Naiman *et al.* 2000). In addition, a recent review examined the relationship between an array of habitat factors and the distribution and abundance patterns of tailed frogs (Wahbe *et al.* 2001). We summarized the important relationships below and considered them as hypotheses to address in this meta-analysis.

Expected Ecological Responses of Streams to Riparian Timber Harvest

There are three primary and three secondary effects of riparian zone management on streams in the PNW (Figure 2):

1. ***Increased incident solar radiation commonly results in an increase in water temperature.*** Warm-season water temperature typically increases immediately post harvest and returns to pre-harvest levels as vegetation regrows, although this general pattern depends on a number of other factors. Water temperature may not increase if

direct solar radiation to the stream is unaffected by harvest or if streams are spring-fed or ground water-dominated.

a. *Increases in solar radiation to the stream can often increase primary productivity.* This response may be short-lived (i.e., < 5 years) unless brush is controlled, or the site is of low productivity (J. MacCracken, *pers. comm.*).

b. *An increase in primary productivity may translate into greater consumer biomass (macroinvertebrate and vertebrate).*
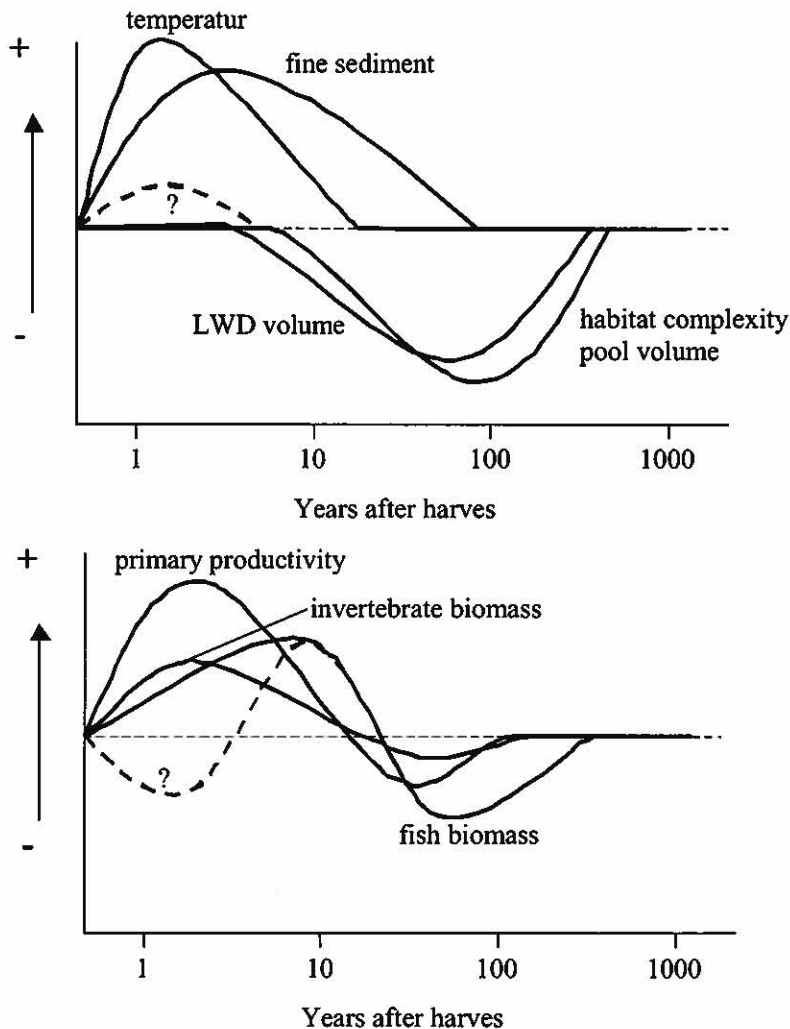
Figure 2. Conceptual models illustrating the temporal response of aquatic systems to riparian forest removal relative to "pre-disturbance" conditions (horizontal line). Top graph: physical components; bottom graph: biological components. Dotted lines indicate alternative hypotheses for a particular response. Adapted from Young (2001); see also Gregory *et al.* (1987) and Murphy and Koski (1989).

2. *Forest management often immediately increases suspended and/or fine sediment delivery rates to stream.* Elevated delivery rates may persist due to loss of tree root stability, presence of roads, stream crossings, etc. The extent to which

sedimentation increases depends on forest management and engineering practices, slope, geology, precipitation, and other factors. In addition, the degree of connection of the road drainage ditches to streams (e.g., road crossing points) appears pivotal in long-term sediment delivery (Jones *et al.* 2000; J. MacCracken, *pers. comm.*).

3. *Volume of woody debris (WD) input to the stream may decline after harvest,* although a temporary pulse of WD to the channel may occur immediately post-harvest. Recovery is generally slow until the surrounding forest ages sufficiently for tree mortality to resume, and as in-stream woody debris declines due to decay and movement downstream.

   a. *Channel habitat complexity (generally a measure of pool frequency or percent area/volume) also declines.* This is particularly important for small pieces of wood. Larger WD may persist over long periods of time.

Expected Ecological Responses of Tailed Frogs to Habitat Factors

Tailed frog habitat can be organized according to macro- (landscape), meso- (watershed-stand), and micro- (site) spatial scales. Geology and climate (temperature, precipitation) may explain macro-scale distribution patterns and abundance of tailed frogs (see references cited in Wahbe *et al.* 2001). At the meso-scale, overall topography (elevation, aspect), watershed (stream gradients, hillslope concavity, road density), channel size, and vegetation (forest age, presence of riparian buffers) appear to influence abundance of tailed frogs. At the micro-scale, tadpole abundances and the age structure of the population seem to be related to substrate composition, channel morphology (heterogeneity, substrate embeddedness, disturbance frequency), sidewall stability, and water flow (depth, flow rate, summer wetted width). Some variables exert influence at more than one scale (e.g., gradient at meso- and micro-scales).

Disturbances to forest vegetation and soils (e.g., loss of vegetation cover, exposure of soils) affect meso- and micro-scale conditions in tailed frog habitat by: (1) changing vegetation cover and flow patterns associated with downed wood (Bunnell and Huggard 1999); (2) changing incident radiation, which affects periphyton productivity and stream temperatures (Richardson and Neill 1998); and (3) changing sedimentation rates (Hawkins *et al.* 1983, Welsh and Ollivier 1998). These changes have the potential to affect tailed frog life stages in complex ways. Primary production, which determines food supply for larvae via growth and availability of periphyton, is related to incident radiation, stream temperature, current velocity, nutrient inputs, and disturbance (McIntire 1966, Murphy and Hall 1981, Beschta *et al.* 1987, Lamberti *et al.* 1991). Rate of sediment deposition, which can affect the extent of substrate spacing that conceals tailed frog life stages, is an inverse function of velocity (Leopold *et al.* 1964). As montane stream sediment volume is related to probability of bedrock failure (Church *in press*) and amount of exposed soil surface (e.g., road surfaces, cutbanks, landslides; Forman and Alexander 1998), surficial geology is likely to influence tailed frog occurrence. Woody debris, which interacts with sedimentation to affect stream channel morphology (Tripp 1998), can influence tailed frog habitat by altering pool:riffle or step:pool ratios, wetted width, or substrate composition.

The interaction of these physical factors has made it difficult to interpret studies of tailed frog-habitat associations. In fact, some studies assessing the effects of timber

management on tailed frogs have produced contradictory results (see Wahbe *et al.* 2001). In part, these apparent contradictions result from failure to recognize the interactions between habitat factors at the macro-scale (particularly geomorphology) with those at finer scales (Sutherland *et al.*, *in prep.*). Contradictory results make it difficult to predict tailed frogs response to habitat change. As an initial step in our process, we described expected tailed frog responses to each individual habitat factor (Tables 1a, 1b, and 1c) in the absence of other factors. Note that many relationships are expected to be unimodal (i.e., the highest values for tailed frogs may occur at intermediate ranges of the habitat factor).

2.0 Methods

Conceptual Approach

In principle, meta-analysis is used to describe quantitative methods for combining research evidence across studies (Hedges and Olkin 1985, Myers and Mertz 1998, Gurevitch and Hedges 1999, Hedges *et al.* 1999). The underlying philosophy in this case is to exploit commonalities in how different populations (from different studies) respond to habitat variables to learn more about how the species as a whole responds to the same suite of habitat variables (Myers and Mertz 1998). Lack of long-term data for any single population has been one of the major motivating factors for the use of meta-analysis techniques in ecological studies. By combining separate estimates of effects of habitat factors on biological responses across several populations, we hope to reach firmer conclusions, and acquire more precise estimates of the parameters describing the relationships between a species and its environment. An overarching assumption is that ecological and physical processes acting across all populations are comparable in a broad sense, and thus may be described by the same probability distribution and combined in a general model.

Meta-analysis techniques vary among applications, but all require estimates of parameters describing an ecological effect measured for each of the source studies or populations, along with estimates of the sampling variances for these effects. The usual approach is to identify a measure of "effect size" that is comparable across populations. The effects are assumed to be related to the measured conditions under study in each population. Usually, "effects" are described with an estimate of a parameter to an underlying statistical distribution specifying the distribution of errors about that parameter (e.g., the mean for normally distributed variables). "Effect size" is determined by comparing differences in the values of these estimated parameters among studies (e.g., by their ratios). Each observed effect size thus serves as an independent observation in the meta-analysis (Osenberg *et al.* 1999). Treated this way, the effect size is treated as if drawn from an underlying distribution representing a grand mean for the species, plus true inter-population variation, plus estimation error (Myers and Mertz 1998). Thus an estimate of the parameter for any particular population provides information about the true value of the parameter for all the other populations in the analysis. By capitalizing on this combined information, the uncertainty in the estimate for any particular population can be reduced (Myers and Mertz 1998). Given our goal of building a general ecological habitat model for *Ascaphus*, meta-analysis techniques both help to identify the complete suite of variables that must be included in such a model, and to increase the

precision and accuracy of estimated parameters for the relationships in such a model.

Table 1a. Habitat factors and their expected influence on tailed frog presence and abundance at a landscape or macro- scale.
Unless noted otherwise, the source is Wahbe *et al.* (2000).

Predictor Variable[a]		Response Variable[b]		Comments
Class	**Type (units)**	**Presence/ Non-Presence**	**Abundance**	
Climatic	Mean annual precipitation (mm) [MeanAPrecip]	+ Monotonic	Unimodal	Daily data averaged by year for period 1961-1990
	Mean summer precipitation (mm) [MeanSPrecip]	+ Monotonic	+ Monotonic	Precipitation for April-Sept (1961-1990) averaged by year
	Mean annual air temperature (°C) [MeanATemp]	Unknown	Unimodal	Daily data averaged by year for period 1961-1990
	Mean air temp warmest month (°C) [MTWM]	Unknown	Unimodal	Daily data averaged by month for period 1961-1990
Geologic	Parent lithology type (geocodes) [Geology]	Categorical	Categorical	Based on origin (e.g., sedimentary) and weathering rate; intrusives or rocks with low weathering appear favored
Distance	Latitude [Latitude]	Unimodal	Unimodal	Theoretical expectation: Decreasing abundance away from center of ranges.

[a] Type is the name of the variable within a particular class predictor variables (e.g., topography). Codes in brackets following the variable type indicate the name used in subsequent analyses (e.g., CART).

[b] Shape of the curve describing the relationship between the response and predictor variables is provided for each of occurrence (i.e., presence/non-presence) and abundance data. Curve shapes are described as categorical (category or step function), monotonic (continuous function in one direction), unimodal (continuous function with one mode; an n-shaped curve), bimodal (continuous function with two modes; a u-shaped curve), variable (curve changes depending on conditions or latitude; see comment line), and unknown. We use a "+" or "-" to describe the positive (increasing) or negative (decreasing) forms of monotonic functions.

Table 1b. **Habitat factors and their expected influence on tailed frog presence and abundance at a watershed-stand or meso-scale.** Unless noted otherwise, the source is Wahbe *et al.* (2000).

Predictor Variable[a]		Response Variable[b]		Comments
Class	Type (units)	Presence/ Non-Presence	Abundance	
Topography	Elevation (m) [Elevation]	Unimodal	Unimodal	Variable across range[c]
	Aspect (degrees) [Aspect]	Categorical	Categorical	Highest on north-facing aspect but variable across range
	Stream gradient (%) [Gradient]	Unimodal	Unimodal	Geology dependent
Watershed Disturbance	Area recently logged (%) [RecentLog]	- Monotonic	Bimodal	Highest post-harvest and old growth; Time since harvest and topography dependent
	Road density (km/km^2) within 100 m of stream [RoadDensity]	- Monotonic	- Monotonic	Geology/fine slash dependent (Sutherland 2000)
Forest Descriptors	Bordering forest stand age (classes)[d] [ForestAge]	Unknown	Variable	Time since harvest and buffer dependent; Expect a relationship such as in Figure 2 (bottom)
	Riparian buffer occurrence [Buffer]	Unknown	Variable	Sites with buffer on one side were scored no buffer

[a] Type is the name of the variable within a particular class predictor variables (e.g., topography). Codes in brackets following the variable type indicate the name used in subsequent analyses (e.g., CART).

[b] Shape of the curve describing the relationship between the response and predictor variables is provided for each of occurrence (i.e., presence/non-presence) and abundance data. Curve shapes are described as categorical (category or step function), monotonic (continuous function in one direction), unimodal (continuous function with one mode; an n-shaped curve), bimodal (continuous function with two modes; a u-shaped curve), variable (curve changes depending on conditions or latitude; see comment line), and unknown. We use a "+" or "-" to describe the positive (increasing) or negative (decreasing) forms of monotonic functions.

[c] In Oregon, responses appear highest at intermediate elevations.

[d] Bordering was within 100 m of the stream. Forest age classes were: (1) 0-10 yrs; (2) 11-20 yrs; (3) 20-60 yrs; (4) 60-100 yrs; and (5) 100+ yrs. For sites with buffers, we used the youngest forest stand age class represented.

Table 1c. Habitat factors and their expected influence on tailed frog presence and abundance at a site or micro-scale. Unless noted otherwise, the source is Wahbe *et al.* (2000).

Predictor Variable[a]		Response Variable[b]		Comments
Class	Type (units)	Presence/ Non-Presence	Abundance	
Morphology	Pool:riffle (ratio) [PoolRif]	Unknown	+ Monotonic	Abundance increases with increasing pool: riffle ratio
	Mean wetted width (m) [MeanWW]	Unknown	Unimodal	Width of permanent water flow at sample period. Intermediate sized streams expected to have highest abundances
	Mean bank width (m) [MeanBW]	Unknown	Unimodal	Determined by break in topography from side gully to stream substrate. Stream with seasonal floods (e.g., wide streams) may have lower abundance.
Temperature	Water temperature (°C) [Temp]	Unknown	Variable	Increases in north; decreases in south
Substrate	Detritus index (categories)[c] [WD]	- Monotonic	- Monotonic	Higher amounts of slash lower physical space available and stream productivity
	% cover of boulders (> 256 mm) [PCNTBoulders]	- Monotonic	- Monotonic	Large substrate size related to stream stability and epiphyton availability
	% cover of cobbles (64-256 mm) [PCNTCobbles]	+ Monotonic	+ Monotonic	Large substrate size related to stream stability and epiphyton availability
	% cover of fines (< 64 mm) [PCNTFines]	- Monotonic	- Monotonic	Large substrate size related to stream stability and epiphyton availability

[a] Type is the name of the variable within a particular class predictor variables (e.g., topography). Codes in brackets following the variable type indicate the name used in subsequent analyses (e.g., CART).

[b] Shape of the curve describing the relationship between the response and predictor variables is provided for each of occurrence (i.e., presence/non-presence) and abundance data.   Curve shapes are described as categorical (category or step function), monotonic (continuous function in one direction), unimodal (continuous function with one mode; an n-shaped curve), bimodal (continuous function with two modes; a u-shaped curve), variable (curve changes depending on conditions or latitude; see comment line), and unknown. We use a "+" or "-" to describe the positive (increasing) or negative (decreasing) forms of monotonic functions.

[c] Index of small (< 4 cm diameter) woody debris in streams; classes are 1 = nil, 2 = low, 3 = medium, and 4 = high.

If a general model can describe the ecological effects in the various populations, the most interesting task is estimating meaningful parameters for a probability model that captures the effects observed in each study. Gelman *et al.* (1995), Osenberg *et al.* (1999) and others discuss three possibilities: 1) the studies are essentially replications of each other, and sample results can be treated as outcomes from the same population; 2) the studies are so different that the results from any study provide no information about the results of any other; and 3) studies are neither identical nor unrelated and the underlying population distribution may be governed by related sets of parameter values. In this last case, which is typical of most dataset complexes assembled for meta-analysis, it is critical that specification of the underlying model be done explicitly as part of the meta-analysis protocol (Osenberg *et al.* 1999). We expected that our studies would fall into this case, and so inferring the key factors and relationships an underlying ecological model formed a pivotal part of our approach.

We undertook this pilot meta-analysis in several steps (e.g., Shekelle and Morton 2000):

(1) we assembled data from habitat association studies on *A. truei* and *A. montanus* and screened the data using criteria for acceptance (see below);
(2) we used Classification and Regression Tree analysis among other techniques to extract the dominant habitat relationships governing *Ascaphus* distribution and abundance patterns;
(3) we developed estimates of effect size for each study, along with information on other habitat factors of interest. Together with the results of (2), these form the core of the ecological model. Finally,
(4) we analyzed trends and drew conclusions about the effects of management on the ecological processes of most importance.

Data Sources

Five datasets from field surveys on tailed frogs were included in this study (Table 2). For all datasets, the original sample information was supplemented with additional topographic, geologic, climatic and watershed status information that may describe macro- and meso-scale factors that influence stream productivity and disturbance regimes (see Table 3 below). We did not analyze a sixth data set (Kelsey 1995) because we could not derive all the necessary habitat information for it in time to complete the analysis. This dataset will be included at a later stage of this project. More details on the sampling designs employed in the original studies are provided in Appendix I.

We treated these datasets as follows. First, we examined each dataset for consistency and completeness in the habitat factors measured at each sample site, eliminating records for which the accuracy of measured variables was suspect, or where measurements were incomplete. To do this we examined diagnostic plots for each variable, searching for outliers or sequences of identical data. If causes for such suspect values could not be determined, or their true values could not be located, they were eliminated. Second, to reduce redundancies among closely related predictor variables, we used correlation analysis to select one variable from highly correlated pairs ($r > 0.75$). We retained the variable with the highest overall correlation to the response variables. The remaining samples for each tailed frog dataset actually used are listed in Table 2. For the Kootenays

A. montanus dataset, we used only the subset of original sites searched that were within 20 km of the nearest recorded tailed frog record, as searched sites too remote from recorded areas were thought to have non-ecological influences on the likelihood of occurrence that would bias model construction. Finally, because of the broad spatial scope of the coastal BC data for *A. truei* (approximately 60,000 km^2), we partitioned sampled sites it into two broadly similar (topographic and ecologic) subsets using the BC Ecoregion Classification System (Demarchi 1993): (1) a North and Central Coast dataset (including the North Coastal, Nass Ranges, and Coastal Gap Ecoregions), and (2) a south coastal dataset (including the Pacific Ranges, Lower Mainland, Cascade Ranges, and Interior Transition Ranges Ecoregions). Appendix I includes descriptions of how the habitat information was measured.

Table 2. Tailed frog datasets used in this pilot meta-analysis.

Ascaphus Species	Study Location	Years	Sites		Total Habitat Variables	Response Variables	Principal Investigators
			Total	Used[1]			
truei	Coastal BC	1994–1998[2]	585	143	25	P/NP[3](all sites) Counts (n/20 min) Density (n/m^2) Cohort distribution	Dupuis Bunnell
	Squamish watershed, (BC S Coast)	1994-1996	9	9	25	Counts (n/20 min) Density (n/m^2) Cohort distribution	Wahbe
	Chilliwack watershed, (BC S Coast)	1996-1999	11	10	2	Density (n/m^2) Cohort distribution	Richardson
	Chehalis-Willapa watershed (SW WA)	1994-1995	71	71	17	P/NP[2] (all sites) Counts (n/10 m)	Runde
montanus	Kootenays (BC)	1996,1998	250	115	25	P/NP[2] (all sites) Density (n/m^2)	Dupuis

[1] Sites meeting criteria for inclusion in this meta-analysis. For Olympic tailed frog, all datasets except the Chilliwack watershed were used in the CART analysis.
[2] Includes scattered data outside the 1994-1998 interval
[3] P/NP = Presence/non-presence

Table 3. Sources of supplementary habitat information included in this study. All
other habitat factors were measured at the sampling sites, as described in the text.

Predictor Variable	Source
Macro scale (landscape)	
climate (precipitation, air temperature)	BC: Reynolds (1997)[a] WA: PRISM database[b]
geology (bedrock lithology)[c]	BC: Geological Survey of Canada 1:250,000maps WA: DNR 1:64,000 maps
Meso scale (watershed - stand)	
stream gradient (%)	BC: 1:50,000 and 1:20,000 topographic maps
area recently logged (%)	BC: 1:250,000 Base Thematic Mapping (BTM)
road density (km/km^2)[d]	BC: 1:20,000 TRIM mapping (1988 data)

[a] Based on data for 1961-1990 and averaged by biogeoclimatic zone and variant, thus partially corrected for
   elevation and aspect.
[b] Model projections based on long-term average (1961-90 data) corrected for elevation and local
   topography.
[c] Categories for bedrock lithology (BC); geocodes (WA).
[d] Within 100 m of the stream.

Statistical Analysis

Analyses of species-habitat associations require alternatives to linear models because
variation in broad- and fine-scale habitat factors are confounded and are also non-linear
(Huggard 2000; Sutherland and Bunnell 2001). Several ecological and methodological
difficulties exist in studies relating species occurrence or abundance to habitat features.
First, variability in animal abundance is affected by behavioral processes, stochastic
events (such as severe weather) and other factors that confound the determination of the
relative importance of habitat and non-habitat factors (Van Horne 1983; Wiens *et al.*
1987; Hansen *et al.* 1993). Second, empirical studies of habitat relationships are
necessarily imperfect (e.g., some distinct habitat types are not sampled separately, or
important elements may not be measured at all [Huggard 2000]). Third, spatial structure
in either the dispersion of habitat types, or in species' distributions can lead to spurious
habitat relationships and/or excessive confidence in actual relationships (Legendre and
Fortin 1989; Thomson *et al.* 1996). These difficulties virtually guarantee that statistical
analysis methods dependent on well-stratified sampling designs, or on particular
assumptions about the variance structure of samples (e.g., independence of habitat
elements, or known distributions of errors in variables) will generate models that are
unreliable when tested at new sites (e.g., Van Horne and Wiens 1991).

Initial explorations of some data used in this study (the occurrence and abundance data
from B.C. for *A. truei*) using a generalized linear modeling approach (e.g., logistic
regression, and quasi-likelihood models) produced models that accounted for less than
20% of the observed variation in the data. Accordingly, we chose a non-linear, dendritic
Classification and Regression Tree (CART) analysis techniques in this study because of
the utility of this method in screening habitat factors that may interact in complex ways,
and to devise prediction rules that can be evaluated among datasets (Mathsoft 1998).

Classification trees are used to model the probability of particular states or categories of the response variable (e.g., presence/non-presence in this study) depending on the values of the predictor variables. Regression trees are used to predict the value of a continuous response variable (e.g., abundance) given the values of the predictor variables. Other advantages CART models offer (see Verbyla 1987) include easier interpretation than models produced by other multivariate approaches when both continuous and categorical predictor variables are used. They assume no specific multiplicative relationship between predictor variables, so resulting models are robust to both the shapes of frequency distributions of predictor variables, and the presence of outliers. Once developed, they can be tested on other datasets for further refinement and verification. They can generate predictions even if variable values for some sites are missing. In short, they are appropriate for the types of survey data analyzed here.

CART models create hierarchical trees by recursive partitioning of sets of numeric and/or categorical habitat predictor variables into subsets which are most homogeneous with respect to a variable describing the biological response of interest (i.e. species occurrence or abundance; Brieman *et al.* 1984). The analysis assumes each response variable is assumed to follow a multinomial distribution with respect to the predictor variables. Each step in splitting the sample finds the variable most important in reducing remaining variation in the response variable of the subset (dependent on all previous steps) and the subset is then split into two further subsets that are mutually exclusive in their values of the selected predictor variable. Residual variation remaining in the response variable at each splitting point in the model fitting process, termed "deviance", is measured by the log-likelihood function (Mathsoft 1998), and is analogous to the residual sum-of-squares in a generalized linear model. In CART analysis, the fitted value at each node is the mean value of the response variable, and for classification trees, the misclass rate can be used as a measure of goodness-of-fit. The output tree 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. More details on the methods used in developing the trees can be found in Sutherland and Bunnell (2001).

3.0 Results

General Tailed Frog Response Variables

Overall, *A. truei* was widely distributed and occurred in 48% (107 of 223) of sampled sites that met our data selection criteria. In the coastal mountains of British Columbia, the species appears more or less continuously distributed, although occurrences become scattered north of latitude 54° N. Although there was reduced sampling north of this latitude, Dupuis *et al.* (2000) suggested that the decrease in occurrences reflects unsuitable conditions for tailed frog populations rather than an artifact of reduced sampling effort even though they did not test this suggestion. This pilot analysis did not include enough datasets to delineate distributional variation within the range of *A. truei* in the United States (Figure 3). Other summaries (e.g., Leonard *et al.* 1993) have suggested that the species is also continuously distributed in the coastal mountains of Washington

and Oregon with the distribution becoming more scattered in the western Cascades (see Figure 3).

Larvae (tadpoles) were present at 39% (88 of 223) selected sites, whereas metamorphic and post-metamorphic juveniles or adults were found in 23% (51 of 223) of the selected sampled streams. Tadpoles co-occurred with other life stages in 27% (60 or 223) of selected streams (although we note that sampling was focused on tadpoles and so other life stages are likely under-represented in these samples). We found a considerable range of variation in *A. truei* tadpole density (when tadpoles were found) among sites within and among datasets (north-central coast BC: 2.18 individuals/m^2 $\pm$ 0.27 SE, n = 72 samples; south coast BC: 0.47 individuals/m^2 $\pm$ 0.08 SE, n = 50). Measures of relative abundance when tadpoles were found (e.g., counts per distance [10 m] or time [20 mins] sampled) also varied in a similar way among sites and datasets (north-central coast BC: 15.14 $\pm$ 0.38 SE, n = 32; south coast BC: 9.18 $\pm$ 2.22 SE, n = 11; Chehalis-Willapa WA: 9.47 $\pm$ 2.04 SE, n = 23).

In the Kootenays area of BC, *A. montanus* was less widely distributed and less common than *A. truei* was across its range. Individuals were recorded at 23% (27 of 115) of selected sites, and occupied sites were concentrated in only two tributary systems of the Flathead River, and one watershed of the Yahk River west of the Rocky Mountain Trench. Estimates of relative abundances were also significantly lower compared with *A. truei* (3.09 $\pm$ 0.49, n = 25; Mann-Whitney U test; P < 0.01).

Classification of Environmental Relationships

Across the datasets examined, sites with tailed frogs (either *A. truei* or *A. montanus*) occurrences had a broad range of variation among the habitat factors measured. At the macro-scale, tailed frogs were found in climatic conditions ranging from quite dry to very wet (mean annual precipitation range: 378-2824 mm; $\bar{x}$ = 1877 mm $\pm$ 25 SE) and from cool to warm summer temperatures (mean annual temperature warmest month range: 9.2-20.4; $\bar{x}$ = 15.4 °C $\pm$ 0.1 SE). At the meso-scale, tailed frogs occurred in watersheds with levels of recent harvest ranging from 0 to 48% ($\bar{x}$ = 9.8% $\pm$ 0.3 SE), with road density within 100 m of headwater streams up to 4.4 km/km^2 ($\bar{x}$ = 0.5 km/km^2 $\pm$ 0.3 SE), and at all ages of adjacent stands (recent clearcuts [< 5 years] to stands > 100 years old). In addition, occurrence was recorded at elevations up to 1900 m ($\bar{x}$ = 540 m $\pm$ 20 SE), and stream gradients ranged between 2-93% ($\bar{x}$ = 31.3% $\pm$ 0.7 SE). They were present in streams located in all the bedrock types identified in this analysis. At the micro-scale, tailed frogs occurred in streams ranging in wetted width from 0.5-14.0 m ($\bar{x}$ = 3.0 m $\pm$ 0.1 SE), with water temperatures ranging between 5.5 °C - 19.0 °C ($\bar{x}$ = 12.1°C $\pm$ 0.1 SE) and with a variety of substrates ranging from 5% up to 80% boulder cover ($\bar{x}$ = 20.9% $\pm$ 0.7 SE), up to 75% cover of cobbles ($\bar{x}$ = 34.5% $\pm$ 0.6 SE), and up to 77% cover of fines ($\bar{x}$ =17.9% $\pm$ 0.6 SE).

First, we report results for occurrence by examining all datasets combined, and then each separately. CART analysis produced branched tree models of habitat relationships for occurrence (Figures 4 -6) that included 5 to 7 of the 22 environmental variables, with misclassification error rates (our measure of goodness-of-fit) between 11.3% - 18.8%, and coefficients of determination (r^2) between 0.24 – 0.44. Over all occurrence models,

habitat factors at all scales (macro: geology; meso: topographic, watershed disturbance, forest age class; micro: stream substrate, detritus) significantly influenced probability of tailed frog presence (Figures 4 and 5 for *A. truei*; Figure 5 for *A. montanus*). Climate and latitudinal variables were found to be relatively unimportant in site classification, appearing in none of the final models as a distinguishing variable.

Figure 3. Distribution map of the Olympic tailed frog (*Ascaphus truei*:dark gray) and Rocky Mountain tailed frog (*A. montanus*:light gray) in the Pacific Northwest of North America (from Bunnell *et al.* 2001b). The precise range limits of the two taxa are not yet fully determined.

Environmental Relationships in Olympic tailed frog (Ascaphus truei) Occurrence and Abundance Patterns

Across all datasets, as well as for most datasets separately, we found that *A. truei* was more likely to occur in streams located in bedrocks of selected classes of igneous intrusive origin, including breccias, granodiorites, quartz diorites, than in those of basaltic or sedimentary origin (Figures 4 and 5; see also Table 4). However, in southwestern

Washington, where the landscape was either basaltic or marine sedimentary formations, Olympic tailed frog occurred more frequently on basaltic formations. In addition, streams in stands of older age classes, containing larger-sized substrates (i.e. lower % cover of fine sediments and higher cover of boulders or cobbles), and with less small woody debris were more likely to contain tailed frogs than other types of streams. The branching structures of each the classification trees suggest other more complex interactions between habitat factors. It is not apparent from the residual deviance values that the separate CART models for each region explain relatively more of the variation than does the combined model.

Differences among datasets also emerged from inspection of the separate trees (Figure 5), notably in the topographic variables elevation and aspect. For example, relationships between probability of occurrence and elevation appeared generally positively related in BC, whereas they tended to be negative in the Washington (i.e., Chehalis-Willapa) dataset. *Ascaphus truei* tended to be found in a wider elevation band in BC than in the Chehalis-Willapa dataset, but was more likely to be found in elevations below 600 m in southwestern Washington (~200-300 m below the maximum elevations in that area). Interpretation of the influence of elevation is difficult given the differing topography across the range of the datasets examined, and the fact that most sampling was done from roads which were often constrained within selected elevational bands. A more useful measure might be the elevation band of occupied streams as an indicator of habitat availability. In addition, *A. truei* was more likely to occur in streams with an easterly or southerly aspect in BC, but aspect did not appear to be a discriminating variable in the Chehalis-Willapa dataset. The relative "effect size" of both elevation and aspect on tailed frogs are likely moderated by local climatic regimes and may possibly be surrogates for effects of precipitation, temperature, and insolation on stream flow and condition. These results also imply that latitudinal clines in insolation, temperature, precipitation may be interacting to influence *Ascaphus* populations. For example, at high latitudes (e.g., BC), a northerly aspect might be less insolated and thus colder than northerly aspects at lower latitudes (e.g., SW Washington). We plan to investigate this possibility in future analyses.

The tree diagrams produced by CART analyses identify important conditional dependencies in relationships among habitat factors, as the relationships on each individual branch below a higher level node are independently derived from each other. Two fundamental types of dependencies are suggested by our results: compensatory (e.g., effects of reductions in some habitat factors on populations may be compensated by increases in another) and substitution (replacement of the effects of one habitat factor with those of another). First, tailed frogs had a higher probability of occurrence in streams with coarser substrates than streams with fine substrates in BC when those streams were located in partly disturbed watersheds (i.e., in stands of younger age classes, or with roads in the riparian zones), and when those streams contained fine woody debris. This suggests either that substrate composition may partially compensate for other effects of harvesting or that harvesting can alter the substrate characteristics depending on precedent conditions. Second, in the Chehalis-Willapa dataset, higher stream gradients appear to substitute for increased forest age in maintaining tailed frog abundance in easily weathered bedrock geologies. Perhaps higher flushing rates in these streams compensate for impacts of disturbance due to forest harvesting activities

disturbance. However, widely applicable and simple rules are difficult to infer from these empirical trees – non-linear relationships between habitat factors (variables occurring in more than one place in each tree) are prevalent, and the influence of the same factor can differ depending on antecedent conditions (see Table 4).

At sites where *A. truei* occur, CART analysis illustrated that micro-scale habitat factors (particularly stream substrate composition) were more important than meso-scale or macro-scale habitat factors in predicting abundance, although the residual (unexplained) deviances are higher than for the occurrence models (Figure 6; see also Table 4). Too few samples were available to fit a CART model separately to the south coast BC data for abundance. *Ascaphus truei* were generally more abundant in streams with < 25% cover of fine sediments, although this relationship appeared in the BC data only and may not be reflected in the southwestern Washington State dataset. In part this is likely because the substrate data from Chehalis-Willapa identified only the category (size class) rather than the percent cover of the dominant substrate(s) thus preventing us from reaching a definitive conclusion. *Ascaphus truei* abundances appear higher in steeper streams. This is important only if their substrate has moderate or high cover of fine sediments (e.g., > 22.5% cover; Figure 6). *Ascaphus truei* also tend to be more abundant in streams with bedrocks of volcanic origin. The CART models also suggest negative relationships between abundance and watershed-level disturbances in some areas. In the North Coast BC data, abundances appear higher in watersheds with intermediate proportions of their areas logged within the last 20 years. In the southwestern Washington, streams dominated by intermediate-sized substrates have higher tailed frog abundances. We distinguished no other obvious patterns in abundance with CART, and the explained variation was very low in this model.

Environmental Relationships in Rocky Mountain tailed frog (Ascaphus montanus) Occurrence and Abundance Patterns

Generally, *A. montanus* was more likely to occur in streams with warmer temperatures (first splitting node in Figure 7), or in streams with intermediate-sized substrates (e.g., cobbles or boulders). Abundances appear higher in higher elevation streams located in less erodable sedimentary rocks (quartzites, limestones) than softer siltstones or argillites. As all streams in the Kootenays samples occurred in geologies of sedimentary origin, clear discrimination between effects of widely different geology and other factors was not possible. As we found for abundance patterns in *A. truei*, CART models for *A. montanus* had high residual deviance (e.g., > 50%), suggesting that other factors than those captured in these variables explain a majority of observed abundances. Detailed interpretation of habitat relationships is hindered by the highly localized distribution of *A. montanus* in this area. This localized distribution pattern may be the result of habitat factors and the low recolonization opportunities (see Ritland *et al.* 2000 for a more developed discussion on this point).

Relationships between the habitat factors and occurrence and abundance patterns for *A truei* across the datasets were inferred from these analyses, some of them apparently non-linear and exhibiting partial dependencies on the values of one or more other habitat factors. An interaction between geology and extent of prior development of a watershed, as measured by road density in riparian areas and % of watershed logged in the last 20

years, appears to influence occurrence patterns. Tailed frogs in watersheds with more granitic and volcanic origin bedrocks appeared more resistant to disturbance than those in watersheds with less competent bedrocks, such as highly fractured granitics, or rocks of sedimentary origin. Similarly, tailed frog abundance was influenced by stream substrate composition, which is in turn a function of stream morphology, disturbance and bedrock composition. However, the form of these habitat relationships can only be weakly inferred (see Table 4). Such conditional, non-linear relationships may truly represent the habitat associations for *Ascaphus*, but they are difficult to understand and to use for developing and testing predictive relationships.

We examined the overall quantitative effect of each factor on the likelihood of occurrence and on abundance despite considerable variation between datasets in the associations between habitat factors and responses by *Ascaphus*, and complex relationships within datasets. We did this for each dataset by calculating the net change in each response variable (occurrence probability or abundance) created by the contribution of each factor in the CART trees, weighted by the % of deviance explained by each branch of the tree (occurrence: Figure 8; abundance: Figure 9). This analysis emphasizes the independence of the factors, and ignores the conditional relationships between them. Consistent with previous results, the contributions of each habitat factor in determining occurrence probability differed between datasets. In descending order of importance lower amounts of fine woody debris in streams, decreased fine sediments, north and east aspect, and an increasing trend to bedrocks of volcanic origin had the strongest positive effect on occurrence probability. Increasing levels of fine woody debris in streams, increased fine sediments, sedimentary and composite bedrock, and south or west aspect decreased the likelihood of tailed frog occurrence. Effects were less discernible from abundance data (Figure 9). Across both datasets (north-central coast BC and Chehalis-Willapa), increasingly coarse substrate size appeared to positively influence abundance; no other factor appeared in both datasets. In the north-central coast BC dataset, increased extent of disturbance in watersheds, as well as fine sediments appeared to positively influence abundance.

BC and Southwest Washington State Sites
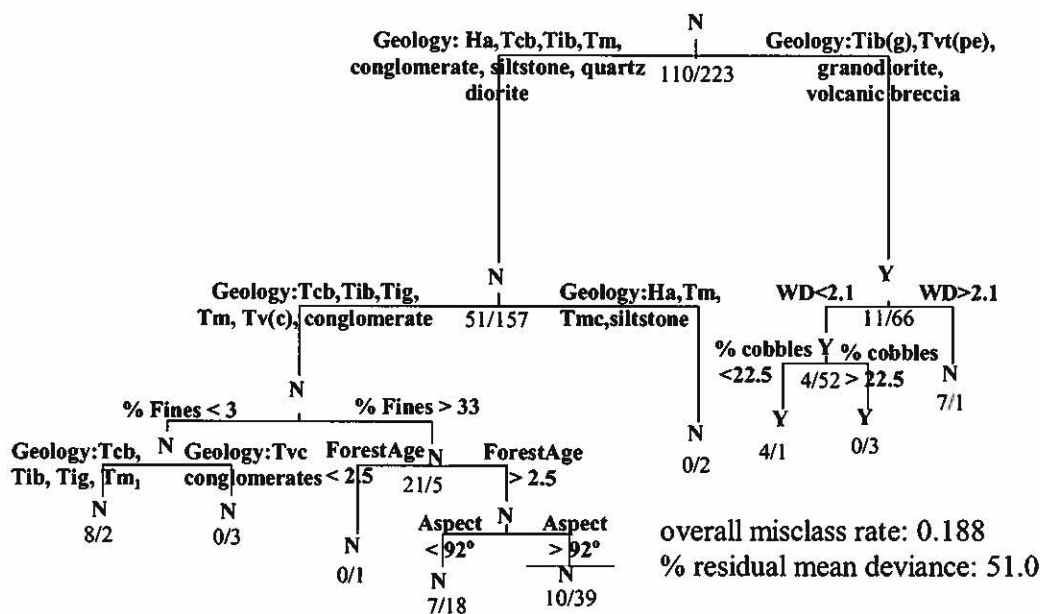
Figure 4. Classification and Regression Tree (CART) models for Olympic tailed frog (*A. truei*) occurrences in the combined sites for British Columbia and southwestern Washington State. Occurrence codes (Y or N) indicate the predicted conclusion (Y = yes; N = no) for sites represented by that node. Numbers below the rectangles (end nodes) are the number of misclassified (numerator) sites of the total number of sites (denominator) given the prediction for that node. The splitting predictor variable and its threshold value is shown for each branch of each node as a label. The length of each branch is proportional to the percent of deviance explained by the splitting variable at each node. Abbreviations for habitat factors are as given in Tables 1a, 1b, and 1c, and geology codes are defined in Appendix Table 1.

North-Central Coast BC Sites

Figure 5a. CART model for Olympic tailed frog *(A. truei)* occurrence in north-central coast British Columbia sites. Notation is as described in the caption for Figure 4. Abbreviations for habitat factors are as given in Tables 1a, 1b, 1c, and geology codes are defined in Appendix Table 1.

South Coast BC Sites

Figure 5b. CART model for Olympic tailed frog *(A. truei)* occurrence in south coast British Columbia sites. Notation is as described in the caption for Figure 4. Abbreviations for habitat factors are as given in Tables 1a, 1b, 1c, and geology codes are defined in Appendix Table 1.

Chehalis-Willapa (S Wash.) Sites
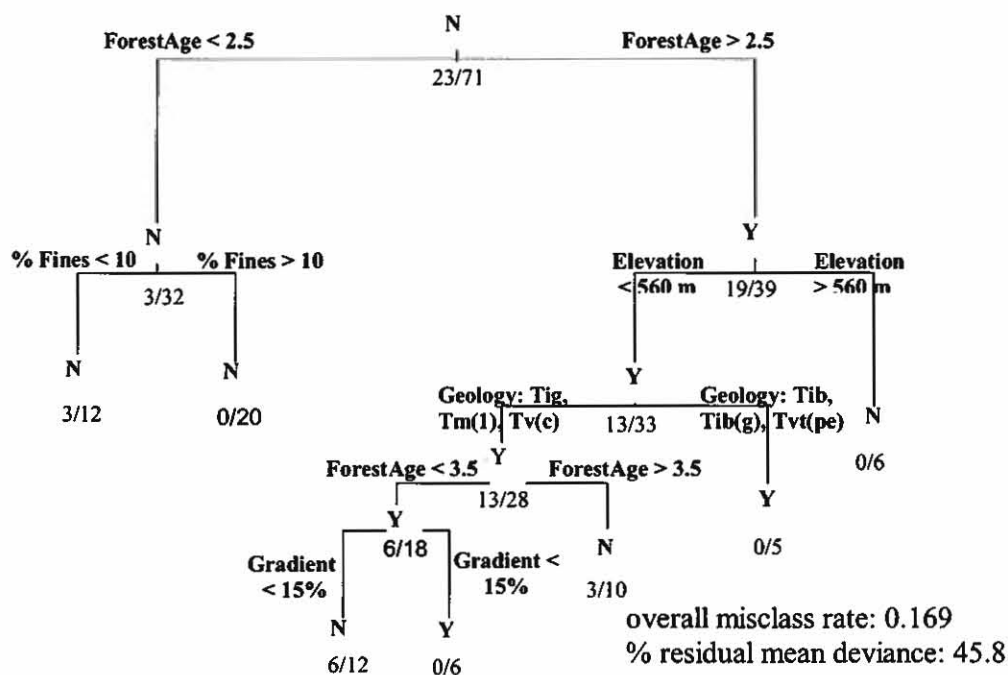
Figure 5c. CART model for Olympic tailed frog *(A. truei)* occurrence in Chehalis-Willapa (southwestern Washington State) sites. Notation is as described in the caption for Figure 4. Abbreviations for habitat factors are as given in Tables 1a, 1b, 1c, and geology codes are defined in Appendix Table 1.

BC and Southwest Washington State Sites
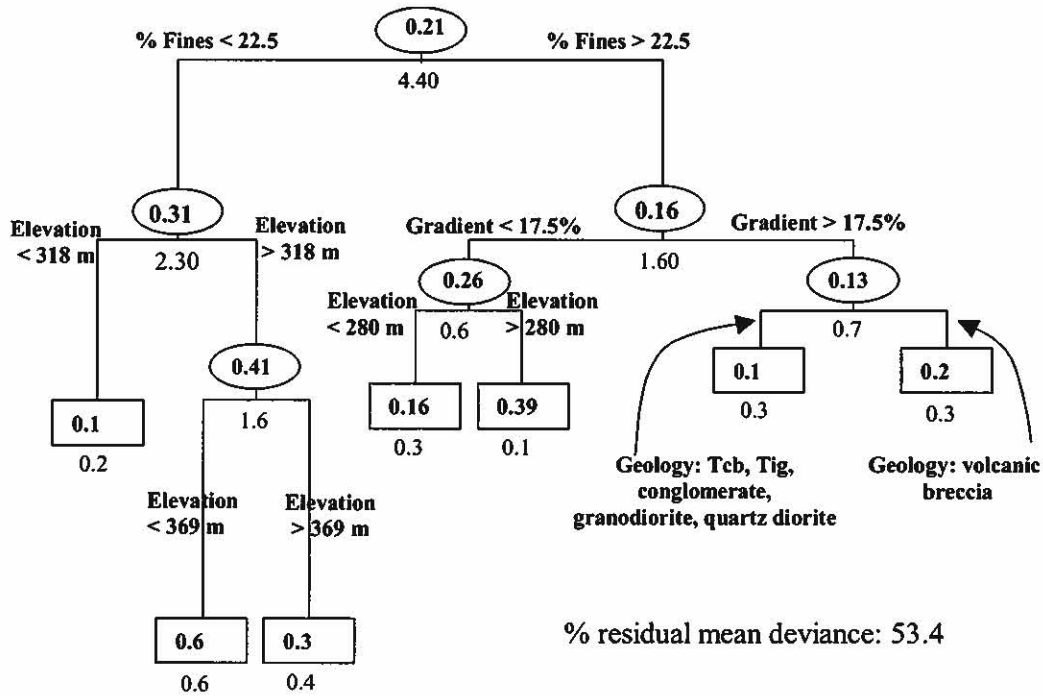
Figure 6a. CART model for Olympic tailed frog (*A. truei*) standardized abundances for all datasets combined. Only sites where *A. truei* occurred are included. Numbers inside each node are the mean standardized abundance for each dataset (range: 0.0-1.0). The numbers below each node is the deviance remaining for sites in the node. Other notation is as described in the caption for Figure 4. Abbreviations for habitat factors are as given in Tables 1a, 1b, 1c, and geology codes are defined in Appendix Table 1.

North-Central Coast BC Sites
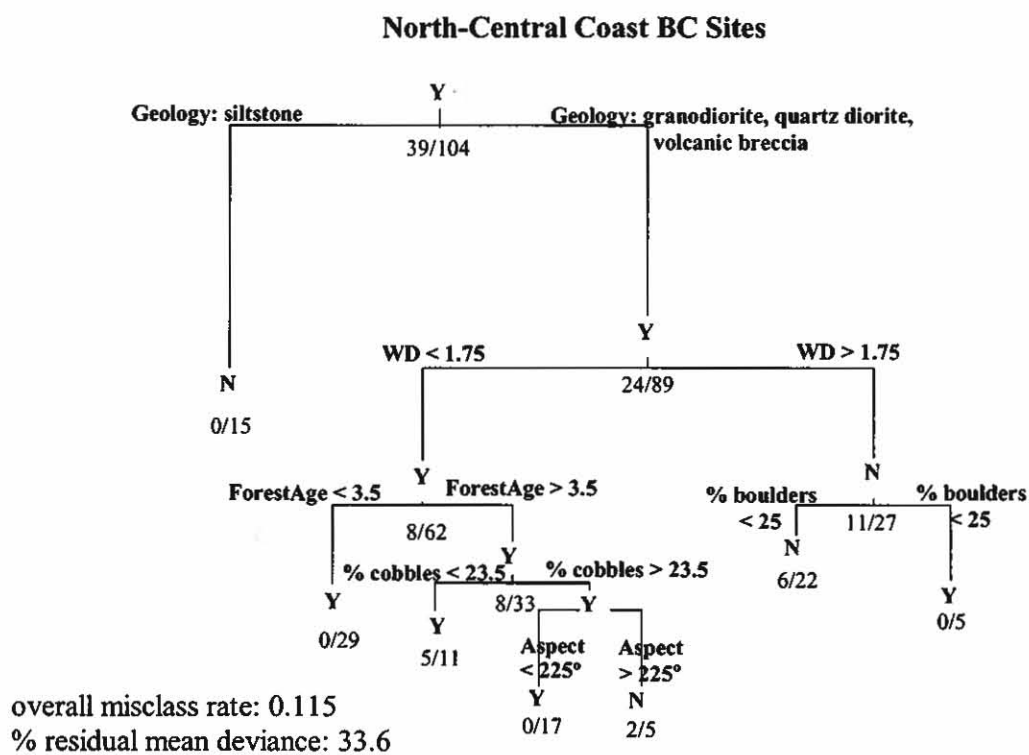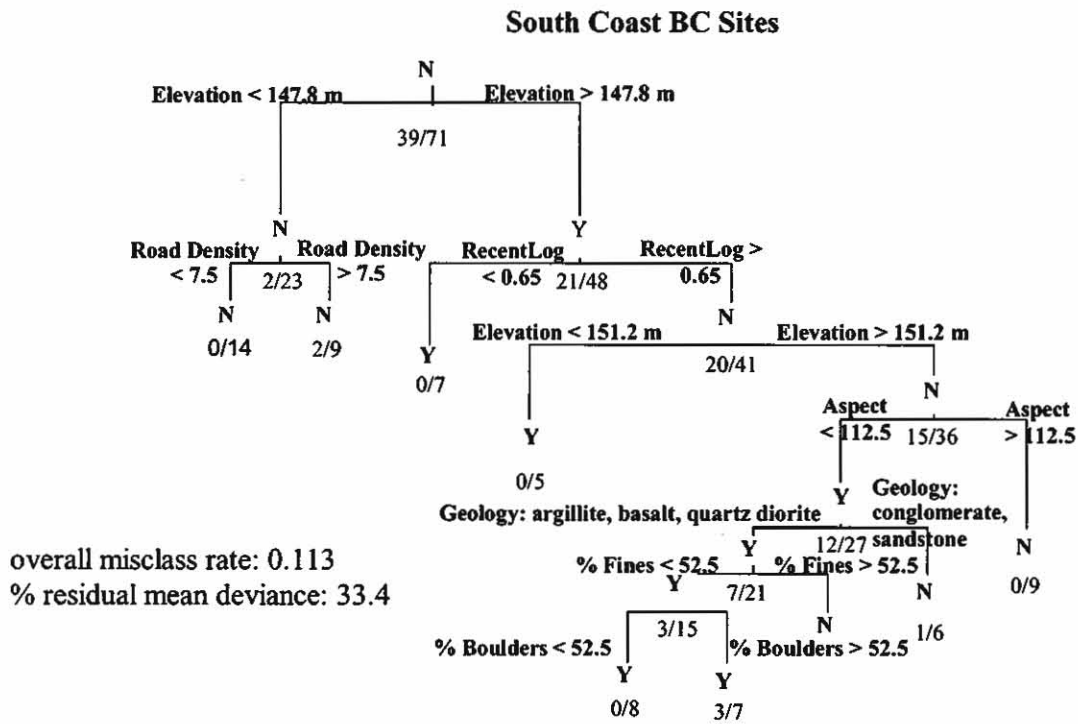

Figure 6b. CART model for Olympic tailed frog (*A. truei*) standardized abundances for north-central coast British Columbia sites. See Figure 6a for definitions and interpretation.

Chehalis-Willapa (SW Wash.) Sites
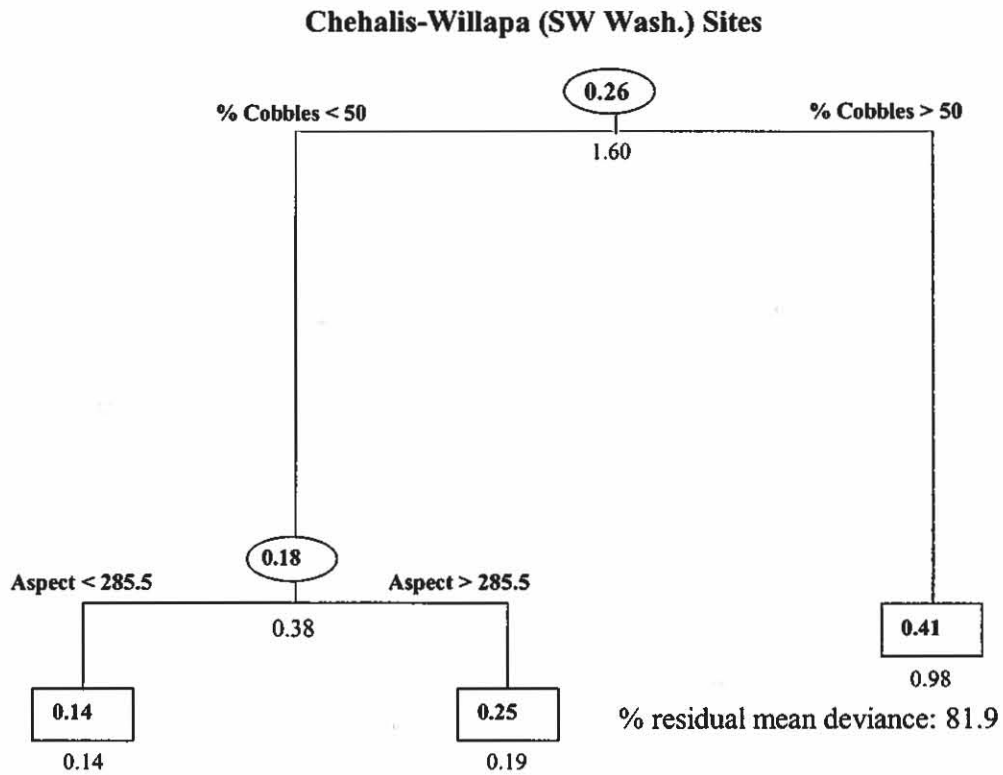
Figure 6c. CART model for Olympic tailed frog (*A. truei*) standardized abundances for Chehalis-Willapa (southwestern Washington State) sites. See Figure 6a for definitions and interpretation.

Kootenay Mountains (BC) Sites

Figure 7a. CART model for Rocky Mountain tailed frog (*A. montanus*) occurrence in the Kootenays area of southwestern British Columbia. Codes are as described in the captions for Figure 4. Abbreviations for habitat factors are as given in Tables 1a, 1b, and 1c, and geology codes are defined in Appendix Table 1.

Kootenay Mountains (BC) Sites
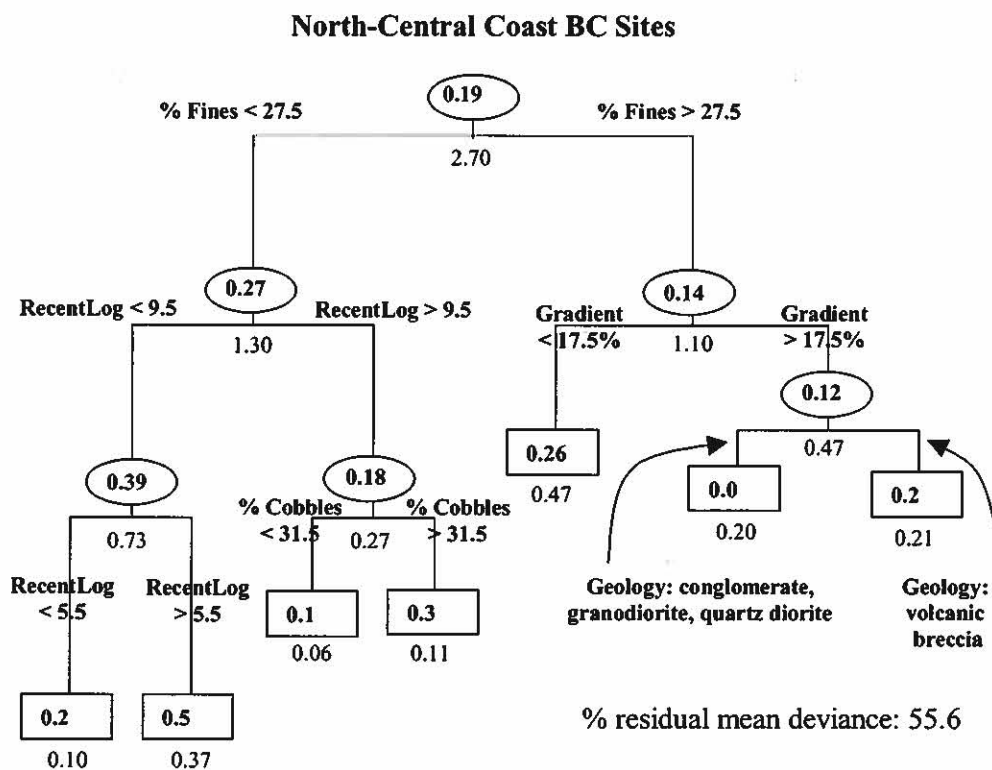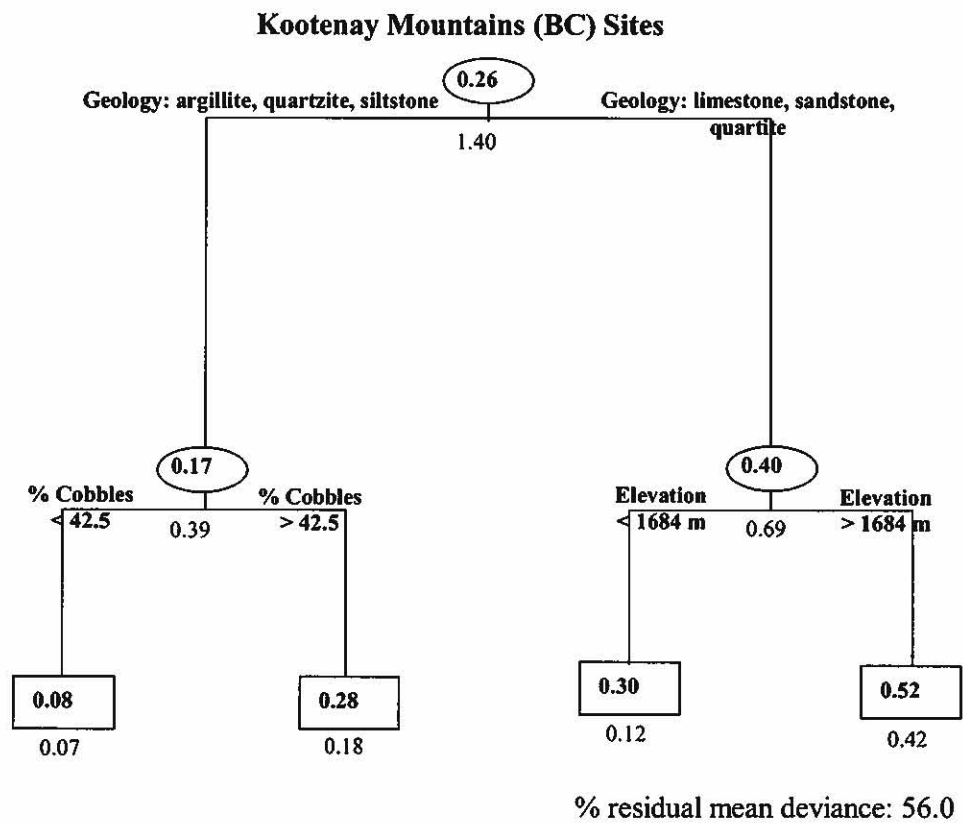

Figure 7b. CART model for Rocky Mountain tailed frog (*A. montanus*) standardized abundance in the Kootenays area of southwestern British Columbia. See caption for Figure 7 for definitions and interpretation.
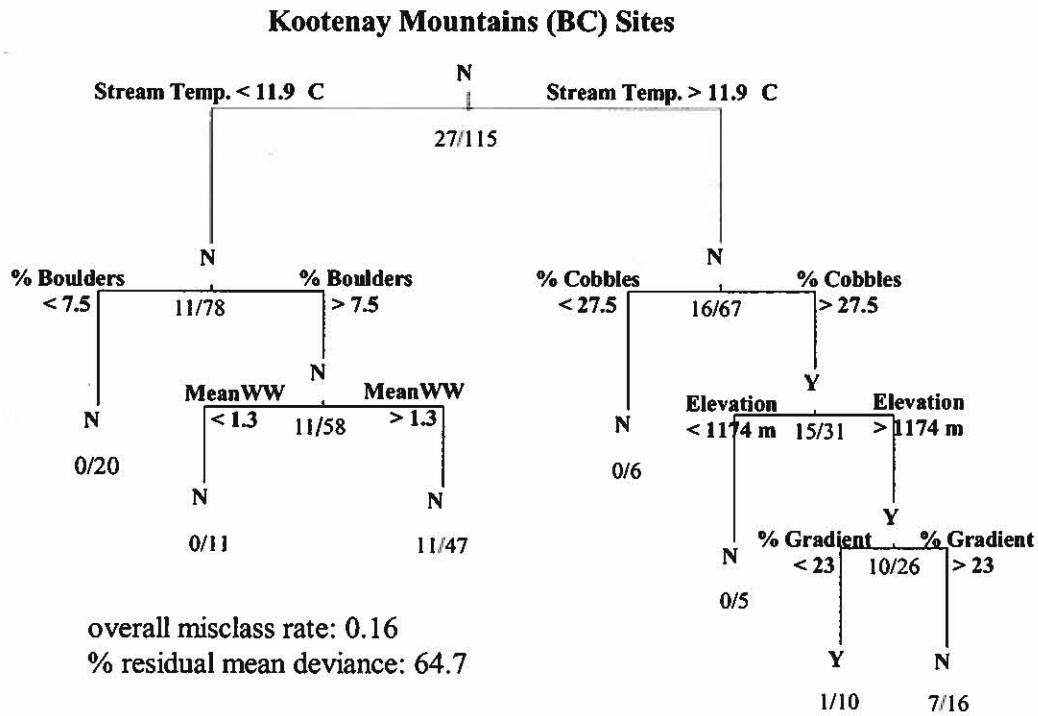
Table 4a. Summary of the CART analyses for occurrence of the Olympic tailed frog (*A. truei*). Arrows indicate the direction of effect (positive with an up arrow [↑]; negative with a down arrow [↓]) and antecedent habitat factors on the response variable. Only effects derived from the top three levels of the CART models are shown for each response variable and dataset. Additional levels are less easy to interpret and so are not included here.

Dataset	Probability of Occurrence	Antecedent conditions		
All	+	↑ volcanic or granitic intrusive rocks	↓ detritus	↓ % cobbles
	-	↑ volcanic or granitic intrusive rocks	↑ detritus	
	-	↑ sedimentary or composite intrusive rocks	↑ sedimentary deposits	
	-	↑ sedimentary or composite intrusive rocks	↑ composite intrusive rocks	↑ % fines
NC	+	↑ volcanic or granitic intrusive rocks	↓ detritus	↓ stand age
	+	↑ volcanic or granitic intrusive rocks	↓ detritus	↑ stand age
	-	↑ volcanic or granitic intrusive rocks	↑ detritus	↓ % boulders
	-	↑ sedimentary or composite intrusive rocks		
SC	+	↑ elevation	↓ watershed recently logged	
	+	↑ elevation	↑ watershed recently logged	↑ north and east aspect
	-			↑ south and west aspect
	-	↓ elevation	↑ roads in riparian zones	
WA	+	↑ stand age	↓ elevation	↑ volcanic or granitic intrusive rocks
	-		↑ elevation	
	-	↓ stand age		

Table 4b. Summary of the CART analyses for abundance patterns of Olympic tailed frog (*A. truei*). See Table 4a for descriptions of table contents.

Dataset	Probability of Occurrence	Antecedent conditions		
All	+	↑ % fines	↓ stream gradient	↑ elevation
	-	↑ % fines	↑ stream gradient	↑ composite intrusive rocks
	+		↑ stream gradient	↑ volcanic intrusive rocks
	+	↓ % fines	↑ elevation	
	-		↓ elevation	
NC	+	↓ % fines	↓ watershed recently logged	
	-	↓ % fines	↑ watershed recently logged	↑ composite intrusive rocks
	+		↑ watershed recently logged	↑ volcanic intrusive rocks
	+	↑ % fines	↓ stream gradient	
	-	↑ % fines	↑ stream gradient	↑ composite intrusive rocks
WA	+	↑ % cobbles		
	-	↓ % cobbles		

Table 5a. Summary of the CART analyses of effects of first three levels of habitat predictor variables on occurrence patterns for the Rocky Mountain tailed frog (*A. montanus*). This analysis is based on the Kootenays dataset. See Table 4a for description of table contents.

Probability of Occurrence	Antecedent conditions		
-	↓ stream temperature	↓ % boulders	
-	↓ stream temperature	↑ % boulders	↓ stream wetted width
+	↑ stream temperature	↑ % cobbles	↑ elevation
-	↑ stream temperature	↓ % cobbles	

Table 5b. Summary of the CART analyses for abundance patterns of the Rocky Mountain tailed frog (*A. montanus*). This analysis is based on the Kootenays dataset. See Table 4a for description of table contents.

Probability of Occurrence	Antecedent conditions		
+	↑ limestone, quartzite, or sandstone rocks		
+	↑ quartzite, argillite, siltstone, or unclassified sedimentary rocks	↑ % cobbles	
-	↑ quartzite, argillite, siltstone, or unclassified sedimentary rocks	↓ % cobbles	

Figure 8a. Net change in occurrence probability of the Olympic tailed frog (*A. truei*) for the habitat factors identified in north-central coast British Columbia sites. Note that interactions between factors (e.g., "compensation" and "substitution"; see Results) can create situations where the influence of a factor can appear in the figure as having both positive and negative effects. Magnitude of influence of factors are rank ordered from most positive (left) to most negative (right). The sign in front of each factor indicates the direction of the response, e.g., a decrease in (-) detritus increased the probability of occurrence by approximately 10 percent; a decrease in the proportion (-) of the watershed recently logged decreases the probability of occurrence by roughly 10 percent.
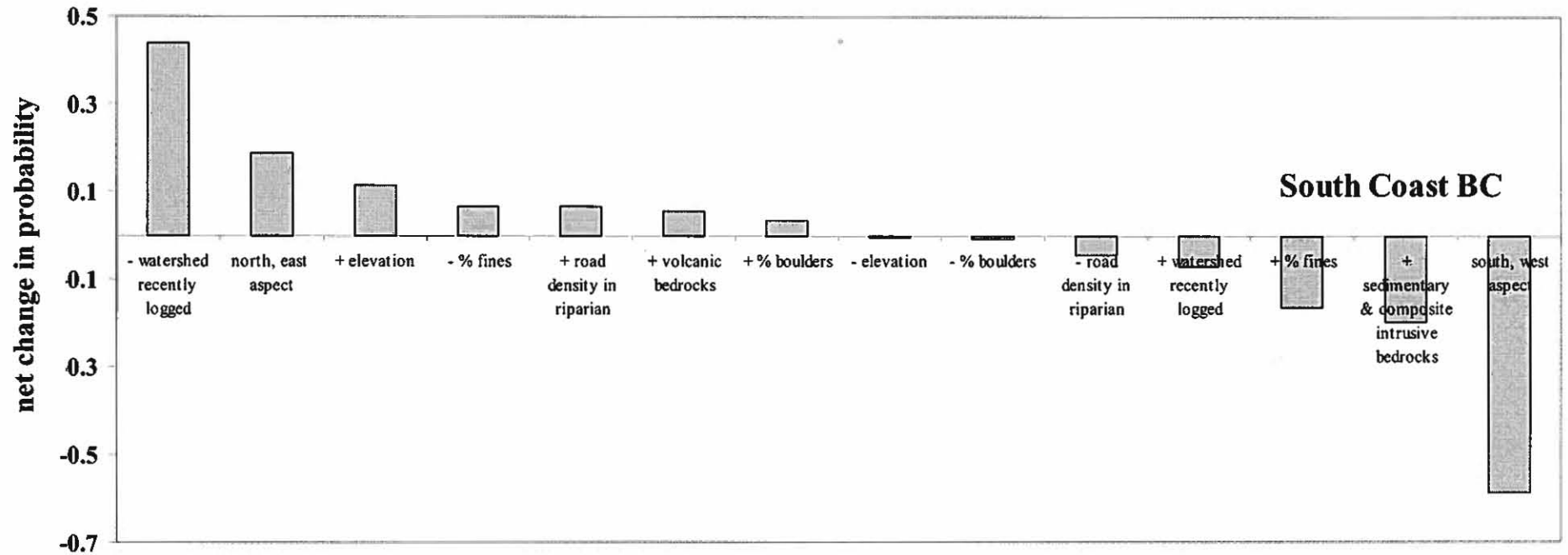
Figure 8b. Net change in occurrence probability of the Olympic tailed frog (*A. truei*) for the habitat factors identified in south coast British Columbia sites. See Figure 8a caption for codes and interpretation.

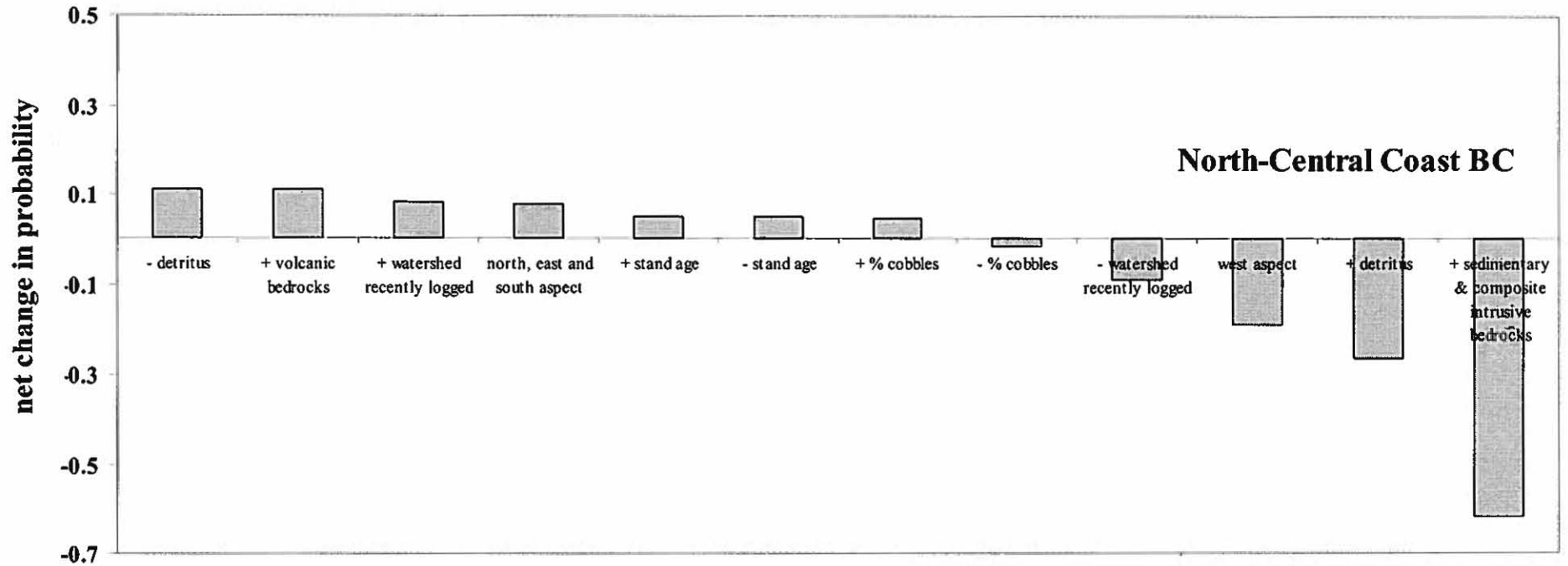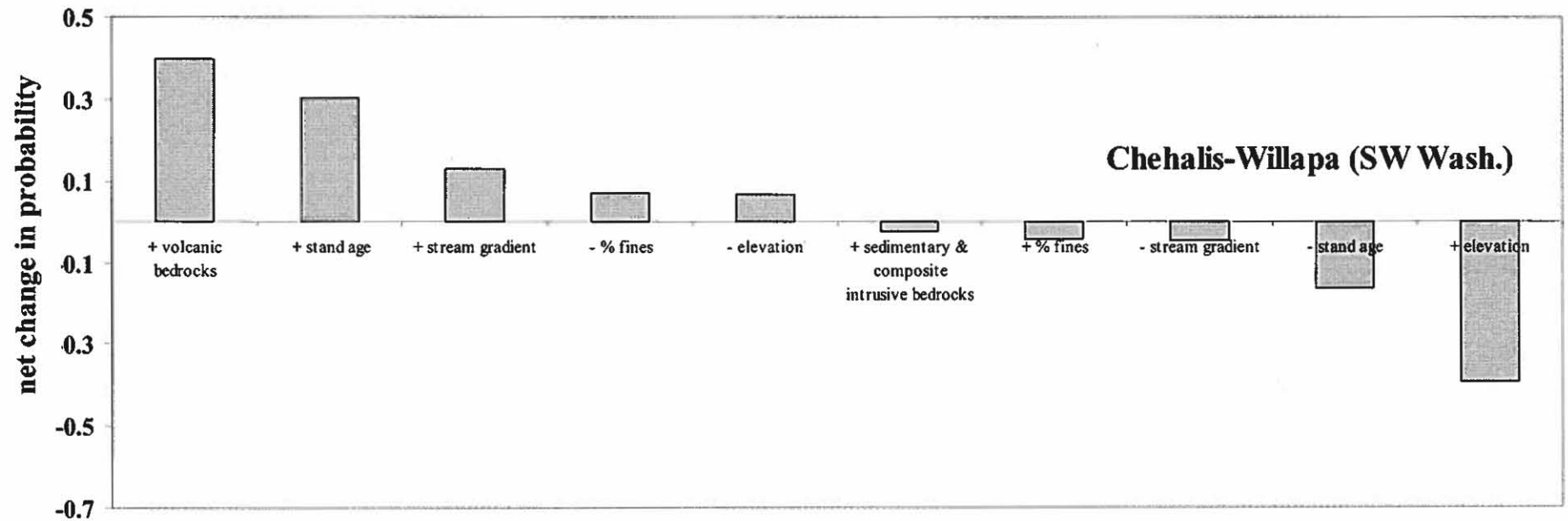**Figure 8c. Net change in occurrence probability of the Olympic tailed frog (*A. truei*) for the habitat factors identified in the Chehalis-Willapa (southwestern Washington State) sites.** See Figure 8a caption for details on codes and interpretation.
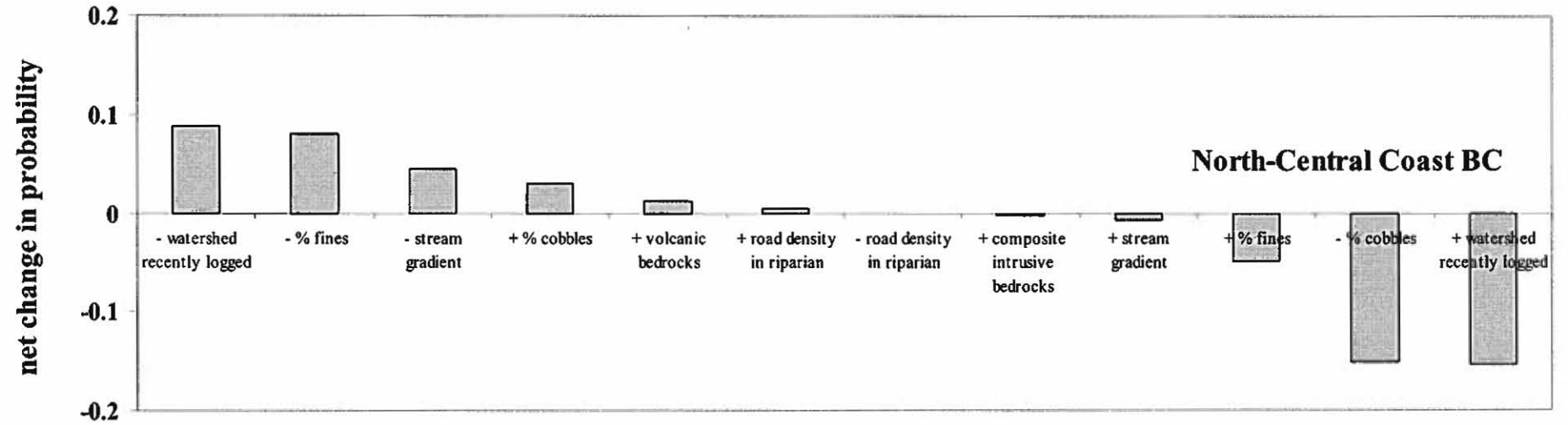
Figure 9a. Net change in standardized abundances of Olympic tailed frog (*A. truei*:y-axis) resulting from the influence of each habitat factor (x-axis) in north-central coast British Columbia sites. See Figure 8a caption for details on codes and interpretation.
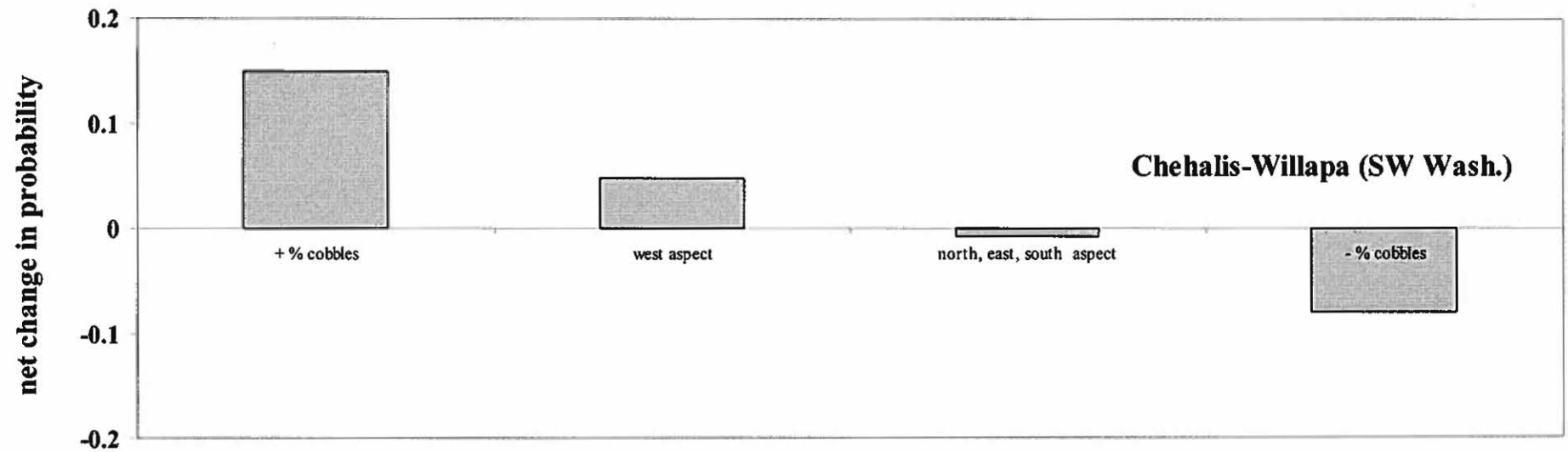
Figure 9b. Net change in standardized abundances of Olympic tailed frog (*A. truei*:y-axis) resulting from the influence of each habitat factor (x-axis) in Chehalis-Willapa (southwestern Washington State) sites.   See Figure 8a caption for details on codes and interpretation.

4.0 Discussion

Overview

We believe that clear trends exist across data sets despite the fact that studies from which we extracted data were designed for purposes other than a systematic analysis of habitat association patterns in *Ascaphus*. Our results suggested that both occurrence and abundance of the Olympic tailed frog in British Columbia and southwestern Washington State are positively associated with bedrock lithologies that are both resistant to weathering and whose products are generally coarser-grained (e.g, intrusives weathering to cobble-sized rocks, granitics to sands, marine sediments to fine silts). Occurrence and abundance of this species appears negatively associated with factors promoting intrusion of fine sediments and small woody debris into streams. Underlying geology consistently separated streams with and without *A. truei* and fine-scale stream substrate composition emerged as an important influence on abundance. Several determinants of stream structure are themselves influenced by bedrock geology (Church *in press*) in headwater streams. Although parallel data were unavailable across studies , increasing area of recent harvest in a watershed (as measured by % of watershed area disturbed in the last 20 years) was consistently associated with both low probabilities of occurrence and lower abundance across the range of both *Ascaphus* taxa.

We found complex relationships between patterns of occurrences and abundances of tailed frogs and macro-, meso- and micro-scale habitat factors. At the macro-scale, parent bedrock lithology interacted with several other habitat factors and was a major determinant of occurrences in both BC and southwestern Washington state. Consistent with conclusions reached by Hunter (1998) for tailed frogs in Oregon, we found meso- (topographic and forest management-related habitat factors) and micro-scale (stream substrate) factors were also related to patterns of occurrence and abundance in both regions. The characteristics of streams most related to physical space for larval attachment and response to disturbance were most important in influencing abundance. Given these results, interacting effects of geomorphology, topography, and channel morphology on fine-scale stream structure may drive patterns of occurrence and to a lesser extent the abundance of this species in headwater streams in these parts of its range. Where these factors create settings with high sediment or debris loads, the potentially additive (or synergistic) effects of forest management may result in the strongest negative effects on tailed frogs.

Some general differences in our results between regions may be related to combinations of climatic and terrain factors that are most strongly expressed at the scale of one or a few watersheds. For example, mean annual precipitation systematically decreases from coastal to interior locations in the PNW due primarily to orographic effects. High precipitation levels can lead to high pore water pressures in soils, slope destabilization, and ultimately slope failure. However, Tertiary to Mesozoic volcanics dominate in the Inner Coast Mountain region of BC whereas acidic to intermediate intrusive rocks are found in the Outer Coast Mountain region of BC and in the Coast Range of southwestern Washington State. Soils derived from intrusive rocks are typically coarser textured and, as a result, are often better-drained and less prone to failure than soils derived from

volcanic rocks depending upon their history of compression and fracturing. Yet, landslides are seen in the Outer Coast Mountain region, which is dominated by intrusive rocks (Trainor 2001). This pattern may reflect precipitation levels, as discussed above, which are greater in the Outer Coast Mountain region than further inland. Local topography and surficial geology may be the most important elements related to sideslope failure. Forest harvesting methods may increase the frequency of landslides, but whether this actually occurs is also a function of surficial geology and local climate (Trainor 2001). These complex interrelationships at the sub-regional and watershed scale suggest that translation of the patterns that emerged from this meta-analysis into management guidelines will require a thorough review of the physical relationships involved.

Different regional geologies facilitate substrate substitution. Basaltic instrusives, which Olympic tailed frogs used less frequently in BC, were the substrates on which tailed frogs were most often found in southwestern Washington; the only alternative substrates were highly erosive marine sedimentary formations. This finding agrees with that of Wilkins and Peterson (2000), who recorded Olympic tailed frogs only on basalt in near-coastal southwestern Washington.

Although our CART models generated average misclassification error rates of less than 20%, there was considerable unexplained variation remaining in all trees (ranging from 33%-82%). Considerable unexplained variation is common in other habitat association models for tailed frogs (e.g., Kelsey 1995; Wilkins and Peterson 2000) and our residual variation values are as small and often smaller than observed with other models. However, such substantive unexplained variation raises the question of whether a predictive and robust habitat model can feasibly be constructed for this species, even with meta-analysis. While a complete discussion is beyond the scope of this analysis, we consider three points. First, at all three spatial scales, low accuracy in the values of many variables used (e.g., regional averages for climate data), use of surrogate values (e.g., % cover of different sized substrates in streams as a surrogate for stream heterogeneity), missing values in many variables (e.g., stream width) probably contributed to residual uncertainty in estimating relationship between the species and its response to the habitat factors. Second, no attempt was made here to "partial-out" (c.f. Borcard *et al.* 1992) or otherwise control for small-scale spatial structuring in the data, although in other analyses for this species, spatial variation due to several causes has been shown to influence the effects of many habitat factors (Sutherland 2000). Third, we expect that the increased power obtained with the inclusion of a number of additional datasets into the analysis will improve the strength of several of these observed relationships.

Coarse-scale Responses of PNW Stream Systems to Riparian Timber Harvest

A recent meta-analysis examining the relationship between riparian zone management and the physical and biological components of fish-bearing streams (Young 2001) has yielded results that could help focus subsequent analyses. First, Young found that riparian zone logging increased water temperatures immediately (0-15 years) following harvest, and riparian buffers moderated this effect. Only two studies beyond 20 years were identified, but these studies suggested that temperatures return to normal within 30 years. Second, he found that fine sediment loads increased following timber harvest of riparian stands, but no biophysical factors (e.g., presence or absence of riparian buffers, stream gradient and size) were related to the increase in fine sediments, possibly because

most sediment comes from road drainage networks that deliver directly to streams. Third, riparian harvest increased WD loads in small streams. Fourth, riparian harvest tended to increase habitat complexity (measured as pool:riffle ratios) in small streams through increased inputs of WD immediately after logging, although habitat complexity appeared to decrease to control levels through time (Young 2001).

In general, Young (2001) concluded that substantial variation existed in the response of different physical and biological components of stream ecosystems to riparian zone harvest. Departures from expected responses are likely due to variation in channel morphology, geology, topography, and natural disturbance histories at both the stream and watershed scale.

In large measure, our results for headwater streams are consistent with this analysis. We suggested in the Introduction that the primary ecological processes affecting *Ascaphus* are primary productivity, stream carrying capacity, and effects of disturbance on survival and reproduction. Because of the types of variables we used, our results emphasize the longer-term, cumulative effects of forestry as mediated by bedrock geology and topography. Shorter-term impacts on primary productivity (e.g., increases in stream temperature) are less detectable in our results, either because their effects are more transient, or our selection of variables could only indirectly capture these effects.

Potential Habitat Models for Tailed Frogs

The results of this pilot study are preliminary, but broad-based. Our findings suggest several testable hypotheses and identify topics that may be helpful in future discussions of the relationships between tailed frog habitat and management practices in forested headwaters. We expect additional analyses to test and refine these findings.

1. *Like other species, habitat relationships of tailed frogs bridge spatial scales, and compensation and substitution among factors results in interactions varying among sites.* Across its range in BC and Washington State, we found that geology, topography and disturbance as measured at macro- and meso-scales are important factors affecting habitat for tailed frogs. From these patterns, it seems clear that not all headwater streams occupied by tailed frogs are equally susceptible to disturbance. We expect that the negative effects of disturbances on tailed frogs will be greatest on geological substrates that favor fine sediment production (Dupuis and Steventon 1999; Dupuis *et al.* 2000). Populations located in streams with higher productivity (e.g., generally warmer temperatures and moderate precipitation) may be better able to recover from effects of disturbances than are populations in less productive sites, because of faster growth rates of tadpoles (Kiffney and Richardson 2001).

2. *Streams in which tailed frogs are most likely to occur can be characterized on the basis of region, topography, geology, and recent disturbance history* (e.g., < 20 years since riparian zone harvesting). Our results suggest that tailed frogs are most likely to occur in: a) streams situated in volcanic or intrusive bedrock formations; b) streams of intermediate (> 15% and < 30%) gradients with significant (> 25%) boulder cover (creating a step-pool morphology [Chin 1998] and also trapping logs); and c) streams in watersheds with low levels (e.g., < 3%) of recent (< 20 years) harvest. Tailed frog populations will be less resilient in

streams flowing through sedimentary formations, which typically produces fine-grained stream sediments, as well as in low-gradient (< 15%) streams.

3. *Tailed frogs appear most sensitive to increased sedimentation in small streams with intermediate to low gradients (i.e., < 15% slope).* Accumulation of fine sediments in streams appears to generally depress larval tailed frog carrying capacity (Welsh and Ollivier 1998; Dupuis and Steventon 1999). The small size and intermediate gradients of many tadpole-bearing tributaries may slow the rate at which streambeds recover from increased sedimentation (e.g., Hogan *et al.* 1998). Selected sedimentary geologies (e.g., marine sedimentary formations) may exacerbate this pattern. Thus, maintaining the natural substrate dynamics of small headwater streams with low to intermediate gradients (< 15% slope) on selected sedimentary geologies may be of primary importance in designing conservation strategies for this species.

4. *Substantial uncertainty remains in determining the risk to this species from natural variation and forest practices.* Results of this pilot analysis, combined with those from related work, highlight several sources of uncertainty that affect evaluation of management options for conserving headwater stream habitats and populations of tailed frogs. First, variability in habitat factors and processes determining responses is a central theme of our preliminary results (see also Kelsey 1995; Bull and Carter 1996). Second, further uncertainty exists in the source data, in part because few sites have been re-sampled, and because differing methods were sometimes used between studies to quantify variables (including tailed frog abundance estimates). Finally, inferences about the effects of forest practices on this species are primarily drawn from in-stream life stages; estimation of disturbance impacts on demographic rates of sub-adults and adults is virtually non-existent.

Meta-Analysis Protocol for Further Analysis

In this pilot study, we conducted a partial meta-analysis of associations between predictor habitat factors and *Ascaphus* responses. Of the four steps in the traditional meta-analysis approach outlined in the Methods, we conducted three (steps 1, 2, and 4). The third step – development of measures of effect size common to all studies – was only partially completed in this pilot analysis. That is, we needed first to assess whether a common model appeared to exist across all studies that could form the basis of effect size estimates. Determination of an appropriate measure of effect (often a ratio between outcomes [e.g., abundances] under different treatments [e.g., treatment-control pairs]) was difficult to do in our analysis. For example, few "controls" exist in any of the studies – most sampled sites were located in sub-basins or watersheds with differing levels of disturbance. In addition, the evidence for complex and conditional interactions between habitat factors illuminated by CART suggests that non-linear, nested models may be needed, and that replicated samples (samples with a similar suite of parameter values) are difficult to find. We are exploring ways in which parsimonious models estimated from these data (e.g., using the information-theoretical methods of Burnham and Anderson [1998]) could be combined with Bayesian parameter estimation for conditional models such as are apparent from our pilot analysis.

The general statistical basis for informative measures of effect size and model selection is an underlying probability model (Osenberg *et al.* 1999) and the chosen effect sizes represent parameters that can be estimated for that model. In general, an appropriate strategy for further analysis in this study may be to model habitat associations in *Ascaphus* hierarchically, choosing simple probability models for the important processes (Gelman *et al.* 1995). For example, it may be possible to assume a multinomial distribution for effects of bedrock geology, but a normal distributions for extent of watershed development and for stream morphology (e.g., substrate composition). For example, if we assume that site-to-site and annual variation in abundances can be represented by a negative binomial distribution, and variation in occurrences by a Poisson distribution, then we could form joint probability models for predicting effects of watershed development given underlying bedrock geology, and so on. Inclusion of additional studies (see below) will likely provide enough samples to fit appropriate probability distributions for key habitat variables. To follow this approach requires us to accept the assumption that a general habitat relationships model holds across the geographic ranges of the respective tailed frog species. To date, our results suggest that while some habitat conditions vary across regions, the species' responses to some key relationships appears consistent among regions, implying that a general model does exist. Further analysis will allow us to more rigorously test this assumption.

Strengths and Limitations of this Study

Our analytical approach represents the first time population and habitat data from such a large set of samples over a very large geographic area has been assembled for this amphibian genus. Part of our study objective was to identify additional studies to include in the full meta-analysis. Currently, we have identified no fewer than five other studies that will extend both the geographic range, as well as improve the accuracy of abundance estimates. With more studies available, we have the opportunity to more thoroughly test estimated habitat models derived from the full meta-analysis. If sample sizes permit we could develop the models on subsets of the data, and test them on the remaining subsets – a method of cross-validation. In addition, our principal analytical method (CART analysis) avoids many of the restrictive statistical assumptions of other techniques that render drawing inferences from among diverse sources studies of habitat associations untenable. In particular, this method emphasizes the subtle ways in which habitat factors may inter-relate rather than simply depending on a relative weighting of each factor. Evidence of substitution and compensation among habitat factors confirms that this focus is important when interpreting a geographically extensive analysis such as this.

In the "Potential Habitat Models for Tailed Frogs" section above, we noted several sources of uncertainty that affected our ability to interpret results. We elaborate briefly on these, and then follow with a description of specific improvements to the data that will help strengthen further meta-analysis results. First, one source of the substantial residual variability in habitat factors and processes determining responses is the nature of the survey sampling methodology forming the bulk of our source data in this study. For example, most of our occurrence and abundance data came from one-time samples obtained for a wide geographic area over a period of several years. Because local abundance estimates are strongly influenced by local heterogeneity in stream substrates and local distribution of egg-masses, such estimates are expected vary considerably from

year-to-year. Such "observation error" makes it difficult to predict how the physical and biotic component of streams will respond to changes in forest practices (see also Young 2001). Second, further uncertainty exists in the source data because differing methods were often used between studies to quantify variables (including tailed frog abundance estimates). These uncertainties contribute additional imprecision and potential bias into estimates of frog response, and perhaps more so in managed landscapes. Finally, the predominant focus on the in-stream juvenile life stage is a problem when assessing habitat changes on populations. While larval stages may be adapted to infrequent or moderate levels of disturbance, older age classes may or may not be relatively tolerant to disturbance. The potential for differential effects of disturbances resulting from forest practices on larval and terrestrial life stages contributes to substantial uncertainty about effects of forest management on future reproductive success (Sutherland 2000).

Not all of these limitations can be overcome by inclusion of additional studies. Nonetheless, we suggest further data collection and analysis should address these particular weaknesses in the data:

1. A key missing habitat factor in the BC data was reliable stand age for stands adjacent to the sampled stream reaches. The data for this preliminary analysis came from a number of sources, ranging from forest cover maps as old or older than 1990 to actual known ages of stands at the sites. Present mapping efforts in the BC Ministry of Forests are nearing completion of a new composite Base Thematic Map for forest age class current to 2000. This will permit more accurate calculation of stand ages across the study sites.

2. Similarly, quality of road density data for coastal BC are poor and reflect GIS data from 1988. The same improved BTM should be updated with road density data.

3. The differing geological histories between British Columbia and the PNW states (e.g., glaciated vs relatively unglaciated) combined with differing methods of classifying lithologies and bedding patterns suggests that a review and refinement of the bedrock geological classifications used in the source data is required for improving this portion of the analysis.

4. Standardized methods of characterizing stream morphology (e.g., step:pool morphology) were not used in much of the source data. Given the importance of fine-scale stream structure revealed in several studies, developing a reliable method of estimating stream morphology from the presently available data (substrate composition, presence/absence of large wood in streams) would be useful.

5. The most difficult parameter to estimate in the source data is primary productivity of streams. If a subsample of streams exist where this data (e.g., incident light, algal growth, etc.) can be included in the analysis, we should attempt to use it to infer simple productivity models for inclusion into the overall habitat model.

6. We have data on tadpole cohort distributions based on length-frequency from several sites (northern BC, Chilliwack, Chehalis-Willapa, central Washington Cascades) as well as body-mass data. Time did not permit analysis of this data for this report. However, these data could potentially be used to infer productivity

of streams, and possibly effects of time-since disturbance, although there are also scientific difficulties in tracing effects of stream productivity directly through changes in tadpole biomass.

7. Clearly, additional data from other sources farther south in the range of *Ascaphus* are required to test the assumptions of latitudinal variation in effects of some climatic and productivity factors.

8. Recent surveys (summer 2001) of streams in the range of *A. montanus* in the Kootenays area of BC by one of the authors (Dupuis and coworkers) has both extended the known range of this species, and found stronger evidence of climatic control over its abundance patterns. Inclusion of this data will strengthen the habitat association models for *A. montanus*.

As described above, we anticipate extending our meta-analysis techniques to include maximum likelihood estimation, Bayesian model evaluation, and information theoretical approaches to utilize information contained in these additional sources of data.

5. Acknowledgments

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Appendix I
Study Area Descriptions

Washington State

Chehalis-Willapa Area

Data on occurrence and abundance of tailed frogs was collected in 1994 and 1995 from streams across ~42,500 ha of managed forestlands in southwestern Washington State, USA near Pe Ell (46° 32' N; 123° 17' W) in western Lewis and eastern Pacific Counties. All streams fall into one of three watersheds: the Chehalis Headwaters, Stillman Creek (a major tributary of the Upper portion of the south branch of the Chehalis River), or the southern half of the Willapa Headwaters. All three watersheds are in the Willapa Hills, at the northern end of the Coast Range physiographic province (Franklin and Dyrness 1973).

The climate is classified as coastal marine with a mean annual precipitation of 1800-2300 mm (as high as 2800 mm) along the west-side of the Divide between Stillman Creek and the Chehalis headwaters: on BawFaw Peak), characterized by cloudiness with mild temperatures and heavy rainfall from October through June. Summers are drier and with milder temperatures due to the presence of high pressure systems over the region (Franklin and Dyrness 1973). Of the 3 watersheds Willapa (WIL) is closest to the coast (just East of the Sitka spruce coastal forests) and adjacent to this and east is Chehalis (CHE). Stillman Creek (STL) is adjacent and east of CHE. The divide between CHE and STL is along the highest point in this area.

The watersheds are comprised of steep, mountainous uplands; low, moderately sloping hills and relatively level alluvial plains that are limited in areal extent. The uplands are commonly developed in volcanic or intrusive igneous rocks with ridgetops ranging in elevation from 395-760 m. The Grays River Divide to the west has high points of KO Peak at 835 meters (Chehalis headwaters) and Ten Peak at 800 meters. Baw Faw Peak (aka. Boistfort Peak: on the Divide between Chehalis and Stillman) is the highest point at 945 m. Moderately-sloping hills in the basins are developed in fine- and medium-grained sedimentary rocks. Ridgetops range from 182-486 m in elevation, many having flat ridges and knolls falling to the creeks at slopes ranging from 30-75%. Inner canyons are a mix of rock outcrops and colluvium that range from 50 to >100% slope. Stream density is high: ~4 km/km^2 (40 m/ha)[1] compared to the average of 2.5 km/km^2 (25 m/ha) for coastal rain forests in the Pacific Northwest (Naiman and Anderson 1997:133). Lengths of non-fish-bearing streams total ~4 times that of fish-bearing reaches. Valley bottoms are generally narrow. Small bedrock-based creeks locally erode the sides of the valley. Alluvial floodplains extend a short distance upstream in the tributaries to the major alluvial channels. These floodplains are developed in Holocene alluvium at relatively flat inclinations (0-10%), although river and creek banks are typically steeper than 75%. The valley fill is provided by the erosion and mass wasting of the surrounding uplands.

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[1] This is an overestimate of stream density based on GIS and DTM models, not stream density based on the Washington State Department of Natural Resources hydrological layer (D. Runde, *unpubl. data*).

Eocene and Miocene basalts, along with Tertiary marine deposits, dominate geology. Tertiary intrusive volcanics, and a small area of Holocene outwash sediments are also present. None of the watersheds was glaciated. The chief geologic processes active in the watersheds now include mass wasting in steeper topography, erosion along creeks, bare ground and road cuts and alluvial depositions in the flatter gradient streams (Weyerhaeuser 1994). Soils are generally deep and gravel-free. Due to erosion patterns, deep soils occur not only on alluvial plains, benches and fans but also on broad ridge tops associated with marine sediment geology. Soils are shallow on steep side slopes and at the heads of minor streams (Steinbrenner and Gehrke 1966, Steinbrenner and Duncan 1969).

Appendix Table 1. Geological codes for Washington State. Source: Washington DNR 1:64,000 geological maps.

Class	GeoCode	Interpretation
Igneous	Tib and Eib	Tertiary (Eocene) intrusive basalt, gabbro
	Tig	Tertiary (early and middle Eocene) intrusive basalt and gabbro
	Tib (g)	Tertiary (Eocene) intrusive basalts – granitic
	Tv (c)	Tertiary (Eocene) volcanic composites
	Tvt (pe)	Tertiary (Eocene) volcanics (Pe Ell member of the Cowlitz Formation)
	Tcb	Tertiary (lower and middle Eocene) composites: breccias, basalts, siltstones, and sandstones – (Crescent Formation)
Sedimentary	Tm(1)	Tertiary (Eocene) marine deposits
	Tm(2m)	Tertiary (Eocene) marine deposits (McIntosh Formation)
	Tmc	Tertiary (middle to upper Eocene) marine sedimentary rocks
	Qa	Quaternary (Holocene) alluvial deposits

The survey area lies just east of the coastal Sitka spruce (*Picea sitchensis* [Bong.] Carr.) zone in the Western hemlock (*Tsuga heterophylla* [Raf.] Sarg.) zone (Franklin and Dyrness 1973). Major conifers in these zones are western hemlock, western redcedar (*Thuja plicata* Donn.), Douglas-fir (*Pseudotsuga menziesii* [Mirb.] Franco) and Sitka spruce, which is abundant near the coast. Grand fir (*Abies grandis* [Dougl.] Forbes) occurs throughout the lowlands of the hills, but becomes more abundant in the drier eastern portions of the hills. Pacific silver fir (*Abies amabilis* [Dougl.] Forbes) is occasional in the higher elevations. Noble fir (*Abies procera* Rehd.) has a limited distribution in the higher elevations. Red alder (*Alnus rubra* Bong.) is the most abundant deciduous tree in the area, often occurring in riparian and recently logged sites. Bigleaf maple (*Acer macrophyllum* Pursh) and cascara (*Rhamnus purshiana* DC.) are also common. The understory is typically dominated by salmonberry (*Rubus spectabilis* Pursh), thimbleberry (*R. parviflorus* Nutt.), salal (*Gaultheria shallon* Pursh), huckleberries (*Vaccinium* spp.), coast red elderberry (*Sambucus racemosa* L.), vine maple (*Acer circinatum* Pursh), and swordfern (*Polystichum munitum* [Kaulf.] Presl).

Disturbance and Land Use History

Since 1940, winter storms have produced several large floods, including two that were estimated to have been larger than 100-year events. Numerous mass-wasting events were associated with these and other storms. No records of very large fires were found in historical accounts, however, burn scars on stumps indicate that at some point fires burned many of the slopes in the study area.

Logging in the Willapa Basin began in the mid-1800s and was limited to areas adjacent to tidewater where the logs could be rolled into the rivers or bay. By the late 1800s, ox teams were used as the loggers and farmers reached out into areas further from tidewater. Splash dams were used to move logs to major rivers to float them to sawmills in Raymond and South Bend. Early logging in the Willapa Hills was concentrated in the flat floodplain along the Willapa River and occurred primarily for agricultural conversion. Completion of the Northern Pacific Railroad from Chehalis to South Bend in the late 1880s precipitated logging in the upland areas of the Willapa Headwaters. Steam donkeys replaced ox teams, and small sawmills and their associated communities developed along the railway. In the late 1890s and early 1900s short rail lines were built to access many of the upper tributaries, and the Pacific and Eastern Railroad was constructed along the northern divide of the watershed. Loggers used steam donkeys and ground lead to move logs to the rail heads during this period.

High-lead logging with steam engines and spar trees replaced steam donkeys and ground lead logging in the 1920s. Caterpillar logging became prominent in the 1930s. Road-building and truck hauling replaced railroad lines in the mid-1940s. By the mid-1960s most of the Willapa Headwaters had been logged at least once. The floodplain along the Willapa River had been converted to agricultural land by the turn of the century. As new farmers moved into the valley they were forced to farm the steeper uplands which had already been logged. These "stump ranchers" burned off the logging slash and allowed grass to re-vegetate to slopes to graze livestock. Trees eventually replaced the grass on slopes that were too steep for farm equipment, and the northern three-quarters of the watershed returned to a mosaic of second-growth stands. Many of these second-growth stands were logged from the mid-1970s through the 1980s and are currently stocked with third-growth stands of conifer.

Timber harvesting in the Chehalis was completed in three phases over the past 50 years. The northern part of the basin (Crim Creek) and Stillman Creek was railroad-logged in the 1940s and allowed to naturally regenerate. The middle third of the Chehalis watershed was logged from the 1960s to mid 1970s with conventional high-lead tower logging and off-highway truck hauling. The southern third of the Chehalis watershed was logged 20-30 years ago during the transition from railroad logging to truck logging systems.

Current harvesting utilizes both cable and ground-based yarding techniques. As a general rule, slopes under 30% are logged with ground-based equipment, and steeper slopes are cable-yarded with full or partial suspension. Most harvest units are clear-cut with some commercial thinning and selective cutting. Second- and third-growth Douglas-fir and western hemlock forests in various stages of development now dominate the landscape. Within this landscape, naturally regenerated stands comprise ca. 50% of the area with the

rest in planted stands. With minor exceptions, planted stands are third-growth forest. Interspersed with these conifer stands are patches dominated by early successional deciduous shrubs and trees, as well as a variety of water- and topographically-related gaps in the landscape.

High-yield intensive timberland management has been practiced here since the mid-1960s. This management has included: planting with nursery-grown seedlings, pre-commercial and commercial thinning, pruning, fertilization, hardwood competition control, and clearcutting on 45-60 year rotations.

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British Columbia

Data on occurrence and abundance of tailed frogs, as well as site-level characteristics of streams were obtained in three ways. A broad scale survey ($n = 453$ sites) using time-constrained headwater stream searches was conducted in 1995, 1996 and 1998. Streams in the Coast and Mountains Ecoprovince of British Columbia, as well as the Southern Interior Mountains Ecoprovince (see Demarchi 1993 for definitions) were surveyed. All ecosections in the Coast and Mountains Ecoprovince were sampled. Additional survey data was obtained for some streams in the Northern Boreal or Sub-boreal Mountains Ecoregions. These data were supplemented with data compiled from scattered tailed frog samples made by other researchers ($n = 260$ sites) between 1961-1996. These records were primarily located in southwestern BC.

Area-constrained search (ACS) data from headwater streams in three field study areas, the Squamish Valley and Chilliwack Valley in southwestern British Columbia were used here to estimate larval densities, distributions of cohorts in streams. More detailed descriptions of these areas are provided in the sections below. With the exception of the use of ACS in the Chilliwack and the Squamish sites (south coast area) compared with TCS searches in the broad survey, all other variables were measured similarly in sampled streams.

South Coast (Squamish and Chilliwack Areas)

Stream and amphibian sampling took place in the Squamish study area (centered at 49° 55'N 123° 20' W) in 1995 and 1996. This area is located in the Coastal Western Hemlock (CWH) biogeoclimatic zone (Meidinger and Pojar 1991) with Pacific silver fir (*Abies amabilis*), western hemlock (*Tsuga heterophylla*), western red-cedar (*Thuja plicata*), and at lower elevations, Douglas –fir (*Pseudotsuga menziesii*) comprising the main overstory tree species. Annual precipitation in the Squamish sites averages 2810 mm and mean annual temperatures are 8.5°C (National Climate Data Centre, Environment Canada).

In total, eleven streams were sampled distributed among four drainages: the Squamish (3 streams), Elaho (3 streams), Mamquam (4 streams), and Ashlu (1 stream) Rivers, all flowing into Howe Sound. Ten of these streams were sampled in both years. One stream in the Squamish drainage was replaced in 1996 with the Ashlu site due to loss of road access. In each watershed, streams flowing through three forest stand types were selected: old-growth forest (> 250 years old), second-growth forest (approximately 70 years old), and clearcut (5-10 years old). In the Mamquam drainage, one site was a stream buffered with 30-m strips on either side of the stream with clearcuts located upslope of the buffers. The replacement site in the Ashlu drainage was a clearcut type.

In the Chilliwack study area (centered at 49° 6'N 121° 36' W), streams in 7 drainages were sampled in 1996–1999. These sites have many similarities to the Squamish study sites. Sites are also located in the Coastal Western Hemlock (CWH) biogeoclimatic zone (Meidinger and Pojar 1991) with a similar composition of overstory tree species. Annual precipitation at Chilliwack sites is considerably less than in the Squamish (mean = 1800 cm), but average annual temperatures are similar between the two areas (mean = 9.8 °C; National Climate Data Centre, Environment Canada).

Sampled streams were selected in three forest stand types: old-growth (2 sites: Chipmunk Creek and Foley Creek drainages), second-growth (4 sites: Promontory Ridge, Thurston Mountain, Tamihi Creek, and Chilliwack Lake), and recent clearcut (3 sites: Foley Creek, Chipmunk Creek and Nesakwatch drainages). Site selection was limited by the availability of tailed-frog bearing streams in each of the forest cover types. Streams were not selected if they were within 1 km of each other and in the same forest cover type.

Kootenays Area

Data on occurrence and abundance of tailed frogs (*Ascaphus montanus*) in the southeastern corner of British Columbia were collected in 1996 (Dupuis and Bunnell 1997) and in 1998 (Dupuis and Wilson 1999) using time-constrained searches. The area is located in the East Kootenay region of British Columbia, and is within the Southern Interior Ecoprovince (Demarchi 1993). All sampled streams are in the Englemann Spruce/Sub-Alpine Fir biogeoclimatic zone with Englemann Spruce (*Picea englemanni*) and sub-alpine fir (*Abies lasiocarpa*) comprising the main overstory tree species. Sampled creeks ranged in elevation from 1189 to 1905 m, had low gradients, were small in size and were not deeply incised (Dupuis and Wilson 1999). Riparian vegetation varied considerably along sampled creeks, and included alder (*Alnus rubra*), white spruce (*Picea glauca*) and lodgepole pine (*Pinus contorta*) as canopy species. Mean annual precipitation in the Kootenays sites was lower than the coast sites (mean = 801 mm), but mean annual temperatures was higher (11.5°C; National Climate Data Centre, Environment Canada).

Tadpole Sampling

At each site where area-constrained searchers were performed, stream and larval population characteristics were measured for selected reach segments of the stream depending on the area (Squamish: 3 reaches of 5 m each separated by 25 m; Chilliwack: 10 reaches of 5 m in length). Streams were characterized by elevation (m), water temperature (°C), and wetted widths (m) (Bury and Corn 1991). Tadpoles and adults within a stream were enumerated by area-constrained search methods (Bury and Corn 1991; Schaffer *et al.* 1994) as follows. All individuals found within sampled stream reaches were counted and measured. Results were averaged for the stream as a whole. Searches included an initial scan of the stream surface for active animals, followed by an in-depth search of all creek substrates (hand-raking sand and gravel, upturning cobbles and small boulders, sweeping large boulders by hand, and scanning streambanks. Surveys began at the downstream end of a reach (at least 20 m above the nearest road) and proceeded upstream in 1-m increments, using aquarium nets (of 0.05 or 1 mm mesh) to catch dislodged animals. Surveys terminated with a final visual sweep of the surveyed area. Measurements to the nearest mm were taken on each captured individual included snout-vent length (SVL), hind-leg length, and total length. Each individual was weighed to the nearest 0.1 g. All captured individuals were replaced in the stream reach after being measured.