RISK ASSESSMENT FOR CONSERVATION UNDER ECOLOGICAL
UNCERTAINTY: A CASE STUDY WITH A STREAM-DWELLING
AMPHIBIAN IN MANAGED FORESTS

by

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ABSTRACT

Quantifying risks of forest and habitat management options are often limited by uncertainties in habitat associations, life history and population trends for resident species. Using the tailed frog (*Ascaphus truei*), a headwater stream-dependent amphibian, I: 1) developed hierarchical models of habitat relationships across this species' range in British Columbia; 2) examined plausible life history responses to habitat change, and 3) investigated population persistence outcomes within and among streams to uncertain effects of forest harvesting and disturbance scenarios.

To develop habitat association relationships I used classification and regression trees (CART) together with simple and partial Mantel tests. Variables describing biophysical setting at meso- and micro-scales had a greater influence on occurrence and abundance of larval frogs than adjacent forest practices, possibly because most sampling sites were in disturbed watersheds. Underlying geology was a consistently important determinant of occurrence patterns, with fine-scale stream structure more important in determining abundance.

Using life stage-based population matrix models, I explored consequences of different life history strategies and ranges of habitat productivity and environmental variation on population persistence. Persistence is decreasingly sensitive to changes in growth rates, tadpole and adult survival, and fecundity. Populations also appear more sensitive to changes in survivorship of in-stream stages (eggs, hatchlings and tadpoles) than riparian stages (juveniles/adults). Clinal, elevational, and local reductions in habitat productivity (e.g., shorter growing seasons, reduced light penetration in mid-seral forests) appear as dominant factors mediating how local fluctuations in demographic rates determine risks of loss of small populations, even if environmental variation is relatively low.

Using a spatially explicit metapopulation-landscape dynamics model, I explored six plausible hypotheses linking habitat alterations to population dynamics in response to forest harvesting and disturbances. Risks to populations from disturbance depend strongly on assumptions about age at first reproduction. Incremental effects of forest harvesting on risks were small compared with those already incurred through stochastic events (floods, debris flows, climatic variation) or state of the landscape. Once extirpated, population recovery through dispersal appears unlikely. However, key uncertainties about the impacts of harvesting and
forest succession on demographic rates render evaluation of alternative riparian protection systems difficult with present knowledge.
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ARCHIVE LOCATION OF ORIGINAL DATA

The original field data used in this thesis were collected by several researchers funded under different research grants, and are not reproduced here. However, archives of all the source data I used have been provided to the B.C. Conservation Data Centre (British Columbia Ministry of Environment, Lands, and Parks, Victoria, B.C.). This data may be requested from the Centre by phone: (250) 356-0928, or via their website: http://www.elp.gov.bc.ca/rib/wis/cdc/.
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CHAPTER 1. GENERAL INTRODUCTION

INTRODUCTION

Forest ecosystems are diverse in species, are structurally complex, and provide products of worldwide economic importance. Among terrestrial biomes, diversity of vertebrate species tends to be greater in forested ecosystems than in non-forested ones (Wilson 1988; Bunnell and Kremsater 1990). Forests provide a renewable supply of highly valued wood fibre, and economic returns from timber harvests contribute significantly to regional and national economies. Charged with managing a finite land base to meet economic targets while maintaining ecological functions, forest resource managers often find themselves confronting potential conflicts between desired timber harvests and maintenance of biological diversity (Montgomery 1995; Bunnell et al. 1999a). The costs of not achieving either economic or conservation targets are high: local economies may suffer and species can be lost. Assessing strategies to conserve the range of species in managed ecosystems is an important issue in applied ecology (Franklin 1993; Haight 1995; Boulanger et al. 1999) and has become central to many current forest management problems and debates (Bunnell et al. 1999a).

What are the cumulative effects of forest practices on the structure and function of forest ecosystems? Processes driving forest dynamics cross many scales in space and time, and our ability to predict responses of many components of forest ecosystems to human interventions is limited (Bunnell and Huggard 1999). Some effects of past and current forestry practices on forest structure (e.g., spatial distribution of seral stage classes) may persist for many decades (Wallin et al. 1994; Bunnell et al. 1999b). Other effects are not predictable (e.g., location of lightning strikes leading to stand-modifying fires) or are as yet poorly known (e.g., relationships between survival rates of most forest-dwelling vertebrates and patch sizes of mature stands of trees). Most current methods for conserving species in forests are based on the premise that providing habitat of sufficient quantity and quality will maintain ecological processes of interest including species survival (Franklin 1994). Progress is being made in linking structural elements provided by forests to requirements of a number of vertebrate species (see Bunnell et al. 1999a for a recent review). However, evaluating likely responses of single species or
communities of species to habitat changes is difficult because of the scale-dependent nature of each species' life history (Holling 1992; Hansen et al. 1993; Bunnell and Huggard 1999). More troubling, uncertainties about population sizes and trends, critical gaps in present understanding of how habitat changes are linked with species' demography, and the generally low power of monitoring to detect changes in populations limit interpretation of management options in terms of consequences to species (Thompson 1997; Beissinger and Westphal 1998; Boulanger et al. 1999). Nonetheless, management decisions must be made, and actions taken (Peterman and Peters 1998). Managers thus require practical methods for managing habitat that confront uncertainty in how impacts of forest practices may affect the long-term viability of species over large and diverse areas.

Many research and monitoring studies on the effects of forest management on biodiversity focus primarily upon stand-level measures of habitat (e.g., tree species composition, stand density, percent shrub cover, etc.) and relating these to abundance of study species. From these relationships, researchers develop predictive statistical models of species abundance as univariate or multivariate combinations of these stand-level variables (e.g., Hansen et al. 1995; Bunnell et al. 1999a). This approach is attractive because stand-level data are relatively easy to gather on the ground and map from remote-sensing data. For many species (especially birds, small mammals and some amphibians), indices of abundance can often be obtained from short-term surveys. Disadvantages of this approach include: 1) the imprecision of animal density or other measures of abundance as an indicator of habitat suitability (Van Horne 1983; Conroy and Noon 1996); 2) lack of knowledge about long-term population trends undermining confidence in any long-term predictions; 3) inappropriate extrapolation of findings from a few intensively studied locations to wider geographic scales where different environmental factors constraining populations may apply; 4) the small number of species and taxa for which these relationships have been calculated; and 5) the absence of landscape context information for any but the simplest systems (but see McGarigal and McComb 1995).

Ecological processes governing species' dynamics span a wide range of temporal and spatial scales (Holling 1992). As a consequence, a range of inventory, projection and
assessment methods have evolved to assist in conservation planning problems and to overcome some of the shortcomings of simple habitat suitability models. Representative examples include: 1) "coarse filter" approaches (Hunter 1990) such as gap analysis (Scott et al. 1993) intended to capture whole community types and processes; 2) quantitative comparisons of future pattern and area of habitat types against current conditions (White et al. 1997); 3) spatially-explicit decision support tools combining forest management models with habitat variables or population models (Hansen et al. 1993; Daust and Sutherland 1997; Bunnell et al. 1999); 4) use of fuzzy sets to assist with the difficult problem of defining practical criteria for assessing sustainability (Ducey and Larson 1999); and 5) population viability analysis of selected species of conservation interest where substantial population-level data permit (e.g., Crouse et al. 1987; Lande 1988; Lindenmayer 1995, 1996; Sæther et al. 2000). Through development and application of these approaches, practitioners are increasingly aware that for many decisions that they make, there is simply not enough information to adequately identify outcomes or the probabilities that particular outcomes may occur (Peterman and Peters 1998). Thus decision-makers remain fundamentally unsure of the possible ecological repercussions associated with forest management decisions (Marshall et al. 1998).

In general, uncertainties about life history attributes of species, the environmental factors governing population dynamics, and the difficulty of detecting changes in population trends must be taken into account when evaluating management options (Ludwig et al. 1993; Conroy and Noon 1996; Marshall et al. 1998; Ludwig 1999). In all but a very few well-studied species of conservation interest (e.g., the loggerhead turtle, Crouse et al. 1987; northern Spotted Owl, Lande 1988; the California gnatcatcher; Akçakaya and Atwood 1997), the autecological data and demographic studies necessary to estimate the risks of loss faced by a species if their habitats are altered are unavailable (Boulanger et al. 1999; Ludwig 1999). In most cases, given fundamental uncertainties about the form of many ecological processes and estimation of parameters (process and observation errors respectively; Hilborn and Mangel 1998), our ability to infer probabilities of species viability under present or future conditions is usually severely limited (Marshall et al. 1998).
In this thesis, I examine the problem of evaluating potential risks to a species over a large spatial scale given uncertainties in habitat relationships, demographic structure, and stochastic events and disturbances affecting both habitats and populations. For a particular species of considerable conservation interest, I combine results of habitat association analyses, potential population responses to changes in physical habitat and productivity, and incorporation of spatial effects of disturbances and management actions. Using a stream-dwelling amphibian (the tailed frog, *Ascaphus truei* Stejneger) dependent on headwater stream networks as my model system, I focus on estimating the likelihood of local and large-scale population loss over time given uncertainty. For the purpose of this research, I consider headwater stream systems as composed of one or more streams without tributaries (J.S. Richardson *personal communication*). In this research, I do not explicitly consider other species, although some findings may be transferable to species with similar life histories. One purpose of my work is to assess the contribution of different sources of natural and anthropogenic sources of disturbance in these systems upon measures of long-term persistence of populations. A second purpose is to evaluate how uncertainties in key ecological processes confound the task of assessing risk, and ultimately, design of effective management options. In the next section, I introduce the conceptual foundation for my research. I then describe in more detail the study system I used for analysis. Lastly, I present an outline of my dissertation.

CONCEPTUAL BASIS FOR ANALYSIS

The general context for my research is the problem of how to allocate managed forest lands among competing uses: timber extraction, protection of water quality, protection of habitat, and recreation objectives. Decision makers and the public are concerned not only with foregone economic benefits of additional habitat protection, but also with uncertainty about how wildlife populations respond to habitat protection (Montgomery *et al.* 1994; Haight and Travis 1997). Morgan and Henrion (1990) describe risk as an exposure to a chance of injury or loss, and state that the probabilistic nature of risk necessarily leads to a need to describe and deal with uncertainty. I begin with a general conception of the components of risk, followed by a description of how I chose to apply these concepts to my study system.
A fundamental problem in managing ecological systems is that the eventual "state of nature" resulting from a management action or set of actions is unknown. It is clearly important to consider what all the possible "states of nature" may be in order to evaluate management options. Statistical theory provides a methodological foundation for estimating the likelihoods that different states of nature will arise given our uncertainty about the true state of nature (Berger 1985). Decision theory provides a means by which a decision maker can gain further information about the true state of nature, and act on the basis of this information (Pratt et al. 1995). Although a formal treatment of decision theory is beyond the scope of this thesis, some key ideas that guided my research are briefly presented here.

In general, to understand how risky a set of actions might be for a management system of interest, we need to ask three questions: "what can happen", "how likely are each of those to happen", and "what are the consequences if they do happen" (Kaplan 1997). Expanding on the approach proposed by Kaplan (1997), I define risk $R$ as the complete set (enclosed in { }) of computed answers to this triplet of questions (enclosed in <> below) as:

$$R = \{S_i, P_i(\phi_i), P_i(V_i)\}$$

where:

$S_i = \text{a particular scenario } i \text{ from a set of possible scenarios. Each scenario is composed of a sequence of events (including management actions) and outcomes;}$

$P_i(\phi) = \text{the probability that a particular scenario } i \text{ will occur with a frequency } \phi.$

$P_i(V_i) = \text{the probability of a consequence having a value } V_i \text{ resulting from scenario } i.$

When you have not done experiments to determine what that frequency is, a statistical distribution of probabilities that each scenario can be used to estimate the likelihood that each scenario could occur;

Consequences of outcomes have different values (or utility) depending on context, and on the perceptions of decision makers. Uncertainty about the value attached to a consequence is also represented by a probability distribution.
\[ c = \text{the complete set of all possible triplets.} \]

Because the true state of nature is unknown, we represent our current knowledge about these triplets as hypotheses referring to possible shapes and parameters of the component processes and probability distributions, or as values of state variables such as abundance (Berger 1985; Robb and Peterman 1998). The goal of analysis is to gain information about these hypotheses, through empirical studies and statistical investigation, and to evaluate alternative management actions. This framework thus defines the scope of the ecological risk assessment problem for management situations when an event (or series of events) may occur with some unknown frequency that may cause outcomes we wish to avoid.

Decision-making when some element of risk is involved requires that decision-makers identify the range of potential outcomes for each scenario that is possible, along with an estimate of the probability that each outcome will be achieved. In British Columbia’s forest sector, one decision-making process that embodies many of these elements of scenario exploration, estimation of uncertainty, and evaluation of outcomes is the timber supply review process (e.g., Ministry of Forests 1996). In timber supply reviews, planners assess the expected long-term impact on harvest levels of changes in such factors as land base classifications, silvicultural techniques, or management objectives and policies (Ministry of Forests 1996). Although not usually termed “risk assessment”, the analytical methods employed in a timber supply forecast are intended to account for the effects of uncertainty in any of these factors upon projected long-term timber supply.

For the more specific problem of conservation of species in managed areas, we wish to minimize the chance that one or more species will be lost from a given area. Thus, this chance can be stated as the probability that the species (or set of species) of interest will not persist in the area under consideration over a selected period. Minimizing the probability of species loss is an implicit objective of most guidelines for large-scale land-use management (e.g., Forest Ecosystem Management Assessment Team 1993; Ministry of Forests and Ministry of Environment 1995a), and, more explicitly, the objective of protecting wildlife zones, or setting aside reserves and parks (e.g., Ministry of Forests and Ministry of Environment 1999). Because population dynamics of any
species are uncertain, there is always some chance that the populations in any area of
habitat will go extinct from causes other than anthropogenic factors (Haight 1995).
Applying the framework above, we want to know what ecological factors and events
affect populations (e.g., habitat productivity, disturbance events, interactions with other
species), how the behaviour of these factors and events are changed by management
actions, and what the consequences are of such changes. For completeness, the set of
possible actions under consideration needs to include a "no management" or "default"
action. The "no management" scenario can be used to calculate the background
probability of species loss (Haight 1995). Incremental changes in this probability
resulting from different management activities can be investigated either through field
studies of different management regimes, through simulation studies, or both.

For a given species, estimating \( R \) thus requires a set of linked problems to be
solved:
1. from an array of environmental features and variables, determining which are
   required for each species to persist in an area.
2. developing a relationship between these components of habitat and expected
   responses of populations (e.g., occurrence and abundance);
3. developing relationships between different management actions and their effects
   on these components of habitat and populations;
4. evaluating probabilistic outcomes of alternative management policies expressed in
   terms of the risk \( R \) to the species in the management area of interest.

Even for well-studied species each of these tasks is a substantial research challenge. The
problem of determining the characteristics of habitat necessary for a population to persist
is a central problem in conservation biology. Estimating relationships among the
components of habitat requires knowing which habitat elements are used by each species
to meet their life requisites (e.g., Hansen et al. 1993; Bunnell et al. 1999a), and how their
spatial dispersion affects their availability to individuals (Wiens et al. 1993). Populations
of species are subject to disturbances, and to random fluctuations in numbers. Thus
designing a feasible method to link patterns of habitat types to long-term population
trajectories is also difficult - the dynamics of spatially divided populations (sensu
Merriam 1998) can be highly variable for reasons that are not strongly dependent on
habitat, e.g., demographic or environmental stochasticity, and connectedness among populations. Finally, the time scales over which risks need to be evaluated for vertebrate species are much longer than those over which a typical field study is conducted.

For complex management problems involving comparisons between alternative management policies, uncertainties in estimating the outcomes of each policy, and trade-offs between objectives (often expressed in terms of values, such as net economic value), decision analysis is often applied (Raiffa 1968; Pratt et al. 1995; Peterman and Peters 1998). Although the formal, quantitative aspects of decision analysis may not be applicable in every situation, its conceptual framework assists in breaking a decision problem down into tractable components. In a simple example involving reserve design in managed forests, Conroy and Noon (1996) outlined the following general approach. The set of possible decisions is the operational planning area \( A \) under study, the area of each type of habitat in \( A \) to be conserved \( A_h \), and the area to be harvested \( A_f \). Both \( A_h \) and \( A_f \) are parameters varied by management policy. The decision space is thus composed of different combinations of habitat area available for conservation, and forested area available for harvest. Because the areas of habitat available for conservation and that are required to sustain populations of the species are unknown, there are 2 eventual uncertain outcomes: either the species is eventually lost from the area, or it persists. Estimating the probability that either persistence or loss will occur under different combinations of habitat protection and forest harvesting is a major task in solving the decision problem for conservation. It is this part of the decision analysis framework that I focus upon in this research.

To complete their decision analysis framework, Conroy and Noon (1996) stated that there is likely to be a utility (or valuation of outcomes; Morgan and Henrion 1990) associated with each combination of decision (choice of \( A_h \) and \( A_f \)) and species outcome (eventual persistence or loss). The conservation utility of conserving the species is maximally 1, and is minimally 0 for loss of the species. Economic utility also depends on the cost or effort expended on conservation, proportional to \( A \). For simplicity, this can be specified as 0 when the whole area \( A \) is conserved, and 1 when no area is conserved, and otherwise neglecting any changes in utility related to amount of area managed for timber harvest. Other, more reasonable economic functions might be used to express the
relationship between area conserved and cost, and the different types of habitat (e.g., riparian areas, harvesting of different tree species, slopes, harvesting method, etc.; see Montgomery et al. 1994 for an example). Finally, an overall utility can be defined as the joint utility of the decision-species persistence outcome. Overall utility is 0 when either no individuals persist, or all available land $A$ is used in the conserved areas, implicitly creating a trade-off between costs (resources foregone), and benefits (persistence probability). While overall utility is unarguably subjective in many cases, certain outcomes (e.g., the total loss of the target species over a large area) is unequivocally the worst possible, and at the other extreme the persistence of all populations with no economic tradeoffs are the best. Expected overall utility is a function of $A_h$, and $A_f$, and the optimal decision is to select $A_h$ and $A_f$ such that overall utility is maximized. Because of the substantial uncertainties in calculating species persistence outcomes in my case study, I do not attempt explicit calculation of optimal decisions.

A formal decision analysis framework such as shown above is challenging to apply to actual forest management areas because of its quantitative requirement that probabilities of outcomes on species be estimated (see also Haigh 1995 for a similar example; Peterman and Peters 1998 for briefly developed examples related to silviculture and design of adaptive management experiments). Other approaches, such as the species-habitat and species-area projection approach (White et al. 1997), or a fuzzy set approach for evaluating sustainability of management actions (Ducey and Larsen 1999), do accomplish the task of placing management objectives and biodiversity outcomes in an evaluation framework. Although these methods include the effects of uncertainty in the evaluation criteria, they are less specific about just how ecological uncertainties about effects of management on habitat elements confound or limit interpretation of results. For this reason, I retained the framework of decision analysis developed by Conroy and Noon (1996) as described above as a conceptual guide to my research. Ultimately, effective and general methods for assessing risks of management activities on biota will likely combine tools for making both quantitative and qualitative predictions (see Ducey and Larson 1999; Walters and Korman 1999).
Selection of Case Study System

A major challenge in ecosystem diagnosis is to identify early warning signs of detrimental changes in ecological processes (Rapport and Regier 1995). Odum (1992) suggested that early signs of stress in ecosystems usually occur at the population level, affecting species with narrow ecological tolerances. If such species respond predictably to the major sources of environmental variation in an ecosystem, abnormal fluctuations may suggest ecosystem dysfunction (Welsh and Ollivier 1998). Although focus on ecologically sensitive species is subject to many pitfalls, monitoring such species has the advantage of shortening the relatively slow response time of the whole ecosystem to stress by shifting attention to much quicker response time of sensitive species (Rapport 1992).

Some species of amphibians are widely thought to be sensitive to perturbations in both terrestrial and aquatic environments because of their biphasic life histories, and specific microhabitat requirements (Bury 1988; Blaustein et al. 1994). In the majority of amphibian species, larval stages are aquatic and subject to different selective pressures than the more terrestrial reproductive stages (Duellman and Trueb 1994). Many stream-dwelling amphibian larvae are highly specialized in their uses of lotic microhabitats for both foraging and cover (Welsh and Ollivier 1998). In these stages, they may be susceptible to even minor environmental fluctuations that alter their ability to seek cover from predators, and to forage for epiphyton, phytoplankton, zooplankton, and invertebrates. Even small amphibians can be relatively long-lived (up to 55 years in some species of salamanders; Hairston 1987). Finally, amphibians are often quite philopatric compared with most fishes or other vertebrates. This combination of attributes renders amphibians susceptible to both short-term and cumulative effects of environmental changes in ecosystems and makes them potentially useful indicators of ecosystem dysfunction.

Montane forests at higher elevations are of considerable management interest because of their present and future economic value, public concerns about water quality, aesthetics, and their value as habitat for forest and riparian-dependent species (Vyse 1997; Bunnell et al. 1999a). Yet fundamental ecological processes in these areas, such as rates of forest regeneration, disturbance dynamics, and hydrology are less well known.
than those in lower elevation sites (Huggard et al. 1999; Church in press). Of most relevance to my study species, montane headwater streams may display different responses to effects of forestry when compared with larger streams (Bunnell et al. 1999a). For example, smaller streams are more quickly shaded as riparian vegetation regenerates than are larger streams (Corn and Bury 1989). Yet other effects (e.g., sedimentation, recruitment of downed wood into streambeds) may have greater and longer-lasting impacts on headwater streams than on larger streams due to their small size and steep gradients (Church in press). We do not yet know how resilient these systems are to large-scale forest management or to the variety of silvicultural systems that may be applied in them. This uncertainty is increasingly motivating research and monitoring efforts in these ecosystems.

As a case study system for exploration of the risk assessment framework, I chose the tailed frog (Ascaphus truei) and its montane headwater streams and associated riparian habitat. Five reasons make this a suitable system for this study: 1) tailed frogs are designated “vulnerable” in British Columbia (Ministry of Forests and Ministry of Environment 1999) and “sensitive” in Oregon (see review in Bunnell et al. 1997); 2) available data on the long-term effects of forest practices on this species are contradictory, suggesting that broader scale phenomena may be acting (compare Metter 1964 or Bury 1968, with Bull and Carter 1996 or Wahbe 1996); 3) generalized conservation measures, such as buffers around headwater streams, could have enormous impact on annual allowable cuts in B.C. forests; 4) the species richness in riparian areas of small streams is usually higher than upslope areas (Bunnell and Dupuis 1995; but see McGarigal and McComb 1992 for birds), hence other species could benefit from protection of tailed frog habitat; and 5) given the number of studies on the tailed frog, it is worthwhile developing an approach that permits analysis of geographically scattered data (e.g., Bunnell and Huggard 1999) and their evaluation in terms of long-term persistence in ecosystems of conservation interest.

General Life History of the Tailed Frog (Ascaphus truei)

Tailed frogs are considered sensitive to habitat alteration because of their fundamental life history characteristics, and specialized characteristics of their habitats.
The species has a long in-stream larval period, ranging from 1-4 years in some locales (Metter 1967; Daugherty and Sheldon 1982; Brown 1990; Kelsey 1995; Wallace and Diller 1998; Bury and Adams 1999). In general they have a small clutch size (30-70 eggs; Leonard et al. 1993). In high elevation montane sites they may have a biennial reproduction (Rocky Mountains; Metter 1967), while in others, reproduction may be annual. Current evidence indicates that adults are strongly philopatric (Daugherty and Sheldon 1982), and movement potential appears to be low, as determined from both local-scale behavioural studies (Bury and Corn 1988; Wahbe and Bunnell in press) and broader-scale genetic analysis (Ritland et al. 2000). In one study, tadpoles were more abundant in lower stream reaches, and metamorphs more likely found in the small headwater areas of stream networks (Hunter 1998). It is not known with certainty whether reproductive adults are also concentrated in the headwater areas.

Adult tailed frogs are most abundant in streams flowing through cool, moist forests (Metter and Pauken 1969). Laboratory studies show that tailed frogs cannot tolerate temperatures above 18 to 24° C depending on life stage (Brown 1975, Claussen 1973a). Breeding occurs in the fall and proceeds by internal fertilization. Sperm is stored by the female until the following June or July when she deposits the eggs in cracks and crevasses in stream substrate. Hatchlings emerge in late August through October. Metamorphic juveniles and adults are seldom found far from streams (Daugherty and Sheldon 1982; Nussbaum et al. 1983), although they have occasionally been caught in large numbers in upslope pit traps in conifer forests (Bury and Corn 1988). Pitfall trap records from the coast ranges of Oregon found adult tailed frogs as far as 400 m from the nearest stream (McComb et al. 1993). Adults appear to be less tolerant of dessication than many other frogs (Claussen 1973b), and removal of forest cover may hinder their movements. Although there may be links between removal of overstory cover and reduced movements by juveniles or adults, field evidence has yet to support this expectation (Matsuda and Richardson in press).

OVERVIEW OF THESIS

In this chapter, I have introduced both the problem of assessing consequences of alternative management policies on populations and the framework I will be considering.
in subsequent chapters using the headwater stream – tailed frog system as my case study. In Chapter 2, I focus on developing associations between key habitat variables and current patterns of distribution and abundance of tailed frogs in British Columbia. To apply this approach, I combine data from several field studies and evaluate relationships within and among biophysical variables on response variables representing current status indicators for tailed frogs.

In Chapter 3, I explore the issues involved in the estimation of long-term population loss under conditions of substantial uncertainty in demographic parameters, habitat characteristics, and stochastic environmental and disturbance effects. I ask “what key interactions between life history attributes and demographic and environmental uncertainties may distinguish future probabilities of species persistence at the local scale”. I use sensitivity analysis of a population matrix model to examine the influence of plausible life history scenarios on likely responses of populations to disturbance and environmental variation.

In practice, management of species and evaluation of habitat protection options requires examining outcomes over a large spatial scale. In Chapter 4, I use a stochastic, spatially explicit model to explore a set of non-exclusive hypotheses linking impacts of management to population demography in riparian zones of the stream network in a medium-sized montane landscape (over 65,000 ha). I ask how important could interacting effects of disturbance, forest management and species’ movement capability be in limiting our ability to predict consequences of landscape change on long-term species’ viability.

In the final chapter, I synthesize the components of my thesis and apply them to my principal objective of evaluating ecological uncertainties on the potential risks to conservation of vulnerable species. I discuss the utility of the risk assessment framework in the broader context of decision analysis for habitat management. I use key results from previous chapters to assess conservation of tailed frogs and similar stream- and forest-dwelling species, including their implications for habitat protection options.
CHAPTER 2. PATTERNS OF DISTRIBUTION AND ABUNDANCE IN RELATION TO BROAD AND FINE-SCALE BIOPHYSICAL FACTORS: THE TAILED FROG (*ASCAPHUS TRUEI*) IN BRITISH COLUMBIA

INTRODUCTION

A major contributing factor to long-term likelihood of species extirpation from ecosystems is habitat loss (Mace and Lande 1991; Robinson *et al.* 1992; Fahrig 1997). For species that depend upon attributes of forests altered by harvesting, forestry practices may increase the vulnerability of their populations to declines. Identifying likely impacts of alternative forest management scenarios on populations, species, and communities remains a key research challenge in applied ecology (Hansen *et al.* 1993; Bunnell and Huggard 1999). Individual species operate over a characteristic range of spatial and temporal scales (Wiens 1976; Levin 1992; Holling 1992) and the habitat elements that may explain much of the variation in species' abundance may differ among scales (Hansen *et al.* 1993; Bunnell and Huggard 1999). Animal-habitat relationships must therefore be measured and interpreted over a range of spatial and temporal scales (Verner *et al.* 1986; Pulliam *et al.* 1992).

In this chapter, I examine characteristics of habitat factors associated with distribution and abundance patterns for the tailed frog, a species considered at risk from forest management practices in British Columbia. I address three problems. First, I examine the association of this species with environmental variables at the micro (local stream reach), meso (stand – watershed), and macro (landscape) scales based on geographically extensive inventory data. Second, I develop empirical, species-habitat classification models using Classification and Regression Tree (CART) analysis to identify biophysical and disturbance factors correlated with distribution and abundance patterns of the species in British Columbia. Third, I examine the effects of spatial dependence of ecological variables to help interpret model structure and assess sources of unknown variation on populations. From these analyses, I identify the range of habitat attributes permitting presence of the species across a geographically extensive area, reveal potential differences in habitat relationships within the species range, and identify site conditions where conservation measures may be most effective for this species. From the results, I infer constraints and opportunities for management actions that may
promote long-term persistence of this and similar stream-dwelling species in managed watersheds.

METHODS

General Sampling Design

This research on the relationships between broad- and fine-scale biophysical factors and present distribution and abundance of tailed frogs is part of a larger study of the status and distribution of tailed frogs in British Columbia (e.g., Dupuis et al. 2000; Ritland et al. 2000). The sampling design was intended to provide both information on the genetic and population status of the species throughout its range in the province, and a description of biophysical features of streams relevant to assessment of effects of forest management on conservation of the species.

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 searches (TCS) of headwaters and higher-order streams 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 between July and September each year. All ecossections in the Coast and Mountains Ecoprovince were sampled. Additional survey data were 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 B.C. More intensive surveys based on area-constrained searches (ACS) of streams with different logging histories were conducted in 1994 (Dupuis and Steventon 1999) and 1995 (Dupuis and Friele 1996) near the northern limit of the tailed frog range in British Columbia (the Kitimat and Nass Ranges Ecossections; n = 118 sites), and in 1995-97 in the more southerly East and South Pacific Ranges (n = 14 sites).
Data Collection

For the broad scale survey, access to sites was usually by road, restricting almost all samples to sub-basins (areas containing stream networks up to third-order or larger) with some previous harvesting history. Sites in candidate sub-basins were selected at random with respect to site criteria. Only one sample was taken per stream, although several streams may have been selected within a given sub-basin. Stream sampling usually began at least 10-m or more upstream from the road. Time constrained searches for tadpoles and adults were conducted for 10 minutes by 2 surveyors (total: 20 person-minutes), and recorded as relative abundance.

For the intensive surveys, candidate sample sites were selected in each of three forest harvest treatments: uncut forest; clearcuts (0-10 years) with unbuffered riparian zones; and clearcuts (0-10 years) with 5-60 m forested buffers. The density of tadpoles and adults within a stream was estimated by counting all the individuals found within a given stream length (three randomly selected 5-m reaches in 1994; one 10-m reach in 1995). 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 and proceeded in 1-m increments, using aquarium nets (of 0.05 or 1-mm mesh) to catch dislodged animals. Searches terminated with a final visual sweep of the surveyed area.

Site-specific habitat features of streams were characterized by aspect, elevation (m), water temperature (°C), reach gradient (%), wetted and bankfull widths (m), and substrate composition (Bury and Corn 1991; Welsh and Ollivier 1998). Substrate cover was classified by visual estimate as sand (< 2 mm), pebbles (2-64 mm), cobbles (64-256 mm), and boulders (> 256 mm) in accordance with the Udden-Wentworth size classification (Pettijohn et al. 1972). For each sampled stream, an average percent cover of each class was calculated. In analysis, fines were considered as sand combined with pebbles. Ages of the adjacent forest stand were obtained from forest cover maps and classed as 0-10 years, 10-20 years, 20-60 years; 60-100 years, and > 100 years. Presence
of riparian vegetation and descriptors of stream bank stability were recorded for a few sites.

Synoptic topographic, geologic, climatic, and anthropogenic attributes may describe broad-scale states that influence stream productivity and disturbance regimes. Average stream gradient was determined from the stream or gully headwall (defined as the steep slope at the head of the gully) to the sample sites from 1:50,000 topographic maps. Dominant parent lithology types were determined from Geological Survey of Canada maps. I extracted several climatic variables from the B.C. Ministry of Forests' climate database representing 30-year average values (1951-1980; Reynolds 1997): mean precipitation (annual and summer in mm), and mean temperature (annual, summer and temperature of the warmest month in °C where summer is defined as the May-September period). The temperature data were interpolated using the elevation correction method of Running et al. (1987). Precipitation data were averaged for each biogeoclimatic subzone (Meidinger and Pojar 1991) in the dataset of streams sampled, but not further extrapolated to account for complex orographic effects. Several anthropogenic variables were used to characterize potential impacts of harvesting at the watershed scale (i.e. low-order (0-3) streams). Extent of impacts of recent forest harvesting and disturbance was characterized by: % of watershed area logged or burned within the last 20 years, % of watershed area logged on slopes exceeding 50% slopes, and road density (km/ha). Potential for sediment production from harvesting or road-related surface soil erosion was characterized by road density within 100 m of streams, and a peak-flow index (PFI) based on the elevation-weighted area harvested relationship: PFI = (area logged < 300m) + (area logged > 300 m and < 800 m * 1.5)+ (area logged > 800 m) (Ministry of Environment, Lands and Parks 1998). Road and stream data were obtained from B.C. provincial 1:20,000 TRIM base maps derived from 1987-1988 aerial photography, limiting accuracy and resolution of watershed-scale statistics. In particular, roads built since 1988 and streams < 200 m long are not included in this database.

To assess whether different environmental relationships were acting in different portions of the tailed frog range, I divided sites into regional subsets reflecting influences of coastal and inland climates (Coast Mountain Range and Kootenay Mountains of southeastern BC), and created separate subsets of these for each response variable.
Before analysis, sites with missing or questionable data for two or more of the environmental variables were removed from the datasets. Sample sizes for each of the 5 datasets used in subsequent analysis were: occurrence (Coast n = 180 sites; Kootenays n = 113 sites); relative abundance (Coast n = 31 sites; Kootenays n = 27 sites), and density (Coast: n = 92 sites). Although ACS were conducted in the Kootenays in 1998, too few (6) streams sampled contained tadpoles to use these results in the habitat association analysis.

**Data Analysis**

To evaluate the relationships between habitat characteristics and response variables (presence/absence, density and/or relative abundance), I employed the following methods. First I examined normal quantile-quantile plots of all ecological (predictor) variables to test for departures from normality. I used a \( \log_{10}(x+1) \) transformation for non-normal variables before proceeding to further analysis. Variables with a large number of zero values were retained even though transformations did not necessarily normalize their distributions. To reduce redundancies among closely related predictor variables, I used correlation analysis to select one variable from highly correlated pairs \( (r > 0.75) \). I retained the variable with the highest overall correlation to the response variables. A summary of all habitat and tailed frog response variables used in subsequent analyses, and their ranges of values, are shown in Tables 2.1a and b.

I expected spatial dependence in the values of many of the environmental variables chosen in this study for the following reasons: 1) many climatic and geologic phenomena (e.g., weather patterns, rainfall, bedrock composition) extend over space to occupy regions rather than single point locations (Hinch *et al.* 1994); 2) many survey sites were clustered in the same or nearby watersheds, thus some variable values were the same amongst these sites; 3) nearby sampling sites are more likely influenced by similar abiotic conditions than sites far from one another, and may share similar characteristics (Legendre and Fortin 1989). As an initial step in assessing among-site spatial dependence in my data, I examined plots of lag correlation-coefficient values vs. Euclidean distance (correlograms) for each retained environmental variable measured at each sampling site. Correlograms express spatial covariance (the average product of the
Table 2.1. Definitions and description\(^1\) of the ecological variables used in analysis of the 1992-1998 tailed frog survey data for British Columbia. Sample sizes (\(n\)) indicate the total number of sites for which each variable was measured. Spatial extent of detectable autocorrelation between sample values is estimated by correlogram analysis (see text). Minimum and maximum values for each measurement indicate the total ranges of measured values; numbers in brackets show minima and maxima for sites with tailed frogs present. Box plots, calculated from untransformed data, indicate mean (thick vertical line), median (thin vertical line), quartiles, error bars, and outlying values of the sampled distributions standardized to their respective ranges.

a) Ecological variables

<table>
<thead>
<tr>
<th>Type of variable</th>
<th>Variable</th>
<th>(n)</th>
<th>Distance (km) of detectable autocorrelation</th>
<th>Minimum value</th>
<th>Distribution of measurements</th>
<th>Maximum value</th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td><strong>Macro scale (landscape)</strong></td>
<td>mean annual precipitation (mm)</td>
<td>835</td>
<td>200.0</td>
<td>358.9 (378.1)</td>
<td></td>
<td>3083.5 (2823.8)</td>
</tr>
<tr>
<td></td>
<td>mean summer precipitation (mm)</td>
<td>835</td>
<td>57.7</td>
<td>149.2 (149.2)</td>
<td></td>
<td>838.3 (803.7)</td>
</tr>
<tr>
<td></td>
<td>mean annual air temperature ((^\circ)C)</td>
<td>835</td>
<td>174</td>
<td>-3.2 (0.3)</td>
<td></td>
<td>9.8 (9.8)</td>
</tr>
<tr>
<td></td>
<td>mean temperature warmest month ((^\circ)C)</td>
<td>835</td>
<td>77.0</td>
<td>6.9 (9.2)</td>
<td></td>
<td>20.4 (20.4)</td>
</tr>
<tr>
<td><strong>Geologic</strong></td>
<td>parent lithology type</td>
<td>847</td>
<td>39.2</td>
<td>1 (1)</td>
<td></td>
<td>17 (17)</td>
</tr>
<tr>
<td><strong>Meso scale (watershed - stand)</strong></td>
<td>elevation (m)</td>
<td>686</td>
<td>111.0</td>
<td>0 (10)</td>
<td></td>
<td>1905 (1905)</td>
</tr>
<tr>
<td></td>
<td>aspect (degrees)</td>
<td>578</td>
<td>19.1</td>
<td>0 (0)</td>
<td></td>
<td>360 (340)</td>
</tr>
<tr>
<td></td>
<td>stream gradient (%)</td>
<td>631</td>
<td>98.0</td>
<td>0 (2.4)</td>
<td></td>
<td>107 (93)</td>
</tr>
<tr>
<td><strong>Watershed</strong></td>
<td>% area logged or burned since 1978</td>
<td>796</td>
<td>86.7</td>
<td>0 (0)</td>
<td></td>
<td>47.7 (47.7)</td>
</tr>
<tr>
<td><strong>disturbance</strong></td>
<td>% of stream lengths logged</td>
<td>557</td>
<td>28.9</td>
<td>0 (0)</td>
<td></td>
<td>51.6 (51.6)</td>
</tr>
<tr>
<td></td>
<td>density of roads within 100 m of streams (km/km(^2))</td>
<td>557</td>
<td>3.6</td>
<td>0 (0)</td>
<td></td>
<td>354 (354)</td>
</tr>
<tr>
<td></td>
<td>peak flow index (PFI)</td>
<td>696</td>
<td>&lt; 1</td>
<td>0 (0)</td>
<td></td>
<td>61.2 (61.2)</td>
</tr>
<tr>
<td><strong>Forest</strong></td>
<td>age class of adjacent forest stand(^2)</td>
<td>431</td>
<td>3.5</td>
<td>1 (1)</td>
<td></td>
<td>5 (5)</td>
</tr>
<tr>
<td>Type of variable</td>
<td>Variable</td>
<td>n</td>
<td>Distance (km) of detectable autocorrelation</td>
<td>Minimum value</td>
<td>Distribution of measurements</td>
<td>Maximum value</td>
</tr>
<tr>
<td>------------------</td>
<td>----------</td>
<td>----</td>
<td>---------------------------------------------</td>
<td>---------------</td>
<td>------------------------------</td>
<td>---------------</td>
</tr>
<tr>
<td>riparian buffer status&lt;sup&gt;3&lt;/sup&gt;</td>
<td>463</td>
<td>&lt; 1</td>
<td>0 (0)</td>
<td></td>
<td></td>
<td>1 (1)</td>
</tr>
<tr>
<td>Micro scale (site)</td>
<td>Stream characteristics</td>
<td>reach slope (%)</td>
<td>594</td>
<td>28.9</td>
<td>0 (3)</td>
<td></td>
</tr>
<tr>
<td>mean wetted width (m)</td>
<td>610</td>
<td>14.6</td>
<td>0 (0)</td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>mean bank width (m)</td>
<td>585</td>
<td>15.0</td>
<td>0 (0.9)</td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>water temperature (°C)</td>
<td>556</td>
<td>57.7</td>
<td>4 (5.5)</td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>detritus index&lt;sup&gt;4&lt;/sup&gt;</td>
<td>531</td>
<td>4.5</td>
<td>1 (1)</td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>% cover of boulders (&gt; 256 mm)</td>
<td>504</td>
<td>15.5</td>
<td>0 (0)</td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>% cover of cobbles (64-256 mm)</td>
<td>581</td>
<td>24.0</td>
<td>0 (2.5)</td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>% cover of fines (&lt; 64 mm)</td>
<td>530</td>
<td>9.7</td>
<td>0 (0)</td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Spatial</td>
<td>UTM coordinate (NAD 83)&lt;sup&gt;5&lt;/sup&gt;</td>
<td>837</td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
</tbody>
</table>

<sup>1</sup> Spatial scales are presented in descending order from coarse to fine resolution (see Wiens 1989).

<sup>2</sup> Age classes defined as 1=0-10 years; 2=11-20 years; 3= 21-60 years 4=60-100 years; 5 = >100 years

<sup>3</sup> 1= stream buffer present; 2= stream buffer not present.

<sup>4</sup> index classes are 1 = nil; 2 = low; 3 = medium; 4 = high.

<sup>5</sup> converted to Albers Equal Area Conic projection.
### b) Tailed frog response variables

<table>
<thead>
<tr>
<th>Variable</th>
<th>$n$</th>
<th>Distance (km) of detectable autocorrelation</th>
<th>Minimum value</th>
<th>Distribution of measurements</th>
<th>Maximum value</th>
</tr>
</thead>
<tbody>
<tr>
<td>Presence/absence</td>
<td>835</td>
<td>99.5</td>
<td>0</td>
<td>-</td>
<td>1</td>
</tr>
<tr>
<td>Density (#/m$^3$)$^1$</td>
<td>95</td>
<td>44.5</td>
<td>0</td>
<td>-</td>
<td>9.8</td>
</tr>
<tr>
<td>Relative abundance(#/20 min)$^1$</td>
<td>80</td>
<td>&lt;1.0</td>
<td>0</td>
<td>-</td>
<td>56</td>
</tr>
</tbody>
</table>

$^1$ Density and relative abundance measures are presented only for sites where tailed frogs were positively detected.
difference between values of each variable and their respective overall means as a function of distance) standardized to the range -1 and 1. I computed correlograms for each environmental variable by dividing the distances between all sampled sites into 10 km distance categories, finding the covariance between pairs of sites whose distance falls into that category, and then dividing by the overall variance (Rossi et al. 1992).

By inspection, most correlograms showed values greater than 0.2 at short distance intervals, and values ranging from –0.2 to 0.2 at longer intervals. Thus I used the value 0.2 as the threshold of detectable spatial autocorrelations. I also examined the bivariate correlations between response variables and each predictor variable for all sampled sites treated independently; and for all sites clustered within the same sub-basin pooled together. Further analyses designed to help interpret the influence of spatial dependence on results, and reduce the risk of spurious correlations, are described below.

**Habitat Analysis and Modelling Using CART**

I chose CART methods over generalized linear models (such as logistic regression) to develop my habitat association models because of the following advantages offered by CART methods (see Verbyla 1987). They are easier to interpret 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 or categorical habitat predictor variables into mutually exclusive 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 top node of the tree contains the entire sample. The classification algorithm for recursive splitting assumes the response variable follows a multinomial distribution (of 2 or more categories). 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. In this analysis the goodness-of-split criterion was least squares deviation from the mean value. The output tree diagram represents a nested set of ecological dependencies among habitat factors, exposing how key environmental variables can act to constrain the ranges of other variables, given the observed species response. By treating the pathway through the tree nodes from the initial node to the terminal node for each site as a set of site classification rules, one can infer how different environmental factors may combine to determine observed patterns in the response variable of interest.

First, I developed initial classification trees using CART for each response variable and dataset by recursively splitting each node until either the proportion of the deviance remaining for sample sites in the node was less than 5% of the original deviance, or there were fewer than 5 sample sites left in the node. For these trees, I used only sites with no missing data for all predictor variables. Next, I “pruned back” each initial tree using a 10-fold cross-validation analysis (see Clark and Pregibon, 1992). That process iteratively removes random subsets of 10% of the original observations, and uses the remaining observations (90%) to refit the classification tree, allowing the analyst to select the number of nodes that provides a parsimonious description of the data. For these data, repeated plotting of the cross-validated deviance against tree size showed fairly flat minima across the range of 8-11 nodes. I therefore restricted the maximum tree size to 10 nodes.

Assessing Effects of Spatial Autocorrelation

Broad-scale variability due to climatic, geologic, and cumulative effects of disturbance, known spatial dependence among sampling sites for some variables, and observed positive autocorrelations in many variable values across sites (Table 2.1a and b), all required that I assess the influence of spatial patterns between variables and sites to help interpret model structure. Accounting for the effects of spatial autocorrelation in irregularly spaced data such as this is not a simple problem. In spatially distributed data, correlations between variables may be related to the spatial position of sampling points. Two general approaches are: a) attempt to remove the spatial dependency among observations by filtering it out using “prewhitening” transformations, trend-surface...
analysis, or partial regression methods; or b) leave the autocorrelation structure intact, and take it into account in inference through additional spatial analysis (see Legendre 1993 for discussion). The first approach requires some a priori model of how ecological gradients are spatially autocorrelated, and the scale at which these gradients may be influencing patterns in nature. Because in my analysis an appropriate spatial model is not known, I chose to follow the second approach using Mantel tests.

Mantel tests quantify the degree of concordance between two matrices of data values (Legendre and Fortin 1989). They can be used with ordinal, interval, and ratio data, even in mixtures (Legendre and Fortin 1989). Applied to the problem of examining how ecological relationships may be influenced by the spatial structure among sampling sites, they can be used with the following approach. The spatial relationship between sampling sites is represented by a matrix of geographic (Euclidean) distances among all pairs of sampled localities. In a simple Mantel test to examine the degree of association between geographical distances among n sampling points and values of ecological variables at each point, the products of corresponding elements of the n by n matrix of geographical distances and a matrix of differences between the value of the ecological variable (or variables) measured at each point (termed the ecological distance matrix) is computed. This product is standardized such that it behaves as a product-moment correlation coefficient r varying between −1 and +1 (termed the Mantel statistic), and represents the average magnitude of spatial autocorrelation of the ecological variable over the entire range of sampled points (Fortin and Gurevitch 1993). The statistical significance of the Mantel statistic is assessed by random permutations of elements of one of the matrices to construct a reference distribution of values of the Mantel statistic. In my analyses, I used 10,000 permutations of one distance matrix relative to the other, a value typically sufficient to ensure stability of the probability estimates (Jackson and Somers 1989).

Determining if there is a true or spurious spatial autocorrelation among measures of ecological variables can be done by computing a partial correlation between two distance matrices A and B while controlling for the effect of a third matrix C (Smouse et al. 1986; Legendre and Fortin 1989). For example, spurious relationships between two ecological variables may be driven by a spatial gradient, or by a third variable (or
variables) that follows the spatial gradient (Fortin and Gurevitch 1993). This partial correlation is computed by first calculating a matrix of residuals of the regression between matrices A and C and a similar matrix of residuals of the regression between B and C. Computations for the partial Mantel test are as described above for the simple Mantel test except that they use these two matrices of residuals. As for simple Mantel tests, significance of the resulting partial Mantel statistic $r_{AB\times C}$ is determined by computing its associated probability by permutation (Legendre and Fortin 1989). Further elaboration on the Mantel test plus a discussion of the types of hypotheses evaluated by this approach are given in Legendre and Fortin (1989).

To examine the role of spatial gradients in structuring the distribution of tailed frog responses among sampling sites, and the classification of sites by CART analysis, I constructed several similarity matrices as described below. First, for each dataset, I constructed a matrix of site descriptors using the CART node structure as a classifier of ecological habitat relationships of sites, and expressed similarity among sites as the difference between the node numbers generated by CART for each site (matrix ABIOTIC). Because the CART algorithm I used constructs trees using a depth-first approach (Mathsoft Inc., 1998), increasing divergence in node numbers is an index of decreasing similarity in the rules used to classify sites. Second, I constructed matrices of the absolute differences between values of the biological response measured (presence/absence, density or relative abundance) among sites (called RESPONSE below). Third, I calculated the Euclidean geographic distances between each sampling site based on UTM coordinates that I converted to Albers Equal Area Conic projection, and assembled the distances between sites into a matrix of spatial similarity (matrix SPACE).

I used partial Mantel tests (Smouse et al. 1986) to create datasets corrected for linear gradients in spatial structure. The Smouse et al. (1986) approach performs more reliably than other three-matrix permutation tests (Oden and Sokal 1992). With this technique, the upper triangular off-diagonal elements of each $n$ by $n$ distance matrix were regressed against the corresponding values from a geographic distance matrix based on sampling site positions. Placing the residuals from this regression relationship into a new
distance matrix created geographically corrected datasets. This procedure removes only simple linear spatial patterns from a given data matrix (i.e. employing the assumption that spatial patterns follow a linear gradient). More complex spatial patterns (e.g., non-linear, non-monotonic gradients) were not evaluated (e.g., see Borcard et al. 1992).

RESULTS

Overall, tailed frogs occurred in 38.3% or 324 of 845 headwater stream sites sampled across British Columbia during the July and September period between 1992 to 1998 (Figure 2.1). Of those sites occupied, tadpoles were present in most (85.5%; \( n = 277 \) sites), and metamorphic juveniles or adults were also found in 26.5% of the streams (\( n = 86 \) sites). At only 14.5% (\( n = 47 \)) of sites with tailed frogs were adults detected without tadpoles also being detected. Average tadpole densities (determined at \( n = 92 \) sites from ACS surveys) of 0.385/m\(^2\) (± 2.184 SE) were similar to mean densities found in Washington and Oregon (range of reported means for streams where tailed frogs were found: 0.37-4.4; Hawkins et al. (1988); Corn and Bury (1989); Kelsey (1995). Relative abundance estimates (/20 minute search) averaged 1.82 (± 1.02 SE) in this study.

Along the coastal mountains of British Columbia, the species appears more or less continuously distributed in the CWH Biogeoclimatic zones (excluding Vancouver Island and the Queen Charlotte Islands where no frogs were detected). Occurrences become scattered and tadpole densities (e.g., mean 0.19/m\(^2\); \( n = 50 \) sites searched) are low north of latitude 54° N. Tailed frogs were not found north of the Nass River and Portland Canal (approximately 55° N 130° W). In this survey, the range of the species appears disjunct in western B.C. (between 120° 30’ W and 116° 20’ W). A few (\( n = 12 \) populations) appear to exist in up to 10 headwater streams in the ESSF Biogeoclimatic Zone in the Rocky Mountain Foothills (approximately 49° N and 49° N 114° N 50’ W) and 6 tributaries in the Columbia Mountains (49° 5’ N 116° 20’ W), an area extending no more than 25 km north of the United States border (Dupuis and Wilson 1999). Sites with tailed frogs present exhibited nearly the complete range of observed values for the 22 environmental variables that I used in my analysis (Table 2.1a).
Equation 1

At the micro scale, tailed frogs were present in headwater streams ranging in wetted width from 0.5-14 m ($\bar{x} = 3.01 \text{ m} \pm 0.09 \text{ SE}$), with water temperatures ranging between 5.5 °C- 19 °C ($\bar{x} = 12.1^\circ \text{C} \pm 0.10 \text{ SE}$) and with a variety of substrates ranging from up to 80% boulder cover ($\bar{x} = 20.9\% \pm 0.73 \text{ SE}$), up to 75% cover of cobbles ($\bar{x} = 34.5\% \pm 0.56 \text{ SE}$), and up to 77% cover of fines ($\bar{x} = 17.87\% \pm 0.63 \text{ SE}$), (Table 2.1a). At the meso-scale, tailed frogs were present in watersheds with levels of recent harvest ranging from 0 to 47.5% ($\bar{x} = 9.8\% \pm 0.29 \text{ SE}$), with road density in riparian areas up to 3.54 km/km² ($\bar{x} = 0.504 \text{ km/km}^2 \pm 0.331 \text{ SE}$), and at all ages of adjacent stands (recent clearcuts to stands > 100 years old). In addition presence was recorded at elevations up
to 1905 m (\( \bar{x} = 538.3 \text{ m} \pm 17.68 \text{ SE} \)), and stream gradients ranged between 2.4 – 93% (\( \bar{x} = 31.25\% \pm 0.70 \text{ SE} \)). At the macro-scale, tailed frogs were present in 21 of the 30 biogeoclimatic subzones sampled in the survey, in climatic conditions ranging from quite dry to very wet (mean annual precipitation range: 378.1 - 2823.8 mm; \( \bar{x} = 1876.5 \text{ mm} \pm 24.58 \text{ SE} \)) and from cool to very warm summer temperatures (mean annual temperature warmest month range: 9.2 - 20.4; \( \bar{x} = 15.4 ^\circ \text{C} \pm 0.07 \text{ SE} \)). Finally, tailed frogs were present in streams located in all the bedrock types distinguished in my analysis.

To determine how significant spatial dependency might be in the patterns of environmental values, I examined their spatial autocorrelation structure. For all sites, among-site positive spatial autocorrelation at distances of less than or equal to 200 km was detected in the values of most environmental variables (Table 2.1a), as well as in 2 of the 3 response variables (Table 2.1b). At distances beyond 200 km, the number of pairs of sites in each distance class became too small to detect meaningful correlations even if they exist. Even in site-level variables representing characteristics of sampled streams, autocorrelations could be detected at distances ranging from 4.5-57.7 km. In part, positive autocorrelations for sites with close geographical proximity are a result of multiple sites sampled within watersheds (see Methods), or within areas that exhibit similar watershed characteristics and/or climatic and geographical features not separable in the sources of data I used. Some observed autocorrelations between variables that may vary from year-to-year may be spurious because values obtained from different years were combined in this analysis (e.g., stream water temperature, species densities or relative abundance). These results clearly warrant further investigation of the influences of even small-scale spatial autocorrelation among streams on habitat association patterns.

To determine how important each predictor variable may be in determining response patterns among the datasets, I examined the bivariate correlation structure of the datasets (excluding the nominal variable bedrock lithology) at two levels of aggregation: a) all sites separately; and b) all sites within the same sub-basin averaged together. Spearman rank correlation analysis was used because some variables (e.g., detritus index, stream gradient) were categorical while the others were continuous. In general, no set of predictor variables dominated observed patterns in response variables among datasets.
(Table 2.2), regardless of whether sites were aggregated or not. In both the coast and Kootenays, occurrences of tailed frogs were generally positively associated with elevation, stream gradient, and cover of boulders, and negatively associated with increasing aspect, reach slope, amount of detritus in streams, and cover of fines, although not all of these relationships are statistically significant. Abundance patterns are more site-specific: on the coast, abundances tend to be positively associated with mean temperature of the warmest month and cover of cobbles, and negatively associated with precipitation and cover of fines.

In the Kootenays, abundances are negatively associated with temperature, cover of boulders and positively associated with cover of fines. Aggregating sites did have an important effect on both the strength and sign of many individual partial correlation coefficients (see Table 2.2; $\delta r_s$ values) suggesting that ecological interrelationships among variables are either complex, and/or influenced by spatial dependence among sites.

Classification of Environmental Relationships

For all 5 datasets, CART analysis produced branched tree models of habitat relationships that included 3 to 8 of the 22 environmental variables, with coefficients of determination ($r^2$) ranging from 0.43 - 0.73 (Figures 2.2 and 2.3). Over all models, stream width and stream substrate variables accounted for the largest reduction in deviance of all response variables, followed by the bedrock lithology variable, sub-basin harvesting, topography and stream temperature (Table 2.3). Variables describing fine organic debris input into streams were least important in terms of deviance explained, and appeared only in the CART model for occurrence on the coast. Climate variables were found to be relatively unimportant in site classification, appearing in none of the final models as a splitting variable.

On the coast, a much higher proportion of sites (0.77) located in competent granodiorite or volcanic breccia lithologies had tailed frogs present than in sites located in other, less competent bedrock types (0.34; conglomerates, quartz diorites and monzonites, sandstone, siltstone). In the former group of sites, a higher proportion of
Table 2.2. Spearman rank correlation coefficients \( r_s \) between predictor variables and the tailed frog response variables before and after values for sites clustered within the same sub-basin were pooled. Bedrock lithology was excluded from this analysis. For each response variable, values shown are the \( r_s \) value for unpoled data (left column), and for pooled data (right column). \( \Delta r_s \) (centre column) is the difference, calculated as an absolute value, in the correlation coefficients for individual variables between original and pooled data. Sample sizes \((n)\) indicates the number of data points used in the correlation analysis. Coefficients in boldface type are significant \(\alpha = 0.05\).

<table>
<thead>
<tr>
<th>Predictor Variable</th>
<th>Occurrence</th>
<th>Coast Density(^1) (#/m(^2))</th>
<th>Relative abundance(^1) (#/20 min)</th>
<th>Kootenays</th>
<th>Relative abundance(^1) (#/20 min)</th>
</tr>
</thead>
<tbody>
<tr>
<td>mean annual precipitation (mm)</td>
<td>(-0.14)</td>
<td>(-0.19)</td>
<td>(-0.27)</td>
<td>(-0.04)</td>
<td>(-0.26)</td>
</tr>
<tr>
<td>mean summer precipitation (mm)</td>
<td>(-0.05)</td>
<td>(-0.17)</td>
<td>(-0.23)</td>
<td>(-0.02)</td>
<td>(-0.10)</td>
</tr>
<tr>
<td>mean annual air temperature (°C)</td>
<td>(-0.24)</td>
<td>(-0.14)</td>
<td>(0.45)</td>
<td>(0.03)</td>
<td>(-0.43)</td>
</tr>
<tr>
<td>mean temperature warmest month (°C)</td>
<td>(-0.21)</td>
<td>(0.11)</td>
<td>(0.42)</td>
<td>(0.01)</td>
<td>(-0.12)</td>
</tr>
<tr>
<td>elevation (m)</td>
<td>0.00</td>
<td>0.18</td>
<td>0.29</td>
<td>0.15</td>
<td>0.29</td>
</tr>
<tr>
<td>aspect (degrees)</td>
<td>0.09</td>
<td>0.14</td>
<td>0.19</td>
<td>0.05</td>
<td>0.13</td>
</tr>
<tr>
<td>stream gradient (%)</td>
<td>0.24</td>
<td>0.14</td>
<td>0.06</td>
<td>0.05</td>
<td>0.13</td>
</tr>
<tr>
<td>% area logged/burned since 1978</td>
<td>0.15</td>
<td>0.26</td>
<td>0.29</td>
<td>0.21</td>
<td>0.19</td>
</tr>
<tr>
<td>density of roads within 100m of streams (km/km(^2))</td>
<td>0.24</td>
<td>0.08</td>
<td>0.23</td>
<td>0.20</td>
<td>0.09</td>
</tr>
<tr>
<td>reach slope (%)</td>
<td>0.00</td>
<td>0.02</td>
<td>-0.35</td>
<td>0.00</td>
<td>-0.26</td>
</tr>
<tr>
<td>mean wetted width (m)</td>
<td>-0.16</td>
<td>0.05</td>
<td>-0.11</td>
<td>0.06</td>
<td>-0.26</td>
</tr>
<tr>
<td>water temperature (°C)</td>
<td>0.14</td>
<td>0.10</td>
<td>0.45</td>
<td>0.42</td>
<td>0.54</td>
</tr>
<tr>
<td>detritus index(^2)</td>
<td>0.24</td>
<td>-0.44</td>
<td>-0.39</td>
<td>-0.42</td>
<td>0.61</td>
</tr>
<tr>
<td>% cover of boulders (&gt; 256 mm)</td>
<td>-0.09</td>
<td>0.39</td>
<td>0.17</td>
<td>(-0.14)</td>
<td>0.13</td>
</tr>
<tr>
<td>% cover of cobbles (64-256 mm)</td>
<td>-0.02</td>
<td>0.17</td>
<td>0.13</td>
<td>0.01</td>
<td>0.15</td>
</tr>
<tr>
<td>% cover of fines (&lt; 64 mm)</td>
<td>0.02</td>
<td>-0.30</td>
<td>-0.28</td>
<td>0.10</td>
<td>-0.03</td>
</tr>
</tbody>
</table>

\(^1\) Density and relative abundance measures are presented only for sites where tailed frogs were positively detected.

\(^2\) Detritus index (fine organic material) is scored as: 1 = none visible; 2 = low; 3 = intermediate; 4 = water opaque.
Figure 2.2. Classification and Regression Tree (CART) models for tailed frog responses in the western coastal mountain zone of British Columbia. Separate trees are shown for: A) occurrence (presence/absence); B) density (#/m$^2$); and C) relative abundance (#/20 min). Only sites where tailed frogs occurred were used in the density and relative abundance CARTS. Numbers inside the rectangles (end nodes) are the means of each response variable for the sample sites included in that node (sample size in brackets). The splitting predictor variable and its threshold value is shown for each branch of each node. The length of each branch (growing to the right) is proportional to the percent of deviance explained by the splitting variable at each node. To the right of each end node is the node number assigned by CART to those sites.
B)

- **Elevation**
  - > 10.8
  - > 152.5
    - > 29: % Cobbles
      - > 29: 0.81 (12) 31
    - < 29: 2.13 (12) 30
  - < 152.5
    - 3.5 (5) 14

- **Water temperature**
  - > 10.8
    - > 152.5
      - 3.5 (5) 14
    - < 152.5
      - granodiorite, quartz diorite
        - 0.92 (5) 13
  - < 10.8
    - Bedrock lithology
      - conglomerate, volcanic breccia
        - 0.35 (6) 12
      - > 38.5
        - 1.73 (12) 5
      - < 38.5
        - 6.22 (8) 4

- **Mean wetted width (m)**
  - > 2.16 (n=60)
    - > 1.6: % Fines
      - > 29: 13
    - < 1.6: 12

- **Elevation**
  - > 10.8
    - > 152.5
      - > 29: % Cobbles
        - > 29: 0.81 (12) 31
      - < 29: 2.13 (12) 30
    - < 152.5
      - 3.5 (5) 14

- **Water temperature**
  - > 10.8
    - > 152.5
      - > 29: % Cobbles
        - > 29: 0.81 (12) 31
      - < 29: 2.13 (12) 30
    - < 152.5
      - 3.5 (5) 14

- **Bedrock lithology**
  - conglomerate, volcanic breccia
    - 0.35 (6) 12
  - > 38.5
    - 1.73 (12) 5
  - < 38.5
    - 6.22 (8) 4

32
Mean wetted width (m)

> 4.95

> 10.5

> 2.0

< 10.5

12.19

(n=31)

< 4.95

< 2.0

Mean wetted width (m)

< 1.5

> 2.0

< 10.5

Road density in riparian zone (km/km²)

< 2.0

15.86 (7)

12

> 10.5

6.2 (5)

27

> 2.0

5.38 (8)

7

> 4.95

Mean wetted width (m)

> 10.5

10.67 (6)

26

> 10.5

6.2 (5)

27

< 2.0

15.86 (7)

12

< 1.5

25.8 (5)

2

< 2.0

< 10.5

25.8 (5)

2
Figure 2.3. CART models for tailed frog occurrence records in the southeastern interior (Kootenays) area in British Columbia. As in Figure 2.2, separate trees are shown for: A) occurrence (presence/absence), B) density (#/m^2), and C) relative abundance (#/20 min). Details presented in the trees are as described in the caption for Figure 2.2.
B)

Bedrock Lithology

Argillite, quartzite, sedimentary, siltstone

% Cobbles

> 42.5  2.95 (7)  5

< 42.5  0.85 (9)  4

Elevation (m)

> 1684  5.60 (5)  7

< 1684  3.17 (6)  6

2.79 (n=27)
Table 2.3. Percentages of original deviance explained by the CART models (Figures 2.2 and 2.3) for tailed frog response variables (see text and Table 2.1b) summarized among the various classes of predictor variable. Sample sizes indicate the number of sites meeting all the criteria that were included in each model.

<table>
<thead>
<tr>
<th>Predictor class</th>
<th>Spatial scale</th>
<th>Coast Occurrence</th>
<th>Density (#/m²)</th>
<th>Relative abundance (#/20 min)</th>
<th>Kootenays Occurrence</th>
<th>Relative abundance (#/20 min)</th>
</tr>
</thead>
<tbody>
<tr>
<td>climate¹</td>
<td>macro</td>
<td>n = 180</td>
<td>-</td>
<td>-</td>
<td>n = 113</td>
<td>-</td>
</tr>
<tr>
<td>bedrock lithology</td>
<td>macro</td>
<td>n = 60</td>
<td>21.1</td>
<td>0.24</td>
<td>2.3</td>
<td>24.5</td>
</tr>
<tr>
<td>topography²</td>
<td>meso</td>
<td>n = 31</td>
<td>9.5</td>
<td>8.0</td>
<td>3.5</td>
<td>9.9</td>
</tr>
<tr>
<td>sub-basin harvesting and road density³</td>
<td>meso</td>
<td></td>
<td>9.6</td>
<td>-</td>
<td>7.5</td>
<td>18.8</td>
</tr>
<tr>
<td>stand type⁴</td>
<td>micro</td>
<td></td>
<td>-</td>
<td>-</td>
<td>-</td>
<td>-</td>
</tr>
<tr>
<td>stream substrate⁵</td>
<td>micro</td>
<td></td>
<td>6.9</td>
<td>29.2</td>
<td>13.8</td>
<td>10.6</td>
</tr>
<tr>
<td>stream temperature</td>
<td>micro</td>
<td></td>
<td>-</td>
<td>4.1</td>
<td>-</td>
<td>6.0</td>
</tr>
<tr>
<td>stream width</td>
<td>micro</td>
<td></td>
<td>-</td>
<td>15.8</td>
<td>-</td>
<td>12.1</td>
</tr>
<tr>
<td>fine organic debris</td>
<td>micro</td>
<td></td>
<td>2.1</td>
<td>-</td>
<td>-</td>
<td>-</td>
</tr>
<tr>
<td>reach slope (%)</td>
<td>micro</td>
<td></td>
<td>-</td>
<td>-</td>
<td>-</td>
<td>-</td>
</tr>
</tbody>
</table>

¹ means for: annual precipitation, summer precipitation (in mm), annual temperature, temperature of warmest month (°C), elevation (m), aspect (°), stream gradient (%)
² % sub-basin area logged since 1978; % logged area within 100 m of streams, road density within 100 m of streams (km/km²)
³ age class of adjacent stand (0-10 yrs; 11-20 yrs; 21-60 yrs; 61-100 yrs, > 100 yrs), presence of riparian buffers (yes/no)
⁴ % cover of boulders, cobbles, and fines

36
those with low indices of streambed debris and with low densities of roads in the riparian zone had tailed frogs present than in either more debris-filled streams or with higher road densities. Of those sites in less competent bedrock types, factors associated with lower proportions of sites with tailed frog presence appear to be smaller-sized stream substrates, location in sandstone or siltstone, low stream gradients, or low elevation. At sites where tailed frogs were present, smaller streams with a low cover of fines had higher densities ($\bar{x} = 6.22$) than did sites in larger streams with temperatures below 10.8 °C ($\bar{x} = 1.80$), and at higher elevations ($\bar{x} = 1.5$). For those higher elevation sites, sites with higher densities were associated with lower cover of cobbles relative to other substrates, higher stream temperatures, smaller stream size, and competent bedrock types (granodiorite or quartz diorites). Other more complex interactions between density and stream size, and stream gradient are suggested by the branching structure in Figure 2.2b. Factors associated with higher relative abundance estimates appear to be small stream size, and relatively low density of roads in the watershed (Fig 2.2c). In the Kootenays, a higher proportion of sites with tailed frogs present occurred in watersheds with more recent harvests (0.41), than those with less recent harvesting (0.03). Intermediate stream size, a higher proportion of % cover of boulders, west facing aspect, and higher stream temperatures were associated with sites with higher probabilities of tailed frog occurrence (Figure 2.3a).

For those sites with tailed frogs, higher elevation sites dominated by limestone, or on quartzite and sandstone bedrock had higher relative abundances than did lower elevation sites, or sites on poorly competent argillite or sedimentary bedrock types (Figure 2.3b). Because of the restricted spatial distribution of tailed frogs in the Kootenays, and evidence of genetic differences between members of these populations and those on the Coast (Ritland et al. 2000), CART models developed here may be strongly dominated by historical determinants of tailed frog distribution in this area.

**Assessing Effects of Spatial Structure on Empirical Habitat Models**

Analysis of the relationships between spatial structure of sampled sites, the abiotic models, and the occurrence and abundance of tailed frogs was investigated by taking into account the spatial pattern of the variables using Mantel tests. For each dataset used to
construct CART models, the Mantel statistic was applied to three similarity matrices for all possible pairs of sampled sites as follows. 1) a distance matrix SPACE formed by taking the Euclidean geographic distances between sites; 2) a similarity matrix RESPONSE reflecting unsigned differences in the species response variable (presence/absence or abundance among sites; and 3) a similarity matrix ABIOTIC representing the unsigned differences in CART model node number among sites.

The simple Mantel statistics (computed for RESPONSE and ABIOTIC above the diagonal in Tables 2.4a-c and 2.5a-b) confirmed significant relationships between the abiotic site classifications created by the CART models and presence/absence and abundance variables for coastal sites (Tables 2.4a-c), and the relative abundance variable for Kootenays sites. Additionally, simple Mantel statistics (computed for RESPONSE and SPACE in Tables 2.4a-c and 2.5a-b) indicated a significant direct influence of spatial dependence in patterns of occurrence on the coast but not in the Kootenays (compare Table 2.4a with 2.5a), nor for patterns of abundance (Tables 2.4b-4c and 2.5b) exclusive of more complex effects. These results are consistent with the information suggested by the presence of significant autocorrelation in correlogram analysis of the individual variables, and by the effect of averaging sites clustered within the same sub-basin together on bivariate correlation coefficients (Table 2.2).

Legendre and Trossellier (1988) introduced causal modelling using simple and partial Mantel statistics as a general approach for identifying mechanisms driving patterns in ecological responses among spatially distributed samples. I use their approach here to disaggregate and test implicit or explicit hypotheses relating habitat structure to site classification, species responses, and other spatial dependencies not otherwise accounted for. Several simple causal relations can be inferred with the three types of variables used in this analysis (i.e. matrices RESPONSE, ABIOTIC and SPACE). I exclude models where SPACE is a dependent variable, and those where ABIOTIC is dependent on RESPONSE which do not make ecological sense. Table 2.6 shows the predictions made by the remaining four models, and the evidence for each of them by values of the simple and partial Mantel statistics (Legendre and Trossellier 1988). The first model (Table 2.6; Model 1) states that response patterns of tailed frogs are independently caused by the spatial structure in the ecological determinants of
Table 2.4. Simple and partial Mantel test results for Coastal sites. A separate table is presented for each response variable analyzed. Shown above the diagonal are the simple Mantel statistics (e.g., $r$), partial Mantel statistics (below the diagonal), and associated probabilities for each response variable in relation to ABIOTIC and SPACE factors. One-tailed tests significant at $\alpha= 0.05$ are indicated with an asterisk (*), and “N.S.” otherwise. The matrix held constant is indicated with the dot notation (see Methods).

### a) Occurrence data

<table>
<thead>
<tr>
<th>OCCURRENCE</th>
<th>ABIOTIC</th>
<th>SPACE</th>
</tr>
</thead>
<tbody>
<tr>
<td>OCCURRENCE</td>
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<td>0.05375</td>
</tr>
<tr>
<td>ABIOTIC</td>
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<td>0.4730</td>
</tr>
<tr>
<td>SPACE</td>
<td>$P = 0.0188 *$</td>
<td></td>
</tr>
<tr>
<td></td>
<td>$P = 0.0457 *$</td>
<td></td>
</tr>
<tr>
<td></td>
<td>$P = 0.0008 *$</td>
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</tbody>
</table>

### b) Density data

<table>
<thead>
<tr>
<th>DENSITY</th>
<th>ABIOTIC</th>
<th>SPACE</th>
</tr>
</thead>
<tbody>
<tr>
<td>DENSITY</td>
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</tr>
<tr>
<td>ABIOTIC</td>
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<tr>
<td>SPACE</td>
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<td>$P = 0.5745$ N.S.</td>
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<tr>
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<td>$P = 0.4400$ N.S.</td>
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</tr>
<tr>
<td></td>
<td>$P = 0.4800$ N.S.</td>
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</table>

### c) Relative abundance data

<table>
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<tr>
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<th>ABIOTIC</th>
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<td>$P = 0.1923$ N.S.</td>
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<tr>
<td></td>
<td>$P = 0.01013$</td>
<td>$P = 0.0385 *$</td>
</tr>
</tbody>
</table>
Table 2.5. Simple and partial Mantel test results for Kootenays sites. A separate table is presented for each response variable analyzed. Shown are simple Mantel statistics (above the diagonal), partial Mantel statistics (below the diagonal), and associated probabilities for each response variable in relation to ABIOTIC and SPACE factors. Notation and tests of significance as described in Table 2.4.

a) Occurrence data

<table>
<thead>
<tr>
<th>OCCURRENCE</th>
<th>ABIOTIC</th>
<th>SPACE</th>
</tr>
</thead>
<tbody>
<tr>
<td>OCCURRENCE</td>
<td>-</td>
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</table>

b) Relative abundance data

<table>
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<tbody>
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<tr>
<td>SPACE</td>
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<td>P = 0.1407 N.S.</td>
</tr>
</tbody>
</table>

site classification as described by CART, and by other spatially dependent factors not explicitly mentioned in the model. Model 2 states that spatial structure in the tailed frog response is partially caused by spatial gradients in the site classification rules, and partly by other factors not explicitly separated out in the model. Model 3 states that the responses of tailed frogs are determined in large part by the spatial patterning of the site classification rules themselves. Finally, Model 4 states that both site classification and tailed frog response variables are independently controlled by unknown spatial factors.

No single model of the influences of spatial and site classification rules on responses of tailed frogs could be unambiguously supported by all the simple and partial Mantel statistics calculated from any of the datasets (Table 2.6). Only Model 1 (absence of a relationship between CART site classification rules and tailed frog responses independent of geographic location at the scale of this study
Table 2.6. Four possible models for causal relationships between variables describing patterns of distribution and abundance (RESPONSE), and both an ABBIOTIC variable (representing the site classification rules generated by CART) and a SPACE variable (representing geographic distances between sites) for the tailed frog in British Columbia. Predictions of each model are developed in the text. Support for each model prediction is taken from the simple and partial Mantel analyses given in Tables 2.4 and 2.5.

<table>
<thead>
<tr>
<th>Model</th>
<th>Model relationships</th>
<th>Predictions if model is true</th>
<th>Response Variables</th>
<th>Kootenays Sites</th>
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<td></td>
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<td>Density</td>
</tr>
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</tr>
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</tr>
<tr>
<td></td>
<td></td>
<td>(ABIOTIC•RESPONSE)</td>
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</tbody>
</table>
(predictions: $(SPACE \cdot RESPONSE) \cdot ABIOTIC \geq SPACE \cdot RESPONSE)$ and
$(ABIOTIC \cdot RESPONSE) \cdot SPACE \geq ABIOTIC \cdot RESPONSE)$; Table 2.6) was unsupported for any dataset. Models 2-4 were supported for occurrence patterns in the coastal dataset, indicating that occurrence patterns appear to be controlled by both spatial patterning in the site classification rules themselves and by unknown spatial factors. In particular, there is a partial indication that spatial patterns in the occurrence data and the CART models for site classification in the coastal dataset may both be controlled by unknown factors not captured in the datasets (Model 4 above; prediction $(SPACE \cdot RESPONSE) \times (SPACE \cdot ABIOTIC) \leq (ABIOTIC \cdot RESPONSE)$; Table 2.6). In the Kootenays datasets, causal relationships between the CART model’s classification of sites, and the responses variables occurrence and relative abundance $ABIOTIC \cdot RESPONSE \neq 0$; Table 2.6) cannot be viewed as fully independent of the sampling sites used to construct them. However, not all the predictions necessary to support a particular model against the others were confirmed for that dataset for either response variable.

DISCUSSION

Although the data used here are correlative and thus do not necessarily imply causality, they suggest that both occurrence and abundance of the tailed frog across its range in British Columbia are positively associated with bedrock lithologies resistant to weathering, and negatively associated with factors promoting intrusion of fine sediments into streams. Generally, tailed frogs exhibit a broad distribution pattern in the montane headwater drainages of coastal British Columbia, contrasting with an apparently much more localized and disjunct pattern in the interior mountains of the east Kootenays. Positive occurrences of the species in headwater tributaries were found in sampling sites representing nearly the full range of variation in climatic, topographic, geologic, stream substrate, and forest disturbance variables described in this study. Broadly, variables describing biophysical setting at meso- and micro-scales had a greater influence on occurrence and abundance of larval frogs than did adjacent forest practices. Although higher probabilities of occurrence of tailed frogs in the Kootenays occurred in watersheds with higher levels of recent harvests, this may simply be an artifact of the coincidence of
recent harvesting activity with the present restricted distribution of the species. Underlying geology emerged as a consistently important determinant of occurrence patterns. Fine scale stream structure is important in determining abundance patterns, and several determinants of stream structure (substrate composition and channel morphology are themselves influenced by bedrock geology (Church in press). At all scales of measurement, the presence of unexplained spatial dependence in patterns of distribution and abundance, and in values of habitat variables, appears to contribute substantially to residual uncertainty in these species-habitat relationships.

Three cautions are important when interpreting these results in the broader context of forest management effects on the long-term persistence of this species. First, my source data for extent of recent logging effects are at coarse scale relative to the life history of the organism to reliably detect an influence on a low-vagility species such as tailed frogs. Second, habitat relationships developed here are directly relevant only to the in-stream life stage, because the survey methods used were directed primarily at that stage. Third, the classification tree approach used here is primarily heuristic in nature processes inferred from the results must be treated as hypotheses until their predictions are confirmed by more detailed experimental studies. Habitat classification approaches by themselves cannot infer effects of specific habitat protection measures on future extirpation probabilities, because of basic uncertainties in species’ life histories.

I found complex relationships between patterns of both occurrences and abundances of tailed frogs and macro-, meso- and micro-scales of environmental and harvesting-related variables. At the macro-scale, parent bedrock lithology was a major determinant of occurrences on the coast, and of relative abundances in the Kootenays (Table 2.3; Figures 2.2 and 2.3). Consistent with conclusions reached by Hunter (1998) for tailed frogs in Oregon, meso-scale topographic and harvesting-related variables also were related to patterns of occurrence and abundance in both regions, as was micro-scale stream substrate composition (Table 2.3). In both regions, it appeared that bedrock lithology, topography, and harvesting related variables were important influences on patterns of occurrence, and 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 it appears likely that patterns of occurrence and to a
lesser extent the abundance of this species in headwater streams in the northern part of its range is driven primarily by interacting effects of geomorphology, topography and channel morphology on fine-scale stream structure with characteristics of adjacent forest and harvesting patterns playing a secondary role.

Regional differences are striking when comparing factors influencing occurrence and abundance patterns of tailed frogs in coastal and interior regions of British Columbia. For occurrence patterns, two general biophysical and disturbance interactions appear important in distinguishing sites with a high vs. low probability of tailed frog occurrences. The first interaction, reflecting an apparent negative relationship between probability of occurrence and degree of watershed disturbance, contingent upon the parent bedrock type, is demonstrated most clearly in coastal sites. I found higher densities of roads in the riparian zone to be associated with lower probabilities of occurrence, for those sites located in intrusive and generally massive bedrock formations (e.g., granodiorites; volcanic breccias) and containing little fine organic debris in the stream. Bedrocks of these types are generally coarse-grained and resistant to erosion (Bovis et al. 1998). Higher percentages of riparian areas logged are also generally associated with lower probabilities of occurrence for those sites located in weak and erosion-prone bedrocks (e.g., sandstone or siltstone), although some of these sites are also in erosion-resistant quartz diorites. Streams located in such sites may become increasingly prone to disturbances in the riparian zone as the areas exposed to disturbance increase, possibly because their small size and slow flushing rates of accumulated sediments through the stream (Murphy and Hall 1981; Hawkins et al. 1983) if they have a relatively low gradient. Consistent with this notion is the result that higher stream gradients are associated with higher probabilities of occurrence in disturbed watersheds, even on bedrocks of intermediate erosion and fracturing characteristics (e.g., conglomerates, gneisses, quartz monzonites).

A second set of interactions between disturbance history, stream size and stream substrate size composition is most apparent in the Kootenay’s occurrence data. In more heavily developed watersheds, smaller streams with a higher cover of boulders show a higher occurrence probability of tailed frogs than do larger streams, or those with smaller-sized substrates. In streams within less developed watersheds, occurrence is
associated with sites in weaker cobble-producing bedrock types (e.g., argillite; quartzite). However, given evidence of a significant residual interaction between geographic location and the predictions of the CART models in the Kootenays, it is not possible to determine how general this relationship is. For example, the Kootenays are warmer and drier in summer months than the coast (Reynolds 1997), and these conditions may limit movements of tailed frogs among streams, leading to a potentially more localized distribution and lower abundances if site conditions are poor.

As expected, abundance patterns appear strongly linked to micro-scale stream characteristics and structure (stream width, substrate size composition; Kelsey 1995; Welsh and Ollivier 1998; Dupuis and Steventon 1999). However, factors operating at a larger scale, such as bedrock lithology, stream gradient, elevation, and degrees of disturbance, that may determine local heterogeneity of stream morphology and productivity, also play a role in abundance relationships. Geomorphology, topography, channel morphology, and the presence and age of disturbed soils and roads all interact to determine the dynamics of bedload and sediment accumulation in streams, including the stream’s ability to dissipate impacts from disturbance (Benda 1994; Kelsey 1995). The area harvested or disturbed adjacent to streams, and time since disturbance, combined with elevation and climate, can influence productivity of streams through stream temperature, nutrient releases and light penetration into streams. In a multi-scale analysis of habitat factors and distributions of several amphibian species in Oregon, Hunter (1998) found that landscape-level variables (e.g., watershed area, distance to nearest unharvested stand) contributed significantly to predictive models of occurrence of tailed frogs.

Like environmental factors governing occurrence, regional differences in abundance patterns are readily apparent. On the coast, smaller streams with a low cover of fines have a much higher density of tadpoles than do other small streams with a higher cover of fines (see also Welsh and Ollivier 1998), while large streams with higher temperatures at low elevation, or a low cover of cobbles, have higher densities than do other streams. Although not directly captured by the variables analyzed, potential influences of fine-scale heterogeneity in stream morphology (e.g., step-pool and pool/riffle ratios) is suggested by the effects of stream gradients and bedrock lithology on densities near the end nodes of the CART tree for density (Figure 2.2b). In addition,
intermediate-sized streams with lower disturbance rates in the riparian zone have higher relative abundances than do other intermediate-sized streams. In the Kootenays, higher abundances are associated with weaker bedrocks that typically fracture into divergent size classes (limestone, quartites and limestone mixed with sandstone) in high elevation sites; other site and bedrock types show lower abundances. These patterns may reflect a general interaction between geology and forest disturbance in governing abundance of larvae in streams where tailed frogs are present. In erosion resistant bedrocks, effects of disturbance on sediment accumulation may be reduced by the combination of slower weathering rates of parent material and other factors such as stream gradients. In weaker, more erosion prone bedrocks, effects of disturbances on sediment production may exceed stream flushing capacities, causing a reduction of egg deposition and larval attachment sites (Kelsey 1995). However, the fact that sites containing tailed frogs are located in a restricted number of watersheds confounds simple interpretation of these factors, limiting extrapolations of their importance in the broader regional context.

How do environmental variables operating at a range of scales from the macro (landscape) to the micro (local stream reach) determine patterns of distribution and abundance, and responses to disturbances? After accounting for simple gradients of spatial dependencies inherent in the data, the answers are still equivocal. Clearly, the spatial pattern of each response variable of this species has components at macro-, meso- and micro-scales (see also Kelsey 1995; Bull and Carter 1996), as has also been shown for other riparian-dependent amphibians (Bury et al. 1991b; Welsh and Lind 1996). Long-term cumulative effects of disturbances to riparian and adjacent forest stands mediated by geomorphology and local topography may indeed contribute to changes in the likelihood of populations being present in small streams in managed watersheds. Abundance patterns related to characteristics of stream substrates and channel morphology also appear mediated by factors operating at a broader scale. Yet evidence of residual spatial autocorrelations between environmental variables after accounting for simple geographic gradients suggests that true relationships between environmental variables and species responses in these data have not yet been exposed. This is not surprising, given strong climatic, topographic and vegetation gradients from one part of a watershed to another in the montane environments studied here. Samples were not
sufficient to perform analyses stratified by all of these factors so inferences from existing
samples may not be easily transferable to new environmental conditions found elsewhere
(Thompson et al. 1996).

A primary strength of a geographically extensive analysis such as this is that it
can identify those variables associated with patterns of abundance or distribution for a
species that are strong enough to stand out against a background of extensive among-site
variation in other variables (Hinch et al. 1994). Small scale studies offer only a limited
view of both the dynamics in population and community pattern and consequent insight
into the mechanisms responsible (Levin 1992). Larger-scale studies can reveal the
relative importance of certain variables as predictors against a background of natural or
local variation. The suggestion from this study that interactions between geomorphology,
topography, and stream channel morphology plays as great or greater role in distribution
and abundance patterns of this species than do characteristics of adjacent forests is
consistent with the suggestion that at a regional scale, biogeographical factors are more
important in the organization of forest-dependent amphibian communities than are local
forest habitat gradients (Bury et al. 1991a). It is likely that geographic variation in
habitat relationships, as clearly evidenced by these results, confounds predictions of
effects of timber harvest on tailed frog populations (Corn and Bury 1989; Bull and Carter
1996).
CHAPTER 3. MODELLING LONG-TERM PERSISTENCE OF TAILED FROG POPULATIONS IN RELATION TO LIFE HISTORY AND ENVIRONMENTAL VARIATION

INTRODUCTION

Species with specialized habitat requirements may be vulnerable to the effects of changes in amount or quality of habitat, the frequency and magnitude of disturbance events, random variations in birth and death rates, and consequences of genetic isolation (Soule 1987; Lande 1993; Root 1998). Management strategies to conserve vulnerable species must account for the potential impacts of these factors on the long-term survival of local populations. For most threatened species, our uncertainty about many of the processes and parameters that influence survival, derived from datasets collected over a limited number of study sites and time periods, severely restrict our confidence in predicting chances of population persistence (Ludwig 1996b).

Long-term condition of the physical habitat is critically important in lotic ecosystems (Welsh and Ollivier 1998). Streams and their immediately adjacent riparian zone are one of the most dynamic zones of the landscape because of the influence of the fluvial and hillslope processes (Gregory et al. 1991). Disturbances in streams alter the composition of stream substrates, and extreme events (e.g., landslides, debris flows) may substantially alter streambed morphology (Church in press). Disturbances in riparian zones create diversity in vegetation structure, and provide a variety of microhabitats for riparian-dependent species (Gregory et al. 1991). Direct and indirect effects of forest harvesting may negatively affect the ecological integrity of stream habitats and are widely linked to declines in rearing habitat for fish and stream-dwelling amphibians (deMaynadier and Hunter 1995; Welsh and Ollivier 1998).

The tailed frog (*Ascaphus truei*) is considered a habitat specialist, dependent upon small, clear, montane headwater streams and associated riparian areas for survival (Corn and Bury 1989; Welsh and Ollivier 1998). One group of factors that may increase vulnerability of this species to population declines following disturbances concern habitat alterations, including increases in stream temperature following clearcut logging, and increasing levels of fine sediments in streams following logging (e.g., Murphy and Hall 1981; Dupuis and Steventon 1999). A second set of traits that make this species
potentially at risk concern consequences of its life history, including a long larval period in streams, low mobility, and low reproductive rates (Richardson and Neill 1998). If habitat degradation and/or loss increase the probability of long-term decline of this species, then assessment of sources of variation in habitat quality that may influence population trends is important for evaluating management options.

Current evidence indicates that populations of tailed frogs in unmanaged habitats are relatively persistent (Welsh and Ollivier 1998). However, it is substantially less clear how robust populations may be to altered conditions in managed watersheds, especially because tailed frog-bearing streams currently lack protection of their riparian zone forest cover (Ministry of Forests and Ministry of Environment 1995b). Larval populations show high natural variability in numbers within and among streams (Dupuis and Steventon 1999). This variation is due in part to local patchiness in tadpole distributions within streams (Kelsey 1995), as well as year-to-year variation in their abundance (J.S. Richardson unpublished data). Because tadpole densities are related to local stream characteristics (e.g., substrate composition, water temperatures and presence of woody debris; Dupuis and Steventon 1999; Chapter 2), there remains considerable uncertainty about the influences of other factors at the habitat and landscape scales (Chapter 2). Postulates about the consequences of harvesting on the eventual fate of local populations in managed watersheds range from population increases, neutral effects (e.g., no net decline in the probability of population persistence), to eventual extinction of local populations as harvested streams become population sinks (e.g., Richardson and Neill 1998). Some authors (e.g., Welsh 1990) have argued that recolonization of logged sites is critical to sustaining productive amphibian populations. However, given apparently low mobility of breeding females (Daugherty and Sheldon 1982), persistence of many populations cannot be taken for granted under future conditions of extensive forest harvest in headwater areas.

Clearly, no strong consensus yet exists on the ecological linkages between particular forest harvesting practices and effects on populations of tailed frogs in montane watersheds (Richardson and Neill 1998). Because of this broad uncertainty, I wish to evaluate which key demographic and environmental factors may influence probabilities of long-term persistence of tailed frogs at the local scale. My approach is to use a stage-
based model of tailed frog populations inhabiting two linked habitat types: streams, representing egg and larval stages, and adjacent riparian habitats representing juvenile and breeding adult habitat. Each life stage may be susceptible to extinction from demographic and environmental stochastic events. I focus on long-term persistence of the population, defined as the probability of quasi-extinction (decline to a low threshold level below which population parameters are unlikely to be valid) over a specified time interval. Because field data on demographic structures of tailed frog populations are not robust, I chose to investigate persistence patterns over a range of plausible values for many parameters. I determine: 1) the stage-specific ranges of growth and survival rates required for persistence of populations; 2) the likelihood of persistence, given field-surveyed population structure and habitat conditions; and 3) effects of temporal variation in habitat quality on the probability of quasi-extinction. I use the results to infer potential consequences of habitat alteration on long-term persistence of the species in managed watersheds.

METHODS

Stage-based Population Models

To evaluate life history and environmental sources of long-term risk to population persistence at the scale of local headwater stream habitats, I constructed female-only, stochastic, stage-based population models. I assume tailed frogs to use three habitats throughout their life cycle: the stream-bed for egg-laying and larval development; the adjacent riparian zone for feeding and movement of metamorphosed juveniles and adults; and occasionally non-riparian upslope habitats for movement. Further, I assume the dynamics of tailed frog populations to be governed essentially by autecological processes, and not mediated indirectly through interactions with other species. Both the dynamics of populations and habitat structures are subject to stochastic events, and to effects of anthropogenic disturbances. To make population projections, I used RAMAS-GIS (Akçakaya 1997).

My stage-based models divide the tailed frog life cycle into 5 stages: eggs & hatchlings, small tadpoles (< 1.5 cm snout-vent length [SVL]), large tadpoles (> 1.5 cm
SVL) living in the stream, pre-reproductive metamorphs, and reproductive adults living in riparian and non-riparian habitats (Figure 3.1).

To create stage-based projection matrices, I needed estimates (by stage i) of the mean annual probability of surviving and growing into the next stage (Gi), the probability of surviving and remaining in the same stage (Pi), and fecundity (Fi). The resulting stage class population matrix has the general form

\[
\begin{bmatrix}
    0 & 0 & 0 & 0 & F_i \\
    G_1 & P_2 & 0 & 0 & 0 \\
    0 & G_2 & P_3 & 0 & 0 \\
    0 & 0 & G_3 & P_4 & 0 \\
    0 & 0 & 0 & G_4 & P_5 \\
\end{bmatrix}
\]

(Crouse et al. 1987). To each mean probability estimate, I applied an estimate of the annual variation in these rates due to changing habitat and climatic characteristics. Because we know little about the variability of growth and survival rates among individuals, I assume that all individuals in a given life stage are subject to the same annual probabilities of survival and stage duration.

Estimates of Demographic Parameters

Densities of Different Life Stages

Only densities of tadpoles (#/m²) are typically measured in field studies of tailed frog populations. Both distribution and density of tadpoles exhibit high variation when measured at the micro (stand) and the stream (sub-watershed) scale (Kelsey 1995; Wahbe 1996). This variability may reflect structural heterogeneity in stream characteristics (e.g., pool: riffle or step:pool area (see Chin 1998), stream substrate composition, volume of large downed wood; Kelsey 1995; Chapter 2) on larval substrate availability. It may also reflect effects of productivity, disturbance, and natural variation in population size, all combined with the logistical difficulties in obtaining a complete census of tadpoles. Densities of juveniles and adults are rarely reported as their estimation requires more intensive study using pitfall trapping or other methods. Currently, capture efficiencies
of these latter methods are poorly known for this species.

Across British Columbia, reported mean observed densities of tadpoles vary between 0.19/m$^2$ in second growth stands (J.S. Richardson unpublished data) to 2.4/m$^2$ in clearcuts with riparian buffers (Dupuis and Friele 1996; Table 3.1, range of individual survey values: 0.0145-9.11/m$^2$). Elsewhere in the Pacific Northwest, observed mean tadpole densities show a similar range of variation (Table 3.1: range of study means: 0.088-2.37/m$^2$). After accounting for uncertainty in observations (see below), I estimated the 95% confidence bounds about the true mean densities to be 0.3029 – 4.484/m$^2$ and used these bounds to constrain the low and high estimates of average tadpole densities used in model projections.

Growth
Growth in amphibians is indeterminate, and differences in growth rates between sites are influenced by differences in the physical environment (Duellman and Trueb 1994). Brown (1990) suggested that in-stream food resources might be an important factor limiting growth rates in larval tailed frogs. Forest disturbances may change availability of the algal food supply influencing time to metamorphosis and size at metamorphosis (Kelsey 1995; Richardson and Neill 1998). In particular, increased light due to removal of riparian canopy has been shown to significantly increase both periphyton biomass and tadpole growth in small streams (Kim 1999). However, less is known of growth patterns in metamorphosed juveniles and adults. In one study, annual growth increment appeared constant in post-metamorphic age classes (Daugherty and Sheldon 1982). Because little is presently known of how factors influencing growth rates in older age classes might respond to habitat alteration and disturbance, I did not explicitly model growth rates in the composite age-class representing breeding adults.

In general, time to metamorphosis in tailed frogs varies with geographic location and elevation. Larvae from streams in northern California show a one- or two-year larval period (Wallace and Diller 1998). Studies of populations in Oregon and Washington as well as inland populations have found 2 or 3 distinct size classes of non-embryonic larvae in streams during June – August (Metter 1968; Daugherty and Sheldon 1982; Brown 1990; Kelsey 1995). In northern populations, larval size-frequency patterns suggest a three- to four-year larval period, with metamorphosis beginning in the third year and gradually completing during the fourth summer (Daugherty and Sheldon 1982). All studies examining the influence of elevation show that higher elevation sites have longer larval periods (Wallace and Diller 1998 and sources cited therein). My analysis of size frequency distributions of larvae from sites in the southern coast mountains of B.C. is consistent with this latter pattern: two or three size classes of tadpoles in most streams, with the likely average length of the larval period therefore being three or four years (see Appendix 1 for details).

**Survivorship**

In nearly all amphibian populations that have been studied, survivorship of eggs and larvae is low, and juvenile mortality fluctuates more than adult mortality (Duellman
Table 3.1. Summary statistics for in-stream densities for tailed frogs obtained from studies conducted in British Columbia, Washington, and Oregon. Mean densities (± SE) estimated only for streams where tailed frogs were found. Where available, sample sizes (n) and the type of forest cover in which the study was made are presented (CC = clearcut (0-25 years); BCC = clearcut with buffer; SG = second growth (25-80 years); OG = old growth (+250 years).

<table>
<thead>
<tr>
<th>Province or State</th>
<th>Location</th>
<th>Forest cover</th>
<th>Density (#/m²)</th>
<th>Source</th>
</tr>
</thead>
<tbody>
<tr>
<td>British Columbia</td>
<td>Terrace</td>
<td>CC</td>
<td>0.40 ± 0.20 (18)</td>
<td>Dupuis and Friele (1996)</td>
</tr>
<tr>
<td></td>
<td></td>
<td>BCC</td>
<td>2.4 ± 0.66 (18)</td>
<td></td>
</tr>
<tr>
<td></td>
<td></td>
<td>OG</td>
<td>1.8 ± 0.59 (18)</td>
<td></td>
</tr>
<tr>
<td></td>
<td>Squamish</td>
<td>CC</td>
<td>1.14 ± 0.52 (3)</td>
<td>Wahbe (unpublished data)^1</td>
</tr>
<tr>
<td></td>
<td></td>
<td>BCC</td>
<td>2.15</td>
<td></td>
</tr>
<tr>
<td></td>
<td></td>
<td>SG</td>
<td>0.64 ± 0.24 (3)</td>
<td></td>
</tr>
<tr>
<td></td>
<td></td>
<td>OG</td>
<td>0.89 ± 0.54 (3)</td>
<td></td>
</tr>
<tr>
<td></td>
<td>Chilliwack</td>
<td>CC</td>
<td>0.35 ± 0.22 (4)</td>
<td>J.S. Richardson (unpublished data)^2</td>
</tr>
<tr>
<td></td>
<td></td>
<td>SG</td>
<td>0.19 ± 0.16 (4)</td>
<td></td>
</tr>
<tr>
<td></td>
<td></td>
<td>OG</td>
<td>0.24 ± 0.04 (2)</td>
<td></td>
</tr>
<tr>
<td></td>
<td>Kootenays</td>
<td>various</td>
<td>0.78 ± 0.23 (7)</td>
<td>Dupuis and Wilson (1999)</td>
</tr>
<tr>
<td></td>
<td>central Cascades</td>
<td>managed</td>
<td>1.01 ± 0.33 (17)</td>
<td>Kelsey (1995)^3</td>
</tr>
<tr>
<td></td>
<td></td>
<td>unmanaged</td>
<td>2.37 ± 0.60 (13)</td>
<td></td>
</tr>
<tr>
<td>Washington</td>
<td>central Cascades</td>
<td>managed</td>
<td>1.01 ± 0.33 (17)</td>
<td>Kelsey (1995)^3</td>
</tr>
<tr>
<td></td>
<td></td>
<td>unmanaged</td>
<td>2.37 ± 0.60 (13)</td>
<td></td>
</tr>
<tr>
<td>Oregon</td>
<td>CC - SG</td>
<td></td>
<td>0.37 (20)</td>
<td>Corn and Bury (1989)</td>
</tr>
<tr>
<td></td>
<td>OG</td>
<td></td>
<td>0.76 (23)</td>
<td></td>
</tr>
<tr>
<td></td>
<td>high harvest</td>
<td></td>
<td>0.101 ± 0.08 (10)</td>
<td>Bull and Carter (1996)^4</td>
</tr>
<tr>
<td></td>
<td>moderate harvest</td>
<td></td>
<td>0.088 ± 0.03 (10)</td>
<td></td>
</tr>
<tr>
<td></td>
<td>low harvest</td>
<td></td>
<td>0.162 ± 0.289 (10)</td>
<td></td>
</tr>
</tbody>
</table>

^1 averaged within and among years (1995-1996)
^2 averaged among years (1996-1999)
^3 includes both tadpoles and metamorphosed individuals
^4 the amount of timber harvest in the surrounding drainage
and Trueb 1994) suggesting that age-specific mortality in amphibians is likely to resemble a Type III survivorship curve (Begon and Mortimer 1986). As no reliable mark-recapture data are available to estimate age-specific survival rates for tailed frogs, I used the combined results of analyses of size-frequency distributions of tadpoles among years (see Appendix 1) with: 1) survivorship estimates obtained for amphibian species with a similar life history; and 2) evidence of longevity of females of 14 years or greater (Daugherty and Sheldon 1982) to infer probable ranges of survivorship values by stage.

For the model, I estimated ranges of survivorship values for the different stages (Table 3.2) as follows. First, plausible larval survivorship values for coastal British Columbia estimated from frequency analysis of larval size classes (see Appendix 1) range between 0.263 (Chilliwack) and 0.36 (Squamish) with coefficients of variation of 14% and 9% respectively. Because these estimates demonstrate a skewed distribution (Figure A1.2) and were obtained from a restricted geographic set of sites, I assumed that a possible range of larval annual survivorship estimates for larval stages across British Columbia could be between 0.25 and 0.5 with annual variation of up to 40%. Because I lacked data, I did not develop different survival rates for small and large tadpoles.

Second, survival rates of eggs and hatchlings are not known from field data. Because in most streams, eggs/hatchlings and tadpoles likely share many of the same sources of mortality, I chose the midpoint of the overall range of larval survival (0.375) as an approximation of the unknown annual eggs/hatchling survival rate. Third, I estimated average annual adult survivorship as 0.8 because a generally high survivorship of adults is necessary to achieve a maximum longevity of 14 years or greater (Daugherty and Sheldon 1982). Finally, I estimated survival of metamorphosed juveniles to be slightly lower than adults at 0.7 because of potentially greater mortality risks than adults from disturbances (e.g., severe flooding) and dispersal (Daugherty and Sheldon 1982; Corn and Bury 1989).

**Fecundity**

Tailed frogs breed in the fall. Breeding females store sperm over winter and lay their eggs (range: 37-85) near the end of spring runoff (Noble and Putnam 1931; Daugherty and Sheldon 1982; Leonard *et al.* 1993) in cracks and crevices in stream
substrate in the upper reaches of inhabited streams (Kelsey 1995). Tailed frog eggs have a narrow thermal tolerance range (5-18°C), and their upper limiting temperature is 18.5°C.

Table 3.2. Estimates of annual survivorship in each life stage defined for tailed frogs. Annual survivorship combines \( P_i \) and \( G_i \). Sources of data are given in parentheses.

<table>
<thead>
<tr>
<th>Stage</th>
<th>Range of years in stage</th>
<th>Mortality factors(^1)</th>
<th>Survivorship estimates(^2) (per capita rate/yr)</th>
<th>Quality of knowledge</th>
<th>Source</th>
</tr>
</thead>
<tbody>
<tr>
<td>1) eggs, hatchling</td>
<td>&lt; 1 yr</td>
<td>predation, erosion, disturbance</td>
<td>0.3-0.4</td>
<td>4</td>
<td>Duellman and Trueb (1994)</td>
</tr>
<tr>
<td>2) small tadpoles</td>
<td>1-2 yr</td>
<td>predation, aperiodic floods, debris flows, high temperatures, dessication</td>
<td>0.3-0.7</td>
<td>2</td>
<td>B.C. data – Appendix 1</td>
</tr>
<tr>
<td>3) large tadpoles</td>
<td>1-2 yr</td>
<td>predation, a periodic floods,</td>
<td>0.5</td>
<td>2</td>
<td>B.C. data – Appendix 1</td>
</tr>
<tr>
<td>4) metamorphs, pre-reproductive juveniles</td>
<td>1-3 yr</td>
<td>predation, dessication, floods</td>
<td>0.7</td>
<td>1</td>
<td></td>
</tr>
<tr>
<td>5) breeding adults</td>
<td>7+ yr</td>
<td>predation, senescence, dessication</td>
<td>0.8</td>
<td>3</td>
<td>(Daugherty and Sheldon 1982)</td>
</tr>
</tbody>
</table>

\(^1\) Major sources of mortality for each stage are given in likely order of importance.

\(^2\) The quality of the underlying empirical knowledge was classed as: 1 - high uncertainty; 5 - certain knowledge.

(Brown 1975). Co-existing, stream dwelling amphibians (e.g., Cope’s Giant Salamander *Dicamptodon copei* or Pacific Giant Salamanders *D. tenbrosus*) and/or fish may prey upon tailed frog eggs (Leonard *et al.* 1993).

Females may breed every year in more productive streams, while Metter (1967) and Daugherty and Sheldon (1982) observed females with a biennial reproductive period in high elevation continental streams. In the latter study, located in Montana, Daugherty and Sheldon (1982) did not observe reproductive maturity in either males or females at less than age 7 and it appeared that first reproduction may occur 1 or 2 years after that. Similar information does not yet exist for coastal streams. By extrapolating from length
of the larval development period in some coastal sites (Brown 1990; Bull and Carter 1996; see above), it is likely that age at first breeding in lower elevation, highly productive sites may be at 5 or 6 years.

In general, increasing annual fecundity is positively related to female body size in many amphibians and reptiles (anurans, Salthe and Duellman 1973; salamanders, Salthe 1969; turtles: Gibbons et al. 1982), and body size and age are generally positively correlated in amphibians and reptiles (Halliday and Verrell 1988). As there are no data on body size–fecundity relationships for tailed frogs, I represented fecundity of breeding adults as a single value, varying this to represent a greater or lesser proportion of the number of females laying eggs in any given year due to long-term average productivity of each site (e.g., a shortened growing season at high elevations).

Habitat Carrying Capacity

For tailed frogs, stream characteristics (e.g., step:pool or pool: riffle area ratios, stream substrate composition, volume of large downed wood; Kelsey 1995; Wahbe 1996; Welsh and Ollivier 1998) interact with channel morphology, bedrock geology, and disturbance to adjacent forest cover composition to determine suitability of habitat for tadpoles (see Chapter 2). The importance of specific factors in setting carrying capacity $K$ may change with life stage and season of the year. Rates of changes in the fine-scale structural heterogeneity of montane stream morphologies of between 1 and 100 years (Hogan et al. 1998; Church in press) imply that average stream habitat carrying capacities are dynamic within the generation time of tailed frog populations and over small spatial scales (e.g., < 100 m). Riparian zones are also dynamic, with disturbances such as windthrow, and flood events altering patterns of succession in habitat structures. Combined with silvicultural activities in the productive riparian zones, carrying capacities of riparian zones for tailed frogs can also be expected to vary within and among-years, although empirical data are lacking.

Estimating ranges of variation in carrying capacity $K$ for the aquatic or terrestrial tailed frog life stages is difficult without time series data. Instead, for this simple site-level model, I adopted the simpler approach of modelling different $K$ values within a range of expected annual variation representing fine-scale spatial and temporal
fluctuations in \( K \). The consequences of these assumptions on estimates of population persistence are evaluated in Chapter 4.

**Density Dependence**

In some amphibian species, rates of larval growth are negatively affected by density, and the size achieved by the larvae have been shown to have an important effect upon the success of later stages in the life cycle (Sinsch 1992). For tailed frogs, determining if and how density dependence acts to regulate populations is problematic for three reasons. First, it is unclear whether density-independent factors, density-dependent factors, or both drive the dynamics of populations of tailed frogs. Recent experimental evidence indicates that larval growth rates show density dependence in tailed frogs (Kim 1999) although the extent of the effects appear masked by a suite of co-varying stream characteristics. Second, assuming density dependent factors do regulate overall population sizes for this species, no time series of density estimates of sufficient length exist to fit a density dependent function to population density. In her study, Kim (1999) found both food limitation and interference competition (possibly for substrates used for attachment) interacted to reduce larval growth rates, even at very low larval densities. Third, habitat segregation between larval and terrestrial life stages suggests the possibility that different forms of density dependence may act upon growth and survivorship in the different life stages confounding interpretations of eventual effects on reproductive rates. It is not yet clear from any other study of tailed frogs if density-dependence affects survivorship in either larval or more terrestrial stages of the life cycle.

Unfortunately, how density dependence is modelled has a strong influence on estimates of population persistence in response to habitat alteration (Alvarez-Buylla *et al.* 1996; Pascual *et al.* 1997; Ratner *et al.* 1997; Grant and Benton 2000). Because it is apparent from Kim (1999) that density dependent factors are operating at least on growth rates of larval stages, I chose to model total population sizes of tailed frogs as being limited by density dependence. I assumed the predominant form of density dependence is a simple contest competition for resources (e.g., food and substrate) using a ceiling at overall habitat \( K \). Under this assumption, population growth is exponential up to \( K \), and some individuals acquire enough resources to reproduce even if effects of density
dependence are strong. If projected extinction rates of populations are low, the trajectories of ceiling models compared with logistic models show little difference, although differences will increase with increasing likelihood of extinction (Foley 1997).

In addition, I assumed that the annual probability of successful mating for each female may be disrupted at very low population densities because of apparent high site fidelity of adults (Daugherty and Sheldon 1982). Thus, I included an Allee effect on reproduction at population densities below one-half of the detection threshold, where likelihood of annual reproduction at those densities declines by 50% due to difficulty of locating mates during the short mating season.

Dispersal

For this local site-level model analysis, I did not explicitly model dispersal between adjacent populations because dispersal patterns in tailed frogs are poorly known. Recent studies indicate that larval tailed frogs can move up to 3.6 m/day (Wahbe unpublished data). Other studies suggest that dispersal ranges in tailed frogs are short at both the individual (Daugherty and Sheldon 1982) and population level (Ritland et al. 2000), as they are in other vertebrates (Sutherland et al. 2000). Consequences of different assumptions about dispersal on patterns of population persistence are evaluated further in Chapter 4.

Modelling Environmental Variation

I modelled two types of stochastic environmental effects on simulated populations: 1) annual stochasticity in stage-specific growth, survivorship and fecundity (range of parameter values are shown in Table 3.3); and 2) infrequent, severe disturbances to streambeds and adjacent riparian habitat (parameter values are shown in Table 3.4). Each of these effects is described in more detail below.

Annual Variation in Vital Rates

Effects of annual changes in growing season length, temperature and precipitation could affect demographic rates in field populations, although no data are currently available to develop parameter estimates. Therefore, I treated each stage-specific vital
rate as a random deviate drawn from a log-normal distribution, with expected values from
the midpoint of the range shown in the selected population matrix (Table 3.3), and a
standard deviation as defined by the particular sensitivity scenario (see below).

Table 3.3. Stage-based projection matrices for tailed frogs based on the mid-points of the
demographic parameters given in Table 3.2. Elements of each matrix can be interpreted
using the format shown in the Stage-based Population Models section for the stages
defined in Table 3.2. Fecundity is expressed in number of female eggs/breeding female.

<table>
<thead>
<tr>
<th>Stage</th>
<th>1</th>
<th>2</th>
<th>3</th>
<th>4</th>
<th>5</th>
</tr>
</thead>
<tbody>
<tr>
<td>0</td>
<td>0</td>
<td>0</td>
<td>0</td>
<td>0</td>
<td>30.000</td>
</tr>
<tr>
<td>0.350</td>
<td>0.287</td>
<td>0</td>
<td>0</td>
<td>0</td>
<td></td>
</tr>
<tr>
<td>0</td>
<td>0.214</td>
<td>0.287</td>
<td>0</td>
<td>0</td>
<td></td>
</tr>
<tr>
<td>0</td>
<td>0</td>
<td>0.214</td>
<td>0.540</td>
<td>0</td>
<td></td>
</tr>
<tr>
<td>0</td>
<td>0</td>
<td>0</td>
<td>0.160</td>
<td>0.800</td>
<td></td>
</tr>
</tbody>
</table>

a). Stage-based projection matrix for tailed frogs for a site with good growing conditions,
showing the ranges of parameter estimates simulated.

<table>
<thead>
<tr>
<th>Stage</th>
<th>1</th>
<th>2</th>
<th>3</th>
<th>4</th>
<th>5</th>
</tr>
</thead>
<tbody>
<tr>
<td>0</td>
<td>0</td>
<td>0</td>
<td>0</td>
<td>0</td>
<td>37.700</td>
</tr>
<tr>
<td>0.315-0.385</td>
<td>0.149-0.194</td>
<td>0</td>
<td>0</td>
<td>0</td>
<td></td>
</tr>
<tr>
<td>0</td>
<td>0.306-0.361</td>
<td>0.149-0.194</td>
<td>0</td>
<td>0</td>
<td></td>
</tr>
<tr>
<td>0</td>
<td>0</td>
<td>0.306-0.361</td>
<td>0.170-0.240</td>
<td>0</td>
<td></td>
</tr>
<tr>
<td>0</td>
<td>0</td>
<td>0</td>
<td>0.460-0.530</td>
<td>0.720-0.880</td>
<td></td>
</tr>
</tbody>
</table>

b). Stage-based projection matrix for tailed frogs for a site with poor growing conditions,
showing the ranges of parameter estimates simulated.

<table>
<thead>
<tr>
<th>Stage</th>
<th>1</th>
<th>2</th>
<th>3</th>
<th>4</th>
<th>5</th>
</tr>
</thead>
<tbody>
<tr>
<td>0</td>
<td>0</td>
<td>0</td>
<td>0</td>
<td>0</td>
<td>23.330</td>
</tr>
<tr>
<td>0.315-0.385</td>
<td>0.310-0.357</td>
<td>0</td>
<td>0</td>
<td>0</td>
<td></td>
</tr>
<tr>
<td>0</td>
<td>0.142-0.190</td>
<td>0.310-0.357</td>
<td>0</td>
<td>0</td>
<td></td>
</tr>
<tr>
<td>0</td>
<td>0</td>
<td>0.142-0.190</td>
<td>0.376-0.446</td>
<td>0</td>
<td></td>
</tr>
<tr>
<td>0</td>
<td>0</td>
<td>0</td>
<td>0.254-0.324</td>
<td>0.720-0.880</td>
<td></td>
</tr>
</tbody>
</table>
Table 3.4. Deterministic states and stochastic events defined for the site-level model.

<table>
<thead>
<tr>
<th>Model component</th>
<th>Parameter value</th>
<th>Ecological interpretation</th>
</tr>
</thead>
<tbody>
<tr>
<td><strong>Deterministic states</strong>&lt;sup&gt;†&lt;/sup&gt;</td>
<td></td>
<td></td>
</tr>
<tr>
<td>population “type”</td>
<td>low or high</td>
<td>local habitat productivity</td>
</tr>
<tr>
<td>average long-term survivorship</td>
<td>low (-10%) or high (+10%) from mean for each stage</td>
<td>site by site variation in sources of mortality (predation, disturbance regime)</td>
</tr>
<tr>
<td>habitat area</td>
<td>5 ha or 20 ha</td>
<td>heterogeneity in area of occupiable habitat among headwater streams</td>
</tr>
<tr>
<td>( K ) (females/m&lt;sup&gt;2&lt;/sup&gt; of occupied habitat)</td>
<td>low: 0.038, intermediate: 0.300, high: 0.540</td>
<td>resource limitation (substrate composition; food supply)</td>
</tr>
<tr>
<td><strong>Stochastic events</strong></td>
<td></td>
<td></td>
</tr>
<tr>
<td>severe disturbance</td>
<td>1:33 years or 1:100 years (90% mortality on aquatic stages; 33% on metamorphs; 0% on breeding adults)</td>
<td>Direct effects of debris flows, triggered by floods, and landslides (duration of effect: 1 year)</td>
</tr>
<tr>
<td>annual fluctuations in survivorship, growth and fecundity</td>
<td>10% coefficient of variation (CV) or 30% CV</td>
<td>annual variation in snowpack, temperature, precipitation</td>
</tr>
<tr>
<td>annual fluctuation in ( K )</td>
<td>10% coefficient of variation (CV) or 30% CV</td>
<td>annual variation in stream structure due to local dynamics in channel morphology and riparian vegetation</td>
</tr>
</tbody>
</table>

<sup>†</sup> see text for definition of the growth and survivorship values for population types

**Infrequent and Severe Disturbances**

Infrequent disturbances such as landslides, debris flows, or windthrow occur in steep montane watersheds (Bovis *et al.* 1998; Church *in press*), and may cause mortality to affected life stages, as well as temporarily reduce habitat \( K \). Based on field observations of intensity and magnitude, debris flows are potentially the most severe of these disturbance types on tailed frogs. Only a debris flow can remove all of the stored material in a stream channel as a single event (Church *in press*). Most gully debris flows are triggered by debris slides that start on steep gully walls during winter rainstorms (Fannin and Rollerson 1993). In high-gradient montane streams, debris flows usually run...
the full length of a gully scouring down to bedrock, because channels are both steep and confined (Lamberti et al. 1991; Bovis et al. 1998). I therefore modelled effects of debris flows upon tailed frogs as causing direct mortality to affected life stages immediately subsequent to a debris flow event (Table 3.4). In the model, larval stages were most affected, and adult stages the least. Even if a debris flow occurs, local refugia for tadpoles may remain in streambeds, and so I retained a proportion of the abundance for each life stage affected. Modelling the effects of other types of disturbances on populations is treated further in Chapter 4.

Design of Sensitivity Analysis

The problem of assessing degrees of risk to a population from an array of possible causes has three components: identifying events that can happen, determining how likely they are to happen, and the consequences if they do happen (Kaplan 1997; Chapter 1). In this analysis, I assumed that eventual loss of the population was the negative consequence of greatest interest for conservation. Therefore my primary indicator of long-term sustainability of the population is probability of quasi-extinction (declining to a low threshold) before a preassigned time period, starting with an initial population size (Haight 1995; Ludwig 1996b, 1999). I also calculated the time (in years) required for 50% of the simulated populations to become quasi-extinct. Other indicators of population status (e.g., population growth rate) were used as needed to evaluate shorter-term behaviour of simulated populations.

Interactions of many biotic and abiotic processes may yield complex outcomes on persistence of populations. In this system, uncertainties about population structure, long-term habitat dynamics, and disturbance regimes are large. Calculation of outcomes rapidly becomes intractable as the number of uncertain parameters increases, because it must be done over a grid of parameter combinations that increases geometrically with the number of parameters (Walters and Ludwig 1993). To evade that difficulty, I chose high contrasts in parameter values to identify plausible bounds for the outcomes. To do this, I designed a complete block, factorial simulation experiment to assess the relative importance of productivity of habitat on growth, survivorship, area of habitat size, K,
infrequent catastrophes, and year-to-year variation in demographic rates and $K$ on eventual outcomes for populations in headwater streams.

I designed a total of 192 scenarios as follows:

1. **Population type:** I defined 2 population types as a function of habitat productivity (increased average growth rates with higher habitat productivity): a “higher productivity” population, with age at first reproduction of 5 years, females breeding every year, and a realized rate of increase of 0.29, compared with a “lower productivity” population with age at first reproduction of 8 years, 40% of females breeding every other year, and a realized rate of increase of 0.02. The chosen values represent growth rates and fecundity levels that capture ranges of these parameters reported in the literature.

2. **Survivorship.** To capture effects of uncertainty in the long-term sources of mortality across the extensive geographic range of the species, I defined two survivorship types: average annual survivorship of each stage increased by 10% or decreased by 10% relative to the assumed mean survivorship for each stage.

3. **Habitat area:** Tailed frog-bearing streams vary in length and width within and among watersheds (see also Chapter 2). Habitat area is an important co-variate of the probability of extinction (Foley 1997), and artificial pond studies show that variation in habitat size affects both survival and growth rates in *Bufo americanus* and *Rana clamitans* tadpoles, although the effects on fitness are complex (Pearman 1993). I defined 2 sizes of montane headwater streams: small (500 m representing source streams), and large (2 km - representing longer streams or a local stream network). For each stream type, I assumed the maximum width of riparian zone to be 60 m, and an average stream width of 2 m.

4. **Carrying capacity $K$.** True population sizes and carrying capacities in tailed frog populations are unknown because of measurement error in stream surveys, difficulties in capturing the terrestrial stages, and lack of among-year samples. After correcting for observation bias (see Appendix 1), I defined 3 levels of maximum population density (females/m$^2$ of habitat): low = 0.038 (approximately double the density at the detection threshold); intermediate (0.30); and high (0.54). These values cover 90% of the observed range of tailed frog densities in
Table 3.1. I assumed a stable age distribution to initialize abundances by stage (but see Bierzychudek 1999).

5. **Severe disturbance events.** I defined two levels of the average annual frequency of a severe disturbance event (storm/runoff events or floods causing a stream-destroying debris flow) occurring at the site: low = 0.01 and high = 0.03, each with a CV of 10%. I assumed that each average debris flow would affect approximately 400 m of stream (Bovis *et al.* 1998), and that the event would remove 90% of the in-stream stages, 30% of the metamorphosed juveniles, and none of the adults per unit of habitat affected. Recovery of the ecological productivity (in particular the epiphytic food supply) of the disturbed stream was assumed to be rapid and linear (i.e. within 2 years; Lamberti *et al.* 1991) although this rate may be unrealistic for some small montane streams.

6. **Annual stochasticity in vital rates.** I assumed two levels of annual coefficients of variation in growth, survivorship and fecundity: low (10%), and high (30%) representing effects of annual variations in climate, habitat productivity, and small scale demographic uncertainties on each life stage.

7. **Annual stochasticity in $K$.** I assumed two levels of annual coefficients of variation in $K$, low (10%) and high (30%), representing different assumptions about the non-catastrophic dynamics of habitats.

The particular scenarios I used are summarized in Table 3.4. Each scenario was replicated 100 times with an annual time step and a time horizon of 100 years. Populations were initialized at 80% of their maximum $K$.

The primary objective of this analysis was to identify the relative contributions of different types of demographic and stochastic variation upon predicted outcomes of population status. Accordingly, I used three methods of analyzing the results. First, under the simplifying assumption that populations are stationary, I calculated proportional sensitivities ("elasticity") in population growth rate caused by proportional changes in one of the life cycle parameters, using Caswell’s (1989) equation:

$$e_i = \frac{\partial \log \lambda}{\partial \log a}$$  \hspace{1cm} (3.1)
where:

\[ \lambda \] is the population growth rate (dominant eigenvalue of the population matrix);
\[ a_i \] is the parameter value for stage \( i \);
\[ e_i \] is the elasticity of \( \lambda \) with respect to \( a_i \).

Because proportional sensitivities of stationary populations sum to 1 (deKroon et al. 1986; Grant and Benton 2000), the relative contribution of each life cycle parameter to the overall population growth rate can be directly compared.

Second, I evaluated the contribution of each factor to the indicators of population loss. My primary indicator of model population vulnerability is the probability of quasi-extinction (dropping below the detection threshold) over the 100 simulation periods (hereafter termed PrQE\(_{100}\)). I also estimated median time to quasi-extinction (number of years required for 50% of the simulated populations to drop below the detection threshold). Note that these populations may not become extinct, just decline to levels below our ability to detect them with current survey efforts. I examined resultant levels of population vulnerability in relation to the different values of the input parameters to understand relationships between the contributions of each simulated factor to PrQE\(_{100}\) in the modelled populations. Because most of the factors used were dichotomous contrasts, and their effects were unlikely to act linearly upon population vulnerability, I used Classification and Regression Tree (CART) analysis to define the relative contribution of each factor to the predicted patterns of probable loss of the populations in preference to other linear methods (see Robinson and Hurst 1997). In addition, I examined relationships between patterns of PrQE\(_{100}\) and ranges of variation in the key life history parameters and levels of annual environmental variation using isocline plots. From these I made inferences about the relative effects of different types of habitat change on long-term risks of loss to populations.

RESULTS

Eigenvalues and intrinsic rates of increase for the population projection matrices in Table 3.4 range from 0.9163 to 1.3700 for \( \lambda_m \) and: -0.0874 to 0.3148 for \( r_m \), covering a
range of potential source-sink population trajectories. Resultant ranges of the stable age
distribution $w_m$ and the vector $v'_m$ of reproductive values showing the value of each
individual of stage $i$ as a seed for future population growth (Caswell 1989) are given in
Table 3.5.

Table 3.5. Ranges of the stable stage distribution ($w_m$) and reproductive values ($v'_m$) for a
hypothetical tailed frog population (expressed as percentages) using the ranges of
parameter estimates contained in the population matrices of Table 3.4.

<table>
<thead>
<tr>
<th>Stage class</th>
<th>Stable stage distribution</th>
<th>Reproductive values</th>
</tr>
</thead>
<tbody>
<tr>
<td>1 (eggs, hatchlings)</td>
<td>58.5-67.0</td>
<td>1.00</td>
</tr>
<tr>
<td>2 (small tadpoles)</td>
<td>22.7-30.4</td>
<td>2.9-3.6</td>
</tr>
<tr>
<td>3 (large tadpoles)</td>
<td>6.5-7.4</td>
<td>11.4-12.6</td>
</tr>
<tr>
<td>4 (subadults)</td>
<td>1.9-2.2</td>
<td>36.8-54.6</td>
</tr>
<tr>
<td>5 (reproductive adults)</td>
<td>2.1-2.8</td>
<td>76.7-118.8</td>
</tr>
</tbody>
</table>

Across the range of population types I investigated, eggs/hatchlings and small
tadpoles dominated stable age distributions. Even in good growing conditions, breeding
adult females are projected to be rare. Reproductive value is low for the first three in-
stream stages, jumps substantially for metamorphic juveniles, and is very high for the last
breeding stage.

**Sensitivity of Population Growth Rate to Variation in Demographic Rates**

The ranges of some of the population parameters for various tailed frog life
history stages (Tables 3.2 and 3.4) indicate that some populations could experience
substantial changes in survivorship or fecundity relative to the estimates in my initial
population matrix. Large reductions could be caused by catastrophic habitat degradation,
while increases may represent improved habitat stability and productivity. To further
investigate this, I simulated 50% changes (reductions or increases) in these parameters
for each life history stage with the remaining matrix components held constant (Figure
3.2). Changes in stages 2-4 were made by reducing (or increasing) the probability of
individuals in that stage surviving to the next year $P_i$, along with the average stage
duration $d$, and recalculating $P_i$ and $G_i$ for each stage using the equations in Crouse et al.
(1987):
Figure 3.2. Changes in the intrinsic rate of increase $r$ of population resulting from proportional changes (50% increase or decrease) in fecundity and survival of individual life history stages in the tailed frog population matrix in Table 3.2 (holding survival/fecundity of the other stages at their baseline rate). The dashed line on both graphs indicates the $r$ estimated for the initial (baseline) matrix.
Reductions of this magnitude in fecundity and survival rates in any stage reduces $\lambda_m$ sufficiently to place populations at or below the point of decline. The effects of such reductions on expected population persistence are most severe for small tadpole and metamorphosed juvenile stages. The remnant pool of older, more fecund individuals may buffer effects of reduced survivorship in breeding adults for a time. Populations experiencing substantial increases in stage-specific survivorship and/or increases in fecundity are most responsive to improvements in these respective rates in the small tadpole and breeding adult stages. In general, any improvement of the chances of surviving in any life stage and/or increasing the fecundity of breeding females may create substantially more robust conditions for long-term persistence.

Under the simple assumption that populations are stationary, for each population matrix $m$ I examined the sensitivity of its finite rate of increase ($r_m$) to proportional changes in the key annual life cycle parameters: stage-dependent growth and survivorship rates, and fecundity of breeding adult females. I examined elasticity in $r_m$ over a range of assumed ages at first reproduction. Resulting elasticities of $r_m$ with respect to $G_i$, $P_i$ and $F_i$ (Figure 3.3), revealed that, on average, $r_m$ was more sensitive to the probability of survival with growth into the next stage (average elasticity for $G_i = 0.545$), than to either the probability of survival and remaining in the same stage (average elasticity for $P_i = 0.319$) or fecundity (average elasticity for $F_i = 0.111$). This suggests that alterations in habitat conditions that affect average habitat productivity will have a proportionally greater influence on population vulnerability than will effects on survivorship or fecundity of females alone.
Figure 3.3. The elasticity, or proportional sensitivity of $\lambda_m$ to changes in survival with growth into the next stage ($G_i$), survival without growth into the next stage ($P_i$), and fecundity ($F_5$). Because the elasticities of these matrix elements sum to 1, they can be compared directly in terms of their contribution to the population growth rate $r$. 

---

5 6 7 8

age at first reproduction (yr)

sensitivity (elasticity)

---

$P_i$

$G_i$

$F_i$
Sensitivity of Persistence Estimates to Environmental Stochasticity and Catastrophes

A major objective of this work is to examine how populations may respond to environmental variation that may be density independent or density dependent in their effects. In general, the majority of scenarios I simulated (127/192 or 66%) created conditions of PrQE\textsubscript{100} > 0.90, while few (4/192 or 4.2%) resulted in PrQE\textsubscript{100} < 0.10. Similarly, more scenarios (55/192 or 28.6%) led to shorter median time to quasi-extinction of < 10 years than median time to quasi-extinction intervals of > 90 years or greater (28/192 or 14.6%). Over all factors, I found that PrQE\textsubscript{100} was significantly negatively associated with factors representing \( K \), and overall survival rate (Spearman correlation coefficients \( r_s = -0.25 \), and \(-0.23\) respectively; \( P < 0.05 \)) and positively associated with any factor representing annual variability (annual probability of catastrophe, annual variation in vital rates, and annual variation in \( K \); \( r_s = 0.28, 0.23, \text{and 0.21} \) respectively; \( P < 0.05 \)). Increased population densities, survival rates, areas of continuous habitat, and growth rates were all significantly positively correlated with increasing median times to quasi-extinction (Spearman correlation coefficients \( r_s = 0.62, 0.48, 0.41, 0.24 \) respectively; \( P < 0.05 \)). No factor examined was negatively associated with median time to quasi-extinction.

Over all scenarios, CART analysis revealed complex interactions between population structure, habitat characteristics and environmental stochasticity in determining PrQE\textsubscript{100} (Figure 3.4). Out of a total explained deviance in the predicted PrQE\textsubscript{100} of 64.1%, \( K \) and extent of occupied habitat accounted for 30.9% of the explained deviance, while survival and growth rates accounted for 21.6%. Sources of annual stochastic variation (variation in vital rates, in \( K \) and probability of catastrophes) together accounted for 11.6% of the explained deviance in PrQE\textsubscript{100}.

Consistent with the among-factor correlations described above, populations with high relative survival rates, higher habitat \( K \) and larger contiguous areas showed generally lower PrQE\textsubscript{100}, than did sites with lower relative survival rates or low \( K \) (Figure 3.4). Of those populations with low overall survival rates, those with slow growth rates (i.e. lower productivity population types) are extremely vulnerable to long-term loss.
Figure 3.4. Hierarchical relationships between different parameters and their effects on the probability of quasi-extinction of a population within 100 years (PrQE\textsubscript{100}). Factors are indicated in bold, along with the percentage of the total deviance in the results explained by that split. Numbers within the end points (rectangles) are the mean probability of quasi-extinction of the population (number in brackets are the number of parameter sets in each node).
Those with higher growth rates are also vulnerable if they experience higher variation in either probability of severe disturbances (average PrQE_{100} = 0.98) or high annual variation in life history rates (average PrQE_{100} = 0.95). Populations with higher survival rates are much less vulnerable to potential losses, only those with low $K$ (average PrQE_{100} = 0.58), or high annual variation in either catastrophes or life history rates have PrQE_{100} above 0.30 (a level consistent with the IUCN "endangered” risk category, IUCN 1994).

Currently we have little empirical understanding of the ecological linkages between alteration of either in-stream (aquatic) habitats, or adjacent riparian forest habitats, and basic life history factors (survivorship, growth, and fecundity rates) for most stream-dwelling species (including tailed frogs). A major question is how sensitive may populations be to potential effects of habitat alteration on life history parameters across the wide range of environmental conditions to be expected over an extensive geographic distribution? To examine this issue, I projected population trajectories for medium density populations occupying the larger habitat type described above (2 km linear length). I systematically varied the survivorship of both the aquatic and terrestrial life stages through four levels (-20%, -6.7%, +6.7% and +20%) of the average survivorship rates for those stages (Table 3.2) across a range of estimates of fecundity and age at first reproduction. I projected each life history scenario under two levels of annual environmental variation: low (using the lower limits of catastrophe probabilities and annual variability in $K$ and vital rates shown in Table 3.4), and high (using the upper limit of those parameters shown in Table 3.4) and examined patterns in PrQE_{100} (Figure 3.5a and b).

In general, fast-growing populations with higher natality appear relatively less vulnerable to loss than are slow-growing populations with lower annual natality. Projections indicate that under conditions of low natural environmental fluctuations, populations reaching age at first reproduction at 6 years can absorb decreases of all but the lowest estimate of survivorship, in either aquatic or terrestrial stages (see left panels in Figures 3.5a and 3.5b). However, under conditions of higher environmental variation, all populations show moderate to very high probabilities of quasi-extinction (0.15 <=
Figure 3.5. Isocones of PrQE_{100} for projected populations in relation to variation in three life history factors (average annual natality rate: number of female eggs/female/year, age at first reproduction, survivorship of aquatic and terrestrial life stages), and environmental stochasticity (compare left and right panels). Shown are a) (this page) annual survival rates for terrestrial stages held constant, and those of aquatic stages varied between the values shown in the four panels. b) (following page) annual survival rates for aquatic stages held constant, and those of terrestrial stages varied between the values shown. See text for description of other assumptions about the model populations.
b)
PrQE_{100} <= 0.90; see right panels in Figures 3.5a and 3.5b) even at high average natality, and lower age at first reproduction, although enhanced survivorship does significantly depress PrQE_{100}, even in fluctuating conditions.

These results suggest that uncertainties in values of basic life history parameters combined with environmental stochasticity have a substantial influence on our ability to project potential long-term sustainability of populations under many site conditions. Eventual extirpation of populations is possible in a wide range of possible site types and population structures (conditional on uncertainty in environmental variation). However, because some forestry practices (road construction, stream crossing, cross-stream yarding) and other disturbances will likely have different degrees of impact on streams and adjacent riparian habitats, the question arises: could differential habitat disturbance affecting growth and survivorship in larval vs. juvenile/adult stages potentially alter the risks of such losses?

To examine this question, I re-expressed results of Figure 3.5 by examining how PrQE_{100} responds to a range of survivorship rates in stages primarily dependent on conditions on one habitat (holding those in the other constant) across variation in age at first reproduction and natality (Figure 3.6). Although results are dependent on the suite of parameters chosen for study, I found that altered survivorship in either larval stages, or older terrestrial stages, yielded very similar patterns of PrQE_{100}. Effects of altered life history parameters on PrQE_{100} for populations with contrasting levels of environmental stochasticity are lowest for fast-growing sites and highest for slow-growing populations (Figure 3.6). This result is intuitive because the dominant factors affecting potential loss of populations in fast-growing sites are variation in environmental conditions themselves. Incremental changes in life histories have comparatively less impact. At the other extreme (slow-growing populations), most populations are already at some risk, and incremental changes in life history become relatively more important in altering the patterns of risk than do levels of environmental variation. However, there is little detectable difference on long-term risk of variation in survivorship rates between larval versus juvenile/adult stages.
Figure 3.6. Effects of uncertainties in age at first reproduction, survivorship $S_i$ in each habitat (stream or riparian), fecundity and annual environmental variation on $PrQE_{100}$ of a simulated local population of tailed frogs. Left panels represent variation in annual survivorship of stream-dwelling stages while holding survivorship in terrestrial-dwelling stages constant. Right panels represent variation in annual survivorship of terrestrial stages while holding survivorship in stream-dwelling stages constant. Assumptions for environmental variation are 10% CV each year (top panels) and 30% CV each year (bottom panels). Each lines represents a different assumption (--- 17.5; ---- 20; ----- 25; ------ 30; -------- 35) of average annual natality (# female eggs/female/yr). Error bars show the 90% prediction interval of the dependent variable over all sources of variation (demographic, environmental, survivorship).

DISCUSSION

Population models for amphibians are difficult to parameterize (Halley et al. 1996). The analyses here are intended to clarify likely responses of populations to plausible ranges of variation in key demographic parameters rather than prediction (Grant and Benton 2000). The results indicate that if life history traits of tailed frog populations across its geographic range are within the ranges estimated here, then habitat protection
measures should be aimed at both maintaining habitat productivity within and along headwater streams and reducing mortality risks for terrestrial stages. In portions of their range with higher year-to-year variability in habitat productivity, or in zones of higher disturbance frequency (e.g., steep stream escarpments or unstable slopes; Bovis et al. 1998), small populations may become vulnerable from the cumulative effects of habitat alteration due to loss of forest cover and sedimentation into streams. Even if stream habitats recover quickly following disturbances (Corn and Bury 1989; Lamberti et al. 1991), even small increases in likelihoods of local extirpation of tailed frog populations is of conservation concern. Many northern populations appear to be locally disjunct (Dupuis et al. 2000; Ritland et al. 2000). Distribution patterns in more southerly populations have yet to be described. If populations in at least some parts of the range are partially or wholly isolated, and if adults in at least some populations show high site fidelity (Daugherty and Sheldon 1982), then recolonization of many formerly occupied sites may be unlikely following habitat-altering disturbances in occupied streams and their associated riparian zones.

The effects of three types of uncertainties on eventual outcomes (persistence or probable extirpation) for tailed frog populations may be ordered as: 1) fundamental demographic characteristics of tailed frogs; 2) area and carrying capacity $K$ of aquatic and terrestrial habitats; and 3) both among-year and among-site variability in these parameters. In the first category, survivorship, earlier age at first reproduction, and fecundity were primary determinants of eventual outcomes for populations; effects of all other factors are conditional on assumptions about these values. In the second, size and $K$ of both terrestrial and aquatic habitats determined responses to perturbation; populations in larger and/or more productive habitats remain robust to environmental fluctuations for many possible growth and survivorship conditions, although effects on aquatic stages have greater consequences. In the third, annual variation in $K$, vital rates and probability of catastrophic losses influence the probability of long-term extirpation for many populations, but the added increases in probability of loss through these effects do not substantially alter the already high likelihood of declines in populations occupying slow-growing, unproductive site types. From these results, I infer that many populations of the tailed frog are likely to be at higher risk from slow-acting, cumulative effects of
habitat alteration (loss of riparian habitat area, and gradual declines in habitat $K$) than from short-term impacts of streambed disturbance, or the immediate impacts of forest harvest.

Can these projections of potential threats to tailed frog populations under different sources of uncertainty be interpreted in terms of criteria determining threats to species? Under present World Conservation Union criteria, a species is considered vulnerable if its probability of extinction is greater than 10% over 100 years (IUCN 1994). From my results, most populations with age at first reproduction averaging 6 years or greater should be considered vulnerable (see Figure 3.5a and 3.5b). Climatic conditions associated with increasing latitude and elevation may increase age at first reproduction and thus more northerly and higher elevation populations may be at increasing risk. Over a large geographic area and time frame, eventual losses of such vulnerable populations may accumulate to have significant conservation consequences (such as loss of genetic substructure, or potential to recolonize habitats). If realized environmental variation becomes as high as I have assumed in my disturbance scenarios, then all populations are likely to eventually become vulnerable by these criteria. Protection measures that effectively reduce long-term variance in demographic rates should be investigated, at least in less productive sites.

**Life History Strategies and Potential Responses to Habitat Perturbation**

Life history characteristics for a species present a balance among the relative benefits of growth, and reproduction, with risks of mortality (Schaffer 1974; Roff 1992; Stearns 1992). Tailed frogs demonstrate a multi-year larval period in streams (Appendix 1), a long-lived breeding adult stage (Daugherty and Sheldon 1982), and probable low average fecundity (Kelsey 1995) compared with other amphibians (Duellman and Trueb 1994). These general life history traits seem to fit the profile of a species adapted to conditions of higher and more variable risks of juvenile mortality compared with those of adults (Duellman and Trueb 1994). In general, aquatic larval habitats for amphibians are generally more productive but less predictable than terrestrial habitats (Werner 1986). Consequences of disturbances and habitat alterations upon long-term sustainability of tailed frogs and other stream-dwelling amphibian species could therefore depend strongly
on how these processes alter relative growth and mortality schedules in each habitat (stream versus the adjacent riparian zone). In this analysis, I found the relative risks faced by juveniles and adults were similar in their effects on long-term probabilities of persistence. Shaffer (1974) noted that the evolution of reproductive schedules and energy allocation in organisms depends on the relative degrees of uncertainty faced by juveniles and adults. In most vertebrate species, juveniles and adults experience the environment on different time and space scales but it is less clear how different these scales actually are in tailed frogs. Under the assumptions I used, both larval and adult stages experience a time scale of between 0 to over 5 years, and a spatial scale of 1 m up to 1 km. Better information on the scale over which adults range would clarify the roles of stage-dependent susceptibility to risks in shaping overall population responses.

Disturbances and harvesting in riparian forests alter physical, chemical and biological processes and features that structure stream ecosystems and determine abundances of stream-dwelling fish and amphibians (Murphy et al. 1986; Lamberti et al. 1991; Young et al. 1999). Studies comparing tailed frog abundance in streams flowing through stands of different ages show high variation in results within and among studies (Richardson and Neill 1998; Dupuis and Steventon 1999; Bunnell et al. 1999a). Some show negative effects following harvest (see Metter 1964; Bury 1968; Corn and Bury 1989; Kelsey 1995), others have found no apparent or even positive effects following clearcutting (see Bury et al. 1991b). Ecological and methodological factors may contribute jointly to creating these ambiguous results. Broadly, topographic and geological determinants of stream carrying capacities vary considerably over the known range of the species (Chapter 2) and sampling is often not designed to account for this source of variation. Natural variation in year-to-year climate regimes between sites may also affect rates of growth, reproduction and mortality. Fine-scale stream channel morphology (e.g., pool-riffle and step:pool ratios) composition of stream substrates are related to observed densities of tailed frog larvae (Kelsey 1995; Wahbe 1996; Dupuis and Steventon 1999; J.S. Richardson unpublished data). In headwater streams, processes that structure these morphological characteristics appear to operate at approximately the same spatial scale as do many stream surveys (10 – 1000 m; Bovis et al. 1998; Church in press) potentially confounding the two sources of variation. Finally, most current data
are obtained primarily from chronosequence studies of larval stage abundances across stands of different ages. Sampling in larval surveys exhibits considerable measurement error (J.S. Richardson *unpublished data*). Experimental studies of the processes by which habitat structure determines growth, mortality and reproduction in stream-dwelling amphibians remain rare. When such studies have been done they indicate tight coupling between forest and stream structures determining growth, and density dependence (Kim 1999). Whether such coupling also exists in habitat factors determining survivorship (e.g., catastrophic mortality, predator-prey relationships) is not yet studied.

Richardson and Neill (1998) and Bunnell and Huggard (1999) suggested that a useful way to interpret the multiple effects of forestry practices on headwater stream-dwelling amphibians is to consider how each effect influences primary production, rates of sedimentation, and inputs of organic debris. At present, three major processes linked to logging and related disturbances appear important in determining responses of stream-dwelling amphibians: (1) changes in cover, aeration and flow patterns associated with downed wood; (2) changes in incident radiation affecting periphyton productivity and stream temperatures; (3) changes in sedimentation rates (Hawkins *et al.* 1983; Welsh and Ollivier 1998). Primary production determines food supply for larvae via growth and availability of periphyton, and is directly 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 is an inverse function of velocity (Leopold *et al.* 1964). In high elevation streams, volume of sediment is strongly related to the probability of bedrock failure (Church *in press*), and the degree of exposed soil surface (e.g., created by roads, cutbanks; Forman and Alexander 1998). Inputs of large woody debris affects stream channel morphology in small montane streams, and such habitat characteristics as pool:riffle or step:pool ratios, wetted width, and substrate composition are determined by the combined effects of sedimentation and the volume of woody debris entering the stream (Tripp 1998).

How these processes interact to affect populations is contingent on geomorphological characteristics of watersheds (Chapter 2). Populations in high gradient streams may benefit from increased primary productivity due to harvesting, while for populations in lower gradient streams such putative benefits may be negated by the
effects of accumulation of fine sediments. In addition, some effects may be transient because regrowth of trees after clearcutting happens quickly in small streams (Corn and Bury 1989). Long-term negative consequences of shading due to second-growth stand structure may become more important to populations than the initial short-term increases in productivity in clearcut areas (Wahbe 1996; Richardson and Neill 1998). The results of this study suggest that even relatively small decreases in survival and growth rates related to habitat perturbations place populations at considerable risk of decline and loss, whether those changes occur in the streams, or in adjacent riparian zones. If losses occur, populations in affected streams may recover only slowly because long-distance dispersal events for stream-dwelling amphibians appear rare (Daugherty and Sheldon 1982; Johnston 1988).

Estimating the likely effects of disturbance in the riparian zone, or losses of upslope forest habitats on life stages of tailed frogs dependent wholly or in part on terrestrial habitats (pre-reproductive juveniles and breeding adults) is difficult with present knowledge. Sufficient captures of juveniles and adults to infer demographic consequences of habitat alteration are uncommon in most studies (see Daugherty and Sheldon 1982; Bull and Carter 1996 for examples). Recent evidence indicates that adults in coastal sites are found up to 100 m from the nearest headwaters even in disturbed sites, although most are found within 35 m of streams (Gomez and Anthony 1996; Matsuda and Richardson in press; Wahbe unpublished data). My exploration of the sensitivity of populations to altered growth and survival of terrestrial stages suggests that maintaining long-term persistence of the species is as dependent on maintaining high survivorship in these stages, as it is on the aquatic stages. In addition, although not considered in this study, maintaining the ability of adults to return to streams for reproduction may be a significant additional component of population persistence.

Taken together, the results of this chapter suggest that for this species, prescriptions for protection of their riparian habitats need to account for site-to-site variation in habitat productivity as well as the longer-term cumulative effects of landscape management on $K$. My simulations suggest populations are at greater risk from habitat alterations altering growth and survival rates over a multi-year period than from year-to-year environmental variability, especially if they live in less productive
sites. Habitat protection options for headwaters need to consider sustaining the stability and average productivity of both streambeds and the riparian zone over long time periods to be effective.
CHAPTER 4. EVALUATING EFFECTS OF UNCERTAINTIES AND MANAGEMENT ON LANDSCAPE-LEVEL PATTERNS OF POPULATION RISK

INTRODUCTION

One fundamental goal of maintaining biodiversity in managed ecosystems is preservation of species (Franklin 1993; Montgomery et al. 1994; Bunnell 1997). In forested ecosystems, each species interacts with its environment at a variety of spatial and temporal scales (e.g., centimetres to hundreds of kilometers, and hours to centuries; Holling 1992; Levin 1992). Consequences of forestry practices and disturbances can be measured and assessed across a similarly wide range of scales (Bunnell and Huggard 1999). Thus, scale interdependencies between species demography, key habitat elements, and forest practices currently confound efforts to project consequences of alternative forest management options on species. Developing forest management strategies that have sufficient generality to be practical, and yet are sufficiently linked to causal ecological mechanisms to be effective, remains a key challenge in attaining this goal (Bunnell and Huggard 1999).

The difficulties engendered by considering multiple space-time scales become especially problematic when managing forest-riparian ecosystems. Because of their species richness, productivity, broad range of ecological function, and density on the landscape (Bunnell et al. 1999a), riparian zone management is a central concern in applications of ecosystem management principles to forestry (Swanson and Franklin 1992; Clayoquot Scientific Panel 1995; Young 2000), as well as in more specific strategies to protect water quality and species of economic or conservation interest (e.g., Ministry of Forests and Ministry of Environment 1995b). Forestry practices affect nearly every ecological process in riparian systems (see reviews of Meehan 1991 and Young 2000). Natural disturbances and harvesting in the riparian zone remove cover, change recruitment rates of downed wood into streams, and may increase sedimentation rates (Hartman and Scrivener 1990; Bilby and Ward 1991; Hicks et al. 1991; Nakamura and Swanson 1994; Ralph et al. 1994; Waters 1995). These changes in turn can reduce streambank stability, alter stream morphology and aeration, change flow patterns associated with downed wood, and increase water temperature (Holtby 1986; Murphy et al. 1986; Lamberti et al. 1991; Belt and O’Laughlin 1994). Many of these changes affect
autochthonous and allochthonous energy pathways for stream-dwelling organisms through their effects on incident radiation and the types and timing of organic matter entering and leaving streams (Murphy and Hall 1981; Beschta et al. 1987; Bilby and Bisson 1992). Short and long-term responses of resident species to this complex of biological, physical and chemical changes arise from their integrated responses to these multiple habitat attributes that themselves are changing on different time and space scales (Young et al. 1999).

Two classes of hypotheses have been proposed to explain responses of stream-dwelling amphibians to forest harvesting and disturbances. The first class focuses on developmental rates and relates response patterns in larval abundance to light induced changes in habitat productivity and food supply created by removal and subsequent regrowth and succession of riparian vegetation (Richardson and Neill 1995, 1998; Wahbe 1996; Kim 1999). The second class focuses on effects of changes in stream and riparian areas on survivorship of different life stages to older age classes (Richardson and Neill 1995, 1998; Wahbe 1996; Dupuis and Steventon 1999). For example, clearcuts may reduce larval survival to older age classes through direct mortality due to the harvesting disturbance, loss of habitat refugia from sediment intrusion into streams, or a combination of both processes (Richardson and Neill 1998). Net changes in abundance and distribution over time may occur if harvest-induced changes in habitat productivity and stage-dependent survival exceed the capacity of a species to absorb their effects. However, present uncertainties about life history attributes of most species, and the relative effects of changes in productivity and structural changes in key habitat variables on populations, renders anticipation of most ecological consequences of riparian management options difficult (Walters and Korman 1999).

In this study, I investigate the effects of several sources of uncertainty on our ability to infer long-term consequences of forest management and habitat protection options. I focus on the tailed frog (Ascaphus truei, Stejneger), an amphibian species dependent on small montane headwater streams in western North America. Amphibians are often considered as indicator taxa for monitoring effects of ecosystem perturbations (Blaustein et al. 1994; Pechman and Wilbur 1994) that may have complex local causes including effects of habitat alteration due to forestry practices (see deMaynadier and
Hunter 1995, and Alford and Richards 1999 for recent reviews). Tailed frogs are potentially vulnerable to forestry practices and disturbances throughout much of their range (Dupuis and Steventon 1999), and options for protecting habitat and populations are both potentially expensive and of unknown effectiveness (Bunnell and Huggard 1999).

Using a stochastic and spatially-explicit population-forest/stream disturbance model, I examined the effects of uncertainties in tailed frog demography, ecological responses to disturbance, and the frequencies and extent of anthropogenic and natural disturbances upon projected patterns of population loss and eventual extirpation in a managed landscape. I developed alternative but plausible hypotheses linking demographic parameters to changes in habitat structures, each of which has different implications for the long-term consequences of forest and riparian management. By comparing outcomes of broadly different scenarios, I evaluated the consequences of present gaps in our understanding of linkages between forest management effects and species demography upon our ability to select effective habitat protection options.

METHODS

To simulate effects of uncertainty in ecological relationships and consequences of management governing likely persistence of tailed frog populations in headwater stream habitats, I developed a stochastic, spatially explicit metapopulation – landscape dynamics simulation model. In this raster-based model, I link occupancy of habitats to population and metapopulation phenomena, using models of population growth and mortality, movements among habitats, and habitat dynamics. Fates of tailed frog populations in each occupied stream cell were projected assuming stochastic variation in environmental and demographic parameters. To evaluate uncertainties about the processes linking habitat characteristics to population dynamics, I invoked a partially nested set of plausible models relating effects of disturbances on demographic parameters. Under alternative forest and riparian management scenarios, I examined the consequences of uncertainty about processes and parameter values on patterns of population persistence. I developed all models using SELES (Spatially Explicit Landscape Event Simulator; Fall and Fall in press). Below I present an overview of the models, descriptions of the
scenarios and methods of analysis. A more detailed description of model relationships, parameter values and sources used to develop them is given in Appendix 2.

Model Overview

Stochastic processes I modelled included local (cell-level) population dynamics, movements and dispersal by different life stages, disturbance events in forests and streams, and ecological succession of habitats (stream morphology, riparian and upland forest vegetation). The primary spatial unit is a 1-hectare cell, representing a reasonable lower limit for modelling harvest activities and other disturbances without being too computationally demanding. Component models operated in one-year time steps, although shorter time steps (e.g., several days) were used in selected events (e.g., fires) to simulate contagion among cells. Dynamics were modelled in the following order: population dynamics, summer disturbances to riparian and upland forests, fall succession of streambed structure and forest vegetation, and fall-winter disturbance events (floods, debris flows).

Local Population Dynamics

I considered the landscape as a network of small headwater streams and adjacent riparian forest, non-riparian operable forest, and inoperable areas (including subalpine forest, and non-forested areas such as alpine and lakes). Using this representation as a basis, I projected population dynamics of tailed frogs using a stochastic female-only stage-based population model (see Chapter 3) in each occupied habitat cell. Given uncertainty about the spatial linkages between populations in nature, I use the term “population” to refer to those tailed frogs occupying each habitat cell whether they were isolated from neighbouring habitat cells or not. For a given population, I assume that the population rate of increase in each cell \( \lambda_c \) is largely determined by characteristics of its habitat, with additional components of demographic variation representing the average effects of random events on individuals in the population. I modelled ontogenetic habitat differentiation in this species as follows: egg and larval stages occupy stream cells, metamorphosed juvenile and breeding adults occupy adjacent riparian habitat cells, and both stream and forested cells represent potential dispersal habitats. Each life stage is
subject to annual or supra-annual variation in demographic rates, carrying capacities in each habitat type, disturbance events, and succession of habitat states. Dispersal of larvae and post-larval stages among habitat cells is simulated with an individual-based movement model (see below).

In each occupied cell at location \((x,y)\), I assume that the demographic response of each life stage to its habitat is a function of habitat state, habitat configuration (e.g., the relative spatial position of forest types and age classes, the juxtaposition of substrate types in stream channels), and the effects of events in the landscape (e.g., windthrow, floods, harvest operations, fires) on growth, fecundity, survivorship and movements. The state of each habitat cell is a function of a vector of attributes \(z(x,y)\) at that location (e.g., stream substrate class, area of riparian and upslope disturbance, and forest age class distribution). Processes occurring in cells in other parts of the landscape (e.g., upslope erosion, road construction, and disturbance) may additionally influence this state as a function of distance, topography and type of disturbance. Over the landscape, I estimated patterns of the species’ distribution and abundance through time by combining responses to habitat conditions at each occupied location \((x,y)\), the rate and direction of movements of individuals across the landscape, and random effects.

For simplicity, I ignored potential interspecific effects (such as predation) on modelled populations. Not only are estimates of the importance of these effects unknown for this species, but their inclusion further complicates the transfer of information about population processes to projected persistence patterns.

Movements and Dispersal

Populations in each habitat cell are subject to emigration and immigration by both tadpoles and juveniles/adults. Downstream movements by tailed frog tadpoles occur and both rates and distances moved appear higher in old-growth sites than in clearcut sites, possibly because woody debris in streams adjacent to clearcuts impedes movement, or old-growth sites are less productive (Wahbe and Bunnell in press). Movement data for juveniles and adults are sparse. In one study of a continental population, Daugherty and Sheldon (1982) found that 50% of reproductively mature adults remained within a 20 m segment of stream, although it is possible they could not detect more infrequent long
distance movements. Other studies using pitfall arrays in coastal forests have found metamorphosed tailed frogs up to 400 m from streams, suggesting the potential for dispersal movements through riparian and upland forests (e.g., McComb et al. 1993; Gomez and Anthony 1996), although it is not yet known how forest harvesting may affect that potential.

In general, I modelled tailed frog movements as a stochastic process through habitat cells (cells containing streams or riparian habitat). I modelled movements of individual juveniles and adults, and those of groups of tadpoles, with group size drawn from a negative exponential distribution. The probability of a successful movement of an individual or group from a source to a destination cell was dependent only on the distance to neighbouring habitat, the degree of forest disturbance in destination cells, and site fidelity of animals, with an upper bound placed on the maximum distance moved by any individual. That is, the dynamics of each originating cell are assumed not to affect other populations enough to cause increased immigration from them. These simplifying assumptions avoid complex and detailed density-dependent movement modelling for which data are not presently available.

Both rate of emigration from and immigration to a habitat cell were modelled as dependent on present population density, and thus indirectly on effects of disturbance and habitat carrying capacity. The per capita rates of emigration for both tadpoles and adults groups are assumed to be normal random variables. Emigration could be directional: tadpoles are more likely to move downstream (Wahbe and Bunnell in press), juveniles show no directional preference, and adults are more likely to move upstream (Leonard et al. 1993). I assumed that the likelihood of moving to an adjacent habitat cell is negatively related to the degree of disturbance in the adjacent cell for juveniles and adults, but not in tadpoles. If a selected destination cell is at carrying capacity, animals continue moving, otherwise they are added to the population of that habitat cell. Mortality rates of moving animals were assumed to be constant and thus independent of distance moved.
Landscape Dynamics

I modelled several types of disturbance events and key processes assumed to govern succession and recovery of forest and stream habitats (see Appendix 2 for details). Streambed and surrounding riparian zones are subject to disturbances including landslides, flood events, debris flows, and the effects of forest disturbances such as windthrow, fires, and road construction (Swanson and Dyrness 1975, Gregory et al. 1991, Swanson et al. 1998). Principal disturbances modelled were: natural disturbances (fires, windthrow, floods, and debris flows in streams), and harvesting (clearcutting, and presence of roads), as well as interactions between disturbances. Depending on the type, disturbances may cause direct mortality to affected life stages, or they may cause reduction in habitat productivity and physical space. I chose disturbance events based on their known effects on tree canopy, vegetation succession, microclimate, sedimentation, and stream morphology.

Removal of forest vegetation affects these disturbance processes to varying degrees. For example, an acceleration in the supply rate of both large woody debris (LWD) and sediment to streams tends to occur following harvest (Bovis et al. 1998). Both the frequency and the size of small landslides increase following harvest because of yarding disturbances to sidewalls, through root decay leading to loss of soil strength over time (Sidle et al. 1985), and from the downslope side of forest road segments during heavy rain events (Jones et al. 2000). Depending on topography, terrain stability, frequency of high intensity rainfall events and volume of downed wood in streams, the accumulated bedload may trigger a debris flow (Bovis et al. 1998; Church in press). After the passage of a debris flow, a gully channel is usually scoured to bedrock or to less erodible basal till, and the processes of sediment and LWD recharge begins again.

Flood and debris flow event models were used to simulate effects on stream structure and associated riparian vegetation. Effects of disturbances on montane forest (including riparian forest) structures were simulated using logging and stand initiating fire models. Spatial relationships were simulated for disturbance events. For example fires and harvesting, once initiated in a forested cell, could spread to any neighbouring cell (or cells) unless conditions in those cells prevented further spread. Effects of
disturbances in forested cells on riparian and stream cells accumulated downslope with their severity diminishing with increasing distance. Similarly, debris flows, once initiated within a stream cell, could cascade down a stream reach until one or more conditions prevented further spread. Contingencies between disturbance types (e.g., removal of vegetation increasing the probability of a debris flow) were treated as functions of conditional probabilities between the event types, biophysical characteristics of the landscape, and applicable management policies.

Substrate condition in each stream cell was modelled as one of three disturbance states ("aggraded", "stable", "degraded") derived from the classification system presently used to assess condition of fish-bearing streams in British Columbia (Ministry of Forests and Ministry of Environment 1996). A particular stream cell may undergo a number of state transitions during a sufficiently long time interval, with probabilities determined by the state of neighbouring stream and forest cells, topography, climate and time since last transition. Each state determines carrying capacities $K$ for larvae, and state transitions affect larval survival. Effects of vegetation changes in forested cells were modelled as accumulating downslope to the nearest stream cells, and these accumulated changes influence the probabilities of transitions between states of stream cells, as do debris flow events.

Forest and streambed recovery from disturbance was also modelled. Vegetation succession after disturbance was modelled as a function of time since the last stand-initiating disturbance, and type of forest (riparian and non-riparian forest). For the purposes of this study, I made no attempt to model details of vegetation structure and species composition as functions of biogeoclimatic context, site characteristics, and previous disturbance history.

Probabilities and processes defining disturbances and habitat succession were modelled at three spatial scales (0-1 ha, 1-1000 ha, > 1000 ha) depending on type, and at two temporal scales (1 day to 1 month, and 1 year).
Response Variables

I tracked the projected numbers of tailed frogs in each occupiable habitat cell in each year. For this analysis, I considered 3 as the minimum threshold for breeding female abundance in each cell. If populations in cells were below this threshold, I considered them not to be viable (i.e. "quasi-extinct"; Akçakaya 1997) because of potential Allee effects, and difficulty in observing individuals at these low numbers (see Chapter 3). In addition, I required that a viable population be present in a cell for a minimum period of 8 years (the assumed generation time for northern populations of this species) in order to consider that population as established. The occupancy status of each habitat cell was tracked as follows. I considered two pools of cells: the unoccupied pool containing cells not presently occupied by an established breeding population, and the occupied pool containing cells with established populations. If cells changed pools, their last transition status was also determined. Occupied cells became unoccupied if their number of breeding females dropped below the threshold and were tagged as "extinct". If immigrants recolonized extinct cells the cells were considered "newly established". If recolonized cells met the above criteria for successful occupancy, they were tagged as "successfully reestablished" and were added to the occupied cell pool.

From these pools and transition changes, I calculated the following types of response variables indicating the likelihood of potential loss and recovery of the species in time and space. As an overall measure of likely long-term risk of loss of populations, I calculated the proportion of occupied habitat cells that drop below the minimum threshold number of breeding females at least once over a given simulation interval (PrE, where i = length of simulation; see Chapter 3). Interpreted as a probability, this measure is widely used as a measure of threat (Akçayaka 1997), although over very long time intervals PrE values will tend to unity as a consequence of the theory of stochastic processes (Ludwig 1996b). In addition, I calculated the time (in years) required for 50% of the populations in the initially occupied cells to become extinct, expressing this as "median time to extinction" (MedTE) for the landscape (where extinction is interpreted as "quasi-extinction" sensu Akçayaka 1997; see above). Finally, as a measure of the potential for population recovery, I estimated the proportion of unoccupied cells that become successfully colonized or recolonized from the "successfully established"
transition described above. Where appropriate, 90% prediction intervals about each response variable were calculated from the results of Monte Carlo runs (see below), and give an estimate of the effects of uncertainty in parameter values on the stochastic response variable (Sæther et al. 2000).

**Hypotheses Linking Habitat State and Demography**

Present data suggest several causal pathways linking effects of harvesting and disturbance events to population dynamics (Richardson and Neill 1995, 1998; Wahbe 1996; Dupuis and Steventon 1999): 1) removal of riparian vegetation increases growth rates of larvae through increased light, temperatures and inputs of organic material and other nutrients into streams; 2) reduced light penetration in second-growth forests reduces food supply for both tadpoles and terrestrial stages via decreased algal production in streams; 3) cumulative sedimentation effects in streams and disruption of log-jam dynamics reduces survivorship in streams and riparian edges; 4) cumulative consequences of riparian and upslope disturbances reduce habitat $K$ for juvenile and breeding adults through loss of physical space. The null ("no effect") hypothesis is that neither disturbances or forest harvests have a detectable impact on populations. Except for "no effect", these pathways are not mutually exclusive and combinations of processes are likely (Richardson and Neill 1998). To date, no study has attempted to distinguish the likelihood of each of these hypotheses on the basis of empirical data.

For tailed frogs, I modelled putative consequences of disturbances and habitat structures predicted by these hypotheses by 1) altering the habitat $K$ of streams and riparian areas for each affected life stage; and 2) altering stage-specific survivorship, growth, and fecundity rates (see Table 4.1). Because few of the specific parameters can be estimated with certainty given present knowledge, I constrained parameters as follows. Parameter changes were bounded such that if the maximum possible cumulative impacts were observed at each cell, the combined effects of all potential impacts would differ by a maximum of $\pm 80\%$ from the mean parameter value. This assumes that very local effects of habitat refugia and habitat heterogeneity could partially buffer populations from extreme environmental effects.
Scenario Design and Analysis

To control the distribution and range of variation in topographic and geomorphological variables related to tailed frog distribution and abundance (Chapter 2), I developed a hypothetical 65,637 ha montane landscape with topographical characteristics similar to many medium-scale watersheds within the range of the tailed frog in British Columbia (Figure 4.1). Biophysical features representative of the southern coastal mountains were assigned using the neutral model capabilities of SELES (see Fall and Fall in press). A quantitative description of the principal features of this landscape is given in Table 4.2.

For the analyses presented below, I simulated 432 scenarios defining combinations of disturbance types, extent of previous habitat disturbance, hypothesized effects of habitat alteration on demographic responses, and dispersal. My approach was to maximize the contrast between effects of each component process by turning each component process (e.g., dispersal) or context (e.g., forest harvesting, natural disturbances) on or off. The resulting scenario combinations are therefore intended to bound plausible ranges of variation about the effects of that component on outcomes. Specifically, I modelled the following processes and contexts:

1. Disturbances (6 states). The primary disturbance types included: (1) no disturbances; (2) natural disturbances (fires, and small (1-2 ha) windthrow events); (3) clearcut forest harvesting without protection of riparian areas; and (4) clearcut forest harvesting with riparian protection using buffers (100% retention of forest volume within a 50m strip on each side of the stream). By combining states (e.g., 2 and 3, 2 and 4), a total of 6 different disturbance regimes were possible.

2. Antecedent disturbance conditions (2 states). I contrasted landscapes that had either been previously harvested, or not. I developed initial landscapes that defined whether or not cumulative effects from previous harvesting and other disturbances on forests, streams, or tailed frogs were present at the start of each simulation (see below).
Table 4.1. Hypotheses relating demographic consequences to tailed frogs of cumulative changes in the habitat variables in each occupied cell. Effects of $H_1$ and $H_2$ relate changes in fecundity and growth of different life stages to changes in habitat productivity, while those of $H_3$ – $H_5$ specify stage-dependent effects on survivorship and carrying capacity $K$ of changes in habitat structure. Changes are relative to baseline rates. For the purposes of this analysis, forest age classes are: $S_0 = 0-10$ yrs (regeneration); $S_1 = 11-20$ yrs; $S_2 = 21-40$ yrs; $S_3 = 41-80$ yrs; $S_4 = 81+$ yrs. Subscripts on demographic variables refer to affected life stages.

<table>
<thead>
<tr>
<th>$H_i$</th>
<th>General description</th>
<th>Relationships</th>
<th>Description $^2$</th>
</tr>
</thead>
<tbody>
<tr>
<td>$H_1$</td>
<td>Fecundity $F$ of breeding adults is related to changes in vegetation succession</td>
<td>linear $\uparrow$ in $F$ with increasing proportion of forest age class $S_0$</td>
<td>$F \uparrow$ up to 30% $\cdot$ yr$^{-1}$ at 100% $S_0$</td>
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<td></td>
<td></td>
<td>linear $\downarrow$ in $F$ with increasing proportion of forest age class $S_3$</td>
<td>$F \downarrow$ up to 30% $\cdot$ yr$^{-1}$ at 100% $S_3$</td>
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<tr>
<td>$H_2$</td>
<td>Growth rates $G$ of larvae and metamorphosed juveniles determined by changes in vegetation succession</td>
<td>linear $\uparrow$ in $G_{2,4}$ with increasing proportion of forest age class $S_0$</td>
<td>$G \uparrow$ up to 30% $\cdot$ yr$^{-1}$ at 100% $S_0$</td>
</tr>
<tr>
<td></td>
<td></td>
<td>linear $\downarrow$ in $G_{2,4}$ with increasing proportion of forest age class $S_3$</td>
<td>$G \downarrow$ up to 30% $\cdot$ yr$^{-1}$ at 100% $S_3$</td>
</tr>
<tr>
<td>$H_3$</td>
<td>Survivorship $S$ of larvae and metamorphic juveniles declines as a function of extent of disturbances in riparian and upland forest</td>
<td>linear $\downarrow$ in $S_{2,3}$ with increasing area of forest disturbed</td>
<td>$S \downarrow$ up to 20% $\cdot$ yr$^{-1}$ at 100% area disturbed</td>
</tr>
<tr>
<td>$H_4$</td>
<td>Survivorship $S$ of larvae and metamorphic juveniles is related to changes in vegetation succession</td>
<td>linear $\downarrow$ in $S_{2,3}$ with increasing proportion of forest age class $S_0$</td>
<td>$S \downarrow$ up to 20% $\cdot$ yr$^{-1}$ at 100% $S_0$</td>
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<tr>
<td></td>
<td></td>
<td>linear $\downarrow$ in $S_{2,3}$ with increasing proportion of forest age class $S_3$</td>
<td>$S \downarrow$ up to 20% $\cdot$ yr$^{-1}$ at 100% $S_3$</td>
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<tr>
<td>$H_5$</td>
<td>$K$ of metamorphosed juveniles and adults declines as a function of extent of disturbances in riparian and upland forest</td>
<td>linear $\downarrow$ in $K_{4,5}$ with increasing area of forest disturbed</td>
<td>$K_4 \downarrow$ up to 50% $\cdot$ yr$^{-1}$ at 100% area disturbed</td>
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<td></td>
<td></td>
<td></td>
<td>$K_5 \downarrow$ up to 25% $\cdot$ yr$^{-1}$ at 100% area disturbed</td>
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<tr>
<td>$H_6$</td>
<td>no effect</td>
<td>-</td>
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</tbody>
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$^1$ Life stages are: 1 - eggs/hatchlings, 2 - small larvae; 3 - large larvae; 4 - metamorphosed juveniles; 5 - breeding adults.

$^2$ Variable codes for each life stage $i$ are: $G$ = growth (proportion of each stage growing into the next stage); $S$ = annual survival; $F$ = annual fecundity (# female eggs/female), $K$ = carrying capacity (maximum number of individuals/ha of habitat).
Figure 4.1. Hypothetical montane coastal landscape (65,637 ha) used in modelling and analysis. Shown are age classes of operable forest, principal streams (black), and non-operable forest combined with alpine areas (gray shading to white).
Table 4.2. Biophysical features of the 65,637 ha landscape used in analysis of scenarios. Values for dynamic features (e.g., forest age) represent initial conditions. Percentages are of operable forest.

<table>
<thead>
<tr>
<th>Feature</th>
<th>Range of Values</th>
</tr>
</thead>
<tbody>
<tr>
<td>Elevation</td>
<td>220 m - 2,010 m</td>
</tr>
<tr>
<td>Land cover types</td>
<td></td>
</tr>
<tr>
<td>riparian forest</td>
<td>5,694 ha</td>
</tr>
<tr>
<td>operable forest (riparian + non-riparian)</td>
<td>40,451 ha</td>
</tr>
<tr>
<td>non-operable + alpine</td>
<td>25,186 ha</td>
</tr>
<tr>
<td>Operable forest ages</td>
<td></td>
</tr>
<tr>
<td>0-10 years (regeneration)</td>
<td>991 ha (2.5%)</td>
</tr>
<tr>
<td>11-20 years (sapling)</td>
<td>4,117 ha (10.2%)</td>
</tr>
<tr>
<td>21-60 years (pole)</td>
<td>3,849 ha (9.5%)</td>
</tr>
<tr>
<td>61-140 years (early mature to mature)</td>
<td>12,183 ha (30.2%)</td>
</tr>
<tr>
<td>140+ years (mature to old growth)</td>
<td>19,311 ha (47.7%)</td>
</tr>
<tr>
<td>Stream classification1</td>
<td></td>
</tr>
<tr>
<td>S5 (channel width &gt; 3 m)</td>
<td>5.01 ha</td>
</tr>
<tr>
<td>S6 (channel width ≤ 3 m)</td>
<td>25.94 ha</td>
</tr>
</tbody>
</table>

1 stream classes based on the Riparian Management Area Guidebook (Ministry of Forests and Ministry of Environment 1995.)

3. Effects of habitat on demography (6 states). I modelled hypothesized effects of current habitat condition on the demographic response of particular life stages by combining hypotheses described in Table 4.1 into biologically plausible sets. In order of increasing complexity, these sets are: H6 (no effect), H1 (fecundity effects), H2+H3 (growth effects), H4+H5 (survivorship effects); H2-H5 (growth+survival effects), H1-H5 (growth+survival+fecundity effects).

4. Age at first reproduction (3 states). A priori, I specified one of three ages at first reproduction for each landscape (i.e. age at first reproduction was set externally, not dynamically for each habitat cell), and stage-specific growth and survivorship rates for each age at first reproduction according to the methods described in Chapter 3.
5. *Dispersal of larvae and juveniles/adults* (2 states). I assumed dispersal of instream (larvae) and terrestrial (juveniles/adults) either did or did not occur.

Each scenario was replicated 10 times with an annual time step and a time horizon of 100 years. Pilot Monte Carlo runs showed that increases in overall variance were small after 6-7 runs. For each scenario, populations in habitat cells were initialized from a normal distribution with mean size at 80% of the maximum carrying capacity for that cell, and a standard deviation as specified by the particular scenario. Stream state for each cell was initialized according to probabilities obtained from Hogan *et al.* (1998). For simulations involving landscapes that had previously been harvested, I randomly chose a landscape dynamics scenario, and after projecting it for 100 years, saved the forest age and stream status maps. These maps (defining cumulative effects of previous disturbances affecting tailed frogs) were then used as input to subsequent simulations.

Probability values used in analysis were obtained as follows. For probabilistic outcomes (e.g., PrE_{100}) each model run yielded a proportion of the cells in that simulation meeting that criteria. Because this proportion includes the stochastic variability inherent in the modelled processes, I assumed it was a reasonable estimate of the probability that the outcome would occur for a randomly chosen cell. I assumed that the distribution of probability values obtained from Monte Carlo runs would follow a normal distribution, truncated at 0 and 1. To estimate an upper (conservative) bound on the probability distribution, I computed the value at the 90% percentile obtained from the sample of probability values.

**Statistical analysis**

Prior to statistical analysis, I arcsine transformed all response variables expressed as probabilities. I next examined normal quantile-quantile plots of all data to test for departures from normality, finding most response variables remained significantly non-normal after transformation. I therefore used statistical methods of inference that do not depend strongly on the theoretical form of the likelihood function. I used the following methods to examine results of the model scenarios. First, to assess the overall contributions of the different demographic factors, disturbances, and management options
to variation in the response variables, I used generalized linear models (GLMs, McCullagh and Nelder 1989; Hastie and Pregibon 1992). GLMs can represent a greater variety of relationships between response and explanatory variables than can linear regression models, and do not assume constant variance. For these data I used quasi-likelihood estimation methods (McCullagh and Nelder 1989; Hastie and Pregibon 1992). Quasi-likelihood estimation allows inference about the significance of relationships without requiring that the error distribution of the response variable conform to a particular theoretical distribution. Here, I assumed an approximate log error distribution for the response variable in relation to a set of \( n \) explanatory variables, with its variance centered on the mean (McCullagh and Nelder 1989). I examined other possible error models (e.g., gaussian, poisson, and gamma) and found that inferences were not sensitive to the choice of error model.

Next, I used analyses of variance modelled using GLMs in order to evaluate the relative influence of landscape disturbance types, the habitat change-demographic effect hypothesis, and selected demographic characteristics upon each response variable. For each response variable, I selected the most influential explanatory variables from the candidate set by a forward and backward stepwise procedure (Hastie and Pregibon 1992). At the ends of the spectrum were the null and full model. The null model was simply the mean of the response variable over all scenarios (no effect of explanatory variables) while the full model included all the explanatory variables. Intermediate models used subsets of the variables selected by the forwards and backwards stepwise procedures. For each response variable, I used Akaike's Information Criterion (AIC, Akaike 1974) to select the most parsimonious statistical model. AIC measures the tradeoff between model goodness-of-fit (measured as the log-likelihood) and model parsimony measured by the number of parameters included in the model. Model strength was measured using the percent of deviance explained. This measure is analogous to the multiple coefficient of determination (\( R^2 \)), and measures the proportion of the deviance in the independent variables associated with the deviance in the dependent variable (Cameron and Windmeijer 1997).

Finally, to investigate possible interactions between effects of each management action, disturbance regime and demographic uncertainty, I examined the outcomes
obtained for each input variable with each value of the other input conditions using combinatorial scenario trees. In scenario trees each node represents an uncertain quantity or event, and the path through the tree from root to terminal outcome represents the sequence of conditions and uncertain events forming a specific scenario (Morgan and Henrion 1990).

All statistical modelling was conducted with S-Plus (Mathsoft, Inc. 1998).

RESULTS

Populations in occupied habitat cells exhibited a wide range of trajectories and eventual fates depending primarily on the demographic characteristics of each population, and the assumed effects of habitat changes on the life cycle. Of significant interest in evaluating management are the projected likelihoods that populations will become extirpated. Of the 432 scenarios modelled, 170 (39.4%) resulted in low probabilities of quasi-extinction after 100 years (PrE<sub>100</sub> ≤ 10%), while high PrE<sub>100</sub> (PrE<sub>100</sub> ≥ 90%) were observed in 152 (35.2%) of the scenarios. The suite of demographic characteristics associated with age at first reproduction appeared more influential than did either the presence or absence of other factors such as dispersal, natural disturbances or forest management in determining whether populations in habitat cells are likely to persist or not (Table 4.3). Almost all (96.7%) of the low PrE<sub>100</sub> results came from scenarios using an age at first reproduction of 5 or 6 years. In contrast, 58% of runs resulting in a high PrE<sub>100</sub> came from scenarios based on an age at first reproduction of 7 years. Of the other factors that varied between scenarios, no simple relationship emerged between their state (present or absent) and low PrE<sub>100</sub> (Table 4.3). However, scenarios occurring in previously disturbed landscapes, and occurring in the presence of forest harvesting were more likely to result in a high PrE<sub>100</sub> (Table 4.3).

Movements and dispersal of larvae and juveniles/adults had no apparent influence on projected patterns of long-term persistence of populations (measured in terms of PrE<sub>100</sub>, Table 4.3). Using the assumptions of the movement model, 23.9% (range: 0-60.2%) of habitat cells in which tailed frogs became extirpated were recolonized by immigrants. Over all runs in which movements by tadpoles or juveniles and adults were
Table 4.3. Summary results of simulations across the model’s main factors upon probabilities of quasi-extinction over the 100 year interval (PrE100). Shown are percent of simulations (sample sizes in brackets) resulting in low (≤ 10%) or high (≥ 90%) projected PrE100 results obtained from all habitat cells with established populations. In the table, all scenarios had a specific age at first reproduction (5, 6 or 7), while other treatment factors were either turned on or off for a given simulation. For a given result, columns (response categories and status in each scenario) are mutually exclusive as are ages at first reproduction.

<table>
<thead>
<tr>
<th>Projected response</th>
<th>Age at first reproduction (yr)</th>
<th>Status in Scenario</th>
<th>Treatment factor</th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td>5</td>
<td>6</td>
<td>7</td>
</tr>
<tr>
<td>PrE100 ≤ 10%</td>
<td>(144)</td>
<td>(144)</td>
<td>(144)</td>
</tr>
<tr>
<td></td>
<td>Off</td>
<td>14.2</td>
<td>14.6</td>
</tr>
<tr>
<td>11% &lt; PrE100 &lt; 90%</td>
<td>41.7</td>
<td>20.8</td>
<td>19.4</td>
</tr>
<tr>
<td></td>
<td>Off</td>
<td>13.7</td>
<td>15.3</td>
</tr>
<tr>
<td>PrE100 ≥ 90%</td>
<td>11.1</td>
<td>44.4</td>
<td>77.8</td>
</tr>
<tr>
<td></td>
<td>Off</td>
<td>22.2</td>
<td>18.1</td>
</tr>
</tbody>
</table>

1 landscapes were classed as “previously disturbed” if they were initialized from maps containing prior projections of disturbances and “initial” otherwise (see Methods for details).

2 “natural disturbances” in forests include fires and windthrow, while floods and debris flows occur in streams (potentially also affecting adjacent riparian areas).

3 note that riparian protection is only applicable if there is also forest harvesting being simulated.
modelled, newly established populations persisted for an average of 2.49 (± 1.96) years. However, in only a few cases (< 2%) did populations in recolonized cells persist long enough to become permanently established. To assess potential influences of the basic assumptions in the movement and dispersal model on these results, I systematically altered the effect of each of the following relationships while holding the others constant, as follows: (1) reduce the negative effects of cumulative forest area disturbed on the probability of dispersing to a new habitat cell to 0; (2) increase the maximum distance moved by juveniles and adults to 2 km, (3) increase the proportion of juveniles and adults moving by 50%, (4) decrease the mortality rate of moving animals to 10% (from an average of 50%), and (5) reduce the time interval required to be considered an established population by 50%. Although three of these alterations increased the mean number of habitat cells recolonized per year (reduced disturbance effect, 36.6%; increased maximum movement distance, 99.8%; decreased mortality rate, 49.1%), the other two did not (increased proportion of population moving, -0.31%; decreased time interval for reestablishing a population, 0%). Overall PrE\textsubscript{100} remained unaffected, as did PrE\textsubscript{50} and MedTE. It is likely that in these models stochastic variation in the population growth parameters predominates over the influence of immigration as a process controlling population dynamics.

The apparent importance of local demographic characteristics of populations and alternative hypotheses linking habitat changes with demographic effects on different life stages in determining outcomes was statistically confirmed by the results of GLM analysis. Over all scenarios, the suite of demographic characteristics associated with different ages at first reproduction together with the hypothesis linking habitat change to effects on demography were selected as the most parsimonious factors determining projected population responses across the landscape (Table 4.4). In general, the alternative statistical models I considered explained between 43.8 and 53.4% of the projected variation in the response variables (Table 4.4). From the analysis of deviance results obtained from the statistical model fitting, I found that age at first reproduction accounted for most (> 95%) of the reductions in residual deviance for all response variables, while the particular hypothesis linking habitat changes to demography
Table 4.4. Summary of the GLM analysis of effects of different possible input conditions on the response variables. Shown for each response variable are the most parsimonious statistical model (in bold) along with the next two most parsimonious models for comparison. Summary statistics include the analysis of deviance results and the resulting AIC value. Degrees of freedom for all models are 431 for null model deviance, and 425 for residual deviance. The different input conditions included in the models are described in the Methods section.

<table>
<thead>
<tr>
<th>Response variable</th>
<th>Statistical model</th>
<th>Null model deviance</th>
<th>Residual deviance</th>
<th>% deviance explained</th>
<th>AIC</th>
</tr>
</thead>
<tbody>
<tr>
<td>PrE$_{100}$</td>
<td>AFR + $H_0$</td>
<td>42.67</td>
<td>19.96</td>
<td>53.2</td>
<td>20.53</td>
</tr>
<tr>
<td></td>
<td>AFR + $H_0$ +</td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td></td>
<td>InitialLandscapeState</td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td></td>
<td>AFR + $H_0$ +</td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td></td>
<td>InitialLandscapeState + NatDist</td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>PrE$_{50}$</td>
<td>AFR + $H_0$</td>
<td>42.28</td>
<td>23.70</td>
<td>43.9</td>
<td>24.37</td>
</tr>
<tr>
<td></td>
<td>AFR + $H_0$ + NatDist</td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td></td>
<td>AFR + $H_0$ + NatDist + MgmtType</td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>MedTE</td>
<td>AFR + $H_0$</td>
<td>261.14</td>
<td>146.91</td>
<td>43.7</td>
<td>151.16</td>
</tr>
<tr>
<td></td>
<td>AFR + $H_0$ +</td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td></td>
<td>InitialLandscapeState</td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td></td>
<td>AFR + $H_0$ +</td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td></td>
<td>InitialLandscapeState + NatDist</td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
</tbody>
</table>

1 PrE$_{100}$ and PrE$_{50}$ are probabilities of each cell becoming extinct over 100 and 50 year time horizon respectively. MedTE is the time (years) by which 50% of the populations have become extinct. See Methods for more detailed interpretation of response variables.

2 Codes and their interpretation for input conditions appearing here are: AFR (age at first reproduction), Ho (habitat change-demographic effect hypothesis), InitialLandscapeState (whether landscape was set at initial conditions, or previously disturbed), MgmtType (forest management type), and NatDist (natural disturbances).

accounted for 3.5 - 4.6% of the remaining reductions in residual deviance. Relative to these demographic variables, other factors (e.g., the state of the initial landscape, the type of forest management, presence of natural disturbances, and dispersal capability) contributed little to the projected patterns in the response variables. Residual unexplained variation in all response variables (46.6 – 66.2%) are likely attributable to
the combined effects of stochastic variation in both population dynamics and habitat structures upon projected outcomes.

Projected trajectories of probability of extinction for occupied habitat cells differ substantially among the hypotheses linking changes in habitat state and effects on demography (Figure 4.2), given the particular age at first reproduction. Uncertainties in projecting probabilities of extinction contributed by the selection of the causal hypothesis greatly exceeds that created by the disturbance scenario chosen (compare left and right panels of Figure 4.2). In most cases, all hypotheses linking effects of disturbances on demographic parameters lead to long-term vulnerabilities at least as great or greater than the null (H0: no effect) hypothesis, even if some hypothesized effects may be positive in the short-term (e.g., H2 and H3: project enhanced growth of tadpoles and adults with initial removal of vegetation; enhanced fecundity).

As a framework for ranking the different disturbances and management actions, I constructed scenario trees that combined the uncertain “states of nature” and their projected population outcomes (Morgan and Henrion 1990). In this analysis, uncertain “states of nature” include stochastic events (e.g., whether or not a flooding event occurs), alternative management actions (e.g., whether or not a particular cell is harvested this year), and alternative hypotheses of the effects of each event on the population. Effects of initial landscape state, and the various combinations of disturbance and management policies on eventual population outcomes are apparent, despite wide uncertainty in outcomes due to demographic characteristics (Figures 4.3a and 4.3b). Under any scenario, projected probabilities of losses of populations are significantly more likely in previously disturbed landscapes than on initial landscapes (one-tailed Wilcoxon paired sample tests: \( P_{0.05(1),51} < 0.0025 \) for both PrE100 and PrE50; \( P_{0.05(1),51} < 0.005 \) for MedTE). However, the presence of natural disturbances increased both probabilities and rates of projected loss of populations only in initial landscapes (one-tailed Wilcoxon paired sample tests comparing “natural disturbance” with “no disturbance” scenarios: initial landscapes, PrE100, \( P_{0.05(1),26} < 0.001 \); PrE50, \( P_{0.05(1),33} < 0.01 \); MedTE, \( P_{0.05(1),22} < 0.025 \); disturbed landscapes, \( P_{0.05(1)} > 0.10 \) for all response variables). I found that the presence of forest harvesting activity (with or without riparian protection) significantly increased probabilities of projected loss of populations although not the time to extinction.
Figure 4.2. Upper 90% percentiles of the probabilities of extinction (PrE) of simulated tailed frog populations in occupied habitat cells as a function of simulated period. Left panels are results under conditions of no forest harvesting or natural disturbances, and right panels for both forest harvesting and disturbances. Shown are results for 6 different hypotheses linking habitat structure to population dynamics for a range of ages at first reproduction: 5 years (top panels) to 7 years (bottom panels) in initial landscapes. Individual hypotheses are explained in Table 4.1 and their combinations are described in Methods.
Figure 4.3 (following pages). Scenario trees illustrating the population outcomes associated with each combination of management option, natural disturbance regime, and demographic assumption. Projections over 100 years were made for a landscape that was set to initial conditions (a) and previously disturbed (b). In each figure, the square at the left is the "decision node", and circles represent "chance nodes". The population outcomes shown represent probabilities of extinction at 100 and 50 years (PrE_{100} and PrE_{50} respectively), as well as the median time to extinction for all populations (MedTE). All outcomes represent the upper 90% percentile of their respective prediction interval obtained from Monte Carlo simulations.
(one-tailed Wilcoxon paired sample tests comparing “harvesting without riparian protection” scenarios to “no harvesting” scenarios: PrE100, PrE50, P0.05(1), 26 < 0.0001; PrE50, P0.05(1), 30 < 0.0001; MedTE, P0.05(1), 32 > 0.5 and comparing “harvesting with riparian protection” to “no harvesting” scenarios: PrE100, P0.05(1), 26 < 0.0001; PrE50, P0.05(1), 50 < 0.002; MedTE, P0.05(1), 26 < 0.0001). In addition, riparian protection significantly reduced the probability of loss of populations for harvesting scenarios, although not the time to extinction for those populations that did become extinct (one-tailed Wilcoxon paired sample tests: comparing all “harvesting with riparian protection” scenarios to all “harvesting without riparian protection” scenarios: PrE100, P0.05(1), 34 < 0.005; PrE50, P0.05(1), 40 < 0.0001; MedTE, P0.05(1), 32 > 0.5).

Given the alternative management strategies, and alternative models of the demographic effects of habitat changes on projected outcomes, I asked which of the management strategies, if followed, could minimize long-term likelihood of loss of populations if each model were true. For each initial condition of the landscape, I calculated the expected probability of loss of populations for each management strategy and model, averaging across all ages at first reproduction (Table 4.5). By inspection, no “robust” management strategy (a strategy associated with the lowest probabilities of eventual extinction across the array of alternative hypotheses) is evident under the conditions I simulated.

As expected from the analyses presented earlier, differences in outcomes among alternative management strategies are small relative to the differences created by the alternative hypotheses, and to the levels of disturbance created by each management strategy itself (Table 4.5). Harvesting strategies associated with riparian protection appear potentially as able to minimize the likelihood of species loss as the null “no harvesting/no disturbance” case under a number of the hypotheses examined. However, if the more complex hypotheses relating both short- and long-term effects of disturbances to growth and survivorship are in fact true, then conclusions become contingent upon characteristics of historic and on-going disturbances. Given wide uncertainty in outcomes contributed by demographic parameters, it is not yet possible to decide which harvesting and riparian protection strategies are unambiguously capable of reducing the probability of eventual loss of populations.
Table 4.5. The average probability of long-term extinction of populations over 100 years projected for each management strategy and alternative demography-habitat change hypothesis. All values are averaged among ages at first reproduction. For each initial landscape condition and hypothesis combination, the management strategy projected to be least likely to result in long-term losses of populations is indicated in bold. In the last column is average probability for each management strategies across all hypotheses with each hypothesis considered as equally likely. For comparison, I also show the mean (± SD) areas disturbed and harvested per year for all runs comprising each management option.

<table>
<thead>
<tr>
<th>Landscape management strategy</th>
<th>Mean area disturbed (ha/yr)</th>
<th>Mean area harvested (ha/yr)</th>
<th>H6</th>
<th>H1</th>
<th>H2+H3</th>
<th>H4+H5</th>
<th>H2-H5</th>
<th>H1-H6</th>
<th>Mean for all Hₘₛ</th>
</tr>
</thead>
<tbody>
<tr>
<td>No harvesting</td>
<td>0</td>
<td>0</td>
<td>0.163</td>
<td>0.131</td>
<td>0.338</td>
<td>0.628</td>
<td>0.719</td>
<td>0.733</td>
<td><strong>0.452</strong></td>
</tr>
<tr>
<td>No riparian protection</td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>No natural disturbances</td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>No harvesting</td>
<td>261.1 (± 168.0)</td>
<td>0</td>
<td>0.183</td>
<td>0.170</td>
<td>0.342</td>
<td>0.633</td>
<td>0.716</td>
<td>0.761</td>
<td><strong>0.466</strong></td>
</tr>
<tr>
<td>No riparian protection</td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Natural disturbances</td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Harvesting</td>
<td>0</td>
<td>574.3 (± 379.1)</td>
<td>0.181</td>
<td>0.215</td>
<td>0.340</td>
<td><strong>0.627</strong></td>
<td>0.740</td>
<td>0.747</td>
<td><strong>0.475</strong></td>
</tr>
<tr>
<td>No riparian protection</td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>No natural disturbances</td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Harvesting</td>
<td>398.0 (± 323.1)</td>
<td>692.5 (± 675.1)</td>
<td>0.201</td>
<td>0.168</td>
<td>0.345</td>
<td>0.633</td>
<td>0.780</td>
<td>0.757</td>
<td><strong>0.481</strong></td>
</tr>
<tr>
<td>No riparian protection</td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Natural disturbances</td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Harvesting</td>
<td>0</td>
<td>734.6 (± 881.8)</td>
<td>0.171</td>
<td>0.165</td>
<td>0.367</td>
<td>0.635</td>
<td>0.718</td>
<td>0.716</td>
<td><strong>0.462</strong></td>
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<tr>
<td>Riparian protection</td>
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<td></td>
<td></td>
</tr>
<tr>
<td>No natural disturbances</td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Harvesting</td>
<td>359.8 (± 308.9)</td>
<td>689.7 (± 332.5)</td>
<td>0.173</td>
<td>0.160</td>
<td><strong>0.335</strong></td>
<td>0.640</td>
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Previously Disturbed Landscape
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<th>Landscape management strategy</th>
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<th>Mean area harvested (ha/yr)</th>
<th>H6</th>
<th>H1</th>
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<th>H4+H5</th>
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<td>0</td>
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<td>No harvesting</td>
<td>486.7 (± 429.1)</td>
<td>0</td>
<td>0.182</td>
<td>0.178</td>
<td>0.340</td>
<td>0.634</td>
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<tr>
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<td>668.6 (± 309.2)</td>
<td>0.231</td>
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<td>592.5 (± 475.3)</td>
<td><strong>0.160</strong></td>
<td><strong>0.154</strong></td>
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<td>488 (± 410.9)</td>
<td>0.223</td>
<td>0.190</td>
<td>0.340</td>
<td>0.641</td>
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DISCUSSION

This spatial analysis shows that projected long-term survival patterns of populations of tailed frogs in managed forests can be affected by the degree of habitat disturbance to either forests or adjacent streams, conditional on the demographic characteristics of the populations in managed streams. Relative vulnerability of populations to different sources of habitat disturbance depends strongly on assumptions characterizing the rates at which individuals reach reproductive maturity. It is not yet clear if specific measures to protect riparian habitats (e.g., riparian buffers) could be effective in reducing projected long-term risks of loss, although much of this uncertainty is due to presently unknown consequences of disturbances on the fundamental demographic rates of growth and survivorship. Yet the utility in preventing long-term loss is high because extirpated habitats appear unlikely to become successfully recolonized again under a wide range of assumptions about movements and dispersal.

Metapopulation theory (e.g., Levins 1970, Hanski 1991) regards extinctions of populations divided in space as a natural component of a species' regional dynamics (Sjögren 1991). In pond-dwelling amphibians, empirical evidence does suggest that probabilities of loss of populations and their reestablishment in spatially-divided populations (Merriam 1998) are driven by spatial factors such as interpopulation distance, habitat size, the presence of potential barriers (such as roads), and the degree of spatial correlation between environmental conditions at occupied and unoccupied habitat sites (Sjögren 1991, Sjögren Gulve 1994, Vos and Chardon 1998; Funk and Dunlap 1999). While I did not attempt here to formally define the spatial structure of tailed frog populations on the basis of connectedness among habitats, my findings suggest that persistence of populations of tailed frogs is not simply predicted from the characteristics and spatial dispersion of key habitat variables, but is also dependent upon dynamics of habitat disturbance and rates of recovery of populations.

One important result of my study is the finding that transient (severe but short-lived) consequences of disturbance on mortality and habitat carrying capacity appear less important to population survival than do slower and cumulative effects of vegetation removal, sedimentation and loss of physical habitat (see also Chapter 3). In part, this
result may be a structural consequence of the way I modelled downslope effects of disturbances on populations (see Methods and Appendix 2). Many effects of forest disturbances upon temperature, stream morphology and habitat area accumulate downslope (Young et al. 1999; Church in press), and slightly elevated losses to resident biota associated with them may persist for years or decades (Trombulak and Frissell 2000). In complex stream and riparian systems, disturbances associated with floods and small landslides are extremely varied in severity (Swanson et al. 1998, Jones et al. 2000) perhaps permitting local refugia to buffer populations from some of the immediate mortality effects created by these events.

In general, the habitat value of riparian areas to stream-dwelling species appears influenced both by ecological gradients operating at broad scales (regional climate, geomorphology; Chapter 2), local channel morphology, persistent legacies from past forest practices and disturbances (Trombulak and Frissell 2000) and the structure of adjacent forests (Bunnell et al. 1999a). The life histories of native stream-dwelling organisms do appear to be congruent with natural stream-flow and disturbance regimes (Reeves et al. 1995; Poff et al. 1997). However, increased frequencies (Thomas and Megahan 1998) and severity of such disturbances as floods and debris flows in forest stream networks with roads (Jones et al. 2000) may increase the vulnerability of resident species to the negative consequences of both transient and cumulative effects of disturbances to riparian habitat. If many of the cumulative effects of natural and anthropogenic disturbances in headwater areas upon stream-dwelling species are unlikely to be adequately mitigated by such management strategies as provision of riparian buffers (see Belt and O’Laughlin 1994; Young 1999 for discussion), then management options may be limited. The results of my study imply that in many headwater areas, the management decision of greatest impact appears to be whether to initiate activities associated with forest harvesting, or not. Subsequent efforts to mitigate long-term detrimental consequences of disturbances through fine-scale management of forestry practices, including provision of riparian buffers, may or may not be efficacious in the long-term.

Several spatial factors (the location of forest harvest, spatial correlation between physical disturbances and likelihood of stream degradation, movement capability of
different life stages within streams and along riparian areas) were examined in this study. Among vertebrates generally, available evidence indicates that short dispersal distances are frequent (Sutherland et al. 2000) and strongly influence age and sex structure, abundance, and relatedness within populations. In many species, long-distance dispersal occurs regularly, but at a relatively low frequency. Nonetheless, long dispersal distances are important in invasion and recolonization processes (Shaw 1995), and in the genetic structuring of populations (Ibrahim et al. 1996). I found that the probability of recovery of habitat cells where populations have gone extinct (as well as those exhibiting severe declines in abundance) via "rescue" with movements or dispersal from nearby habitats appears low in all scenarios I examined. Many of the biophysical effects of the original disturbances for this stream-dwelling species (even if transient) may therefore accumulate in streams and watersheds, creating significant long-term consequences that may be quite difficult to reverse. This modelling result is consistent with empirical observations that recolonization rates of altered sites by tailed frogs may be slow (Welsh 1990). Detailed radiotelemetry data on amphibians are uncommon (for recent examples see Madison (1997) for Ambystoma maculatum; Johnston (1998) for Dicamptodon tenebrosus), and indicate seasonal movements of less than 1 km in these species. Higher genetic heterozygosity among tailed frog populations in the presumably harsher environmental conditions in the B.C. interior compared with those found on the coast are consistent with these observations of low vagility in stream-dwelling amphibian species (Ritland et al. 2000). At least in part, lack of success in recolonizing sites may not be because moving individuals cannot reach unoccupied habitats, but because the time required for establishing a reproductively viable population is insufficient to escape irrecoverable losses from stochastic events operating at the local scale. The life history strategy of tailed frogs appears to resemble that of a species adapted to an environment where the primary factors driving survival are locally correlated (Hanski 1991). Until better dispersal data become available, it appears that certain management options (such as large-scale, progressive forest removal or disturbance) may extend this spatial autocorrelation of effects of disturbance significantly beyond the range of movements and dispersal of individuals (see Frank and Wissel 1998). If so, then the spatial scale of
habitat protection strategies to retain continuity and ecological functioning of riparian areas must also extend considerably beyond the riparian zone itself.

These results, based on the data presently available, raise some troubling questions. Figures 4.2 and 4.3 show that although populations in which females reach age at first reproduction at 5 years can persist in the face of the types of disturbances considered in this study, populations with longer maturation periods become vulnerable to both random environmental effects and incremental effects of disturbances. It is not unexpected that such primary demographic characteristics as length of the larval cycle, survivorship, and fecundity rates should strongly interact with the direct and cumulative effects of disturbances in both stream and riparian habitats to determine population persistence. However, in a species with a complex life history involving multiple habitats (streams, riparian zones, upland forest), attempts to decompose sources of variation in critical demographic parameters may simply uncover a daunting tangle of responses and uncertainties. Unless these demographic parameters are relatively fixed for tailed frogs (which is unlikely at least for the periphyton-grazing larval stages), then developing a sufficiently robust understanding of headwater stream-riparian system functioning to critically evaluate alternative riparian management measures is uncomfortably remote.

Could populations in nature actually be as vulnerable to effects of forest harvesting as many of these results imply? At present, evidence from both field surveys and genetic analysis in British Columbia suggest that the answer is “likely”, depending upon details of geographic location, local watershed and stream geomorphology, and patterns of forest harvesting in watersheds. While tailed frogs are widely distributed and often locally abundant in montane streams in the coastal mountains of British Columbia, they are sparsely distributed and generally uncommon in interior areas (Chapter 2 and references cited therein). At a regional spatial scale, genetic distances among clusters of sample streams (e.g. north, mid and south coast; interior) increase uniformly with physical distance (Ritland et al. 2000). At finer spatial scales (e.g., within each cluster of sampled streams), genetic differentiation among populations is strongly linked to physical distance among streams in the interior, although that trend is not apparent in coastal streams (Ritland et al. 2000). These results imply that migration and
recolonization rates are very low at least in some populations (Ritland et al. 2000). At more immediate time scales, larval densities and biomass appear to be strongly influenced by removal of riparian cover and increased sedimentation even in coastal populations (Dupuis and Steventon 1999; Kim 1999), and local stream characteristics appear to determine whether populations in disturbed sites will persist. Broad surveys in Washington and Oregon indicate a general negative trend in tailed frog abundance with increasing amounts of timber harvest in watersheds (Corn and Bury 1989; Bull and Carter 1996), although high local variability in numbers often prevents statistical confirmation of the relationship (see also Kelsey 1995).

From this analysis, it is clear that there are likely to be quite important effects of removal of forest vegetation influencing the long-term population dynamics of tailed frogs in British Columbia. In this analysis I included two major effects of these: 1) a causal linkage between vegetation removal, establishment, and growth on variables such as light availability, temperature, and nutrient inputs; and 2) a linkage between vegetation succession and hydrological variables such as streamflow, probability of debris flows, and streambed structure. I represented these as “event” changes in state (e.g., age of vegetation, stream substrate class, etc.) with consequent recovery dynamics at longer time scales. However, our current knowledge of these relationships is only preliminary. For example, streamflows show complex, high-frequency variation related to other biophysical factors such as regional climate, and complex topography (Benda 1994) about which few predictive relationships are known for headwater streams (Church in press). I have had to make assumptions about the sensitivity of population sizes to streambed substrate composition, and to the various processes by which sedimentation, temperature, and inputs of organic debris could affect growth and survivorship of both larval and riparian-dependent stages. As a consequence, I have been unable to eliminate alternative hypotheses about the cumulative effects of most forest disturbances on eventual persistence of this species. These difficulties highlight the depth of study that will be required to produce effective guidelines for conservation of stream-dwelling amphibians in watersheds subject to forest harvesting activity.

For forest-riparian zones generally, forest practice regulations designed to afford protection of the riparian vegetation, streambank stability, and thermal regime of
headwater streams ranges from no protection, to 20-50 m of buffering on each side of the stream (Young 1999). Buffering of streams effectively reduces many of the impacts of forest harvesting on stream systems by maintaining water quality, providing shade and reducing sedimentation (Newbold et al. 1980, Murphy et al. 1986, Beschta et al. 1987, Budd et al. 1987, Belt and O’Laughlin 1994). Given the potential economic costs of riparian zone protection, the potential for infrequent events (e.g., windthrow, fire) to disturb both regenerating and protected forests, and the uncertain likelihood of persistence of stream-dwelling species (such as the tailed frog), planning silvicultural activities in areas containing vulnerable or threatened species must involve some means of comparing trade-offs among management options (Montgomery 1995). Quantitative evaluation methods, such as decision analysis, are often used to explicitly compare options when the probabilities of different outcomes and the utilities of different decisions can be estimated (Conroy and Noon 1996; Peterman and Peters 1998). In this study, basic ecological uncertainties so dominate the pattern of outcomes that broad overlaps occur among outcomes for different management policies. Because strong overlaps between consequences of alternatives are not uncommon in riparian systems, prediction methods need only be accurate enough about outcomes to correctly order the choices for the purposes of choosing among policies (Walters and Korman 1999). The data summarized in Table 4.4 suggests that protection of the riparian zones of headwater streams where stream-dwelling amphibians are present may be the policy most likely to improve the likelihood of retaining populations over the long term. However, the uncertainties about consequences of vegetation succession on growth, survivorship and fecundity of these species implies that we cannot yet choose a single “best policy” that will do well no matter which ecological model is correct.

At the broad time and space scales of forest-level planning (e.g., over thousands of hectares and over decades), decision-support tools are now frequently used to examine options by linking management actions to consequences for species survival (see reviews in Thompson 1997 and Beissinger and Westphal 1998). These linkages are made through projections of habitat suitability (e.g., Hansen et al. 1993; Daust and Sutherland 1997), projections of population sizes using detailed demographic models (e.g., Crouse et al. 1987; Lande 1988; Pulliam et al. 1992; Lindenmayer 1995,1996; Sæther et al. 2000),
criteria for classifying likelihood of species persistence (Haight 1995; Conroy and Noon 1996; Marshall et al. 1998; Ducey and Larson 1999), and comparisons of the economic costs of different habitat protection options (Montgomery 1995). All these approaches implicitly or explicitly assume that ecological processes that link indicators of population status to the spatial distribution and rates of change in habitat attributes can be adequately represented by the spatial and temporal resolution structure of the models used to generate alternative outcomes. Although the critical details of many animal-habitat processes are difficult to capture in riparian ecosystem models (Walters and Korman 1999), my results show that uncertainties present in those relationships presently cloud our capability to distinguish many consequences of even broadly different management alternatives in long-term projections. This problem is not unique to this study, or to forest-riparian systems as a whole. Generally there is a loss of certainty as information passes from the real forest, to local research sites, to simplified research summaries, to management policy (Bunnell and Huggard 1999). Consequently, our ability to anticipate consequences of alternative management actions upon most species remains strongly limited by the uncertain relationship of predicted outcomes to parameter estimates (Conroy and Noon 1996) and to the imperfect representation of ecological processes affected by habitat change.
CHAPTER 5. SUMMARY AND CONSERVATION IMPLICATIONS OF THIS RESEARCH

INTRODUCTION

In this thesis, I investigated consequences of uncertainties in a species' responses to habitat alterations upon our ability to evaluate effects of forest management options. I based my work on *Ascaphus truei* (tailed frogs) because available empirical data for this species are representative of the types of information we typically rely on as a basis for conservation planning. I reviewed basic notions of risk in assessing effects of forest management on biodiversity, and how a number of those concepts implicitly underlie principles of habitat protection for single species management (Chapter 1). In subsequent chapters, I: 1) examined habitat factors related to present abundance and distribution of this species (Chapter 2); 2) evaluated properties of this species' demographic structure and life history that appear to condition its likely responses to habitat perturbation (Chapter 3); and 3) examined our present uncertainty about just how habitat changes link to projected patterns of persistence, and how the consequences of that uncertainty constrain our ability to evaluate alternative management options (Chapter 4). In this chapter, I bring this work together. Here I provide an evaluation of the results, techniques, and recommendations and examine in which ways my approach could assist in developing more effective management for tailed frogs and other species of similar management concern.

SUMMARY AND EVALUATION OF RESEARCH RESULTS

The majority of habitat studies of forest-dwelling vertebrates have focussed on the association between presence, density (or sometimes biomass), and/or richness of species and the structural elements of stands or landscapes to which those species are closely linked (e.g., Hansen et al. 1993, 1995; Bunnell et al. 1999a). For stream-dwelling amphibians in the Pacific Northwest (including British Columbia), most habitat studies have examined these associations in relation to such fine-scale variables as stream size, substrate composition, as well as broader-scale variables as adjacency to previous timber harvesting, areal extent of previous timber harvests in watersheds, or size of watershed area (e.g., Murphy et al. 1986, Corn and Bury 1989, Bury and Corn 1991, Bury et al.)
1991b, Kelsey 1995, Bull and Carter 1996, Welsh and Lind 1996, Wahbe 1996, Hunter 1998). Below, I review and summarize results of these association studies (including work in my thesis) within a conceptual space-time diagram (Figure 5.1) to aid discussion of the findings from my research are relevant to the general problem of conserving species in managed forest-riparian systems. I discuss how my results assist in teasing apart informative relationships between physical processes and their ecological consequences, and identify key uncertainties about these interactions that hinder development of effective management alternatives across these space-time domains.

Figure 5.1. Space-time domains of associations examined in this thesis between the life history attributes of the study species, and natural and anthropogenic environmental processes affecting them. Major attributes of species' life history are shown in open ovals, and major environmental processes in shaded ovals. Adapted from Stommel (1963), Hunter (1998) and Bunnell and Huggard (1999).
Two fundamental and interconnected research paths in ecology are: (1) the study of how biotic and abiotic temporal and spatial patterns arise and are maintained; and (2) interpreting the consequences of those patterns for the dynamics of population and ecosystems (Levin 1992). In the forest-riparian system I studied, interactions between environmental patterns and dynamics with one or more life history attributes of the study species can be identified across wide scales of space and time (Figure 5.1). At the finest space-time scales (where most current empirical work has been done), local effects of timber harvesting and stochastic events in stream reaches operate on eggs and larvae through their modifications of stream substrate composition, flow rates, and temperature. Aspects of stream-dwelling amphibian life histories that occur at more intermediate space-time scales of streams, forests and sub-basins include habitat use by the different life stages, response to food availability, time to metamorphosis, mortality from disturbances, and local heterogeneity of occurrences, age and size class distributions within stream networks (including movements and dispersal) (Hunter 1998). Biophysical and disturbance factors that may interact with life history attributes at these scales include fluctuations in stream flows, occurrence and severity of debris flows, geomorphologic context (e.g., slope, surficial soils, bedrocks) determining slope stability and material inputs to streams, and the age and composition of riparian and upslope forests (Church in press). At the broadest space-time scales of watersheds and landscapes, changes in the status of the species’s geographic range and genetic structure among populations result from very long-term interactions with changes in climate patterns, volcanic activity, and glaciation (see Ritland et al. 2000 for a discussion of these effects).

Environmental Relations and Risks to Populations

I used classification trees and Mantel tests to uncover ecological and spatial dependencies between habitat factors operating at different spatial and temporal scales and occurrence and abundance patterns of tailed frogs in British Columbia. I used population matrix models combined with a spatially explicit model of landscape dynamics to study effects of uncertainties about the functional interactions between habitat dynamics upon long-term projections of population persistence. With these tools, I found that broad-scale (i.e., coarse-grained, sensu Wiens 1989) variables (especially the
presence of weathering-resistant bedrock lithologies), appeared to be consistently positively associated with tailed frog occurrence patterns over its range in B.C. Local-scale (fine-grained) variables related to intrusion of fine sediments and streambed morphology are generally important in determining abundance. However, lack of a formal sampling design stratified by geomorphology, climate, extent and patterning of forest harvesting in watersheds, and local stream topography and morphology precludes treating these results as predictive. In addition, considerable unexplained spatial dependence in both patterns of distribution and abundance in the study species, and the complex of habitat variables associated with these patterns, resulted in considerable residual uncertainty in the species-habitat relationships I describe. From my demographic modelling, the uncertainties appeared to reside in our poor understanding of the cumulative, often contradictory, effects of forest and stream succession on growth and survivorship rates of tailed frogs.

Despite these difficulties, I believe my exploratory multi-scale habitat classification (Chapter 2) when combined with present uncertainties in demographic responses (Chapter 3) helps reveal why fundamental problems remain in our understanding of how to best manage habitats for long-term conservation of this and similar species (Chapter 4). In general, patterns of distribution and abundance of tailed frogs appear to be determined by a mix of factors that interact across scales in space and time. For example, on the coast, tailed frogs appear regionally common, although locally patchy. In the Kootenays, this species appears to be both regionally rare and locally patchy, although never abundant. I found that wherever weathering products from underlying geology are fine-grained (e.g., sands, silts, or rubble), this species is never abundant and appears always vulnerable to disturbances (see also Dupuis and Wilson 1999; Sutherland and Bunnell in press). On the coast then, broadly applied prescriptive approaches to tailed frog conservation (e.g., “place 30 m riparian buffers everywhere there are positive occurrences”) undertaken in erosion-prone bedrock zones are likely to be less worthwhile than in erosion-resistant bedrocks (such as granodiorites and other intrusive bedrock lithologies). However, if the species is regionally rare (as it is in the Kootenays), the value of retaining all extant populations may remain high because of the low probability of recolonization from nearby sites. Here, protection measures (such as
buffer strips and restrictions on road location in riparian zones) even in sandstone or siltstone-dominated areas may still be of considerable conservation value. Based on my analyses, decisions about whether and how to protect this species can not depend solely on a single criterion (e.g., distributional status, geological type, biogeoclimatic zone, etc.) or prescribed on the basis of forest harvesting practices (e.g., retain 80% of residual stems to a width of 20 m on each side of all streams less than 3 m in wetted width in low-gradient (<20% slope) watersheds). Instead, evaluation of the conservation potential of each potential site depends on: (1) the regional status of the species (the frequency and dispersion of populations), (2) interactions between local habitat structure and growth and survivorship rates, and (3) biophysical characteristics of stream sites determining rates of recovery of stream and riparian habitats from disturbance.

This interdependence of management consequences with ecological processes that interact across broad scales in both space and time forces us to find ways to balance our desire for precise descriptions of causal mechanisms, with an understanding of the generality of the patterns of management interest (Bunnell and Huggard 1999). Levin (1992) suggested that research approaches combining both statistical and correlational studies of ecological patterns with process-level models designed to elucidate mechanisms were essential to decompose cross-scale ecological interactions sufficiently well to interpret them. Using that approach in my study, I found evidence of complex interactions among geomorphology, structure of upland and riparian forests and demographic responses to perturbation. I suggest that approaches for protection of species that ignore either the site-specific physical contingencies that mediate the effects of locally important habitat factors (e.g., in this case the linkages between catchment area, gradient, stream velocity and flushing rates of sediment; Church in press), and the influences of broader-scale patterns (e.g., climate, bedrock geology) will have little long-term conservation value. If preventing the loss of populations and species due to large-scale forest management has a high value for conservation (see below), then evaluation and monitoring programs must themselves be designed to examine options at both local and regional scales.
Implicit throughout the design of this study is the premise that persistence of species over space and time scales relevant to analysis of forest management options arises from: 1) the finite rate of population growth as determined by the state of the array of habitat structures required by the species; and 2) the recovery rates of both populations and habitats from effects of perturbations that occur over these same scales (see Conroy and Noon 1996; Peterson et al. 1998). The results of the habitat-demographic analysis undertaken here clearly points out that our present understanding of consequences of habitat change or degradation to resident species in small headwater streams is not robust. If future forestry practices push these forest-riparian ecosystems into regions of dynamics beyond the recovery rates of either the physical system (e.g., flushing rates of sediments from streams) or the biological system (e.g., decreased productivity in extensive second growth forests), then persistence of stream-dwelling amphibians and other species is questionable.

**Effects of Uncertainties in Estimating Risks**

For ecological problems in general, and resource management problems in particular, Walters (1986) made a distinction between three basic sources of uncertainty, as follows. The first is natural variation or noise inherent in ecological systems (e.g., variation in growth rates of trees, and animals that differ among individuals, sites and years) that produce unpredictable and uncontrollable changes in ecological systems. This stochasticity is usually represented by probability distributions underlying each type of disturbance event, as well as about population variables. The second is statistical uncertainty about the forms and values of the various ecological hypotheses under study (e.g., the growth response of tadpoles to increased light penetration in riparian zones). Contributing sources of this type of uncertainty are sampling biases creating “observation uncertainty” (Hilborn and Mangel 1998), problems in estimating parameters from noisy data, and/or weighting various possible hypotheses expressed as alternative parameter values or models (these latter two are sometimes termed “process uncertainty”; Hilborn and Mangel 1998). The third kind of uncertainty, and the one most difficult to deal with,

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1 Forestry practices can alter habitats over scales important for population survival of forest-dependent species (e.g., spatial scales of 10 m-1000 km, and time scales of 1 month-1 century or more; Wallin et al. 1994, Bunnell and Huggard 1999, Bunnell et al. 1999b).
is basic structural uncertainty about what variables and processes to even consider in representing the system. Among the difficulties created by incomplete structural representations is the likelihood of autocorrelations in time and/or space creating lags in system responses, as well as unexpected and fundamental alterations in response behaviours. All of these sources of uncertainty are interrelated, and they ensure that the predictability of a system decreases at increasing spatial and temporal scales away from a particular viewpoint of analysis (Walters 1986).

Uncertainty in the spatial and temporal abundance of any species may be attributed to sampling error, demographic stochasticity (effects of chance application of vital rates on the fates of individuals; Caswell 1989), environmental stochasticity (effects of variation in weather and disturbances on population and habitat dynamics), or changes in genetic structure (Erb and Boyce 1999). As part of this study, I attempted to include the influence of these effects (except genetics) in my assessment of long-term persistence patterns in tailed frogs. Variation in field estimates of tailed frog abundance can certainly be attributable in part to both sampling error and small-scale stochastic events, although these cannot be adequately partitioned with the data I used. However, I found that uncertainties in this system are dominated by the types of process and structural uncertainties pointed out by Walters (1986) and elaborated on by Ludwig (1996a, 1996b). Our description and sound understanding of how the fundamental population processes of births, deaths and movements are linked to the rates and types of habitat changes found in this system over the space-time scales relevant for management are inadequate. For example, I found that assumptions about timing of age at first reproduction influenced all interpretations of the effects of disturbance and management options on projected long-term persistence. Reducing uncertainty in this dominant factor (e.g., how growth rates of larvae and timing of metamorphosis varies among individuals and populations in conjunction with latitudinal and topographic clines in primary productivity and habitat variability) could allow stronger linkages to be made among other ecological hypotheses and their management consequences.

What are the consequences of these sources of uncertainty upon our ability to infer patterns of risk and evaluate options for alleviating risks? The answer depends on space and time scales relevant to each species and management objective. From the point
of view of biodiversity conservation, loss of species over a large area due to resource harvesting (e.g., Bunnell 1997) is viewed as unequivocally the most serious possible outcome (Conroy and Noon 1996). Expressed in terms of increasing scales of space and time (Figure 5.1), negative consequences of losses generally increase as one moves upwards and to the right. I interpret the consequences of this figure using the tailed frog – headwater stream system as an example. At the finest scales of space and time negative effects attributable to forestry practices, while serious for the fitness of a given individual animal, are of little significance to management. However, the effects of unpredictable, individual stochastic events (e.g., daily streamflow patterns, shifts in log jams and rocks within the streambed) dominate biotic responses measurable at these scales. At the intermediate scales of stream reaches and decades, the management consequences of negative effects on life history stages or sub-populations due to altered disturbance regimes could be of conservation significance depending on which life history attribute (e.g., growth rates, adult movement) is affected. Here, as the modelling work in this thesis shows, the combined effects of process uncertainty (parameter estimation) and structural uncertainty (model complexity) begin to create substantial difficulties in identifying favourable management options. At the broadest scales, negative effects great enough to impact attributes such as geographic range or genetic substructure are likely very rare. However, if they occur, their conservation consequences are very significant. Here, the structural uncertainties about the roles of recolonization distance through stream networks, migration among watersheds, and decadal cycles in climate affecting stream permanency and growing season length become strong impediments to understanding how best to distribute alternative forestry practices now to minimize future losses of this and other similar stream-dwelling species. Some consequences of these uncertainties for planning effective conservation measures are discussed at the end of this chapter.

**Evaluation of Risk Assessment Approach**

Decision analysis was developed as a method of evaluating alternative views of an unknown future, and provides a conceptual basis for explicitly taking uncertainties into account (Raiffa 1968; Pratt et al. 1995). Although I did not conduct a formal quantitative comparison of management objectives in this research (e.g., see Hilborn et
al. 1994; Robb and Peterman 1998; Olson and Orr 1999 for recent applications in fisheries and forestry), I did use the approach as a framework for identifying and assessing the relative plausibilities of uncertain ecological hypotheses about future effects of forestry practices in headwater systems. In particular, I attempted to link multi-scaled descriptors of tailed frog habitat structure (e.g., topography, stream characteristics, extent of forest harvesting, rates of disturbance) with models of their respective functions in determining growth, reproduction and mortality in the study species. I found that because of fundamental uncertainties in the ecology of the study organism and the dynamics of headwater stream ecosystems, quantitative comparison of management options (including economic costs of each) was unlikely to be worthwhile. Therefore I used selected tools from the decision analysis framework (e.g., generation of alternative "states of nature", sensitivity analysis, calculating probabilities of different outcomes) as a means of ranking the effectiveness of possible management strategies. Within the context of a designed experimental management program, it would likely be possible to extend the approach initiated here to include calculations of expected value of perfect information (EVPI; Walters and Holling 1990; Peterman and Peters 1998), and expected value of including uncertainty (EVIU) (Morgan and Henrion 1990).

Two of the approaches I have employed can be challenged: (1) population viability analysis using matrix models; and (2) spatially explicit simulation of population and landscape dynamics. Predictions of population viability models are sensitive to errors in counts of population data, as well as in the fundamental structural assumptions about populations of the study species (e.g., measures of growth and mortality rates, estimates of carrying capacity, and effects of dispersal on population dynamics, Marcot and Murphy 1996; Beissinger and Westphal 1998; Ludwig 1999). Spatially-explicit models require knowledge of population spatial structure, movement rates, dispersal distances, and habitat heterogeneity, in addition to the usual demographic parameters and structural assumptions such as density-dependence (Dunning et al. 1995, Schumaker 1998). They are thus potentially very vulnerable to propagation of model uncertainty (Conroy et al. 1995), and may quickly become misleading. However, both tools are invaluable aids in forcing explicit consideration about the ways in which we think the ecology of a system is linked to management activities. Because long-term persistence of
populations over a wide area is an implicit or explicit goal of present forestry management guidelines (Bunnell 1997), thoughtful use of these tools to explicitly assess impacts of uncertainty at each scale affected by management is a useful step in qualitatively guiding planning efforts.

IMPLICATIONS FOR CONSERVATION

Based on my analyses of habitat characteristics, responses of tailed frogs over a wide geographic area, and sources and effects of uncertainty, I propose 5 main implications of this research for assessing conservation measures for this species, and for future management of headwater riparian zones.

1. Like other species, habitat relationships in the study species appear to cross spatial scales, and interactions among factors vary among sites. Across its range in British Columbia, the habitat factors (and their interactions) that distinguish sites likely to support populations differ substantially from those sites that do not. I found that broad-scale geologic, topographic and watershed disturbance factors are important site classification variables throughout the range studied. For example, small headwater streams underlain by intrusive rocks and with coarse substrates appear better able to support populations than are creeks with rubbly substrates derived from weaker, erosion-prone rocks. In part this may be because these streams are more stable, and in part because such streams may also have a more heterogeneous fine-scale morphology. However, hidden interactions between variables may contribute both to substantial regional variation in processes governing patterns of responses to short and long term disturbance regimes. From these patterns it may be inferred that areas in which the tailed frog presently occurs are not equally susceptible to disturbance. For example, potential short-term effects of disturbances in the watershed on streams and larval populations may therefore be greatest on geological substrates that favour 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.
2. **Areas in which tailed frogs are likely to persist can be characterized on the basis of region, topography, geology, and historical development.** In high elevation streams, volume of sediment is strongly related to the probability of bedrock failure (Church in press), and the degree of exposed soil surface (e.g., created by roads, cutbanks, and exposed soils; Forman and Alexander 1998). The analyses presented above suggest that practices designed to conserve existing tailed frog tadpole populations (e.g., buffers around streams) will be most successful if: 1) they are situated in intrusive or metamorphic bedrock formations; 2) they target streams of intermediate gradients with significant boulder cover (creating a step-pool morphology (Chin 1998) and trapping logs); and 3) they are in watersheds with low or moderate levels of historical harvest. Conservation efforts will be less effective where weathering products from surrounding geology produces fine-grained or rubbly stream sediments, or streams are located on low gradient sites. Although data on metamorphs and adults are scarce, it is likely that in much of the tailed frog range (e.g., many coastal sites), natural factors and variability have more influence than do human-induced changes on patterns of distribution and abundance. Expensive protective measures for tailed frogs in such areas could be limited to selected headwater streams where evidence indicates the presence of established breeding populations, or that appear critical to maintain connectedness between scattered populations. In interior regions, effort could be placed in maintaining extant populations (already known to be rare).

3. **In areas selected to sustain tailed frogs, rates of cut, methods of cut, and locations of roads could allow only small amounts of disturbed area to be exposed at a given time.** In general, management practices should maintain headwater stream channel morphology and natural substrate dynamics regime. As accumulation of fine sediments in streams appears generally important in governing reproduction and carrying capacity for tadpoles (Kelsey 1995; Welsh and Ollivier 1998; Dupuis and Steventon 1999), developing management strategies that maintain a channel’s natural substrate dynamics should be of primary importance in designing conservation strategies for this species. The small size and intermediate gradients of many tadpole-bearing tributaries imply that the rate at which
streambeds could recover from increased sedimentation from active roads, landslides, or reduced inputs of large downed wood that structure stream morphology may be low (e.g., Hogan et al. 1998). My results show that even small increments in sedimentation rates to tailed frog-bearing streams occurring over long (e.g., decadal) periods may have long-term negative impacts on such populations, even if other short-term effects of disturbances may be positive.

4. Substantial uncertainty remains in assessing risk to this species from natural variation and forest practices. Results of this study, 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, spatial variability in habitat factors and processes determining responses of the species is a central outcome of the results presented here, both locally and regionally (see also Kelsey 1995; Bull and Carter 1996). Such variability makes it difficult to forecast response of forest-riparian ecosystems, and the species living in them to different management actions with accuracy or precision (Peterman and Peters 1998). Second, further uncertainty exists in the source data, in part because there are few re-samples of sites, and because estimates of abundance used here are influenced by local heterogeneity in stream substrates. These uncertainties contribute additional imprecision and bias in estimates of response quantities that vary naturally. Third, fundamental demographic characteristics strongly enter any estimate of risk and information about survivorship and growth are not well captured by most studies on this species to date. Tailed frogs may be resident as tadpoles in streams in this area for up to 4 years (Wahbe 1996; Richardson and Neill 1998). This residency period implies particular vulnerability to sources of disturbance in sensitive areas (steep escarpments; highly fractured rock, deep unconsolidated surficial materials; Bovis et al. 1998) or, in areas with relatively frequent extreme discharge events to frequent reorganizations of streambed structure (e.g., Chin 1998). Likewise, we know that tailed frog populations are remarkably discrete within streams, and show genetic differences among streams (Ritland et al. 2000) suggesting low movement potential, particularly in areas with low precipitation during summer.
(see also Daugherty and Sheldon 1982). How management might affect the dynamics among spatially divided subpopulations in a network of tributaries is not easily predicted from current data. My models suggest that a critical source of uncertainty for this species are the interacting effects of forest structure and disturbance characteristics found in the mid-successional period of a managed forest on survivorship and growth patterns. Finally, inferences about the effects of forest practices on this species are primarily drawn from the in-stream life stage; estimation of impacts of site conditions and disturbances on demographic rates of sub-adults and adults is virtually non-existent. While larval stages may be adapted to infrequent or moderate levels of disturbance, older age classes may not and my analyses show that both life stages are susceptible. The potential for differential effects of disturbances resulting from forest practices on larval and terrestrial life stages contributes to substantial uncertainty about effects of management on future reproductive success.

5. **Multiscale study and analysis is essential for uncovering the relationships between effects of disturbance and demography.** Many ecological processes act on multiple scales, or have consequences over a range of scales (Levin 1992; Lertzman and Fall 1998; Peterson et al. 1998). The relationships between fine-scale processes and patterns of abundance within units of habitat (i.e. streams) have generally been the focus of substantial research and analysis effort in population and conservation ecology. Applied research and management prescriptions tend also to focus at smaller scales (Bunnell and Huggard 1999). As a consequence, “bottom-up” application of conservation options derived from results obtained at a limited range of scales (e.g., application of many PVA analyses) may have uncertain efficacy. Larger-scale patterns and processes remain poorly understood, and effects of land-use change upon species generally arise as unplanned consequences of smaller-scale decisions and actions (Lertzman and Fall 1998). I found that the greatest source of uncertainty in my system resides in medium-scale cumulative effects of natural and anthropogenic disturbances on population dynamics within and among streams. At present, assessing the relative benefits of investing in different conservation strategies at
this scale is at the stage of hypothesis development, rather than hypothesis testing. Stand-level prescriptions for wildlife habitat protection are unlikely to meet their objectives unless they are part of a coordinated multiscale landscape management strategy.

Among the methods presently considered for protection of tailed frogs in British Columbia are: 1) providing stream buffers along headwater streams (Kelsey 1995; Dupuis and Steventon 1999); and 2) larger Wildlife Habitat Protection Areas (Ministry of Forests and Ministry of Environment 1999). Stream buffers alone may not protect this species over the long-term, and so their conservation utility may be low. As presently envisioned, provision of Wildlife Habitat Areas would cover a minimum of 500 m along the length of selected streams. They should extend 50 m from the stream edge on both sides including a 20 m riparian core and a 30 m buffer. Based on my research, if the WHA approach is followed, WHAs should be established on several creeks in a drainage to ensure that at least one creek will maintain a viable subpopulation. Within a WHA, roads should not be constructed within 30 m of the stream. It may be possible to partially harvest in streamside buffers using partial cutting methods that maintain approximately 80% basal area. Because WHAs protect more extensive areas than cutblock by cutblock approaches (such as stream buffers), their conservation utility is potentially higher, but so is their cost. Evaluating expected overall utility of such protection options (e.g. area conserved vs. area harvested) remains impractical.

How should policies for design and dispersion of conservation measures (e.g., buffers, WHAs) for tailed frogs be developed? My research shows that not every population is likely to be similarly sensitive to forestry practices due to influences of geology, stream channel morphology, climate, elevation and latitude. However once local populations are extirpated or significantly reduced in numbers then their recovery is uncertain. More generally, riparian areas exhibit considerable variation in macroclimate, microclimate, gradient, underlying substrate, disturbance regime, and community of associated species. As part of their in-depth synthesis of research findings on effects of forestry practices on vertebrates, Bunnell et al. (1999) found that there is no universally appropriate streamside buffer width, buffer placement, or reserve size for maintaining stream-dependent species in riparian zones. Because riparian zones (including
headwaters) are discontinuous in naturally disturbed forested systems, exhibit strong site-to-site variation driven by biophysical gradients and geomorphology, Bunnell et al. (1999) infer that “blanket” or universally applied prescriptions are therefore unnecessarily expensive. Furthermore, sufficient insight to guide management practices for conservation of species in forested systems is unlikely to arise simply from acquisition and analysis of databases of inventory data, or small scale studies designed to identify response thresholds. Given the difficulties I found in identifying simple “best” management strategies for conservation in these systems through explicit consideration of uncertainties, the way forward must be to refocus on process-oriented research and monitoring that exposes ecological variability, rather than constraining it (see also Bunnell and Huggard 1999). This is neither an easy or straightforward task.
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APPENDIX 1 – ESTIMATION OF LARVAL DEMOGRAPHIC PARAMETERS FROM STREAM SURVEY DATA

METHODS

Study Areas

Data from headwater streams in two field study areas, the Squamish Valley and Chilliwack Valley in southwestern British Columbia were used here to estimate ranges of larval densities, growth and survivorship. Studies in both areas form part of a broader project to assess the population and metapopulation ecology of tailed frogs in response to land-use alterations from forestry. Both areas are 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. The Squamish sites tend to receive more precipitation (mean annual precipitation: 281 cm) than do the Chilliwack sites (180 cm) although average temperatures are similar between the two areas (mean annual temperature: 8.5°C and 9.8 °C respectively; National Climate Data Centre, Environment Canada).

Stream and amphibian sampling took place in the Squamish study area (centered at 49° 55’N 123° 20’ W) in 1995 and 1996. 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. Similar to the Squamish study sites, 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.

Stream and Tadpole Sampling

At each site, 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 1mm 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.

Estimation of Larval Demographic Characteristics

For the purposes of this study, the tadpole variables derived for each stream were average density (#/m²), and the distribution of tadpole sizes based on SVL. I did not use weights because too few sites had sufficient samples of larval weights for analysis. Average densities of larvae (#/m²) was determined for each stream by dividing the total number of tadpoles by the area searched (average wetted width X reach length). Snout-
vent lengths for all tadpoles measured in each stream were re-expressed as a cumulative
frequency distribution prior to identification of size classes within streams, and
estimating possible larval survivorship rates. While data from all sites were used in
density estimates, only data from sites with more than 20 tadpoles measured were
included in estimating larval size classes and survivorships (Chilliwack: \( n = 12 \) sites
sampled in 1998-99; Squamish: \( n = 25 \) sites sampled between 1994-96).

In stream surveys for tailed frogs, true population abundances are not observed
directly. Instead, the samples yield estimates of abundance for some life stages (i.e.
tadpoles) derived from counts within streams. Uncertainty in enumeration of tadpoles by
standard stream survey techniques is due to at least three causes. First, a recent pilot
study of tadpole census efficiency indicates that in-stream tadpole surveys using a single
pass through the sampled reach underestimate densities by as much as 73% (average
underestimate: 59%; range 33-73%; \( n = 5 \); J.S. Richardson unpublished data). A bias of
this magnitude in enumerating tadpoles seriously affects interpretation of current
population status estimates, and influences the detection threshold for presence of
populations, as well as the projection of quasi-extinction thresholds (Ludwig 1999).
Second, a lower threshold on tadpole density before tadpoles are detected is likely, given
finite searching times, the heterogeneous nature of streambeds in which tadpoles are
identified, and this evidence of a systematic sampling bias leading to underestimates of
tadpole density. Third, there are likely differences between observers in spotting
tadpoles.

To account for these uncertainties in observations in subsequent analysis, I used
the following model of observation uncertainties to apply to field estimates of tadpole
densities:

\[
D_{\text{obs},t} = \max\{a + qD_t + V_t, 0\}
\]  

(A1.1)

where \( D_{\text{obs},t} \) is the observed population density at sample time \( t \), \( a \) is the detection
threshold below which no animals may be seen, \( D_t \) is the density of animals present at the
start of \( t \), \( q \) is the estimated mean observation bias, and \( V_t \) is the observation uncertainty
(Hilborn and Mangel 1998).
I estimated larval size classes by fitting log-normal functions using the second derivative to the smoothed cumulative frequency distributions of tadpole SVL for each site analyzed. Functions were fit by minimizing the second derivatives in the smoothed input data. I chose the log-normal functional form because larval growth is assumed to be logarithmic with increasing size (Duellman and Trueb 1994). Smoothing was performed using an optimized non-parametric filter for unequally sized classes on the x-axis using a quadratic Gaussian weighting function. This procedure determines the greatest possible noise reduction without distorting the features of peaks fitted to the data. I used Peakfit (SPSS Inc. 1997) to smooth data and fit all functions. Because the method used here for estimating parameters of distributions is based on minimizing the second derivative, it is functionally equivalent to other graphical methods of fitting polymodal distributions using inflection points (e.g., Harding 1949).

For the statistical modelling and analysis of these data to estimate survivorship, I used Bayesian inference based upon Markov chain Monte Carlo simulations to compute the posterior distributions of model parameters. Several uncertainties in these data should be accounted for as part of the analysis. First, there is a significant likelihood that broad biophysical differences between areas (e.g., climate and geology) may affect demographic parameters (Chapter 2; Bunnell and Huggard 1999). The size of these effects is not known a priori. Second, the species of potential predators on tailed frog larvae may differ among sites and between Squamish and Chilliwack. For example, the Pacific Giant Salamander (*Dicamptodon tenebrosus*) is present at some of the sites in Chilliwack, but is not present at Squamish. Third, there was only a limited and not necessarily random sample of the types of sites that tailed frogs occupy available for this analysis. Finally, all estimates below were made from samples of unmarked animals, and both sampling and process errors (e.g., uncertainty about whether growth and survival rates differ between animals) should be taken into account. Given these sampling limits, and sources of variation among sites there is substantial uncertainty about the "true" statistical models to use to estimate demographic parameters. The Bayesian approach to estimating and interpreting the plausibility of various model parameters is thus appropriate (Ludwig 1996b; Bergerud and Reed 1998). The results of a Bayesian analysis consists of a posterior distribution specifying the joint distribution of the various
unknown parameters in the model, missing data, and predictions for future unknown quantities that can be measured in the field or compared with other studies.

For the statistical models used below in survivorship estimates, I estimated parameters and their marginal posterior probability distributions as follows. Unless otherwise specified, I ran 100,000 iterations of each model after an initial "burn-in" of 10,000 iterations. To reduce the effects of potential autocorrelations among iterations, I used every 10th sample yielding 10,000 realizations from the posterior to construct distributions. For categorical analysis, I estimated goodness-of-fits using the $G$ statistic. All statistical models were created and analyzed with the WinBUGS package (Spiegelhalter et al. 2000).

RESULTS AND DISCUSSION

Estimates of Larval Densities

I estimated the detection threshold for tadpoles using data from the Squamish and Chilliwack samples described above, and supplementing them with results from 2 additional research projects (Kelsey 1995 and Dupuis and Wilson 1999) for a total sample of 155 surveys. By inspection, I found the minimum density detected in any of the studies. The lowest reported non-zero density in these individual stream surveys using area constrained search methods was 0.0145 tadpoles/m², and I used this value as an approximation of the detection threshold. The estimated average observation bias noted above (59%) was used for $q$, and observer error was derived by assuming variation about each observed value was normally distributed with a mean of 0 and a coefficient of variation of 50%. (approximately the range of variation found in the census efficiency study, J.S. Richardson unpublished data).

To examine how these uncertainties in observations could affect estimates of tadpole abundances, I simulated the "true" population density for a range of values representing observed densities taken in field surveys. Because the actual survey observations represent a relatively small set of possible samples ($n = 155$), I estimated the mean and variance of this distribution (after $\log_{10}$ transformation) and generated an additional set of sample values ($n = 845$) for a total of 1000 values. Monte Carlo
simulations of the predicted "true" density for each sample value showing the 95% confidence intervals around the relationship between predicted "true" density and observed density are shown in Figure A1.1. I used these relationships to estimate mean and variances in numbers of tadpoles for the models described in Chapter 3 and 4.

Estimates of Larval Size Classes

I found evidence for at least two and sometimes up to three co-resident size classes of larvae in streams (Figure A1.2) in both the Squamish and Chilliwack areas. In many streams, there was evidence of young-of-the-year appearing in the samples (particularly samples taken after mid-August). Young-of-the-year may overlap with the first overwintering cohort in fall samples, and so these individuals were included with that cohort before further analysis.

In part, the number of larval size classes observed in each stream may be related to the type of surrounding forest (influencing local growth rates), and to broader year-to-year variation in growing season characteristics (e.g., length of frost-free period). To assess these effects in the samples of larvae that met the criteria above, I treated the number of observed larval size classes \( k \) as a multinomial variable (possible values for \( k=2,3,4 \)), and for each category of number of larval size classes, forest stand type, and year summed the number of sites bearing those attributes. Because of the potential for geographic differences between groups of sites, and because there was no overlap between the years the sites were sampled in Squamish and Chilliwack (see above), I analyzed data from each group separately.

For each set of sites, I modelled the observed vector of counts with a General Linear Model (GLM) assuming a multinomial distribution and logistic link function (Hastie and Pregibon 1992). There were too few sites sampled each year to statistically distinguish year to year variation in Squamish, so before analysis I randomly selected one of the samples taken from sites re-sampled in more than one year, resulting in 22 sites for Squamish used in this analysis. There was insufficient evidence of an association between number of larval size classes observed and forest stand type (3) or year (2) in Squamish sites (log-likelihood ratio test; mean number of larval size classes = 3.582;
Figure A1.1. Monte Carlo realization of effects of the parameters of the observation model on the predicted tadpole density from samples. Shown are the range of predicted densities for the 155 samples examined (black circles), and additional simulated observation points (open circles) assuming parameter values for the observation model described in the text. There were 100 simulations for each predicted value.
Figure A1.2. Length-frequency distributions of larval *Ascaphus truei* found in the forest treatments examined at the Squamish and Chilliwack study sites during 1995 to 1999. Boxplots indicate median (central vertical line), quartiles of the distribution and the limits of the 95% prediction interval (outlying dots).
the range of the 95% credible set of values for $G = 0.75 - 10.14; d.f. = 21$). Similarly, there was insufficient evidence to conclude that number of larval size classes observed in Chilliwack sites was associated with forest stand type (sites (log-likelihood ratio test: mean number of larval size classes = 5.742; the range of the 95% credible set of values for $G = 1.957 - 13.14; d.f. = 11$). For both sites, the distributions of the predictive densities (the posteriors) for the parameters of the multinomial model are very wide-tailed and leptokurtic, leading to a large amount of uncertainty about the true parameter estimates.

**Estimates of Year to Year Larval Survival**

I used the inverse of the cumulative frequency distribution of size classes found in each sampled stream to obtain an estimate of mean larval survivorship rates of larvae, as follows. I assumed that (1) survivorship in larvae is age independent; (2) mortality rate is constant within and between years; (2) immigration and emigration rates of individuals into each reach is approximately in balance within and among years; and (3) the events affecting survivorship between streams or between years are not correlated. Although it is unlikely that these assumptions are true for all sites and times (particularly the assumptions of constant mortality uncorrected with location), no data are currently available to evaluate them. Using these assumptions, we can define $q(t) = \text{Pr}(\text{a particular tadpole is alive at time } t)$, and estimate its value using $q(t) = e^{-\theta}$ (Renshaw 1991).

To make estimates of the posterior distribution of $\theta$, I used the following statistical model. First, the observations of larvae $Y_i$ are assumed to arise from a normal distribution with parameters specifying the degree of uncertainty about the sampling error $\tau$ (where a small value of $\tau$ indicates high precision or low uncertainty), and the correct size class a given larvae is in:

$$Y_i \sim \text{Normal}(\mu_i, \tau_i)$$  \hspace{1cm} (A1.2)

Then, the function relating dependence of the expectation of $Y_i$ on the time $t$ is:

$$\mu_i = e^{-\theta}$$  \hspace{1cm} (A1.3)

Finally, the estimates of $\theta$ are themselves also assumed to have uncertainty due to the assumptions employed (assumptions 1-3 above), and are thus modelled as
\[ \theta \sim \text{Normal}(\phi, \tau_2) \]  

Because there were no other field data available to make a prior probability estimates of the values of either \( Y_i \) or \( \theta \), or their precision (\( \tau_i \) and \( \tau_2 \) above), I assumed only vague, uninformative priors with zero mean and low precision (e.g., wide uncertainty; SD = 1000). These parameters result in the priors being locally uniform over the region supported by the likelihood estimate (Pratt et al. 1995).

Smoothed posterior marginal distributions for the parameter \( \theta \) for larvae indicate large variation in its estimates within and among groups of sites (Figure A1.2). I estimated plausible ranges of the annual survivorship rates for each site group, given these priors, by using the posterior estimates of \( \theta \) to calculate the annual survivorship rates, and using the distribution of sampled values to estimate their probability (Table A1.1). From this, it appears that the posterior annual tadpole survival rate for tailed frogs in southwestern British Columbia may range between 0.263 and 0.365, given the uncertainties in estimation. While there may potentially be differences in survivorship rates between Squamish and Chilliwack sites, it is not clear from present data whether such differences arise from different sources of mortality between sites, or are simply due to other sources of estimation errors.
Figure A1.3. Smoothed posterior marginal distributions for estimates of $\theta$ in the models fitted to cumulative larval size class data for Squamish and Chilliwack sites. The bounds of the upper and lower 95% credible region of estimates on each distribution are indicated with arrows. Estimates were generated with non-informative priors and represent 10,000 samples from the posterior.

Table A1.1. Posterior means and the 95% credible range of values for annual survivorship rates of larvae in Squamish and Chilliwack sites.

<table>
<thead>
<tr>
<th>Location</th>
<th>Mean annual survivorship rate</th>
<th>95% credible range</th>
</tr>
</thead>
<tbody>
<tr>
<td>Squamish</td>
<td>0.355</td>
<td>0.336-0.365</td>
</tr>
<tr>
<td>Chilliwack</td>
<td>0.327</td>
<td>0.263-0.360</td>
</tr>
</tbody>
</table>
APPENDIX 2 – RELATIONSHIPS AND PARAMETER VALUES FOR THE LANDSCAPE-LEVEL SPATIAL MODEL

Table A2.1. Principal relationships and parameters used in the spatially-explicit landscape model developed in Chapter 4. Subscripts refer to tailed frog life stages (1=eggs/hatchlings, 2=small tadpoles, 3=large tadpoles, 4 = metamorphosed juveniles, 5=breeding adults; see also Chapter 3).

<table>
<thead>
<tr>
<th>Model component</th>
<th>Parameters</th>
<th>Default values</th>
<th>Range of values</th>
<th>Description</th>
</tr>
</thead>
<tbody>
<tr>
<td>Population growth</td>
<td>A</td>
<td>1</td>
<td>0-20</td>
<td>Allee parameter used to calculate the proportional decrease in fecundity as the total number of breeding individuals declines.</td>
</tr>
<tr>
<td></td>
<td>CVDemography</td>
<td>0.1</td>
<td>0-1.0</td>
<td>Coefficient of variation about each stochastic demographic parameter in each cell: initial $N_i$ (population size in each life stage), $G_i$, $S_i$, $F_i$.</td>
</tr>
<tr>
<td></td>
<td>deltaF&lt;sub&gt;5&lt;/sub&gt;</td>
<td>1</td>
<td>0-2</td>
<td>Multiplier for $F_i$ in this cell as a result of the combined effects of proportion (area) of total contributing&lt;sup&gt;3&lt;/sup&gt; upland and riparian forest that is 41-80 years old.</td>
</tr>
<tr>
<td></td>
<td>deltaG&lt;sub&gt;i&lt;/sub&gt;</td>
<td>1</td>
<td>0-2</td>
<td>Multiplier for $G_i$ in this cell as a result of the combined effects of proportion (area) of total contributing&lt;sup&gt;3&lt;/sup&gt; upland and riparian forest that is either 0-10 years old, or 41-80 years old.</td>
</tr>
<tr>
<td></td>
<td>deltaS&lt;sub&gt;i&lt;/sub&gt;</td>
<td>1</td>
<td>0-2</td>
<td>Multiplier for $S_i$ in this cell as a result of the combined effects of proportion (area) of total contributing upland and riparian forest that is either 0-10 years old, or 41-80 years old.</td>
</tr>
<tr>
<td></td>
<td>DFEfectS&lt;sub&gt;i&lt;/sub&gt;</td>
<td>0.25&lt;sub&gt;1,3&lt;/sub&gt;, 0.75&lt;sub&gt;4&lt;/sub&gt;, 1.0&lt;sub&gt;5&lt;/sub&gt;</td>
<td>0-1</td>
<td>Multiplier for $S_i$ in this cell as a result of immediate mortality from a debris flow event.</td>
</tr>
<tr>
<td></td>
<td>$F_i$</td>
<td>30&lt;sub&gt;0&lt;/sub&gt;</td>
<td>15-45</td>
<td>Average annual fecundity (# female eggs · breeding female&lt;sup&gt;-1&lt;/sup&gt;) in the landscape.</td>
</tr>
<tr>
<td></td>
<td>$G_i$</td>
<td>0.385&lt;sub&gt;1&lt;/sub&gt;, 0.297&lt;sub&gt;2&lt;/sub&gt;, 0.533&lt;sub&gt;3&lt;/sub&gt;, 0.424&lt;sub&gt;4&lt;/sub&gt;, 0.0&lt;sub&gt;5&lt;/sub&gt;</td>
<td>0-1&lt;sub&gt;i&lt;/sub&gt;</td>
<td>Mean annual proportion of $N_i$ in all occupied cells moving to the next life stage this year. Values taken from Chapter 3.</td>
</tr>
</tbody>
</table>
|                  | HabKDiff    | 0.4            | 0-1             | Maximum percentage difference in stream carrying capacity $K$ between the “stable” (high
<table>
<thead>
<tr>
<th>Model component</th>
<th>Parameters</th>
<th>Default values</th>
<th>Range of values</th>
<th>Description</th>
</tr>
</thead>
<tbody>
<tr>
<td>MaxK_i</td>
<td>2.7054_1</td>
<td>0.003 – 5.0</td>
<td>Maximum carrying capacity K (in # individuals \cdot m^2 of habitat) for each life in the landscape. If the number of individuals exceeds K, in a particular habitat cell, excess individuals are either dispersed, or killed at a rate of 50% of the excess per year.</td>
<td></td>
</tr>
<tr>
<td>OccupiedPropn</td>
<td>0.52</td>
<td>0-1</td>
<td>Proportion of habitat cells occupied by tailed frog populations at the start of simulations. Value taken from Figure 2.2a.</td>
<td></td>
</tr>
<tr>
<td>RpDEffectS_i</td>
<td>0.80_1</td>
<td>0.5 –1.0</td>
<td>Multiplier for S_i as a result of the combined effects of all disturbances occurring in the contributing riparian forest for this habitat cell. Disturbances include harvesting, fires, windthrow, flooding.</td>
<td></td>
</tr>
<tr>
<td>S_i</td>
<td>0.0000_1</td>
<td></td>
<td>Mean annual proportion of N_i in all occupied cells remaining in the same life stage this year. Values taken from Table 3.3.</td>
<td></td>
</tr>
<tr>
<td>S0EffectF_i</td>
<td>1.0_5</td>
<td></td>
<td>Maximum proportional change in F_i in each cell due to effects of area of contributing forest (non-riparian and riparian) in the age class 0-10 years.</td>
<td></td>
</tr>
<tr>
<td>S0EffectG_i</td>
<td>1.0_5</td>
<td></td>
<td>Maximum proportional change in G_i in each cell due to effects of area of contributing forest (non-riparian and riparian) in the age class 0-10 years.</td>
<td></td>
</tr>
<tr>
<td>S0EffectS_i</td>
<td>0.82_3</td>
<td></td>
<td>Maximum proportional change in S_i in each cell due to effects of area of contributing forest (non-riparian and riparian) in the age class 0-10 years.</td>
<td></td>
</tr>
<tr>
<td>S3EffectF_i</td>
<td>0.8_5</td>
<td></td>
<td>Maximum proportional change in F_i in each cell due to effects of area of contributing forest (non-riparian and riparian) in the age class 41-80 years.</td>
<td></td>
</tr>
<tr>
<td>S3EffectG_i</td>
<td>0.82_3</td>
<td></td>
<td>Maximum proportional change in G_i in each cell due to effects of area of contributing forest (non-riparian and riparian) in the age class 41-80 years.</td>
<td></td>
</tr>
<tr>
<td>S3EffectS_i</td>
<td>0.82_3</td>
<td></td>
<td>Maximum proportional change in S_i in each cell due to effects of area of contributing forest (non-riparian and riparian) in the age class 41-80 years.</td>
<td></td>
</tr>
<tr>
<td>StockLevel</td>
<td>0.8</td>
<td>0.5-1.5</td>
<td>Initial proportion of K for each habitat used to calculate the mean initial population size (N_i). From this the actual N_i at the start of the simulation is computed as:</td>
<td></td>
</tr>
<tr>
<td>Model component</td>
<td>Parameters</td>
<td>Default values</td>
<td>Range of values</td>
<td>Description</td>
</tr>
<tr>
<td>-----------------</td>
<td>------------</td>
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</tr>
<tr>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Dispersal</td>
<td>AEmigAmt</td>
<td>0.1</td>
<td>0-0.5</td>
<td>Proportion of the combined juvenile and adult population in all cells eligible to disperse each year. Actual number of dispersers of these stages is calculated as deltaEmigAmt * AEmigAmt0 * Nj with surplus individuals (those above K) added in.</td>
</tr>
<tr>
<td></td>
<td>DeltaEmigAmti</td>
<td>1.0</td>
<td>0.75</td>
<td>Multiplier on the fraction of Nj in each cell eligible to disperse as a result of cumulative disturbances in riparian forest.</td>
</tr>
<tr>
<td></td>
<td>MaxTDnStrDist</td>
<td>600 m</td>
<td>0-2000 m</td>
<td>Maximum number of meters moved downstream by tadpoles. Estimated from Wahbe and Bunnell (in press).</td>
</tr>
<tr>
<td></td>
<td>MaxTUpStrDist</td>
<td>100 m</td>
<td>0-400 m</td>
<td>Maximum number of meters moved upstream by tadpoles. Estimated from Wahbe and Bunnell (in press).</td>
</tr>
<tr>
<td></td>
<td>MinNToDisp</td>
<td>5</td>
<td>0-Ni</td>
<td>Minimum population size of juveniles and adults in each cell below which no dispersal will occur.</td>
</tr>
<tr>
<td></td>
<td>PrEmigi</td>
<td>0.052-3</td>
<td>0 - 1</td>
<td>Probability that emigration of each life stage will not occur from this cell this year, calculated from a uniform distribution.</td>
</tr>
<tr>
<td></td>
<td>PropAUpStrDisp</td>
<td>0.67</td>
<td>0-1.0</td>
<td>Proportion of adult dispersers moving upstream. Estimated from anecdotal evidence that gravid females are often seen moving towards headwaters in the fall (Leonard et al. 1993).</td>
</tr>
<tr>
<td></td>
<td>TEmigAmt</td>
<td>0.1</td>
<td>0-0.5</td>
<td>Proportion of the tadpole population in all cells eligible to move each year. Actual number of individuals moving in each tadpole stage is calculated as deltaEmigAmt * TEmigAmt) * Nj with surplus individuals (those above K) added in.</td>
</tr>
</tbody>
</table>

Non-harvesting disturbances:

<table>
<thead>
<tr>
<th>Parameters</th>
<th>Default values</th>
<th>Range of values</th>
<th>Description</th>
</tr>
</thead>
<tbody>
<tr>
<td>CVNDPatchSizeRp</td>
<td>0.1</td>
<td>0-1</td>
<td>Coefficient of variation of non-logging disturbance patch sizes in riparian forest</td>
</tr>
<tr>
<td>CVPropDRp</td>
<td>0.1</td>
<td>0-1</td>
<td>Coefficient of variation of proportion of riparian forest disturbed each year.</td>
</tr>
<tr>
<td>DFSpreadProb</td>
<td>0.3</td>
<td>0-1</td>
<td>Probability that a debris flow will stop in the current stream cell. If the stream cell changes size class, there is a 100% chance it will stop.</td>
</tr>
</tbody>
</table>

\[ N_i = \text{Normal}(\text{StockLevel} \times \text{Max}K_i, \text{SD}) \] where SD is determined from CVDemography.
<table>
<thead>
<tr>
<th>Model component</th>
<th>Parameters</th>
<th>Default values</th>
<th>Range of values</th>
<th>Description</th>
</tr>
</thead>
<tbody>
<tr>
<td>DSSeverity</td>
<td>10%</td>
<td>0-100%</td>
<td></td>
<td>Index indicating the percentage of the maximum severity (expressed in terms of contribution to sedimentation and temperature effects) of each ha disturbed. A value of 100% indicate that one ha would create the maximum possible habitat and demographic effect on the downslope stream cell.</td>
</tr>
<tr>
<td>FireReturnTime</td>
<td>250 years</td>
<td>0-1000 years</td>
<td></td>
<td>Mean interval (years) between successive stand-initiating fires for each ha of forest. The default value is the expected value for coastal forests in disturbance type NDT1 (Ministry of Forests and Ministry of Environment 1995a). Values for coastal streams taken from Church in press).</td>
</tr>
<tr>
<td>FYPerCentury</td>
<td>3</td>
<td>0-10</td>
<td></td>
<td>Mean number of flood events expected per montane headwater stream each century.</td>
</tr>
<tr>
<td>MaxFireDDist</td>
<td>1000m</td>
<td>0-5000 m</td>
<td></td>
<td>Maximum distance (m) from nearest stream that impacts (sedimentation, nutrient leaching) from stand-initiating fires (e.g., sedimentation, nutrient leaching) can be detected. Impacts diminish linearly with distance (uncorrected for slope). Sources: Britton (1990), Spencer and Hauer (1991), Belillas and Feller (1998).</td>
</tr>
<tr>
<td>MaxLoggingDDist</td>
<td>1000m</td>
<td>0-5000 m</td>
<td></td>
<td>Maximum distance (m) from nearest stream that impacts (sedimentation, temperature effects on runoff) from clear-cut logging (e.g., sedimentation, temperature effects on runoff) can be detected. Impacts diminish linearly with distance (uncorrected for slope).</td>
</tr>
<tr>
<td>MaxOtherDDist</td>
<td>500m</td>
<td>0-2000 m</td>
<td></td>
<td>Maximum distance (m) from nearest stream that impacts (sedimentation, temperature effects on runoff, nutrient effects) from non-harvest related disturbances (e.g., landslides) can be detected. Impacts diminish linearly with distance (uncorrected for slope).</td>
</tr>
<tr>
<td>MeanDPatchSizeRp</td>
<td>2 ha</td>
<td>0-1</td>
<td></td>
<td>Mean size (ha) of non-harvest related disturbances in riparian forest.</td>
</tr>
<tr>
<td>MeanPropDRp</td>
<td>0.005</td>
<td>0-1</td>
<td></td>
<td>Mean proportion of total riparian forest susceptible to non-harvest-related disturbances each year. Default value set to a return interval of 200 years.</td>
</tr>
<tr>
<td>MinAgeToDRp</td>
<td>20 yr</td>
<td>0-100 yr</td>
<td></td>
<td>Minimum age (years) of riparian forest required before it becomes susceptible to non-harvest-related disturbances.</td>
</tr>
<tr>
<td>ProbDF</td>
<td>degraded = 0.0005</td>
<td>stable = 0.004</td>
<td>aggraded = 0.02</td>
<td>Static probability of initiating a debris flow, depending on current CAP state of the stream cell. Each time interval the probability that a debris flow is initiated in a stream cell is 0.01 * ProbDF for a flood year, 0.001 * ProbDF for a non-flood year. Estimates derived from Bovis et al. (1998).</td>
</tr>
<tr>
<td>RDRecoveryRate</td>
<td>3 yr</td>
<td>0-40 yr</td>
<td></td>
<td>Recovery rate of non-riparian vegetation from bare-ground disturbances in each disturbed cell, such that their contribution to effects on populations cannot be detected. Value estimated from Lamberti et al. 1991).</td>
</tr>
<tr>
<td>UDRecoveryRate</td>
<td>5 yr</td>
<td>0-100 yr</td>
<td></td>
<td>Recovery rate of non-riparian vegetation from bare-ground disturbances in each disturbed cell, such that their contribution to effects on populations cannot be detected.</td>
</tr>
<tr>
<td>Model component</td>
<td>Parameters</td>
<td>Default values</td>
<td>Range of values</td>
<td>Description</td>
</tr>
<tr>
<td>-----------------</td>
<td>------------</td>
<td>----------------</td>
<td>----------------</td>
<td>-------------</td>
</tr>
<tr>
<td>Logging</td>
<td>AAC</td>
<td>30000 m² yr⁻¹</td>
<td>0 - ∞</td>
<td>Mean annual allowable cut (m² yr⁻¹). Value estimated for the test landscape assuming and average merchantable yield per ha of 270m³ ha⁻¹ for all of the operable timber land base, and a minimum harvesting age of 100 years. From this, the number of cutblocks required to meet the AAC target is: (AAC / YieldPerHa / BlockSizeMean ha). The total number of cells cut may actually be less, if fewer cells can be found at an initiation site than required, but on average this is likely to be minor. In addition, some stochasticity (up to 50%) is added to the AAC using a normal distribution: 68% of the time it will be within AAC +- 25%; 95% of the time it will be within AAC +- 50%, and 5% of the time it will be greater than a 50% deviation from the AAC.</td>
</tr>
<tr>
<td>BlockSizeMean</td>
<td>10 ha</td>
<td>1-40 ha</td>
<td></td>
<td>Mean size (ha) of cutblocks for coastal forests. Once a cutblock is started, it is cut before the next cutblock is initiated. Source: Forest Practices Code guidelines for southern coastal forests (Ministry of Forests and Ministry of Environment 1995b).</td>
</tr>
<tr>
<td>BlockSizeSD</td>
<td>5 ha</td>
<td>0-20 ha</td>
<td></td>
<td>Standard deviation in average cutblock size for coastal forests.</td>
</tr>
<tr>
<td>GreenUpYears</td>
<td>15 yr</td>
<td>0-25 yr</td>
<td></td>
<td>Regeneration interval (years) required before cells adjacent to the harvested cell can be eligible for harvesting. Currently, the width of adjacent unharvested areas (&quot;leave strip&quot;) is set at 100m.</td>
</tr>
<tr>
<td>MaxDistToRoad</td>
<td>2 km</td>
<td>0-5 km</td>
<td></td>
<td>Maximum distance (km) a newly cut cells can be located from the nearest logging road.</td>
</tr>
<tr>
<td>MinStandAgeToLog</td>
<td>100 yr</td>
<td></td>
<td></td>
<td>Minimum rotation age of stands before they are eligible for harvest.</td>
</tr>
<tr>
<td>NewRoadAffinity</td>
<td>0.5</td>
<td>0-1</td>
<td></td>
<td>Relative probability that a cutblock will be located near cells containing active logging roads. In general the probability of initiating a cutblock decreases exponentially with increasing distance from roads, up to MaxDistToRoad. Harvestable cells on the landscape edge cells must be within 2 km of a road.</td>
</tr>
</tbody>
</table>

¹ non-harvesting disturbances include: fires, debris flows, floods affecting riparian vegetation, local windthrow events, landslides in riparian zones