TAILED FROGS (*ASCAPHUS TRUEI*, STEJNEGER) IN NATURAL AND MANAGED COASTAL TEMPERATE RAINFORESTS OF SOUTHWESTERN BRITISH COLUMBIA, CANADA

by

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Abstract

Ten headwater creeks were surveyed for tailed frog tadpoles in the summers of 1994 and 1995 to assess possible effects of timber harvest on their population density and structure. Three watersheds were selected to replicate three treatments: old-growth (250+yrs), mature second growth (60-80yrs) and young clearcut (~5yrs). One buffered clearcut creek was located and sampled but not replicated. Creek and site characteristics modified the response forest harvest had on tailed frog tadpole populations.

Effects on tailed frog tadpoles associated with forest harvest depended on elevation, creek size, percent sand cover and percent riffle cover. Higher tadpole biomass per unit area and density were associated with high elevation sites, small creeks and low percent cover of riffles. Both average tadpole mass and snout-vent length were found to increase with increasing percent sand cover. Tadpoles appear to select microhabitats of pool, run or riffle depending on their body size or stage of development. Higher tadpole densities are also associated with lower creek temperatures. Old-growth and buffered clearcut creeks showed highest biomass per unit area and density of tailed frog tadpoles. Old-growth creeks also exhibited more tadpole cohorts (5 'year-classes'), higher tadpole biomass per unit area but lower average mass than clearcuts. Low (3m maximum) tadpole movements were detected in clearcut creeks, while longer distance (65m maximum) movements were detected within old-growth creeks.

Harvesting history appears to be an indirect measure of the factors influencing the population dynamics of tailed frogs, whereas aspects of microhabitat, which can vary in parallel with forest age, are probably the true limiting factors. Structural features of old-growth forests are also influenced by gradient, elevation and disturbance history. In my study, more than 85% of the variation in tadpole biomass per unit area and tadpole density was associated with creek and site characteristics. History of forest disturbance only had a major impact under specific conditions. When managing for tailed frogs, the variability of creek and site characteristics must be considered prior to making harvesting decisions.

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Chapter 1

Overview

Introduction

Impacts of timber harvest vary among physical habitats and regions of the Pacific Northwest, and this variability is evident in studies of the tailed frog (*Ascaphus truei*, Stejneger). Research has shown differing results when attempting to document tadpole relations to changes in forest cover. Environmental factors such as creek gradient, shading by entrenchment or substrate may modify the response of frogs to forest harvest. Several authors have shown negative impacts on tailed frog tadpoles, where population densities decrease following timber harvest (Noble and Putnam 1931; Metter 1964; Corn and Bury 1989; Aubry and Hall 1991; Dupuis and Friele 1995; Kelsey 1995). Others have found little (no increase or decrease in population densities) or positive (increase in population densities) effects (Gilbert and Allwine 1991; Richardson and Neill 1995). There is no consistent response to forest harvesting, which suggests that other factors play a more important role in the population density and structure of tailed frogs, or that forest harvest has a series of complex effects. This study focuses on the habitat associations and relations of tailed frog tadpoles to different forest practices. The results indicate that effects of forest harvest are modified by creek and site characteristics. Forest harvest does not affect tailed frog tadpoles directly, but modifies the environment which then directly affects them. Therefore, the degree of effect depends on what the initial environment was and how much it changed.

Background Information

Natural History of the Tailed Frog

Distribution and Status of the Tailed Frog

Tailed frogs are endemic to the Pacific Northwest of North America. They occur between the Cascades and the Pacific Coast through Washington, Oregon, northern California and in southwestern, southeastern and northwestern British Columbia, with scattered populations eastward into Montana and Idaho (Capula 1989; Leonard et al. 1993). The Portland Canal (B.C., Alaska divide) is the northern extent of their range (Dupuis and Bunnell 1996). To date, no studies have monitored tailed frog populations for more than three years.

In British Columbia, the tailed frog has been designated as a Blue-listed species (Clayoquot Scientific Panel 1995). Blue-listed designation covers indigenous species, subspecies, or populations that are vulnerable or at risk because of low or declining numbers or presence in vulnerable habitats, and includes populations suspected of being vulnerable, but for which information is too limited to allow designation in another category (Clayoquot Scientific Panel 1995). Wildlife species are evaluated for the provincial lists on the basis of abundance, distribution, habitat integrity, population trend, reproductive potential and national and international status (Ministry of Environment, Lands and Parks 1991).

Unique Features

The tailed frog is the most primitive frog in the world (Nussbaum et al. 1983) and is the only representative of the family Ascaphidae. They are unique among anurans in many ways. Fertilization of the eggs is internal (males possess an extended cloaca). *Ascaphus* is the only anuran known to engage in copulation (Stebbins and Cohen 1995). The only other anurans with internal fertilization are four species of African bufonids (*Nectophrynoides*) and two species of leptodactylids (*Eleutherodactylus*) (Stebbins and Cohen 1995). Other primitive features lie in their skeletal structure. *Ascaphus* have nine vertebrae while other anurans have six to eight (Duellman and Trueb 1994). They also possess ribs, which are only present in three 'recent' anuran families: leiopelmatids, discoglossids and pipids (Duellman and Trueb 1994). The only living frogs that are similar in primitiveness to the tailed frog are three species in the genus *Leiopelma* (Family: Leiopelmatidae) of New Zealand (Green and Cannatella 1993), but the two genera may not be closely related (Green and Campbell 1992).

Life History

Tailed frogs possess one of the longest life spans yet described for anurans, living at least 14 years (Daugherty and Sheldon 1982*b*). Age at metamorphosis can vary depending on the location of populations and the conditions to which they are exposed. The variation is estimated to range from one (southern Oregon; Bury unpubl. data) to four years (Metter 1967; Daugherty and Sheldon 1982*b*; Brown 1990*a*). In a study of northern Idaho and southeastern Washington populations, Metter (1964) estimated that individuals spent three years as tadpoles and reached reproductive maturity four years after hatching. These estimates are based on size cohorts; there is no unequivocal way of establishing tadpole age.

Adults breed in early fall and the frequency of egg-laying can vary depending on the geographic location. *Ascaphus* females lay their eggs every other year in inland areas and probably lay every year in coastal areas (Noble and Putnam 1931; Metter 1964). Generally, sperm is stored by the female until June or July when she deposits the eggs in sticky strings attached to the downstream undersides of rocks (Noble and Putnam 1931; Capula 1989; Leonard et al. 1993). Embryos develop in about one month (Metter 1967, 1964; Brown 1990*a*) and free-swimming tadpoles emerge in late September and October.

Foraging Ecology

Tadpoles hide under rocks during the day, but at night they move to the surface of rocks and graze diatoms (Leonard et al. 1993). Suction to rocks is maintained with a wide flat band surrounding the large mouth, and rows of teeth (2-3 rows on top, 8-13 rows on bottom) are used to scrape algae from the rock surfaces (Corkran and Thoms 1996). As well as diatoms, other items, such as pollen and sand grains have been encountered in the intestines of tadpoles (Metter 1964). During the day, frogs hide under submerged stones then emerge at dusk and during the night to feed on small arthropods found along the creek and in the damp surrounding forests (Capula 1989; Leonard et al. 1993). Metter (1964) found spiders to be the most common food item in the guts of adults, while other food items encountered were Diptera (flies) and adult Trichoptera (caddisflies), Coleoptera (beetles), Lepidoptera (butterflies and moths), Hymenoptera (sawflies, ichneumons, chalcids, ants, wasps, bees), snails, ticks, mites and crickets.

Predation

Tailed frogs are preyed upon by American dippers (*Cinclus mexicanus*), Pacific giant salamanders (*Dicamptodon tenebrosus*), fish species such as cutthroat trout (*Oncorhynchus clarki*), red legged frogs (*Rana aurora*) and garter snakes (*Thamnophis spp.*). In the Squamish Valley, natural barriers to dispersal prevent fish from moving into headwater creeks, and allow tailed frogs to avoid predation and competition with these vertebrates. Pacific giant salamanders are also absent from headwater creeks in the Squamish Valley.

Tailed frog tadpoles possess a characteristic white spot at the tip of the tail fin. Because of the presence of this ocellus, Altig and Channing (1993) suggested that attacks within the water come from the rear while aerial attacks are directed at the tail rather than the cryptically coloured body. Vertical wagging of tail fins was observed during this study and I suspect it provides a visual stimulus for potential predators.

Dispersal

Dispersal is defined as the tendency of an organism to move away, either from its birth site (natal dispersal) or breeding site (breeding dispersal) (Begon et al. 1990). Daugherty and Sheldon (1982*a*) examined age-specific movement patterns of transformed individuals in a Montana population of tailed frogs, which is the only study that looked at movement patterns in this species. Once adults reached reproductive maturity, about 50% of them exhibited high philopatry (remaining within a 20 metre segment of the study site). It was concluded that tailed frogs exhibit an extreme case of site fidelity. Extreme philopatry in *Ascaphus*, as compared with other anuran species, is probably due to the fact that *Ascaphus* has one of the lowest desiccation tolerances among anurans (Claussen 1973). High levels of philopatry in *Ascaphus* would reduce gene flow between populations, and suggests a highly fragmented population structure for the species (Daugherty and Sheldon 1982*a*). This suggests that *Ascaphus* exists as a metapopulation for this particular distribution. There has been a progressive reduction in gene flow among *Ascaphus* populations since the Pleistocene (Metter and Pauken 1969) which is probably due to the progressive fragmentation of forest habitat since the Pleistocene.

The high level of philopatry observed in Montana (Daugherty and Sheldon 1982*a*) may be attributed to the dry conditions surrounding the riparian zone in that region. In the temperate rainforests of British Columbia, tailed frogs may not be as limited in their movement. It is important to note that Daugherty and Sheldon's (1982*a*) findings illustrated the philopatry exhibited by adults, leaving the metamorphs, juveniles and subadults as potential dispersers.

Tadpole movements are completely unknown in B.C. streams. In Oregon streams, Snook (unpubl. data) found that tadpoles moved downstream while adults and juveniles moved upstream. These observations agree with suggestions made by other authors (Metter 1964; Daugherty and Sheldon 1982*a*), except that upstream movement was thought to be done by newly transformed individuals.

Objectives of this Thesis

The objectives of this thesis were to determine what creek and site characteristics tailed frog tadpoles are associated with and to determine if creeks flowing through old-growth forests, second-growth forests and clearcuts supported comparable tadpole population density and structure. My main question was: How are tailed frog tadpoles affected by forest harvest? Determining what creek and site characteristics tadpoles were associated with provided some insight as to what factors played a more important role in regulating tadpole populations (e.g., whether they were related to the creek and site environment or to post-harvest conditions acting on the creek and site environment). I also wanted to know how the population density and structure of tailed frog tadpoles differed among the different forest treatments to determine if tadpoles may be faring better in particular age-classes of forest.

Significance of Doing this Work

Role of Amphibians in Riparian Ecosystems

Amphibians serve to benefit the energy dynamics of both terrestrial and aquatic systems. Physiological functions of ectotherms do not demand maintenance of a constant body temperature which allows a high proportion of metabolizable energy to be used for growth and reproduction (Pough 1980). Where fish are not present, amphibians may be the top predators. In small streams in the Washington and Oregon Cascade Range tadpole and adult amphibian densities of 0.9 to 17.2 individuals/m^2 were reported, with more than 90% of the individuals being tadpoles (Bury 1988). Because amphibians are abundant and at a relatively high trophic level, they are an important link in the energy flow of wetland ecosystems.

Riparian Ecosystems Post-Harvest

Immediate results to riparian ecosystems post-harvest include an increase in solar radiation due to the reduction in forest shading (reviewed by Beschta et al. 1987), followed by an increase in within-stream primary productivity (Murphy and Hall 1981), and increased stream sedimentation due to ground disturbances and road building (Beschta 1978). Increases of 7.78° C in average monthly maximum temperature in clearcut streams were reported by Brown and Krygier (1970) in Oregon's coast range while buffered streams (30 metres on both sides) showed no significant temperature changes. Within-stream primary production increases as more solar radiation reaches the stream, changing the composition and amounts of periphyton (Murphy and Hall 1981; Murphy et al. 1981; Hawkins et al. 1983). Composition of algal communities (e.g., a shift to filamentous species) on rocks may affect tailed frog feeding and their ability to maintain position on rocks (personal observation).

Low gradient streams showed significantly greater amounts of sedimentation as compared with high gradient streams in clearcut, second-growth, and old-growth forests (Murphy et al. 1981). Increased sedimentation rates appear to have a negative impact on stream communities. As sediment fills interstitial spaces, refugia and egg deposition areas of stream amphibians are lost. The ability of tailed frog tadpoles to attach to rocks and to scrape off diatoms is impeded by stream siltation (Nussbaum et al. 1983). High levels of sediment may also clog the gills of tadpoles and impair respiration.

Management Actions Affecting Tailed Frog Populations

Fragmentation and removal of riparian forests are habitat alterations of potential importance to tailed frogs, and their effects are likely modified by creek and site characteristics. Forest fragmentation creates various sizes of "habitat patches" defined by Fahrig and Merriam (1994) as any discrete areas that are used by a species for breeding or for obtaining other resources. Forest fragmentation could reduce habitat patch size to levels of unsuitable habitat (increasing the probability of local extinction), and remove habitat connectivity that supports dispersal among fragments (e.g., Sjögren 1991; Bunnell et al. 1992; Fahrig and Merriam 1994). Connectivity between habitat patches is believed to be a key to metapopulation persistence (Sjögren 1991) because it allows dispersal, or movement from one population to another (Taylor 1990). A metapopulation is defined as a set of local populations (often described as subpopulations) which interact by individuals moving among populations (Hanski and Gilpin 1991). The tailed frog is believed to exist as a metapopulation (e.g., Metter and Pauken 1969; Daugherty and Sheldon 1982*a*), but the evidence is not strong.

Reports have indicated that tailed frogs are negatively impacted by logging practices (see Metter 1968; Bury 1988; Bury and Corn 1988; Welsh 1990; Bury et al. 1991; Walls et al. 1992; Dupuis and Friele 1995). Two factors reported to cause a decrease in tailed frog population densities following timber harvest are increased stream temperatures and increased levels of sedimentation. Research is still needed to identify creek and site characteristics that represent significant problems to tailed frog populations following timber harvest.

Riparian Reserves

Riparian reserves, which I will refer to herein as "buffers," are believed to be effective in reducing timber harvest impacts on stream systems and maintaining water quality (e.g., Brown and Krygier 1970; Dupuis and Friele 1995). Research has shown that the effects of clearcutting on stream temperature, sedimentation rates and invertebrate composition are negligible with a 30-m buffer strip on both sides of a stream (Murphy et al. 1986; Beschta et al. 1987). Dupuis and Friele (1995) found higher abundances of tailed frogs in buffered creeks than in those without buffers.

Chapter 2

Habitat Associations and Relations of Tailed Frog Tadpoles with Different Forest Practices

Introduction

The first objective of this study was to determine if tailed frog tadpoles are associated with the various creek and site parameters measured, and was assessed through individual and multiple linear regressions between tadpole and creek and site variables. The second objective was to determine if creeks flowing through clearcuts and mature second-growth forests supported populations of tailed frog tadpoles comparable to those in creeks running through old-growth forests. This objective was accomplished by comparing biomass per unit area, density, size distribution and movement patterns within four forest treatments (old-growth, mature second growth, clearcut and buffered clearcut).

Questions and Hypotheses

Are there relationships between tadpole variables (biomass per unit area, density, average mass and average snout-vent length) and the creek and site parameters? H_o: There is no relationship between the tadpole variables and the creek and site parameters. Do tadpoles of different sizes select microhabitats of pool, run or riffle? Are mean tadpole biomass per unit area, weight and density different in creeks flowing through stands of different ages or in creeks with different parameters? H_o: $\mu_1 = \mu_2$. Do tadpoles metamorphose in the same number of years in creeks flowing through stands of different ages? Are tadpole movements the same in creeks of the different stands?

Study Area

Research was conducted near Squamish in southwestern British Columbia (Figure 1), within the coastal Western Hemlock (*Tsuga heterophylla*) forest. Sites were distributed within three drainages: Squamish River, Elaho River and Mamquam River, tributaries to Howe Sound, and included old-growth forest (250+ years; unaltered natural forest), mature second-growth forest (60-80 years) and clearcuts (~ 5 years). The Squamish and

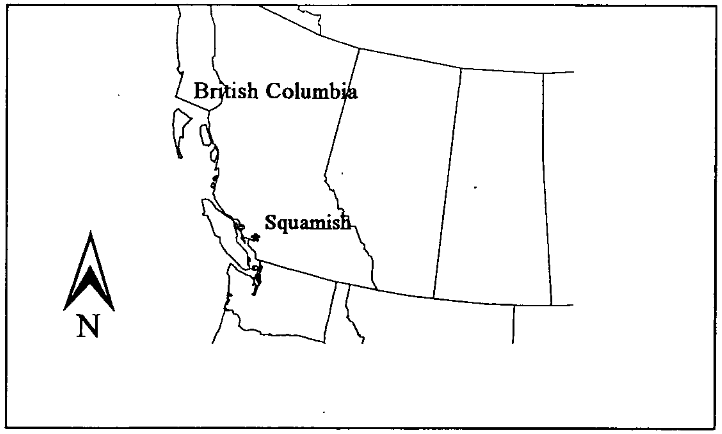
Elaho drainages are managed by International Forest Products (T.F.L. 38). The Mamquam drainage is managed by MacMillan Bloedel (T.O. 726, T.O. 722, T.O. 730), International Forest Products (F.L.A. 19211) and Halrey Logging (F.L.A. 19217). Due to the lack of mature second-growth sites within the Squamish and Elaho watersheds, these sites were selected from just outside Garibaldi Park. Mature second-growth sites selected along the perimeter of Garibaldi Park (not within the park) are managed under Ministry of Forests jurisdiction.

All creeks within the three watersheds were independent of one another, and varied in their characteristics. Topography eliminated any opportunity for nesting relative effects of creek and site characteristics or forest practices. Because this was not a nested design, it was impossible to determine if differences in tadpole populations were due to the different creeks or the different treatments. Creeks were selected on the basis of presence of tailed frog tadpoles, and were chosen upstream (except for the Mamquam clearcut site) from logging roads. Presence/absence searches were conducted for 15 minutes per creek, and tadpole presence was established after one individual was found. Within watersheds, approximate straight-line distances between sites are as follows (where OG = old growth, SG = second growth, CC = clearcut and BCC = buffered clearcut):

Squamish	OG to CC: 2.5 km	OG to SG: 1.7 km	CC to SG: 2.0 km
Elaho	OG to CC: 2.8 km	OG to SG: 7.5 km	CC to SG: 6.4 km
Mamquam	OG to CC: 5.4 km	OG to SG: 16.0 km	CC to SG: 13.7 km
	BCC to OG: 4.7 km	BCC to SG: 15.0 km	BCC to CC: 1.0 km

Riparian buffers around headwater creeks were uncommon, but one buffered clearcut creek was found in the Mamquam drainage (approximately 50 m of old-growth forest was retained on both sides). This creek was surrounded by two recent clearcuts (one 1-year-old and the other 3-months-old in 1994). Three replicates of each forest treatment (except buffered clearcut) were selected. See Appendix I for site information.

For this study, the term "headwater creek" refers to permanent, low order streams without resident game or anadromous fish. Gullies are small, V-sided creeks in the steep headwater areas of a watershed. Headwaters are classified as S4 (may contain fish), S5 and S6 streams in the Riparian Management Area Guidebook of the Forest Practices Code (Ministry of Forests and Ministry of Environment, Lands and Parks 1995). These are stream Class C as described in the B.C. Coastal Fisheries/Forestry Guidelines (1993). Such creeks are afforded no mandatory protection under current laws unless the integrity of fish-bearing streams is at risk.



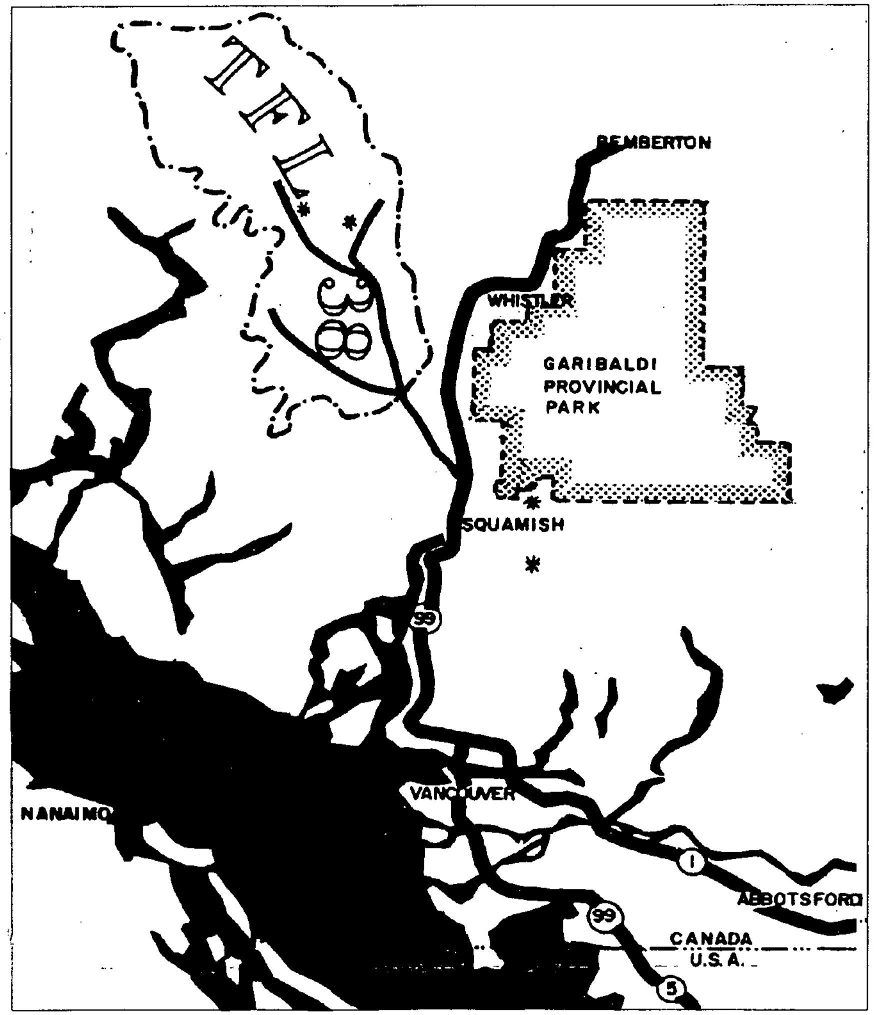


Figure 1: Map of British Columbia showing location of Squamish Valley and enlargement of study area.

Methods

Creek and Site Characteristics

Physical parameters measured for each creek included: wetted width (m), bank width (m), water temperature (°C), aspect (°), creek gradient (°), elevation (m), substrate composition (%) and gully sidewall (m). Water temperature was measured once per month during regular site visits using a digital thermometer. The time of day and day of the month when temperatures were recorded varied for each site. Elevation was obtained using an altimeter and was verified with maps when possible. Using a visual estimation of the area covered, substrate was classified as sand (<2mm), pebbles (2-64mm), cobbles (64-256mm) and boulders (>256mm) (adapted from Bury et. al. 1991). Percent cover of bedrock and percentage of each microhabitat (pool, run or riffle) present was also recorded using a visual estimation. Microhabitat of each tadpole captured was recorded simply by noting whether the tadpole was found in a pool, run or riffle. Pools are generally deep areas of calm water with very little flow. Runs are areas of flowing water with variable depths. Riffles are generally shallow areas of fast-moving and bubbling water. These data were used to determine habitat use by tadpoles of various size-classes. By visual inspection, presence of silt, filamentous algae and detritus were also recorded. Some of the creek characteristics are more integrative of the entire creek (e.g., temperature) while some are specific to the individual sample sites (e.g., percent pool).

Tadpole Variables

Four tadpole variables were used in the various analyses. These are referred to as biomass per unit area, density, average mass and average snout-vent length. Data for all variables were collected through area-constrained creek surveys (adapted from Bury and Corn 1991; Shaffer et al. 1994). Because sampling units were 5-m reaches, values were calculated using the formulae:

1. biomass per unit area (g/m^2) = (Σ tadpole mass)/(average wetted width X 5m)
2. density ($\#/m^2$) = (# of tadpoles)/(average wetted width X 5m)
3. average mass (g) = (Σ tadpole mass)/# of tadpoles
4. average snout-vent length (mm) = (Σ snout-vent lengths)/# of tadpoles

Three 5-m reaches per creek were selected 25m apart (Figure 2a), the first reach chosen at random. Area-constrained searches were performed in all reaches by first scanning the banks for frogs, scanning the creek for surface-active tadpoles, and then by slowly moving up the creek turning and brushing the undersides of rocks and capturing tadpoles with dipnets as they became dislodged. For each reach multiple searches were conducted by each surveyor to ensure that the majority of tadpoles present were captured. Three sizes of dipnets with 1-mm mesh were used for sampling: large, medium and small. Large nets measured 16cm X 12cm, 15cm deep; medium nets measured 13cm X 10cm, 12cm deep; small nets measured 7.5cm X 6.5cm, 8.5cm deep. Selection of appropriate net size was based on dominant creek substrate size, and more than one size of net was always carried while searching reaches.

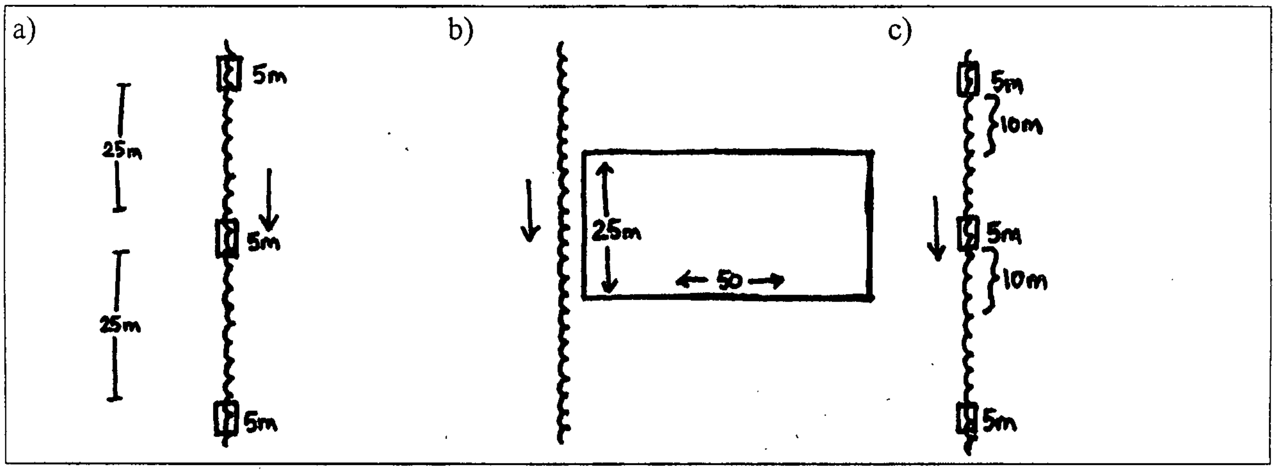


Figure 2: Sampling designs for tailed frog surveys: a) creek surveys for tadpole variables, b) visual encounter survey transect for frogs, c) additional creek surveys for tadpole movements.

During the 1994 preliminary field season, sampling methods were in the developmental stage. Young second-growth forests were selected for the first year of the study, and sites were not sampled consistently. Sites are not comparable with one another for this year of sampling due to this inconsistency of sampling effort and are therefore not comparable with 1995 data. In 1995, creeks within old-growth, mature second-growth, clearcut and buffered clearcut sites were sampled once each in June, July and August (except for the buffered clearcut which was not sampled in June; see 1995 sampling schedule, Appendix II). Only data for July are used in the analyses. All tadpoles had not yet emerged in June due to cold temperatures (sample size was low) and August sample sizes were lower than July which suggested the possibility of tadpoles returning deeper into the substrate due to cooler temperatures. All data not found in this thesis (1994 data, 1995 June and August data) have been archived at the Data Library at the University of British Columbia. These data can be easily accessed through the World Wide Web at http://www.datalib.ubc.ca/datalib/gen/files_unixg/frogs/main.html.

Tadpoles were measured (snout-vent length, total length and limb length), weighed (using a Pesola spring scale, to the nearest 0.05g), marked with unique-to-reach codes, and location in reach (e.g., pool, run or riffle) was recorded. Taking special care not to cut into the central axis of caudal muscle, the dorsal fin of the tail was marked with "V"-shaped notches following Turner (1960; see also Donnelly et al. 1994). Three different notching codes were given to tadpoles captured in the three reaches (i.e. one notch, two notches or three notches). Notches lasted for over one month and allowed for identification of reach-specific recaptures in subsequent creek surveys. After the reach had been completely searched and tadpole measurements were recorded, disturbed rocks were replaced and tadpoles were released 1m upstream from the reach of capture. Releases were always made within a run to maintain consistency.

Size Distribution

Tadpole data were collected through the area-constrained searches described above. Snout-vent lengths were plotted as cumulative frequency distributions to view the size distributions within the different forest treatments. Harding's (1949) approach for analysing polymodal distributions was used to determine where breaks in the data were. This involved plotting the cumulative frequencies of tadpole length on probability graph paper so that inflection points (where the distribution line made a sharp turn in a new direction) were visible. For one site, Mamquam old growth, data were also run through Peak Fit (Jandel Scientific 1990) to assess comparability.

Frog data were collected using evening visual encounter surveys (VES) in the forest adjacent to creeks sampled for tadpoles (Mamquam watershed sites only). Some frog data were also collected during creek surveys. During visual encounter surveys, the field crew walked through riparian and upslope habitat while searching for frogs (after Crump and Scott 1994). VES were only conducted in the Mamquam watershed because of the intensive nature of these surveys, and because these surveys were only intended as a supplementary technique for capturing frogs. Four transects were set up in each of the three creeks within the Mamquam watershed. Permanent distance markers were placed at 10-m intervals along the four transects: two parallel trans-riparian transects extending from creek edge 50 m into the upslope forest, one riparian transect (1 m from the creek) 25 m in length and one 25-m upslope transect, connecting the 4 transects in a rectangle (Figure 2b).

Each transect was carefully searched for frogs within 1 m of the transect path, on each side. The total area searched was 300 m^2 (2 X 150m). Three visits were made to each site in the Mamquam watershed from July until October. Surveys were carried out during rainy or drizzly periods from dusk until midnight when encounters were expected to be highest. Individual frogs were measured, weighed, sexed, given a unique toe-clip code (e.g., A3B2: left forelimb, third digit and right forelimb, second digit), released and the distance from the creek recorded.

Frog toe-clippings were preserved in a 10% formalin acetate solution to explore the feasibility of skeletochronology in aging frogs. Skeletochronology involves the processing of thin sections made with a freezing microtome from decalcified bone (toes) and staining by hematoxylin (Castanet and Smirina 1990). Toe bone sections were prepared by Gary Matson (Matson's Laboratory, Milltown, Montana) using the following methods: toes were decalcified in a dilute solution of hydrochloric acid, embedded in Paraplast paraffin medium, and sectioned transversely in a rotary microtome at a thickness of 14 micrometers. Four sections at 0.3-mm intervals were saved during sectioning in an attempt to obtain sections through bone rather than the more abundant cartilage. The sections were mounted on glass microscope slides and stained with Mayer's Hematoxylin.

Annulus visibility was found to be rather poor in this species (Gary Matson pers. comm.). There are no researchers that I am aware of who have used this technique to age tailed frogs, so I developed a protocol before starting the analyses. Frog toes were examined and aged using a microscope by counting the number of annuli present. I assumed a pair of dark and light rings was equivalent to one year of growth. Counting the number of rings for each individual and adding this number to the number of tadpole size-classes (previously estimated) provided an age estimation. Ages were checked against field observations. Some important indicators of sexual maturity (at least 7 years old for *Ascaphus*; according to Daugherty and Sheldon 1982*b*) include presence and colour of nuptial pads and presence of eggs.

Movement Patterns

Because it is difficult to locate natal sites (in this case, nest sites) to know how far tadpoles have moved from them, the aim of this portion of the study was to determine general movement patterns from the original site of capture. The movements of tadpoles were assessed by conducting area-constrained creek surveys and mark-recapture techniques described above. Two additional 10-m reaches were sampled directly below the second and third reaches to maximize number of captures (Figure 2c). Tadpole data recorded for 10-m reaches included number of notches, distance from upstream end of reach, limb development, predicted age-class (after Brown 1990*a*), tail damage and presence of spot. Each creek was surveyed once in July and once in August (about two weeks apart) and yielded information on the extent of tadpole movements.

Results

Relations of Tailed Frog Tadpoles with Creek and Site Characteristics

Table 1 provides a summary of creek and site characteristics showing both tadpole biomass per unit area and density in July 1995 for old-growth, mature second-growth, clearcut and buffered clearcut creeks. To compare tadpole variable means, t-tests were used (α = 0.05). Both tadpole biomass per unit area and densities were low where silt was present. Average tadpole biomass per unit area where silt was present was 0.16 $\pm$ 0.04 g/m^2, and 0.65 $\pm$ 0.15 g/m^2 where silt was not present showing a significant difference (t=-2.597, p=0.03, n=10). Average tadpole density where silt was present was 0.35 $\pm$ 0.11 tadpoles/m^2, and 1.62 $\pm$ 0.41 tadpoles/m^2 where silt was not present also showing a significant difference (t=-2.419, p=0.04, n=10). Tadpole biomass per unit area and density were also low where percent cover of sand was high. Filamentous algae was present only in clearcuts, and there tended to be lower biomass per unit area and density of tadpoles in these sites.

Table 1: Summary of creek and site characteristics for tailed frog study sites (± SE mean) - SW B.C. July 1995. OG = old growth (250+yrs), SG = second growth (60-80yrs), CC = clearcut (~5yrs). Presence of silt is recorded as 'yes' or 'no.'

Watershed and Forest Age Class	Silt y/n	% Cover Sand	% Cover Pebble	% Cover Cobble	% Cover Boulder	% Cover Bedrock	Tadpole Biomass Per Unit Area (g/m^2)	Tadpole Density ($\#/m^2$)	Water Temp (°C)	Slope (°)	Filam. Algae (y/n)	Wetted Width (m)	Bank Width (m)	Elev. (m)	% Pool	% Run	% Riffle
Squamish OG	y	14	8	26	20	32	0.19	0.43	13.6	18	n	3.1	7.3	500	1	29	69
Squamish SG	n	7	8	45	33	7	0.30	0.85	11.5	20	n	2.1	4.2	585	30	48	42
Squamish CC	y	32	23	23	16	6	0.10	0.04	11.8	5	y	5.6	9.1	635	2	37	61
Elaho OG	n	45	7	40	8	0	0.38	0.74	12.9	6	n	2.6	3.3	430	7	87	7
Elaho SG	y	3	25	22	50	0	0.23	0.58	8.8	11	n	6.6	10.1	645	2	71	27
Elaho CC	y	6	4	17	73	0	0.18	0.36	15.6	10	y	3.0	5.9	520	7	65	28
Mamquam OG	n	1	18	28	28	25	1.02	2.70	12.9	6	n	2.7	5.0	900	26	63	11
Mamquam SG	n	4	36	35	13	12	0.29	0.59	9.2	5	n	2.2	3.0	255	9	84	7
Mamquam CC	n	1	10	43	23	23	0.84	2.08	11.3	9	n	1.6	3.8	775	20	69	11
Mamquam CC w/buffer	n	1	4	68	7	20	1.05	2.77	12.4	3	n	2.0	7.2	875	22	78	0
Mean ± SE mean		11.40 ±4.78	14.30 ±3.40	34.70 ±4.77	27.10 ±6.52	12.50 ±3.72	0.45 ±0.12	1.11 ±0.32	12.00 ±0.63	9.30 ±1.80		3.15 ±0.52	5.89 ±0.78	612.00 ± 63.47	12.6 ± 3.43	63.10 ± 6.15	26.30 ± 7.59

Mean creek temperatures in old-growth forests (13.1 ± 0.23 °C) and clearcuts (12.9 ± 1.36 °C) were not significantly different among the three watersheds (t=0.169, p=0.874, n=6), but this may be due to the inconsistency of temperature sampling. Mean creek temperatures in old-growth forests (13.1 ± 0.23 °C) and second-growth forests (9.83 ± 0.84 °C) were significantly different (t=3.780, p=0.019, n=6). Creek temperatures in second-growth forests were consistently cooler in both average and individual temperatures, suggesting that local shade may be important. Mean creek temperatures in clearcuts and second-growth forests were not significantly different (t=1.920, p=0.127, n=6), which again may be due to the inconsistency of temperature sampling. The maximum creek temperature in clearcuts was 2°C higher than the maximum in old-growth creeks. Tadpole biomass per unit area and density decreased with increasing water temperatures. Creek gradient varied among all forest treatments and ranged from 3° to 10° in clearcut sites, 5° to 11° in second-growth sites and 6° to 18° in old-growth sites.

A forward multiple linear regression (Norusis 1993) showed that 85% of the variation in tadpole biomass per unit area was associated with elevation, wetted width and % riffle (R^2=0.85, p<0.05, n=30). Tadpole biomass per unit area increased with increasing elevation and decreased with both increasing wetted width (Figure 3) and % riffle. Tadpole mass decreased with increasing elevation (Table 2). SE_E (standard error of the estimate) in Table 2 is an overall indication of the accuracy with which the fitted regression function predicts the dependence of Y on X (Zar 1984). Table 2 was created for exploratory purposes to illustrate relationships. Experimentwise correction of α was not applied.

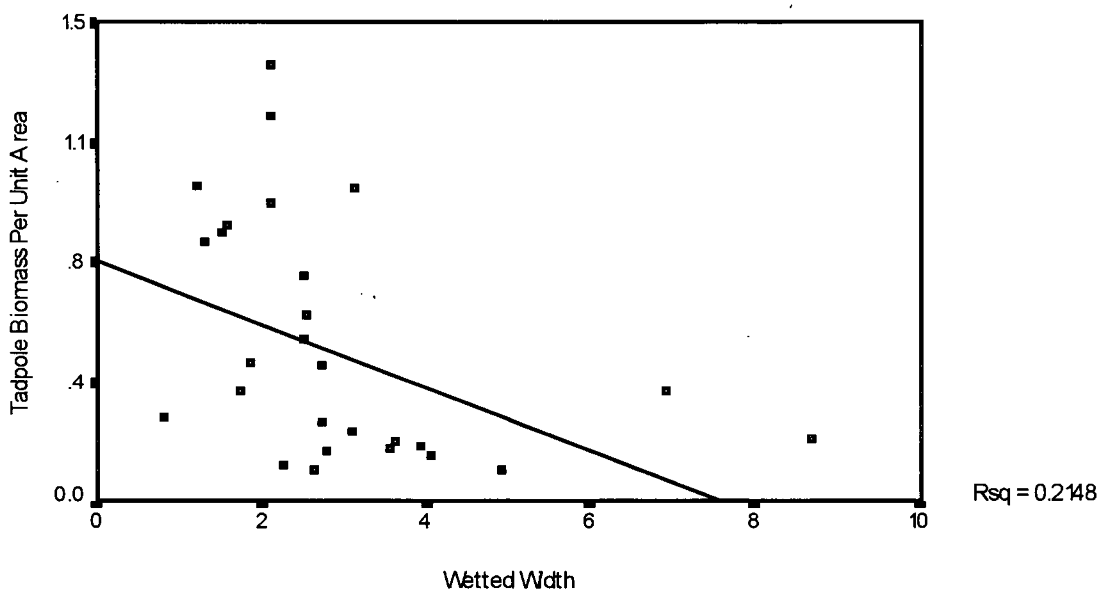


Figure 3: Scatterplot of Tadpole Biomass Per Unit Area vs. Wetted Width

Table 2: Statistically significant relations among tailed frog tadpole and creek and site variables - SW B.C. July 1995. Simple transformations of creek and site variables are employed; only regressions with $p<0.05$ are included.

Dependent Variable	Independent Variable	Relationship +/-	r^2	SE_E	P
density	elevation (1/x)	+	0.654	0.612	<0.001
	% pool	+	0.353	0.838	0.001
	% riffle	-	0.346	0.842	0.001
	slope (1/x)	+	0.286	0.880	0.002
	% sand	-	0.238	0.909	0.006
	gully sidewall	+	0.196	0.934	0.014
	wetted width	-	0.191	0.937	0.016
	% cobbles	+	0.170	0.948	0.023
biomass per unit area	elevation	+	0.453	0.292	<0.001
	% riffle	-	0.350	0.318	0.001
	% pool	+	0.286	0.334	0.002
	wetted width	-	0.215	0.350	0.010
	% sand	-	0.207	0.352	0.012
	slope (1/x)	+	0.204	0.352	0.012
	gully sidewall	+	0.160	0.362	0.029
	% bedrock	+	0.155	0.363	0.032
mass	% sand	+	0.348	0.095	0.001
	% cobbles (1/x)	+	0.171	0.108	0.032
	elevation	-	0.171	0.108	0.032
snout-vent length	% sand	+	0.496	0.729	<0.001

A forward multiple linear regression (Norusis 1993) showed that 87% of the variation in tadpole density was associated with elevation, wetted width, water temperature and % riffle (R^2=0.87, $p<0.05$, n=30). Tadpole density significantly increased with increasing elevation (Figure 4) and decreased with increasing wetted width, water temperature and percent cover of riffles (Figure 5).

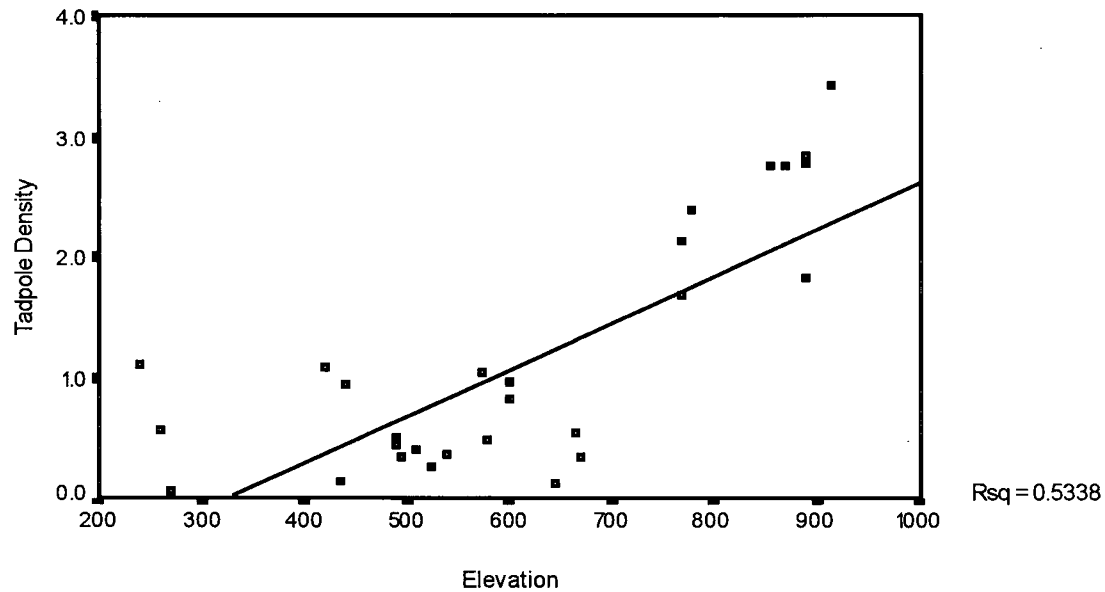


Figure 4: Scatterplot of Tadpole Density vs. Elevation

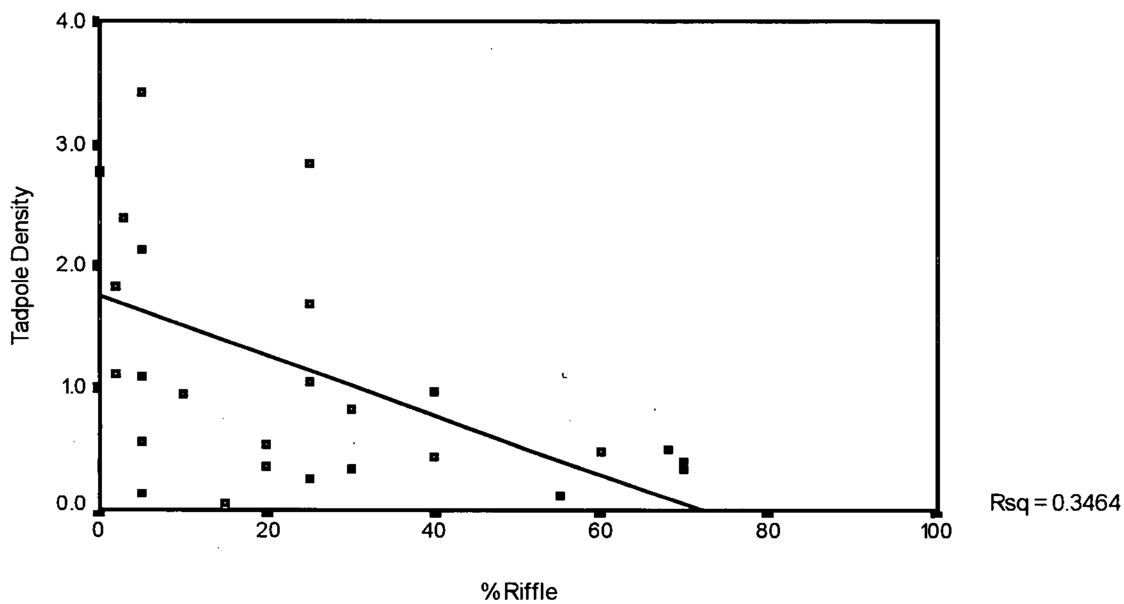


Figure 5: Scatterplot of Tadpole Density vs. % Riffle

A backward multiple linear regression (Norusis 1993) showed that 43% of the variation in average tadpole mass was associated with % sand (R^2=0.43, p<0.05, n=30). Average tadpole mass increased with increasing percent sand cover (Figure 6). A forward multiple linear regression (Norusis 1993) showed that 50% of the variation in average snout-vent length was associated with percent sand cover (R^2=0.50, p<0.05, n=30). Average snout-vent length increased with increasing percent sand cover.

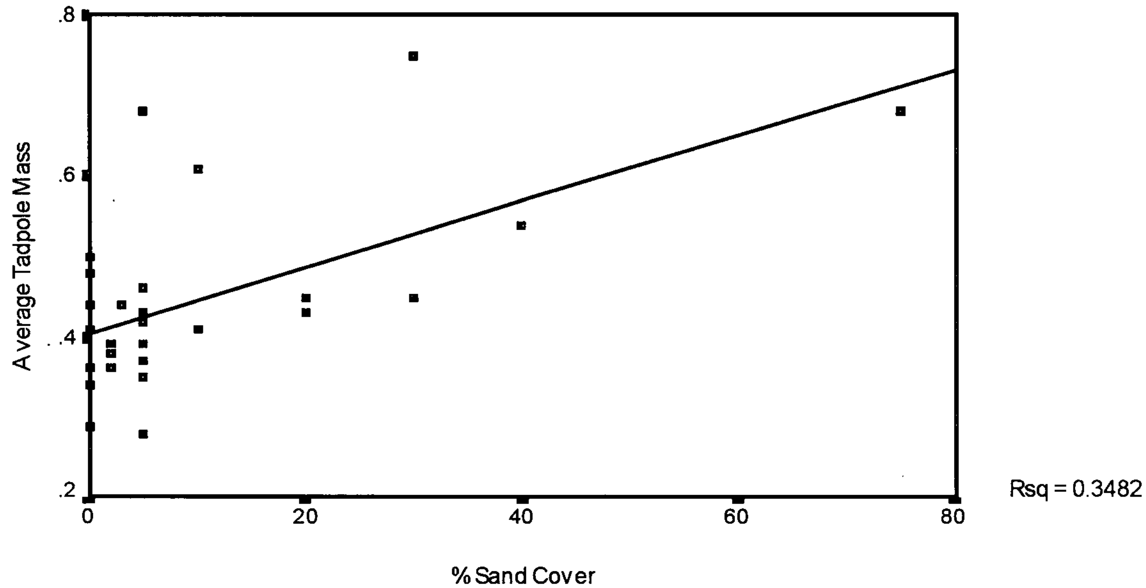


Figure 6: Scatterplot of Average Tadpole Mass vs. % Sand Cover

Relations of Tailed Frog Tadpole Size-Classes with Microhabitat

The majority (66%) of tadpoles captured were found in runs, followed by pools (19%) and riffles (15%) (Table 3). Tadpoles were consistently larger from pools to runs and from runs to riffles. Average snout-vent lengths (SVL) and mass of tadpoles were significantly different from pools to runs (SVL: t=-3.271, p=0.001; Mass: t=-2.236, p=0.026). Average snout-vent lengths, mass and total lengths (TL) were also significant from pools to riffles (SVL: t=-2.994, p=0.003; Mass: t=-2.431, p=0.016; TL: t=-2.363, p=0.019). Two tadpoles captured in pools, and six tadpoles captured in runs had forelimbs, while no tadpoles had forelimbs in riffles.

Table 3: Average length and mass of tailed frog tadpoles in three microhabitats (arithmetic mean ± SE mean) - SW B.C. July 1995

	Pool (N=172)	Run (N=598)	Riffle (N=138)
snout-vent length (mm)	11.50±0.15	12.06±0.08	12.19±0.18
total length (mm)	32.65±0.41	33.48±0.21	34.12±0.47
% with limbs	13.37%	6.69%	7.25%
limb length (mm)*	1.02±0.19	1.23±0.11	1.50±0.23
mass (g)	0.38±0.02	0.42±0.01	0.44±0.02

*Only limb lengths >1.00mm were recorded; N=23 for pools, N=40 for runs, N=10 for riffles.

Tailed Frog Tadpole Biomass Per Unit Area and Average Mass

A total of 941 tadpoles were used in calculations for biomass per unit area (Table 4). Differences in biomass per unit area between old-growth, second-growth, clearcut and buffered clearcut sites were not statistically significant. The buffered clearcut yielded the highest biomass per unit area of all sites sampled. Among the replicated treatments, tadpole populations in old-growth creeks (n=3) yielded the highest (on average) biomass per unit area, followed by clearcut creeks (n=3) and finally mature second-growth creeks (n=3). The Mamquam watershed (not including buffered clearcut) yielded the highest tadpole biomass per unit area overall, with about 3 times that found in the Elaho and Squamish watersheds. Old-growth biomass per unit area values were about 2 times higher than second-growth and 1.5 times higher than clearcuts.

Table 4: Tailed frog tadpole biomass per unit area (g/m^2) in four forest habitat types ($\pm$ SE mean) - SW B.C. July 1995. For average biomass per unit area calculations, n=3.

Forest Habitat Type	Reach Number	Squamish	Elaho	Mamquam	Average Biomass Per Unit Area
Old-Growth	1	0.22	0.59	0.98	0.60
	2	0.16	0.10	1.37	0.54
	3	0.18	0.43	0.71	0.44
	mean =	0.19$\pm$0.02	0.38$\pm$0.14	1.02$\pm$0.19	0.53$\pm$0.25
Second-Growth	1	0.44	0.35	0.52	0.44
	2	0.19	0.20	0.35	0.25
	3	0.27	0.15	0.00	0.14
	mean =	0.30$\pm$0.07	0.23$\pm$0.06	0.45$\pm$0.09	0.27$\pm$0.02
Clearcut	1	0.10	0.17	0.87	0.38
	2	0.00	0.12	0.82	0.31
	3	0.00	0.25	0.85	0.37
	mean =	0.10	0.18$\pm$0.04	0.84$\pm$0.01	0.35$\pm$0.25
Buffered Clearcut	1	-	-	0.94	0.94
	2	-	-	1.21	1.21
	3	-	-	0.99	0.99
	mean =	-	-	1.05$\pm$0.08	1.05$\pm$0.08
Average $\pm$ SE mean		0.20$\pm$0.06	0.26$\pm$0.06	0.80$\pm$0.18	0.42$\pm$0.19

On average, tadpole mass was highest in clearcut creeks, followed by old-growth creeks and finally second-growth creeks (Table 5). Differences in tadpole mass between old-growth, second-growth, clearcut and buffered clearcut sites were not statistically significant. In the Squamish watershed, tadpole mass was highest in clearcuts, followed by old-growth and second-growth creeks. In the Elaho watershed, tadpole mass was highest in the old-growth site, followed by second-growth and clearcut sites. In the Mamquam watershed, tadpole mass was higher in the second-growth sites, followed by clearcut and old-growth sites.

Table 5: Tailed frog tadpole mass (g) in four forest habitat types (± SE mean) - SW B.C. July 1995. For average mass calculations, n=3.

Forest Habitat Type	Reach Number	Squamish	Elaho	Mamquam	Average Mass
Old-Growth	1	0.43	0.54	0.29	0.42
	2	0.45	0.68	0.48	0.54
	3	0.44	0.45	0.39	0.43
	mean =	0.44±0.04	0.51±0.04	0.37±0.02	0.44±0.04
Second-Growth	1	0.41	0.41	0.46	0.43
	2	0.39	0.35	0.61	0.45
	3	0.28	0.42	0.00	0.23
	mean =	0.38±0.02	0.39±0.03	0.50±0.07	0.42±0.04
Clearcut	1	0.75	0.37	0.36	0.49
	2	0.00	0.43	0.38	0.27
	3	0.00	0.68	0.50	0.39
	mean =	0.75±0.43	0.48±0.08	0.41±0.03	0.55±0.10
Buffered Clearcut	1	-	-	0.34	0.34
	2	-	-	0.44	0.44
	3	-	-	0.36	0.36
	mean =	-	-	0.38±0.02	0.38±0.02
Average ± SE mean		0.52±0.11	0.46±0.04	0.42±0.03	0.47±0.03

Tailed Frog Tadpole Density

Among the replicated treatments, densities were highest (on average) within old-growth creeks (n=3), followed by clearcuts (n=3) and finally mature second-growth creeks (n=3) (Table 6), but differences were not statistically significant. The buffered clearcut yielded the highest tadpole densities of all sites. The Mamquam watershed (not including buffered clearcut) yielded the highest densities overall with about 3.3 times the density found in the Elaho watershed and about 4 times the density found in the Squamish watershed. Old-growth values were 1.9 times higher than second-growth values and 1.6 times higher than clearcuts.

Table 6: Tailed frog tadpole densities (#/m^2) in four forest habitat types (± SE mean) - SW B.C. July 1995. For average density calculations, n=3.

Forest Habitat Type	Reach Number	Squamish	Elaho	Mamquam	Average Density
Old-Growth	1	0.52	1.10	3.42	1.68
	2	0.36	0.15	2.84	1.12
	3	0.41	0.96	1.83	1.07
	mean =	0.43±0.05	0.74±0.30	2.70±0.46	1.29±0.71
Second-Growth	1	1.06	0.84	1.12	1.01
	2	0.50	0.55	0.58	0.54
	3	0.98	0.36	0.08	0.47
	mean =	0.85±0.17	0.58±0.14	0.59±0.30	0.67±0.09
Clearcut	1	0.13	0.45	2.41	1.00
	2	0.00	0.27	2.15	0.81
	3	0.00	0.37	1.69	0.69
	mean =	0.04±0.04	0.36±0.05	2.08±0.21	0.83±0.63
Buffered Clearcut	1	-	-	2.76	2.76
	2	-	-	2.76	2.76
	3	-	-	2.79	2.79
	mean =	-	-	2.77±0.01	2.77±0.01
Average ± SE mean		0.47±0.21	0.56±0.11	2.04±0.51	1.02±0.51

Tailed Frog Tadpole Size Distribution

The size distribution of tadpoles from a given site may give insight to some potential effects of forest harvest or may reflect responses to individual creek and site characteristics. Mamquam watershed data were used (except for mature second growth which had a low sample size, N=19) because these sites yielded the highest number of tadpoles. The larger sample sizes provided enough data for graphing to show more defined size classes. Snout-vent lengths were plotted rather than total lengths to reduce the error involved because tail tips were often found damaged.

To make it possible to view the percent of each size class present in the population, snout-vent lengths were plotted in a cumulative percent frequency distribution. Figures 7a-7c are aligned to show where missing or extra size-classes were in the three sites. Figure 7a shows the cumulative frequency distribution for tadpoles captured in the Mamquam old-growth site in July. Snout-vent lengths ranged from 7.15mm to 16.85mm. Using Harding's (1949) approach for analysing polymodal distributions, it was estimated that there were four tadpole 'year-classes' present in the Mamquam old-growth creek in July 1995 (see Appendix III). Inflection points indicated breaks in the distribution. Analyses by Peak Fit (Jandel Scientific 1990) suggests five cohorts with an r^2 of 0.999 (see Appendix IV). In the Mamquam clearcut creek, snout-vent lengths ranged from 9.05mm to 17.25mm in July (Figure 7b). Three tadpole cohorts were estimated using Harding's (1949) approach (see Appendix V). In the Mamquam buffered clearcut creek (Figure 7c), snout-vent lengths ranged from 9.05mm to 15.55mm. Three tadpole cohorts were estimated using Harding's (1949) approach (see Appendix VI). See Table 7 for a summary of tadpole measures in each apparent 'year-class' (based on Harding's approach). A cohort designated as 'year-class' 1 is effectively 0-1 years old and 'year-class' 5 is 4-5 years old.

I elected to use Harding's method because it allowed judgmental decisions incorporating features such as limb length that could not be incorporated into the computer-based approach of Peak Fit. Harding's method involved the use of probability graph paper, where lengths are plotted as cumulative percents, and enables distributions with multiple overlapping size classes to be analysed. The first 'year-class' is not shown in Table 7 because sampling did not occur during the Fall when this cohort would be detected. Most tadpoles captured were of the second 'year-class,' with 15.2% more of this 'year-class' in clearcut sites than in old-growth sites. Less than 25% of tadpoles were 'year-class' 4 or 5. Tadpoles were larger in length and mass in clearcut sites compared with the old-growth and buffered clearcut sites. The fifth 'year-class' in the old-growth site has near the same mass and snout-vent length as the fourth 'year-class' of the clearcut but has longer limbs. The apparent size- or 'year-classes' are not known to be true year-classes. Differential growth between sexes could confuse the analysis.

Figure 7a: Cumulative frequency distribution of tailed frog tadpole snout-vent lengths - Mamquam old-growth creek SW B.C. July 1995

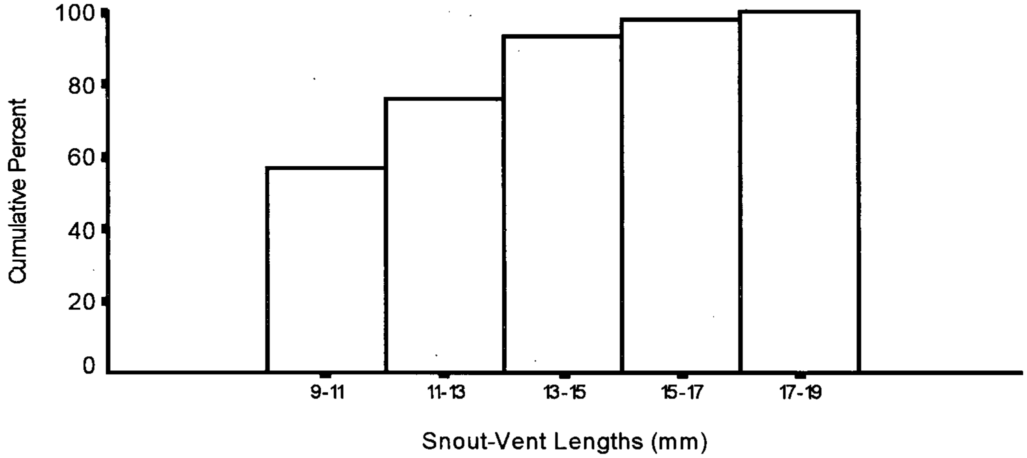


Figure 7b: Cumulative frequency distribution of tailed frog tadpole snout-vent lengths - Mamquam clearcut creek SW B.C. July 1995

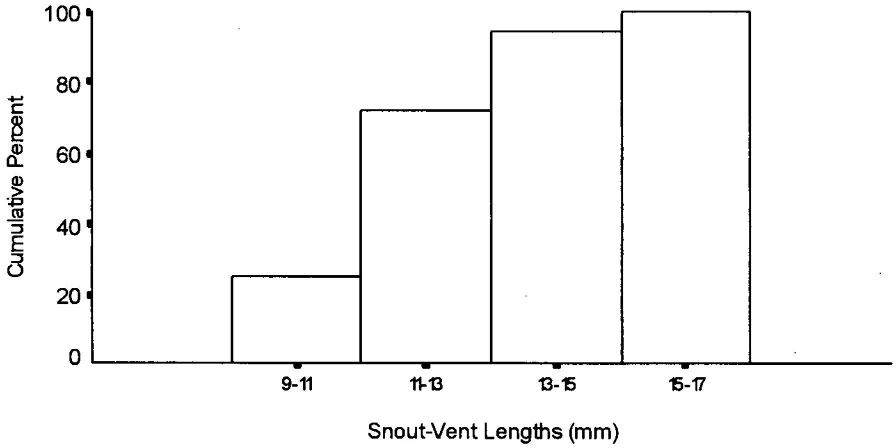


Figure 7c: Cumulative frequency distribution of tailed frog tadpole snout-vent lengths - Mamquam buffered clearcut creek SW B.C. July 1995

Table 7: Percent of population, ranges and means (± SE mean) of tailed frog tadpole measures in each 'year-class' in the Mamquam watershed - SW B.C. July 1995

	Second 'Year'	Third 'Year'	Fourth 'Year'	Fifth 'Year'
Percent of Population				
OG	54.4%	24.2%	14.6%	6.8%
CC	69.6%	13.0%	17.4%	0.0%
BCC	48.0%	29.3%	22.7%	0.0%
Snout-vent Length				
OG	7.15-10.55	10.55-13.35	13.35-15.35	15.35-16.85
CC	9.05-11.45	11.45-14.35	14.35-17.25	
BCC	9.05-11.35	11.35-13.55	13.55-15.55	
Mean SVL				
OG	9.66 ± 0.09	11.80 ± 0.17	14.14 ± 0.16	15.98 ± 0.17
CC	10.34 ± 0.12	13.04 ± 0.40	15.28 ± 0.37	
BCC	10.79 ± 0.09	12.24 ± 0.14	14.34 ± 0.14	
Tadpole Mass				
OG	0.10-0.60	0.15-1.10	0.40-1.00	0.70-0.90
CC	0.10-0.60	0.30-0.70	0.70-1.00	
BCC	0.10-0.40	0.20-0.60	0.40-0.90	
Mean Tadpole Mass				
OG	0.23 ± 0.01	0.40 ± 0.04	0.62 ± 0.04	0.81 ± 0.03
CC	0.30 ± 0.02	0.49 ± 0.06	0.80 ± 0.04	
BCC	0.28 ± 0.01	0.37 ± 0.02	0.62 ± 0.03	
Limb Length				
OG	0.00-0.00	0.00-11.75	0.00-8.05	5.45-14.35
CC	0.00-0.00	0.00-4.65	3.55-9.25	
BCC	0.00-0.00	0.00-3.85	0.00-13.75	
Mean Limb Length				
OG	0.00 ± 0.00	1.01 ± 0.61	2.58 ± 0.65	9.71 ± 1.27
CC	0.00 ± 0.00	2.30 ± 0.83	5.98 ± 0.68	
BCC	0.00 ± 0.00	0.63 ± 0.26	4.26 ± 0.88	

To increase the number of frogs shown in Table 8, frogs captured during the 1994 preliminary field season are included with the 1995 data. No marked frogs were recaptured during either the 1994 or 1995 field seasons so individual growth rates could not be estimated. The majority of frogs captured (71%) were found in the Mamquam watershed (where VES was conducted as a supplement) (Table 8). Thirty-eight percent of the captures were on land, although only 14% of the captures were during visual encounter surveys (most frog captures occurred along creeks during tadpole surveys). Most frogs were male (69%) (Table 8).

Only during the 1995 field season were frog toes submitted to skeletochronological analyses. Toes prepared by Matson's Laboratory for skeletochronological analyses allowed approximate ages to be assigned to frogs. After using Harding's (1949) method for estimating the number of cohorts present in tadpole size distributions, it was estimated that there were between 4 and 5 cohorts present at one time (3 + 1 or 4 + 1: which includes the unsampled first 'year-class' which had not yet hatched). Skeletochronology was adjusted using 'year-class' estimates by adding the number of rings counted in toe bone cross-sections to the number of 'year-classes' in the three sites analysed (Mamquam old growth, clearcut and buffered clearcut). More accurate frog age estimates could be obtained by estimating the number of tadpole cohorts for each creek. Where the number of 'year-classes' of tadpoles had been estimated, one age estimate was given for frogs captured (the number of tadpole 'year-classes' estimated including the first 'year-class' that wasn't sampled + the number of rings counted in toe cross-sections). Other individuals were given two age estimates corresponding to the tadpole 'year-class' range of 4 to 5. Of those submitted to skeletochronological analysis, most (73%) were reproductively mature (at least 7 years old), confirmed by the presence by nuptial pads or eggs.

Table 8: Locations, measures and ages of tailed frogs captured in 1994 and 1995 in SW B.C.
Wtrshd = watershed, TR = treatment, SVL = snout-vent length, TL = total length

Year	Wtrshd	TR	Survey Type	Distance from H_2O	Habitat	Air Temp (°C)	H_20 Temp (°C)	Sex	Age (yr.) = tadpole yr. + toe rings	SVL (mm)	TL (mm)	Mass (g)	Cloaca (mm)
1994	Squam	OG	Creek	0.25	land	11.70	10.60	F		15.15	26.75	0.60	-
1994	Mamq	BCC	Creek	0.25	land	18.30	12.80	M		39.45	45.35	7.50	7.15
1994	Mamq	BCC	Creek	0.00	creek	18.30	12.80	M		15.85	40.15	0.50	1.95
1994	Mamq	BCC	Creek	0.00	creek	18.30	12.80	M		40.85	46.15	8.50	6.65
1994	Mamq	BCC	Creek	0.25	land	13.33	11.11	M		23.45	26.35	1.35	2.45
1994	Mamq	BCC	Creek	0.00	creek	13.30	11.11	M		37.00	44.45	5.95	5.75
1994	Mamq	BCC	Creek	0.00	creek	13.30	11.11	M		38.00	42.55	5.50	6.85
1994	Mamq	BCC	Creek	0.00	creek	13.30	11.11	M		16.65	43.35	1.00	1.95
1994	Elaho	CC	Creek	0.00	creek	25.56	16.67	M		17.00	20.75	0.80	1.45
1994	Elaho	CC	Creek	0.00	creek	25.56	16.67	M		18.95	27.35	1.00	1.65
1994	Mamq	OG	Creek	0.00	creek	12.78	11.67	M		15.55	30.45	0.70	2.00
1994	Mamq	OG	Creek	0.00	creek	12.78	11.67	M		16.95	33.35	0.65	1.65
1994	Mamq	OG	Creek	0.00	creek	12.78	11.67	M		17.45	36.35	0.80	1.95
1994	Mamq	OG	Creek	0.00	creek	17.78	13.33	M		31.85	41.25	3.80	-
1994	Mamq	OG	Creek	0.00	creek	17.78	13.33	F		11.85	34.75	0.20	-
1994	Squam	OG	Creek	2.00	land	16.67	13.33	F		21.75	25.00	1.60	-
1994	Squam	OG	Creek	1.00	land	16.67	13.33	M		14.00	17.45	0.75	1.85
1994	Mamq	OG	Creek	0.00	creek	16.67	11.11	M		35.00	44.75	5.80	7.00
1994	Mamq	OG	Creek	0.00	creek	16.67	11.11	M		33.95	46.00	5.85	5.85
1994	Elaho	OG	Creek	0.25	land	13.33	11.11	F		25.25	29.15	1.95	-
1994	Elaho	OG	Creek	1.00	land	13.33	11.11	M		17.00	20.55	0.80	2.00
1994	Mamq	CC	Creek	0.00	creek	13.89	9.44	F		25.00	27.55	2.25	-
1994	Mamq	CC	Creek	0.00	creek	13.89	11.67	F		16.15	18.95	0.55	-
1994	Mamq	CC	Creek	0.00	creek	13.89	11.67	M		16.55	18.65	0.55	1.35
1994	Mamq	CC	Creek	0.00	creek	13.89	11.67	M		17.00	20.00	0.60	1.35
1994	Mamq	CC	Creek	0.00	creek	13.33	9.44	M		35.00	45.55	5.90	7.75
1994	Mamq	CC	Creek	0.00	creek	13.33	9.44	M		16.00	18.85	0.75	1.45
1995	Squam	OG	Creek	0.00	creek	-	11.40	M	4 or 5 + 2	38.25	41.95	5.9	9.55
1995	Squam	OG	Creek	2.00	land	-	11.40	F	4 or 5 + 3	46.15	50.75	10.5	-
1995	Mamq	CC	Creek	0.00	creek	-	11.30	F	4 + 3	43.15	45.55	8.85	-
1995	Elaho	CC	Creek	0.00	creek	-	16.90	F	4 or 5 + 3	44.65	48.75	8.05	-
1995	Squam	OG	Creek	0.25	land	-	12.40	M	4 or 5 + 3	37.85	46.05	5.55	6.45
1995	Mamq	OG	Creek	0.00	creek	-	11.60	F	5 + 3	34.15	45.65	5.80	-
1995	Mamq	OG	Creek	0.00	creek	-	13.20	M	5 + 3	35.45	46.35	5.70	5.15
1995	Mamq	SG	VES	1.00	land	19.30	-	F	4 or 5 + 3	23.75	26.65	2.00	-
1995	Mamq	CC	VES	50.00	land	15.80	-	M	4 + 2	21.75	24.05	1.70	1.85
1995	Mamq	CC	VES	15.00	land	18.00	-	M	4 + 3	31.65	41.25	5.20	7.95
1995	Mamq	CC	VES	5.00	land	15.40	-	F	4 + 3	30.15	32.25	3.80	-
1995	Mamq	CC	Creek	0.50	land	19.30	15.00	M	4 + 2	16.15	30.45	0.60	1.45
1995	Gert	SG	Creek	0.00	creek	-	9.44	M	4 or 5 + 3	33.35	43.25	4.85	7.85
1995	Mamq	CC	VES	2.00	land	5.90	6.50	F	4 + 2	31.85	35.85	4.10	-
1995	Mamq	CC	VES	2.00	land	-	-	M	4 + 2	32.45	43.65	4.95	8.45

Movement Patterns of Tailed Frog Tadpoles

During searches for tadpole movement, 499 tadpoles were encountered; 50 were recaptures, 10% of the total number of tadpoles sampled. Because no expected value in a contingency table can be less than five (Rosner 1982) contingency table analyses could not be performed on these data. Although sample size is low, some patterns of movement for tadpoles in different forest age classes can be seen (Table 9). Only distances of 0-15 m, 30-45 m or 60-65 m could be detected because of the two stretches (15 m each) of unsampled creek between reaches one and two, and two and three. The maximum distance moved by tadpoles in old-growth sites was higher than maximum distances moved in clearcut sites. Over the average 18-day period, tadpoles moved up to 65 metres in old-growth sites. In mature second-growth sites, distances moved were up to 35 metres. In clearcut sites, maximum distances moved were only 3 metres.

Table 9: Tailed frog tadpole captures in four forest habitat types (± SE mean) - SW B.C. July 1995. Distances are metres moved over an average of 18 days.

Forest Habitat Type	Squamish	Elaho	Mamquam	Total Recaptures	Mean Distance Traveled (m)	Mean Slope (°)	Mean Wetted Width (m)
Old Growth	3	10	8	21	17.33 ± 4.95	10 ± 4.00	2.80 ± 0.15
Second Growth	2	2	13	17	5.24 ± 1.91	12 ± 4.36	3.63 ± 1.48
Clearcut	0	0	6	6	2.33 ± 0.33	8 ± 1.53	3.40 ± 1.17
Buffered Clearcut	-	-	6	6	3.67 ± 0.42	3	2.0

Clearcut and buffered clearcut creeks have the lowest creek gradient and here, movements are the lowest (Table 9). Old-growth creeks have a steeper gradient and movements were much greater. Second-growth sites, however, had the steepest gradient but much shorter movements than old-growth sites. No patterns were visible when scattergrams of average distance traveled versus creek slope, wetted width and tadpole densities were created. Also, a scattergram of density versus number of recaptures did not show any pattern. Due to the low sample size and unequal distribution of data among the 4 treatments, patterns of movement are difficult to determine, but these results provide useful preliminary information for further research.

Discussion

Relations of Tailed Frog Tadpoles with Creek and Site Characteristics

Results indicate that creeks are very different from one another. Creek and site characteristics are dominating within these data and modify the response of tadpole populations post-harvest. Analyses show that higher tadpole biomass per unit area and density are associated with higher elevation sites, small creeks and low percent cover of riffles. Higher tadpole densities are also associated with low creek temperatures.

In the Southern Washington Cascade range, Aubry and Hall (1991) found that tailed frogs were associated with high elevation sites. In this study both tadpole biomass per unit area and density are greater at higher elevations which would explain the larger sample sizes in three of the Mamquam watershed sites. The old-growth, clearcut and buffered clearcut sites in this watershed were at elevations greater than 775m and were located directly downstream from contiguous old-growth forest. Because low elevation sites are harvested first, higher elevation sites are often either surrounded by or downstream from contiguous old-growth forest. The Mamquam clearcut site yielded higher tadpole biomass per unit area and density than the other two unbuffered clearcuts. Uncut forest upstream may mitigate logging impacts by maintaining cool temperatures or low sedimentation rates, and they are potential sources of animals for recolonization. Other researchers have hypothesized that the presence of uncut timber upstream influences the presence of aquatic amphibians in logged areas. *Ascaphus* were most often found in streams of logged stands when uncut timber still remained upstream (Bury and Corn 1988; Corn and Bury 1989), suggesting that tadpoles may benefit from increased within-stream primary productivity following harvest while evading the effects of increased insolation on water temperature.

Tadpole biomass per unit area and density were highest in smaller creeks, and tadpole densities decreased with increasing creek temperatures. Because creek temperatures were not taken at the same time of day or on the same day of the month, measurements are fairly rough which may influence my data. Lack of correlation between water temperature and abundance of tailed frogs (as in Hawkins et al. 1988), may be due to shaded areas upstream acting as sources of tadpoles which moved downstream to warmer water. Beschta et al. (1987) suggest that increased light and stream temperatures play a role in the shift from an aquatic flora dominated by diatoms to one dominated by filamentous green algae. This suggestion may explain some of the patterns seen in these data. The Elaho clearcut creek is small, receives full sunlight and has a high temperature; filamentous algae were detected in this site and biomass per unit area and density of tadpoles were low. The Mamquam clearcut creek is small, receives full sunlight but has a low temperature (old-growth forest upstream); filamentous algae were not detected here and biomass per unit area and density of tadpoles were high. In a study of streams in the Oregon Cascade Mountains, Murphy and Hall (1981) reported a direct relationship between stream width and the amount of chlorophyll *a* found on experimental tiles, with greater chlorophyll accumulation in clearcuts than in the adjacent old-growth sites. They suggested that in larger streams that were naturally more open, the increase in periphyton production was less than in the smaller streams following clearcutting. In my study I ruled out the possibility that lower tadpole biomass per unit area and density in larger creeks were a result of sampling bias because multiple surveyors sampled side by side moving upstream. Also, repeated intensive surveys were conducted in each reach by swapping creek sections between surveyors to reduce surveyor bias and avoid underestimation of tadpole numbers.

Tadpole biomass per unit area and density are low in creeks with higher percent cover of riffles, but this was only apparent in two sites: Squamish old growth and clearcut. This observation may be due to the reduced sampling ability of surveyors in some reaches of these sites. The inability of surveyors to see through the surface water while removing rocks would bias these results. Other possibilities include the increased levels of filamentous algae growing on substrate (as well as an unidentified moss) in the reaches where percent riffle cover was high and shade was low. Both sites receive direct sunlight at a minimum of two of the three creek reaches. Other amphibians have shown to be affected by riffle habitat. Hawkins et al. (1983) found reduced salamander densities in riffles of unshaded versus shaded stream reaches. Dense growths of green algae in unshaded streams may interfere with access to the rock surfaces and thus to the primary food of tailed frog tadpoles. In my study, filamentous algae was only detected in clearcut sites, possibly linked with the recent increase in solar radiation and resulting temperature increase. Moss growing on the substrate in the exposed reaches of the old-growth site would also interfere with tailed frog feeding by reducing surface area where tadpoles can adhere to the rock. The capacity for within-stream primary production should be greater for riffles than for pools (Murphy and Hall 1981).

Both average tadpole mass and snout-vent length were found to increase with increasing percent sand cover. The positive relationship between snout-vent length and sand cover is difficult to explain. Sites with the high percent sand cover were the Squamish old growth and clearcut and the Elaho old growth. Increases in average mass of tadpoles may be a result of ingestion of sand grains. In northern Idaho and southeastern Washington, Metter (1964) found that 30-40% of all gut contents of tailed frog tadpoles examined appeared to be fine sand grains, which was believed to be a result of grazing along rocks.

Relations of Tailed Frog Tadpole Size-Classes with Microhabitat

Tadpoles appear to use microhabitats of pool, run or riffle depending on their body size or stage of development. The majority of tadpoles captured were in runs, which may suggest that microhabitat underlying these swift moving waters with relatively low turbulence provides more suitable habitat for tadpoles. Average lengths and mass of tadpoles were consistently larger from pools to runs and from runs to riffles which suggests that larger tadpoles may find more suitable forage and cover in the faster moving waters. The presence of larger tadpoles in riffles may also be due to the greater capacity for within-stream primary production in riffles as compared with pools (Murphy and Hall 1981). Smaller tadpoles may be unable to utilize these more turbulent microhabitats, and the calmer microhabitats may be more suitable to their needs at this stage of development. Another hypothesis would be that interstitial refugia increase in size with increasing particle size in pools to runs and from runs to riffles (Richardson pers. comm.).

Microhabitat selection may also be related to temperature preferences. DeVlaming and Bury (1970) observed *Ascaphus* tadpoles in laboratory thermal gradient chambers and determined that they exhibited behavioural thermoregulation. This behaviour was evidenced by an avoidance of temperatures above 22°C and a tendency to select within a 10°C range below that temperature. In species of *Rana* tadpoles, Workman and Fisher (1941) found that thermal selection was related to metamorphic stage. The three microhabitats sampled in this study provide potentially three ranges of temperatures for tadpoles to select from, but this requires research. Tadpoles behaviourally seek microhabitats of optimal temperatures and avoid those areas posing thermal extremes. Sections of the creek which receive more shade will possess lower temperatures and are more likely to be selected by younger individuals. DeVlaming and Bury (1970) found that first year tadpoles in particular selected near-freezing temperatures. The placement of pools within the reaches were along the banks and tended to be well-shaded by overhanging vegetation or the bank itself. Larger individuals would select for microhabitats of higher temperatures especially nearing metamorphosis. Warmer areas would be further away from the banks in runs and riffles where direct sunlight will be absorbed throughout the day. Tailed frog tadpoles only metamorphose at the end of the summer (Brown 1990*a*). Tadpoles kept at 5°C did not undergo the expected metamorphosis at the end of the summer (deVlaming and Bury 1970; Brown 1990*b*) which suggests that behavioural thermoregulation is very important to this species.

Forest Practices and Population Dynamics

Creek and site characteristics play a role in the way forest harvest ultimately affects tadpole populations. Because creeks selected were not continuous through old-growth, second-growth and clearcut sites, it is not possible to determine whether the differences in tadpole biomass per unit area and density are due to forest treatment alone. Responses appear strongly modified by creek and site characteristics. Tadpole biomass per unit area and density are lower in disturbed sites than in old-growth or buffered sites. Some factors which may contribute to low biomass per unit area and density within clearcut sites include an increase in water temperature, filamentous algae and higher levels of fine sediment. All are either known or appear to be unfavourable conditions for tailed frog tadpoles.

Following streamside harvest, an increase in incident solar radiation can last anywhere from 5 to 20 years, depending on the length of time it takes for a canopy to develop. Removal of vegetation causes an increase in average daily temperatures and in the range of daily temperatures (Brown and Krygier 1970; Holtby 1988). Annual maximum temperatures can increase by 15° C (Brown and Krygier 1970) which would present an obvious negative impact to tadpoles. On Vancouver Island, temperature increases above prelogging temperatures ranged from 0.7°C in December to 3.2°C in August (Holtby 1988). It has already been established that first year tadpoles of the tailed frog prefer temperatures below 10° C, whereas second year tadpoles prefer temperatures of 10 to 22° C (deVlaming and Bury 1970). The Elaho clearcut creek, with a temperature of 15.6°C, had very low tadpole biomass per unit area and density; filamentous algae was also present there.

Tailed frog tadpoles primarily feed on non-filamentous diatoms, unicellular algae which grow as thin mats over rocks and logs. Filamentous algae present some problems for tailed frog tadpoles, because they are multicellular and grow in long filaments attached to rocks and logs. Filamentous algae are also tough and therefore highly resistant to grazing. Tadpoles are unable to attach themselves to a surface covered with filamentous algae, and therefore cannot avoid being carried downstream by the current. Tadpoles released in creek sections where filamentous algae were present attempted to suction onto surfaces where these algae grew. Without any success, they moved to other rocks which were not covered with these algae (pers. obs.). Diatoms are a major food resource for both marine and freshwater organisms (Round et al. 1990). Tailed frog tadpoles can easily scrape diatoms off the surface of rocks using their rows of teeth.

When gradient is low, the effects of logging can be more serious (e.g., Hawkins et al 1983). In steeper creeks, fine sediments can be flushed out of the system relatively quickly (or flushed in quickly when upstream disturbance exists). The positive effects of a steep gradient are evident in the Squamish watershed. In the mature second-growth creek, gradient was highest among the three treatments; there was no silt present and tadpole densities were the highest of the three treatments. In two clearcut sites (Squamish and Elaho watersheds) where tadpole biomass per unit area and density were low, gradient was low and both silt and filamentous algae were present. Old-growth forest remained upstream from the Mamquam clearcut site which had high tadpole biomass per unit area and density. This site had a steep gradient and no silt was present. In the Mamquam watershed, the second-growth creek had the lowest tadpole biomass per unit area and density of the three treatments and gradient was the lowest of the three treatments.

There were negative effects of fine sediment on tadpoles. Biomass per unit area and density were low in creeks where silt was present and where percent sand cover was high. Silt and sand can clog interstitial spaces which tadpoles use as refuge. Sedimentation may also interfere with feeding by coating the rock surfaces, making suction to the rock surface difficult and increasing ingestion of these fine materials in the process of feeding. Sediment may accumulate in low gradient streams following timber harvest but detrimental effects may be masked at first by the increased autotrophic production due to increased insolation (Murphy and Hall 1981). In clearcut sites, where filamentous algae were present, biomass per unit area and density of tadpoles were lower. Murphy and Hall (1981) found that the amount of sand-gravel and density of crevices in logged sites were strongly correlated with channel gradient, but storage of fine sediment by organic debris in steep channels reduced these correlations for old-growth sites. The effects of forest harvest are strongly modified by creek and site characteristics.

The buffered clearcut creek had the highest tadpole biomass per unit area and density, and may be due to its situation in a deep gully. The gully sidewall (distance from the base of the gully to where it leveled off upslope) was about 35 metres. The forested buffer strip and the embedded nature of the creek may provide the appropriate microclimate (moisture and air temperature) for frogs to breed and feed successfully in and around this creek. Old-growth forest also existed upstream of the buffered patch. This would provide a potential source of new tadpoles if adults were to deposit eggs upstream. Solar radiation was high because the average bank width was wide (7.2m) and few trees grew on the steep gully sidewall. This allowed for high within-stream primary productivity, providing increased forage to tadpoles.

Cohort Analyses

Among the replicated treatments, tadpole biomass per unit area and average mass were highest in old-growth creeks. These observations may suggest that populations are 'well-fed' in these undisturbed creeks, or there may be more overlapping cohorts present in the old-growth sites at the time of sampling. From the analyses of size distribution data using Harding's (1949) approach and Peak Fit (Jandel Scientific 1990), the latter appears to be more likely. Five cohorts were present in the old-growth site, while only four were found in the clearcut site. Tadpoles may spend one year less in clearcut creeks. Most tadpoles captured in the analysed populations were of the 2^{nd} 'year-class' and less than 25% of tadpoles captured were of the 4^{th}- and 5^{th}- 'year-class.'

The buffered clearcut creek yielded four tadpole cohorts which may suggest that disturbance was great enough to create similar conditions as in the unbuffered clearcut creek. Site conditions may cause tadpoles to grow faster in the buffered clearcut. Canopy closure over this creek was minimal, but this level of insolation did not seem to have any effect on water temperature (12.4°C). Although a buffer strip remained around this creek, some responses to forest harvest may be evident. The gradient was only 3°, and low gradient streams are known to have a negative effect on stream-breeding amphibians with similar larval periods as the tailed frog (Corn and Bury 1989; Diller and Wallace 1996). Diller and Wallace (1996) believed high gradient reaches to be important transport areas where finer sediments do not accumulate and gravel and cobble do not become embedded.

There are many methods for estimating number of cohorts present in a population, each subject to difficulties. The only truly accurate method would be to mark individuals and measure them through time. I chose to create cumulative percent frequency distributions and use Harding's (1949) suggested method for analysing polymodal distributions. Peak Fit (Jandel Scientific 1990) was used as a check against Harding's (1949) approach. One extra cohort was teased out, but I believe that this is an over-estimate. Judging from the figure (see Appendix IV), it appears that two highly overlapping 'year-classes' are shown. Harding's (1949) method was very useful as a check against results of cumulative percent frequency distributions of tadpoles. Although, using snout-vent lengths to look for breaks in the data have the obvious downfall in that size does not necessarily relate to age. Plotting of tadpole lengths to determine number of cohorts has been used by some authors (Daugherty and Sheldon 1982*b*; Brown 1990*a*) to determine the age-classes present within the population in their studies. Brown (1990*a*) estimated that tailed frog metamorphosis was achieved in four years in a sub-alpine population of the North Cascade Mountains, northwest Washington. Daugherty and Sheldon (1982*b*) noted three years in their study in Missoula County, Montana. Both studies used total length (snout to tail tip) in their frequency distributions. This measurement would vary a great deal even among same age individuals due to the roughness of the creek environment as well as predation attempts (i.e. loss of tail tips). Other researchers have used snout-vent length to look at frequency distributions (Dupuis and Friele 1995; Kelsey 1995), but the problem of using size is still evident.

Skeletochronological analysis was found to be helpful in estimating ages of frogs captured. It is important to possess the known age of some individuals in other populations for this technique to be reliable, but this is impossible because there are no voucher specimens in museums with this information (Jamie Reaser, pers. comm.). Researchers who have used this technique are generally comfortable with the error involved. Tailed frogs aged through skeletochronological analyses in this study were only between five and eight years old. Due to the difficulty in separating some lines of arrested growth in the bone sections, it is possible that frog ages were underestimated. Another source of error comes from the process of endosteal resorption. In some climates, endosteal resorption of the inner layers of periosteal bone can alter and disrupt the history of resting lines making age estimates inaccurate in reptiles and in some species of amphibians (Rogers and Harvey 1994). Leclair and Castanet (1987) report that this can account for an underestimate of one to three years but that usually not all of the first rest lines are destroyed. Remaining portions of these rest lines can be counted into the age estimate once enough experience is gained in recognizing lines of arrested growth. It is also possible to overestimate the age of frogs because double rest lines can be formed annually, for instance when both drought and cold successively interrupt growth during the annual cycle (Leclair and Castanet 1987). Aging using bone sections requires further investigation for the tailed frog due to the difficulty in separating out the rings. Using known age individuals (raised in the lab or marked and recaptured through time in the field) to compare the various sections would allow for more accurate age assignments. The three treatments sampled for frogs in the Mamquam watershed required differing sampling efforts because visibility varied among them. Visual encounter surveys were not a very effective method for capturing frogs. Pitfall traps with drift fences along creeks and along transects in the upslope forest would likely yield higher sample sizes.

Movement Patterns

The goal of this portion of the study was to record individual movement events by tadpoles within different forest age classes and view any patterns which may be present. The larval stage of amphibians is believed to be relatively sedentary and dedicated to growth, while the more mobile adult stage is dedicated to dispersal

(Wilbur 1980). Creek-dwelling larvae may also serve as dispersers because the current would allow for significant distances to be reached without much effort expended by the individual. Tadpole movements may indicate when the carrying capacity of the reach is met and when conditions become inhospitable. Some tadpole movements may go undetected due to mortality or movement outside of the sampling area during the sampling period.

Very little data was gathered for this portion of the study but these preliminary results are still useful in showing some potential patterns. The very low (3m maximum) movements of tadpoles within clearcut sites may be due to the low creek gradient or to barriers within the creek post-harvest (such as log jams which were present in all clearcuts). The very high (65m maximum) movements within old-growth creeks may be due to their steep creek gradients and fast flow. The distances moved by tadpoles in old-growth sites may also be due to the continuity that these creeks possess, not having undergone any unnatural disturbances. Tadpoles are more free to move to areas with more food or better cover. The steepest gradient was in mature second-growth sites but low movement rate is difficult to explain with the amount of data collected.

Drift may be associated with density, but I found no relation. Movement allows location of new habitats and forage. It also allows escape from predation, especially from stream birds such as dippers (Jenkins and Ormerod 1996). Other risk-sensitive behaviours that would allow tadpoles to escape predation include nocturnal foraging and interstitial distributions during daylight (Jenkins and Ormerod 1996). Drift responses are also thought to be influenced by substratum size (Walton et al. 1977).

Further surveys will provide more data to help explain these vastly different movements within the forest types. If tailed frogs do follow a colonization cycle as stream insects are believed to follow (Müller 1954), it will be useful to know what distance newly metamorphosed frogs need to travel upstream to reach breeding sites.

Chapter 3

Summary

Forestry practices have significant impacts in some conditions, and these need to be considered when managing for the tailed frog and other stream-dwelling species. Tailed frog populations will respond differently to forest harvest depending on the creek and site environment they inhabit. In my data, creek and site characteristics accounted for more than 85% of the variation in tadpole density and biomass per unit area. Effects associated with forest harvesting depended on elevation, creek size, percent sand cover and percent riffle cover. Historical disturbance appeared dominated by creek and site characteristics.

In B.C., small streams are only protected with buffer strips if they directly or indirectly affect commercial fish or their spawning grounds. The Riparian Management Area Guidebook (Ministry of Forests and Ministry of Environment, Lands and Parks 1995) accords some protection to S5 and S6 streams only if they are temperature sensitive (low seasonal flow, wide and shallow channels and minimum shading from the south), because of the effects they may have on downstream fish habitat. Some trees are retained to maintain streambank or channel stability and provide some shade. Falling and yarding occurs away from the stream, and slash and debris that may enter the stream are removed. For the integrity of tailed frog habitat, this protection should be extended to all S5 and S6 streams where tailed frogs are found.

Management must consider long-term effects of forest harvest on the stream ecosystem. Following forest harvest, increased solar radiation raises creek temperatures and causes the less favourable algal populations to flourish. Unbuffered creeks suffer from bank instability, and runoff can fill creeks with fine sediment. The period of time preceding canopy closure can potentially provide more forage for tailed frogs, but once shade is established, this potential benefit is lost and the more negative effects of clearcutting become evident (e.g., increased fine sediments). Harsh winter conditions are likely to exist in disturbed creeks, with much colder temperatures than in old-growth creeks. Tadpoles are believed to aggregate during the winter, but without sufficient interstitial spaces (which can be clogged by fine sediments associated with clearcuts), this may not be an option. Buffering of creeks would mitigate the effects of clearcutting by providing adequate shade to keep filamentous algae from flourishing to such high levels, and would provide protection from extreme temperatures and increased sediment loads. Road building should be planned carefully to minimize sediment input to streams. Where riparian zone protection is not feasible, upstream forest should be left intact as sources of recolonizers for downstream disturbed sites, and to mitigate logging impacts by maintaining cool stream temperatures and reducing sedimentation rates.

Further research is needed in cohort analysis of tailed frogs. Fewer cohorts estimated in disturbed sites is particularly interesting because tadpoles may metamorphose earlier due to greater amounts of diatoms, or particularly vulnerable cohorts may not be surviving through the harsher winter months. Future research should include location of nest sites, development of in-stream enclosures, marking of newly hatched individuals (those with yolk sacs) and long-term monitoring of marked individuals to establish a known age for a few individuals. Measurements taken each year will provide the data necessary to determine the number of cohorts within these populations. Once some individuals are aged, their measurements can then be used to relate other individuals to the known age.

Because of the difficulty in assessing dispersal of tailed frogs, genetic research could prove very useful. Verification of the extent of dispersal among populations through genetic analysis is important because of the difficulty of capturing transformed individuals. Comparing tailed frog populations in various watersheds using DNA analyses would provide valuable information on the extent of diversity in tailed frogs, and may carry important conservation and management implications.

Forest management decisions should consider the importance of small, headwater streams in providing habitat for tailed frogs as well as other wildlife. It is important to ensure the protection of creeks because they provide tailed frogs with breeding sites, overwintering sites, and potential dispersal corridors for gene flow between populations. Further research is needed to address the question of recolonization by tailed frogs if disturbance events cause population decline over the number of years required for natural reforestation. Providing buffer strips around tailed frog creeks and ensuring that forests upstream are left intact will provide the habitat needed for successful breeding and egg deposition upstream.

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Appendices

Appendix I. Site Information: Location of sites selected for tailed frog tadpole creek surveys. SW B.C. 1995

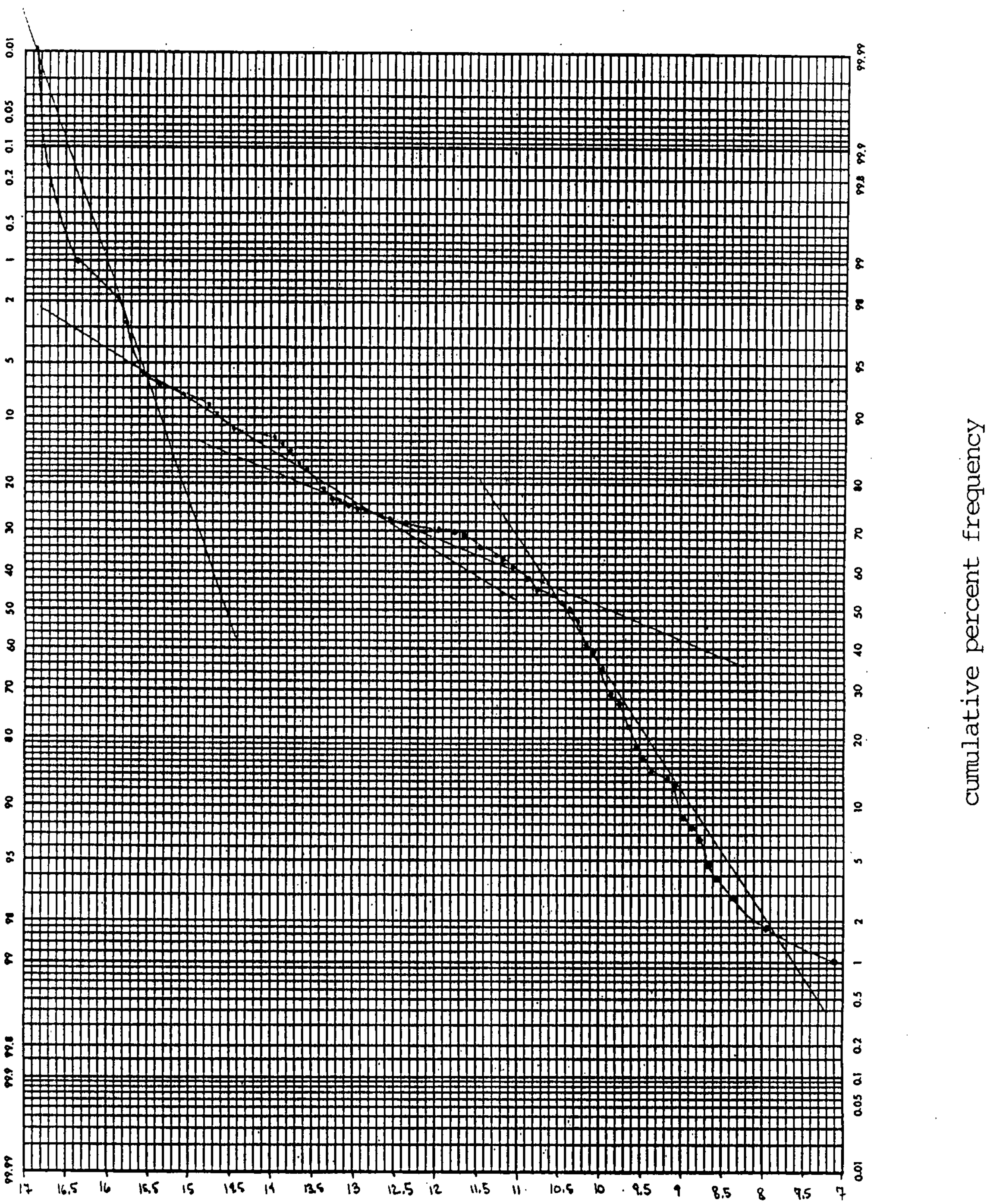
Site	Map Name	Map Number	UTM Zone	Longitude	Latitude
Squamish OG	Camp No. 3	CL3-02-11	10	123^0 23'	50^0 11'
Squamish SG	Garibaldi	92G.075	10	123^0 2'	49^0 44'
Squamish CC	Camp No. 3	CL3-02-11	10	123^0 21'	50^0 12'
Elaho OG	Upper Elaho	CL4-02-18	10	123^0 34'	50^0 20'
Elaho SG	Garibaldi	92G.075	10	123^0 1'	49^0 44'
Elaho CC	Elaho-Sims Junction	CL4-02-14	10	123^0 35'	50^0 17'
Mamquam OG	Mamquam-Raffuse	CL2-09-112	10	122^0 56'	49^0 38'
Mamquam SG	Mamquam-Raffuse	CL2-09-112	10	123° 5'	49° 41'
Mamquam CC	Mamquam-Raffuse	CL2-09-112	10	122^0 55'	49^0 38'
Mamquam BCC	Mamquam-Raffuse	CL2-09-112	10	122^0 55'	49^0 38'

Appendix II. Sampling schedule for tailed frog tadpole creek surveys. SW B.C. 1995

Creek	Sampling	Old-Growth	Second-Growth	Clearcut
Squamish	1	June 28	June 21	June 28
	2	July 17	July 9	July 14
	3	August 13	August 8	August 9
Elaho	1	June 29	June 22	June 29
	2	July 16	July 11	July 15
	3	August 3	August 10	August 9
Mamquam	1	July 6	June 15	June 16
	2	July 22	July 7	July 8
	3	August 4	August 1	August 2
BCC*	1	-	-	July 31
	2	-	-	August 11

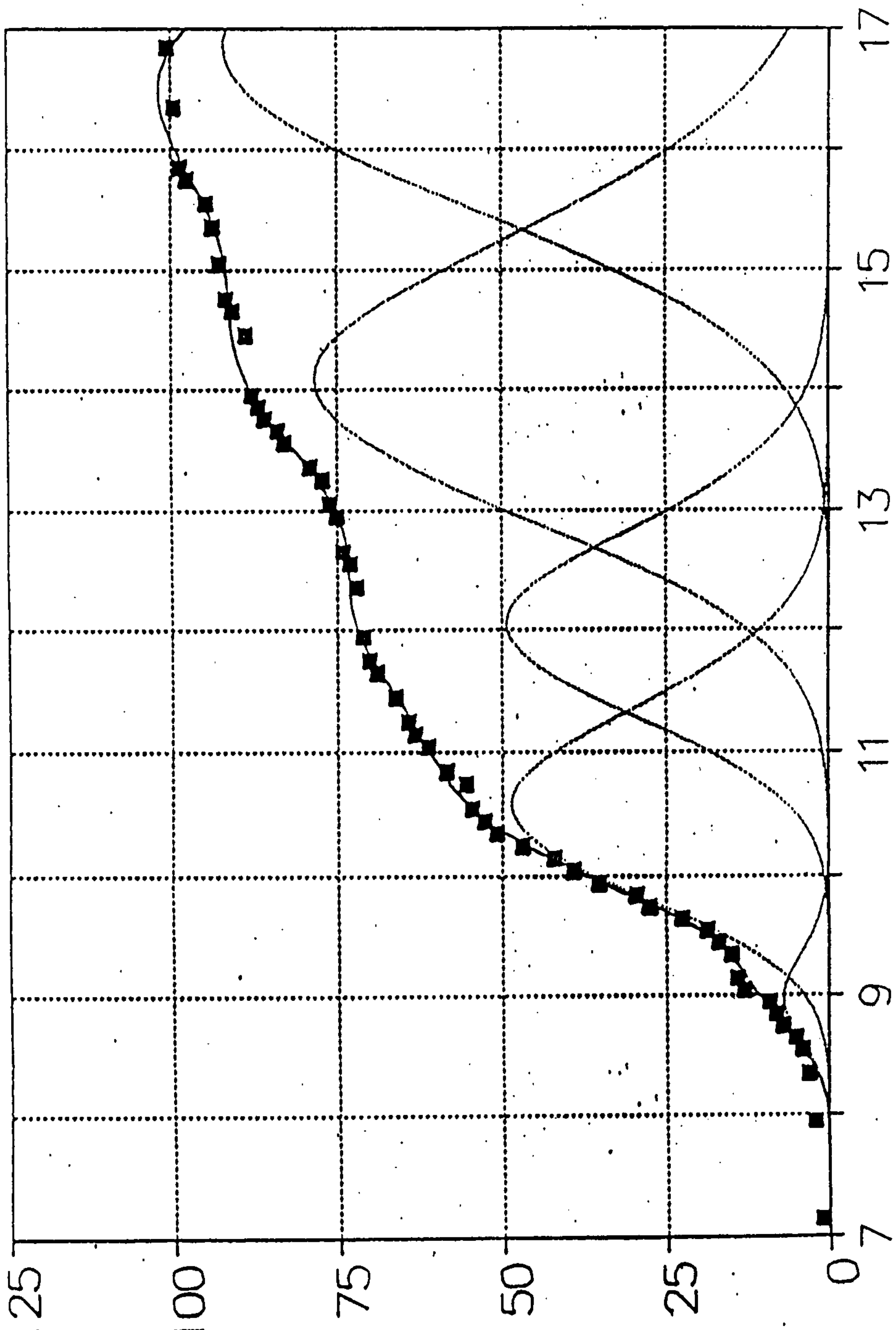
*Buffered Clearcut Creek

Appendix III. Cohort Determination Graph of Mamquam Old-Growth Tailed Frog Tadpoles



snout-vent lengths (mm)

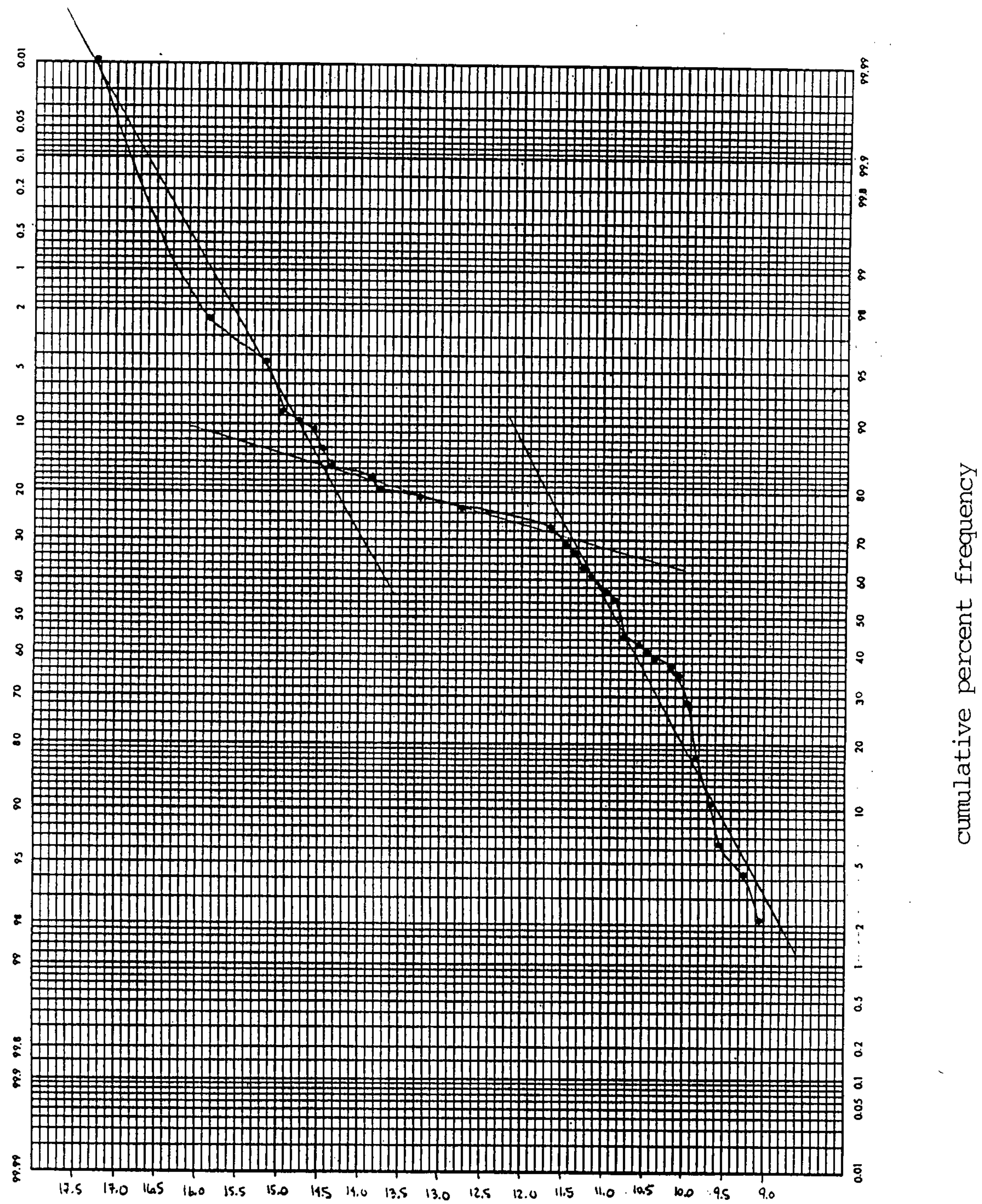
Appendix IV. Peak Fit Graph of Mamquam Old-Growth Tailed Frog Tadpoles



Snout-Vent Lengths (mm)

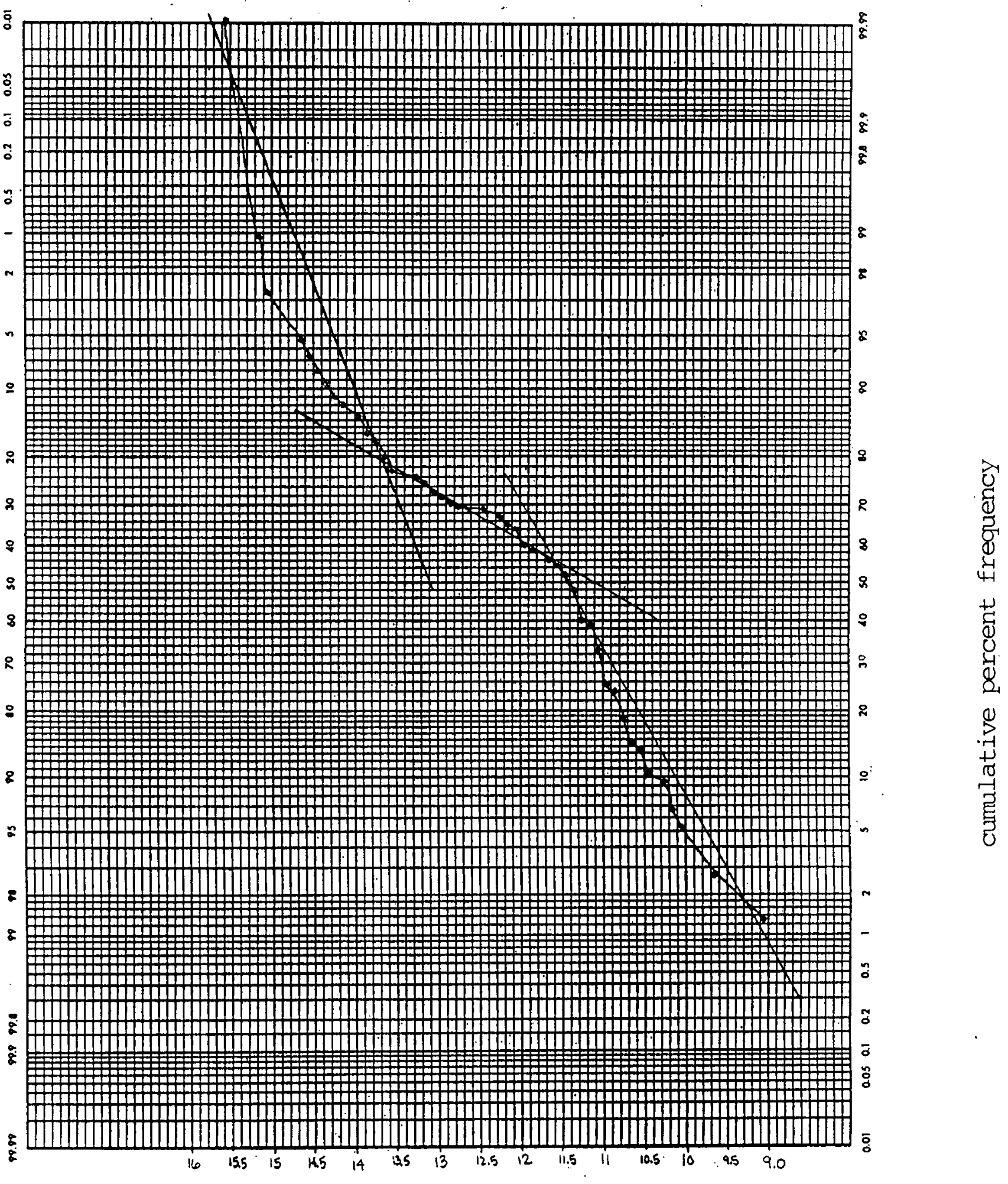
Cumulative Percent Frequencies

Appendix V. Cohort Determination Graph of Mamquam Clearcut Tailed Frog Tadpoles



snout-vent lengths (mm)

Appendix VI. Cohort Determination Graph of Mamquam Buffered Clearcut Tailed Frog Tadpoles



snout-vent lengths (mm)