

Movement and Demography of  
Larval Coastal Giant Salamanders (*Dicamptodon tenebrosus*)  
in Streams with Culverts in the Oregon Coast Range



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*Master of Science Thesis*  
22 July 2004  
*Wildlife Science*  
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AN ABSTRACT OF THE THESIS OF

**Jina P. Sagar** for the degree of **Master of Science** in **Wildlife Science** presented on **July 22, 2004**.

Title: **Movement and Demography of Larval Coastal Giant Salamanders (*Dicamptodon tenebrosus*) in Streams with Culverts in the Oregon Coast Range.**

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Deanna H. Olson

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Barriers to the movement of aquatic organisms can increase the genetic and spatial isolation of populations and may decrease the viability of these regional populations. Focus on culvert passage issues has increased as federal agencies attempt to inventory and replace road-crossing stream culverts that are barriers to the movement of anadromous fish. However, the effect of road-crossing culverts on the movement of other aquatic organisms is not known. The coastal giant salamander (*Dicamptodon tenebrosus*) is an important component of headwater stream communities and their movement may be affected by culverts in the larval aquatic stage. The objectives of this study were to determine the effect of road-crossing culverts on the movement and survival of larval coastal giant salamanders in the Oregon Coast Range. We conducted a mark-recapture study on larval *D. tenebrosus* in 3rd and 4th order streams to: i) determine culvert use and passage by design type (pipe and arch types) relative to reference stream reaches without culverts; and ii) model larval survival by season, age and culvert presence.

We assessed the movement of over 2,000 larval *D. tenebrosus* in 14 streams and found that larvae were highly sedentary. Mean movement distances did not differ with culvert presence. However, a small portion of larvae (20%) moved sufficient distances to assess culvert passage. Larvae moved less frequently through stream reaches with culverts than stream reaches without culverts, suggesting a barrier effect. There was less upstream movement through pipe culverts than arch culverts. Also, there were lower larval densities in pipe culverts, indicating arch culverts provided more larval habitat. Larval density both inside culverts and in the adjacent stream reaches was associated with the presence of large substrates, which may be important in facilitating larval *D. tenebrosus* movement through culverts. Stream reaches with culverts were associated with higher levels of fine sediments, however, which may reduce the suitability of near-culvert habitats.

Survival estimates indicated high selection pressure early in the larval period. Apparent survival was lower in summer, and for first-year in comparison to second/third-year larvae. Larval survival for both age groups was lower in reaches of stream with culverts although this effect was weak.

Culvert effects on movement of coastal giant salamander aquatic larvae indicate they can operate as barriers but their effect on survival remains unclear. Culvert replacements that simulate both the natural stream bed and hydraulic conditions would help provide both habitat and passage opportunities for larval *D. tenebrosus*.

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Movement and Demography of Larval Coastal Giant Salamanders  
(*Dicamptodon tenebrosus*) in Streams with Culverts in the Oregon Coast Range

by

Jina P. Sagar

A THESIS  
submitted to  
Oregon State University

in partial fulfillment of  
the requirements for the  
degree of

Master of Science

Completed July 22, 2004  
Commencement June 2005

Master of Science thesis of Jina P. Sagar presented on July 22, 2004

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I understand that my thesis will become part of the permanent collection of Oregon State University libraries. My signature below authorizes release of my dissertation to any reader upon request.

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Jina P. Sagar

## ACKNOWLEDGMENTS

This project would not have been possible without the support of many people both inside and outside of the graduate school world. I am deeply grateful to have had two wonderful advisors, Dr. Deanna H. Olson and Dr. Richard A. Schmitz, who provided support, advice, and thoughtful editing throughout the process. John Guetterman was a great asset to this project both for providing the initial seed of inquiry and for unlimited logistical support and advice. Committee member Sherri Johnson offered her time and help on edits to the thesis. A special thanks to Manuela Huso for her countless hours of statistical consulting without which the analysis of this research would not have been produced. Pat Cunningham also provided statistical advice and invaluable patience. I thank Gail Olson for conferring on MARK analysis and Mike Furniss for sage culvert advice.

I am especially grateful to those who helped me in the field, Loretta Ellenburg, Kris Fausti, Craig Jacobson, and Jason Lowe. Their good humor through 7,000 salamanders and miles of stream crawling was priceless. Becky Flitcroft was “my fabulous officemate” and lives up to that name. Thank you to my friends and family and especially to Lucas Haley who provided unlimited support, database and otherwise.

Financial support was provided by a cooperative agreement with the Bureau of Land Management, Coos Bay District, the USDA Forest Service Pacific Northwest Research Station (ALI program), and Oregon State University.

## CONTRIBUTION OF AUTHORS

Dr. Deanna Olson and Dr. Richard Schmitz were directly involved in the design of this study and editing of the thesis. They have both made great contributions to the research presented in this thesis and are therefore co-authors on the two manuscripts submitted for publication from this Masters thesis.

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Movement and Demography of Larval Coastal Giant Salamanders  
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Chapter 1  
General Introduction

Road systems and stream networks frequently intersect. Culverts are commonly installed where streams are bisected by a road crossing. Some culverts can alter the stream hydrology and consequently disrupt the physical processes that maintain these systems (Baker and Votapka 1990). Most culverts currently in use were originally designed to pass water most efficiently under a road, and not necessarily with biological passage in mind (McKinley and Webb 1956). On U.S.D.A. Forest Service and U.S.D.I. Bureau of Land Management land in Washington and Oregon, there are approximately 10,000 culverts on fish-bearing streams and over half of these have been found to be barriers to salmonid fish (US GAO 2001). In the U.S., over a million (M. Furniss, personal communication, April 20, 2003) culverts are nearing the end of their life expectancy and are due for replacement on public and private lands (US GAO 2001).

There is a policy framework for maintaining the connectivity of habitats that support aquatic fauna in streams. The Aquatic Conservation Strategy in the Northwest Forest Plan, dictates Forest Service and BLM-administered lands “maintain and restore spatial and temporal connectivity within and between watersheds” and “these network connections must provide chemically and physically unobstructed routes to areas critical for fulfilling life history requirements of aquatic and riparian-dependent species” (USDA and USDI 1994). Furthermore, the ability of vertebrates to “interact with others in the planning area” is protected under the National Forest Management Act of 1976 (CFR) guidelines (USDA and USDI 2001), and connectivity is mandated by the the Clean Water Act (Clean Water Act 1977). For land managers to develop new criteria for culvert design that addresses biological connectivity, we need to have an understanding of how culverts effect the movement of not just fish but other aquatic organisms.

In order to focus the scope of this project, we selected one species from among aquatic stream organisms that may be of culvert passage concern. Larval coastal giant salamanders, *Dicamptodon tenebrosus* (formerly called Pacific giant salamanders, a name now reserved for the family), are an important component of forested headwater streams in the Pacific Northwest and may play a key role in the aquatic faunal community (Parker 1993b; Rundio 2002; Rundio and Olson 2003). Larval *D. tenebrosus* are abundant (Murphy et al. 1981; Hawkins et al. 1983) and are both prey and predators in the aquatic food web (Parker 1993a). Although larval period may vary by location and conditions (Blaustein et al. 1995), they spend between one to four years as stream obligates and may remain in the stream in neotenic form (Nussbaum and Clothier 1973). Larval

*D. tenebrosus* are weak swimmers compared to salmonids and may require different assessment criteria than those currently used for fish. The small streams that larval *D. tenebrosus* inhabit are often bisected by roads due to their position on the hillslope (Jones et al. 1999). For each of these reasons, larval *D. tenebrosus* are an ideal species for studying culvert passage. Culverts may be barriers to their movement, disrupting population structure with subsequent effects on stream communities.

While basic life history patterns have been described for this species, very little is known about their movement. There is some evidence that larvae are sedentary yet may occasionally make longer, colonizing movements to defaunated stream reaches (Ferguson 2000). Metamorphosed adults are capable of long distance movement overland (e.g., up to 305 m over three months; Johnston and Frid 2002) and may be more mobile than their larvae. However, larvae spend approximately two years in streams and may need to move in order to obtain adequate resources for survival (Welsh 2004 in press).

Although coastal giant salamanders occur from Mendocino County, California, to southwestern British Columbia, in both Coast and Cascade Ranges (Welsh 2004 in press), a smaller portion of the range was chosen as a focus for this study. The coastal Oregon Coos Bay region was selected as the study area because the Coos Bay District of the Bureau of Land Management (BLM) was particularly interested in examining the effect of culverts on non-fish aquatic organisms and had already established a list of culvert sites on lands they administer. Furthermore, two culvert design types were apparent in their inventory: pipe and arch culverts. Pipe culverts are the traditional design used over the last several decades. They have been associated with perched outlets and high water velocities, impairing fish passage (Baker and Votapka 1990). Arch culverts represented road crossings where restoration had occurred due to replacement of a fish barrier. Arch culverts span the active channel and allow stream substrates to accumulate within the culvert.

Channel constriction at the culvert can alter stream hydrology (i.e., high water velocity, outlet drop) and influence passage. Rather than examine salamander passage across a broad spectrum of culvert types, we chose to compare these two culvert design types, pipe and arch, that share few common physical characteristics and may represent extremes in hydrologic function. We used reference sites (no culvert) to provide a means of comparing movement through culvert reaches with movement through culvert-free reaches. Most culvert replacements (arch culverts) in the study area occurred on fish-bearing, low elevation streams, consequently reference and pipe

culvert sites needed to match these same physical criteria. We set the study site stream lengths by the maximum movement distances described for the larval *D. tenebrosus* (~50 m; Ferguson 2000) and the length of stream we could reasonably survey in a day. We conducted a two-year mark-recapture study on fourteen streams in the Oregon Coast Range study area on stream reaches with and without culverts.

In Chapter 2, we examined larval *D. tenebrosus* movement to determine if they travel distances that may require culvert passage. We also determined the use and frequency of culvert passage by larvae, compared the frequency of upstream and downstream movement directions, examined habitat features associated with movement and density of larval *D. tenebrosus*, and assessed culvert characteristics that may be related to culvert use and passage.

In Chapter 3, our primary aim was to estimate the growth and survival that occurs during the larval stage of *D. tenebrosus* and assess these demographic rates in the presence of culverts. Although the larval phase is only one stage in the complex life history of *D. tenebrosus*, larvae that survive to metamorphosis replenish the terrestrial adult population. Little is known about how growth and survival of larval *D. tenebrosus* vary both seasonally and temporally. Preliminary research in British Columbia suggested that larval survival may be lower in the winter season due to harsh conditions (Ferguson 1998), however, survival in milder climates such as the mid-Oregon Coast Range may differ. The primary causes of mortality in larval *D. tenebrosus*, cannibalism, predation and stream drying (Nussbaum and Clothier 1973), also may be more prevalent in the summer season in this more southerly location. In order to estimate survival and growth for larvae we used mark-recapture data from study streams and modeled survival for several populations in the Oregon Coast Range. We present robust estimates of survival on streams with and without culverts for two age classes of larvae in two seasons.

In Chapter 4, we summarize our findings and major conclusions and present management implications of this research. We report culvert effects on salamander movement and survival, and instream habitat conditions. We discuss the suitability of arch culverts for improving connectivity for instream larvae in comparison to pipe culverts.

Finally, there are three (A-C) Appendices in which we describe: A) the full set of MARK models used in the survival analysis; B) the density of other aquatic species found in reference reaches, culverts and in reaches adjacent to culverts; and C) an ancillary study on the density of the stream mollusk, *Juga* spp., in reference streams, culverts and adjacent stream reaches.

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## CHAPTER 2

# The Effect of Road Culverts on the Movement of Larval Coastal Giant Salamanders (*Dicamptodon tenebrosus*) in the Oregon Coast Range

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### INTRODUCTION

Barriers to in-stream movement can have multiple ecological impacts on aquatic organisms. Natural and anthropogenic barriers, such as waterfalls and dams, may fragment streams thereby limiting the access to food resources, reproductive sites and refugia by aquatic populations (Hilerbrand and Kershner 2000). As available habitat becomes more spatially limited, adequate resources for population maintenance may be insufficient (Chapman 1966; Hilerbrand and Kershner 2000). Barriers also may subdivide populations and impede or prevent recolonization after disturbance, increasing extinction risk due to fragmentation (Lacy 1987; Fagan et al. 2002). As dendritic ecosystems, river and stream networks are particularly vulnerable to fragmentation (Fagan 2002).

Road crossing culverts can be a barrier to aquatic organisms. Empirical evidence for the biological effects of barriers at road crossings comes primarily from studies of fish (Travis and Tilsworth 1986; Toepfer et al. 1999; Bates and Powers 1998). There are a variety of different culvert types and the type of culvert design may either preclude or facilitate passage (Warren and Pardew 1998). Culverts can act as filters that are passable only in certain seasons, by certain species, or at certain life stages (Warren and Pardew 1998). One barrier culvert can affect communities within the entire stream network by reducing upstream genetic diversity (Dillon 1988; Wofford 2003) or species richness (Peter 1998). Culvert passage issues are gaining national and international attention because they may be implicated in species loss and the more general decline of biodiversity in freshwater ecosystems (US GAO 2001).

The ability of an organism to navigate hydraulic and physical features within a culvert influences its passage success. Primary reasons that culverts serve as barriers for salmonids include a perched outlet, high velocity of water, and shallow water depth inside the culvert (Baker and Votapka 1990). While salmonids are known for strong swimming and jumping abilities (Baker and Votapka 1990), little attention has focused on other aquatic species that have different physical capabilities. Culverts designed to pass anadromous fish may not accommodate the different passage abilities of other stream organisms.

We examined the effect of road crossing culverts on the movement of larval *Dicamptodon tenebrosus* in coastal Oregon. Their use of culverts, ability to pass culverts, and in-stream movement patterns are unknown. This species is often the most abundant vertebrate in small headwater streams of the Pacific Northwest (Murphy et al. 1981; Hawkins et al. 1983) and impacts on passage could have cascading effects through aquatic communities. Larval *D. tenebrosus* are stream obligates for two to three years (Nussbaum and Clothier 1973), suggesting a barrier to movement could affect population structure. Larvae metamorphose into terrestrial adults although in streams with strong flow throughout the year, *D. tenebrosus* may stay in the stream as reproducing adults (Nussbaum and Clothier 1973). The distribution and abundance of larval *D. tenebrosus* is strongly influenced by cover availability in streams (Hawkins et al. 1983; Parker 1991). Although little research has examined territoriality in larval *D. tenebrosus*, larger larvae may displace or eat smaller larvae (Mallory 1996), suggesting that dispersal may play a role in allowing small larvae to secure adequate habitat. Furthermore, larval salamanders primarily move by crawling along the stream bottom and larger substrates (>64 mm) are easier for them to grip than fine sediments (Holomuzki 1991); hence, salamander passage may be affected by the absence of coarse substrates within some types of culverts.

Knowledge of species-specific movement and dispersal patterns is critical to understanding the effect that barriers have on life history (Rosenberg et al. 1998; Rodriguez 2002). Our study objectives were to determine: 1) larval *D. tenebrosus* movement distances and direction to assess the potential for culvert passage; 2) frequency and directionality of larval salamander culvert passage; 3) incidence of culvert use; 4) the relationship of habitat conditions and culvert characteristics to the density and movement of larval salamanders; and 5) the relationship of larval body size to movement distance and direction. Finally, we discuss the potential for fish passage at our culvert study sites and compare these results with our salamander passage findings. In order to compare passage success and use between culverts with different physical features, culverts identified in this study consisted of two design types, conventional pipe design (pipe) and pipe arch design (arch).

## METHODS

## Study Area

The study area was located on U.S. federal lands administered by the Coos Bay District of the Bureau of Land Management (BLM) and private timber lands in the central Oregon Coast Range (Figure 2.1). The three river sub-basins sampled, the Umpqua, Coos, and Coquille, are geologically characterized by basalt and uplifted sea floor sediment consisting of sandstone and layers of siltstone (USDI 2001). Within the Coast Range physiographic province,

precipitation mainly falls as rain between the months of October and March with annual averages in the study area ranging from 1,727 to 2,032 mm (USDI 2002). Air temperatures in the area are mild with seasonal averages between 4.4 and 15.0 degrees C (USDI 2002). Plant communities in the study area are described as the western hemlock (*Tsuga heterophylla*) zone (Franklin and Dyrness 1973), consisting primarily of Douglas-fir (*Pseudotsuga menziesii*) and western hemlock on forested slopes. Riparian areas are dominated by red alder (*Alnus rubra*). Portions of the study area have a high stream density (2.9 km of streams/km<sup>2</sup>) as well as high road densities (3.96 km of road/km<sup>2</sup>) (USDI 1998; USDI 2001).

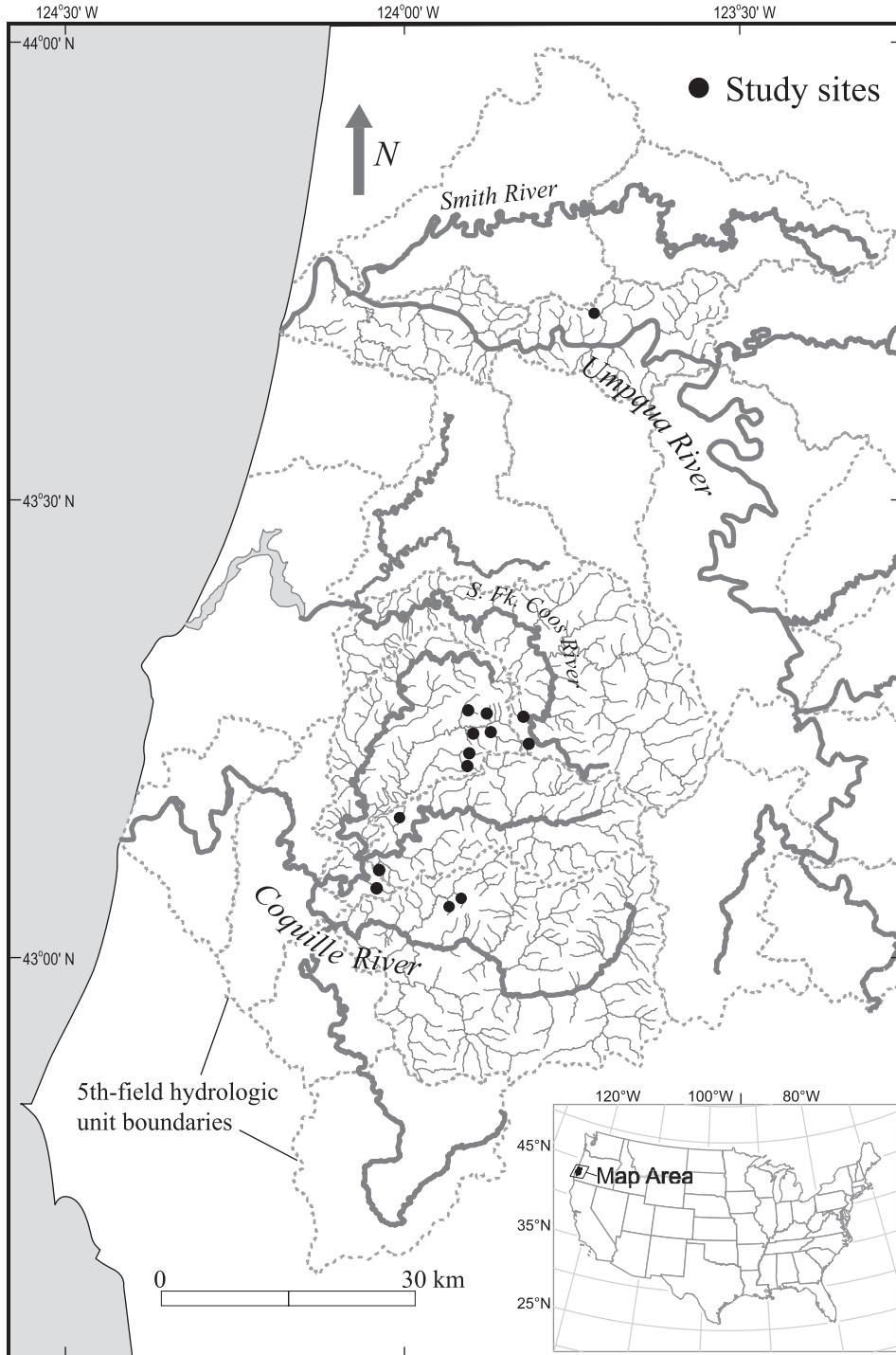


Figure 2.1. Map of southwestern Oregon showing the location of study area and the fourteen study sites within the Coquille, Coos, and Umpqua River basins.

## Study Design

We compiled a list of potential study sites from the BLM database of culvert sites and from map locations of road and stream intersections on Coos Bay BLM and adjacent private timber lands ( $n = 81$ ). Fourteen streams from three drainage basins in the study area were selected for study sites. To enable comparability between streams, site selection criteria sought to minimize heterogeneity in common stream characteristics and maximize habitats where larval *D. tenebrosus* are found. Stream characteristics for study site selection included perennial stream reaches with  $<3$  m low flow wetted width, low gradient ( $< 10\%$  slope),  $> 40$  m from the mainstem junction, sufficient reach length (see below), and a streambed composed of gravel, cobble and boulder substrates (dominant substrates  $> 64$  mm diameter). In addition, sites were selected only if larval *D. tenebrosus* were detected during a preliminary search period.

Study sites were located on different streams and consisted of a section of stream with a culvert in the middle (culvert sites) or a section of stream without a culvert (reference sites; Figure 2.2). Two culvert types were selected for study, pipe or arch culverts. Nine culvert sites (pipe  $n=4$ ; arch  $n=5$ ) and five reference sites were selected. We selected all sites that matched this fixed set of criteria from the list of available sites.

Culverts were grouped by design type (pipe or arch) based on differences in their physical characteristics. The two culvert types differed in their width, perch, and in the presence of stream bed substrates. Pipe culverts were circular with a corrugated metal bottom, lacked stream substrates, were narrower than the active channel width and were perched above the stream. Arch culverts were designed for the active width of the channel and were not perched. Therefore, they had a submerged flat bottom ( $n=5$ ), or baffles ( $n=1$ ), and a bottom covered with stream bed substrates. Culverts of both types varied in length from 13 m to 25 m (Table 2.1)

At each study site, habitat and larval *D. tenebrosus* were sampled along a reach approximately 80 m in length. At culvert sites, the culvert was positioned in the center of the reach with a 30 m

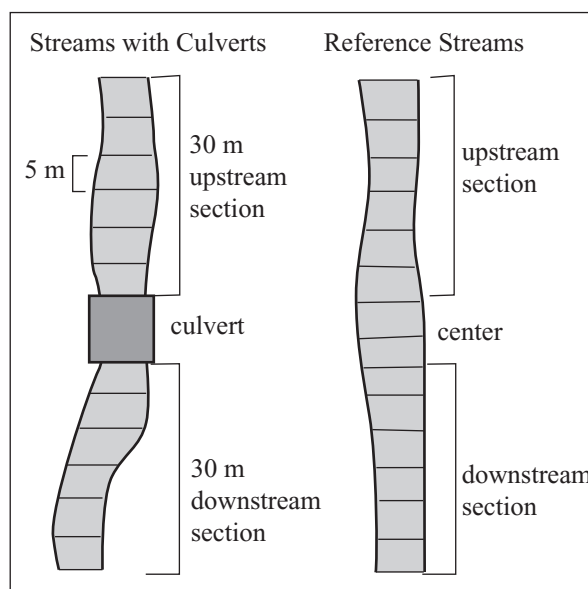


Figure 2.2. Design of survey area within culvert and reference study sites in the Oregon Coast Range.

upstream section above and 30 m downstream section below the culvert. Total stream section lengths for culvert sites varied with culvert length (Figure 2.2). In 2003, an additional 20 m was added to both ends of most study streams ( $n=13$ ) to capture marked salamanders that had moved beyond the study reach over the winter.

## Habitat Variables and Salamander Surveys

To examine possible differences in salamander movement and density in relation to habitat variability, habitat characteristics were evaluated for 5-m sections (using fixed points and a measuring tape) along each study stream in June 2002 and 2003. Habitat measures included wetted width (cm), active width (cm), percent substrate coverage of six classes of rocky substrates (visual estimate; Bury et al.

Table 2.1. Physical and biological characteristics of the 2002-2003 study sites in the Oregon Coast Range. Sites are reference (R), arch culvert (A) or pipe culvert (P). Date after arch culverts indicates year of installation.

| Stream Site       | Watershed area (km <sup>2</sup> ) | Culvert length (m) (perched cm) | Mean elevation (m) | Gradient (%) | Larval density (larvae/m <sup>2</sup> ) |
|-------------------|-----------------------------------|---------------------------------|--------------------|--------------|---|
| Alder (R)         | 8.52                              | n/a                             | 500                | 4            | 1.30                                    |
| Cherry (R)        | 3.86                              | n/a                             | 635                | 6            | 1.33                                    |
| Firecamp (R)      | 1.67                              | n/a                             | 748                | 4            | 2.57                                    |
| Honcho (R)        | 1.95                              | n/a                             | 650                | 6            | 0.96                                    |
| Weatherly (R)     | 2.74                              | n/a                             | 184                | 2            | 0.80                                    |
| Bearpen (A) 1999  | 1.23                              | 20(0)                           | 380                | 3            | 0.70                                    |
| Cherry (A) 1998   | 2.88                              | 22(0)                           | 850                | 6            | 3.58                                    |
| Firecamp (A) 1998 | 1.98                              | 25(0)                           | 747                | 4            | 1.27                                    |
| Vaughn (A) ~1989  | 3.36                              | 13(0)                           | 644                | 4            | 1.29                                    |
| Yankee (A) 2001   | 2.75                              | 17(0)                           | 157                | 2            | 0.78                                    |
| Axe (P)           | 3.75                              | 22(20)                          | 425                | 3            | 2.30                                    |
| Honcho (P)        | 1.81                              | 22(100)                         | 600                | 10           | 2.14                                    |
| Johns (P)         | 0.93                              | 19(30)                          | 244                | 5            | 1.08                                    |
| Weekly (P)        | 1.83                              | 23(100)                         | 292                | 5            | 0.42                                    |

1991), unit type (100% pool = 1.0; 100% riffle = 0), and canopy cover (visual estimate; 0-100%). Gradient was recorded for each stream reach in the field with a clinometer. In addition, in 2004 we recorded specific culvert characteristics related to the velocity, depth and outlet jump at the culvert (see USDA 1999) in order to assess the hydrologic challenge and potential for fish passage of culvert study sites.

We conducted larval *D. tenebrosus* surveys five times in each stream over the course of two summers. The entire length of each study site, including culverts, was surveyed once a month in June, July and August 2002 and again in June and July 2003. Surveys were conducted in an upstream direction through stream and culvert sections. Stream sections were first visually searched for *D. tenebrosus*. We then systematically searched the wetted substrates in 5 m cross sectional belts, by turning over all rock and wood cover objects that could be moved. Boulders that could not be moved were probed with a stick along the underside, dislodging *D. tenebrosus* from underneath. In riffles, where the water surface was agitated, we used a plexiglass box to locate salamanders. We hand-captured all *D. tenebrosus* with small dip nets and put them into a water-filled plastic bag. Overturned substrates and debris were returned to their original position. Cover object type, size of substrate and the location of each capture site were recorded for each individual.

Salamanders were anesthetized, measured (snout vent length, SVL; total length, TL; Fellers et al. 1994), marked, and quickly returned to their initial capture location. Only individuals captured in June and July 2002 were marked. Larvae were anesthetized by immersion in a 0.33g/L solution of MS222 (tricaine methanesulfonate; Cooper 2003). Each salamander was given a unique pattern of colored marks using visible implant fluorescent elastomer (Northwest Technologies; four colors; Davis and Ovaska 2001). Three marks were made at six possible locations on the ventral body wall, on both sides of the body: posterior to forelimbs; anterior to hind-limbs; or posterior to hind-limbs. Small salamanders (<31 mm SVL) or older salamanders that had a dark ventral surface (>90 mm SVL) were given three marks at the base of the tail. In order to minimize disturbance, recaptures were not anesthetized but were measured to the nearest millimeter (SVL) while within a plastic bag. Recaptured animals were checked for marks by using a blue filtered light and amber glasses.

## Statistical Analyses

**Movement.** Movement distance was measured as the difference between the initial position of a salamander and a later location. While we have no way of knowing the true distance an individual may have traveled between intervals, movement distances presented here represent net losses or gains over specified periods of time. Summer movement refers to individuals marked in June and recaptured in August 2002 (n = 499). Overwinter movement refers to individuals captured in August 2002 and recaptured in June or July 2003 (n = 274). If an individual was captured in both June and July 2003, its location in June only was used. Annual movement refers to individuals marked in June 2002, recaptured in June 2003 and those marked in July 2002 and recaptured in July 2003 (n = 238).

In two analyses, summer movement distances and overwinter movement distances were compared among the three stream classes

(reference, pipe and arch) using a mixed effects ANOVA (PROC MIXED). Absolute movement distance per salamander was log transformed to meet the assumption of constant variance. We used SAS (SAS Institute 1990; Littell et al. 2002) for all statistical analyses. For all mixed models, individual stream (n = 14) was included as a random effect.

To examine differences in movement directionality between culvert (arch and pipe) and reference streams, we used the ratio of upstream movements to total movements per stream as a response variable in logistic regression (PROC GENMOD). Ratios > 0.5 indicate upstream directionality. A contrast statement was used to determine the average log-transformed odds of moving upstream versus downstream, provided no differences existed between culvert and reference streams.

The frequency of salamander movement through culverts is purely anecdotal without the context of a reference condition. The study was therefore designed so that on culvert streams, movements greater than 30 m (the length of stream section above or below the culvert) would result in the salamander entering a culvert or leaving the study reach. The frequency of these movements on culvert streams were compared to reference streams to determine if movements were truncated where a culvert was in the center of the transect. We used the ratio of longer distance movements (> 30 m) to total movements as the response variable in a logistic ANOVA (PROC GENMOD). We compared these movements between the three stream classes. Larval salamanders were only included in the analysis if they had passed through the center of the study site in either culvert or reference streams (e.g., recaptures found in 2003 extended survey areas were not included). In this way, the number of salamanders that passed into or through the center reach, from upstream or downstream reaches, could be compared between culvert and reference streams.

As salamanders grow in streams, their movement patterns may change. To investigate the relationship between salamander size (SVL), and movement distance we used linear regression (PROC GLM). We log-transformed the response variable, absolute annual movement, to meet the assumption of equal variance. In a second linear regression model, we examined the relationship between salamander size (SVL) and annual movement direction using movements as the response variable.

**Habitat Associations.** We used regression models (PROC REG; PROC GENMOD) to determine if larval salamander abundance (linear regression), average movements (linear regression), and long distance movements (logistic regression) were associated with specific habitat variables. We used logistic instead of linear regression for long distance movements because of the binary distribution of the response (ratio of longer distance movements (> 30 m) to total movements). The movement analyses contained an additional parameter (density, averaged over the summer) in order to detect broad-scale density dependent effects on movement. We selected a small set of a priori models to describe general habitat characteristics associated with the streams. Habitat features were selected based on prior evidence of which habitat conditions are likely relevant to *D. tenebrosus* abundance and movement (Table 2.2). Sample size limited models to only one explanatory variable (Ramsey 2002).

A total of five habitat parameters (and therefore models) were fit to the monthly density of larval *D. tenebrosus* in the summer of

Table 2.2. Description of habitat variables measured at the stream scale or averaged over the site from the 5-m scale, and references indicating the relevance of a habitat parameter.

| Parameter        | Description  | References                          |
|------------------|--|-------------------------------------|
| Canopy cover (%) | Percent canopy cover by 5-m section averaged over site                                     | Bury et al. 1991                    |
| Wet width (m)    | Mean wetted width over site  | Nussbaum and Clothier 1973          |
| Substrate (%)    | Visual estimate of % of each 5-m section obscured by substrates >64 mm, averaged over site | Hawkins et al. 1983;<br>Parker 1991 |
| Stream Class     | 3 classes: reference, arch, pipe   | -                                   |
| Density          | Number of salamanders/m <sup>2</sup> for each stream averaged over summer                  | Petranka and Sih 1986               |
| Elevation        | Elevation from GPS   | Nussbaum and Clothier 1973          |

2002. Larval density is the total number captured divided by the area searched. In order to meet the assumption of equal variance, we log-transformed density for all three summer capture occasions. We also excluded three streams from movement analysis (one of each stream class) due to low salamander numbers in those streams in 2003. A null model (no effect) was included in all analyses to determine if the response mean was a better fit to the data than any of the habitat measures. To allow comparability of models, the overdispersion parameter was set to the fullest model possible for each analysis (Burnham and Anderson 1998). We separately ranked models for salamander density and movement distance using Akaike's Information Criteria (AICc, adjusted for small sample size). AICc is an estimate of Kullback-Leibler information, which attaches a penalty for additional model parameters and has a lack of fit component (Burnham and Anderson 1998). The model with the lowest AICc value both best approximates the data and is the most parsimonious.

In order to compare streambed fine sediments in arch and pipe culvert streams versus reference streams we used a mixed effects ANOVA (PROC MIXED) and blocked by individual stream. We calculated the mean percent fine sediments per square meter for both the upstream (above culvert) and downstream (below culvert) sections of each study site. We then compared the mean fine sediments/m<sup>2</sup> between upstream and downstream sections and between culvert and reference (above and below center reach) streams and included an interaction between the two terms. We used a contrast statement to determine if fine sediments in culvert streams differed from those of reference streams. Estimates of mean fine sediments/m<sup>2</sup> were log-transformed to meet the assumption of equal variance.

**Culvert Use.** To determine whether the number of salamanders found in culverts was similar to the adjacent upstream and downstream reaches, we compared salamander counts per unit area in a mixed effects ANOVA. We compared differences between the density of salamanders in: 1) pipe and arch type culverts; and 2) adjacent reaches (stream sections immediately upstream and downstream of the culvert). In order to meet the assumption of constant variance, densities were log-transformed. Individual stream was considered a random, not fixed, effect. We included a culvert type main effect; a main effect for location, either inside the culvert

or in the adjacent reaches; and an interaction between culvert type and location, either inside the culvert or in the adjacent reaches. A Tukey-Kramer multiple comparison test was used to examine the relationship among the independent variables (culvert type; inside culvert or in adjacent stream reaches).

In order to assess the potential for fish passage through culverts on study sites, we used the program FishXing (USDA 1999), which models fish swimming capabilities against culvert hydraulics across a range of expected stream discharges. In the program, swimming and jumping capabilities were compiled into species and lifestage specific algorithms from a database based on the literature. To depict expected flows in the study area, we created a flow duration curve. Using daily average flow information from local USGS gauging stations divided by drainage area, a flow duration curve plots a frequency distribution of the average percentage of time specific daily flows are equaled or exceeded. The range of flows was then modeled with hydraulics in the culverts against the swimming and jumping algorithms for salmonids (juvenile and adult) and resident trout to determine potential for culvert passage.

## RESULTS

Over 7,000 captures of *Dicamptodon tenebrosus* were recorded during the summers of 2002 and 2003. A total of 2,215 larval *D. tenebrosus* were individually marked (1,334 in June 2002; 881 in July, 2002). Of those larvae marked, 1,200 (54%) were recaptured at least once during the study. Recapture rates varied by stream and season. Among all fourteen sites, the mean recapture rate over the summer was 38% (SE=3.4%) with an overwinter rate of 12% (SE=1.9%). Mean in-stream densities of all surveys per site ranged from 0.42 to 3.58 larvae/m<sup>2</sup>, in the wetted channel (Table 2.1). The number of individuals captured varied widely among sites, from 10 to 288.

The size distribution on each capture occasion, typical of small streams (Nussbaum and Clothier 1973), was largely made up of first-year larval *D. tenebrosus*, and few older larvae and pedomorphic adults (no. aquatic adults=31; Figure 2.3). We grouped larvae by size estimates from previous studies (Kessel and Kessel 1943; Nussbaum and Clothier 1973) and then used the size of those individuals recaptured after a year to determine the transition between first-year larvae and older larvae. Although most larvae

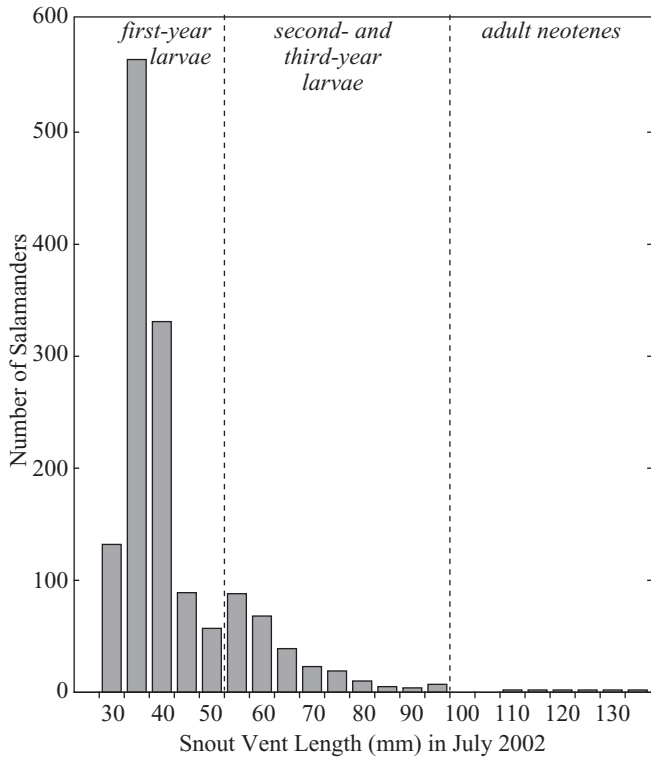


Figure 2.3. Size frequency histogram for larval *D. tenebrosus* captured in July 2002 in the Oregon Coast Range. Salamander captures before the first dashed line are first-year larvae, between the two dashed lines are second/third-year larvae, and captures to the right of the dashed line are aquatic adults.

mature into paedomorphs after reaching 115 mm SVL, the onset of paedomorphosis can occur earlier in some populations (85-107 mm SVL; Nussbaum 1976). We describe paedomorphs as individuals with length = 100 mm SVL in order to address potential size variation. Only four adult terrestrial salamanders were captured during stream sampling and were not marked.

### Movement

Mean movement distances were generally small (Figure 2.4). The mean movement distance for the entire summer season (June to August 2002) was 3.2 m (SE = 0.27,  $n = 483$ ) with a maximum detected movement of 51 m. Average movement distances during the summer did not differ ( $p = 0.63$ ,  $n = 13$ ) between reference (3.6 m, SE = 0.45,  $n = 196$ ) and culvert streams (2.6 m, SE = 0.31,  $n = 303$ ). Movements < 2 m comprised 45% of summer and 13% of overwinter movements. The average movement distance for all streams overwinter was 15 m (SE = 0.88,  $n=274$ ) with a maximum movement distance of 89 m. As with summer movements, mean movement distances did not differ ( $p = 0.27$ ,  $n = 13$ ) overwinter between reference (16 m, SE = 1.44,  $n = 120$ ) and culvert streams (11 m, SE = 1.06,  $n = 154$ ). When the study area was extended in 2003 (20 m at each end), larvae found in these areas had a movement mean more than twice that of the rest of the overwinter captures (30 m, SE = 3.2,  $n = 27$ ). Monthly movement rates (movement distance/no. of months in interval) were similar for the summer (1.6 m/month), winter (1.5 m/month) and full year (1.5 m/month).

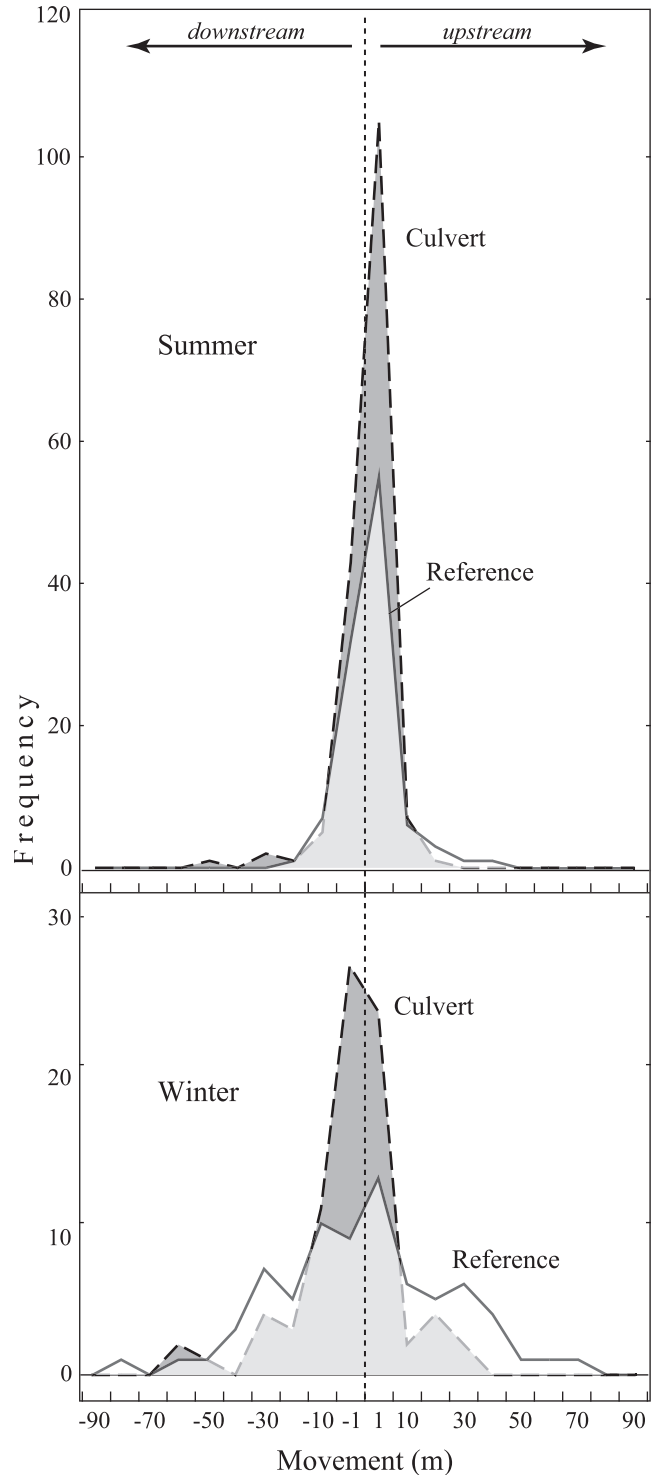


Figure 2.4. Movements by recaptured larval *D. tenebrosus* over summer (upper graph) and winter (lower graph) in culvert and reference streams in the Oregon Coast Range, 2002-2003. Summer is a measure of movement over a three-month interval, while winter is a measure of movement over a ten-month interval. On the x-axis, downstream movement is negative; upstream is positive. The vertical dashed line indicates zero (no movement).

Table 2.3. AICc model selection and ranking results for sets of log-linear and logistic regression models predicting larval *D. tenebrosus* density, average movement and longer movements (> 30 m) as a function of stream habitat variables. Symbols indicate top competing models ( $\Delta$  AICc  $\leq 2$  from top model) for each analysis. A null model (no effect) was included in all analyses to determine if the response mean was a better fit to the data than any of the habitat measures.

| Stream variable                                   | Density |      |        | Mean Movement |        |        | Long Movements |            |
|---|---------|------|--------|---------------|--------|--------|----------------|------------|
|   | June    | July | August | summer        | annual | winter | annual         | winter     |
| Width   |         |      |        |               |        |        |                |            |
| Stream Class<br>Reference (R), Arch (A), Pipe (P) |         |      |        |               |        |        | R+, A-, P-     | R+, A-, P- |
| Substrate   |         | +    | +      | -             |        |        |                |            |
| Elevation   |         |      |        |               |        |        |                |            |
| Canopy Cover                                      |         |      |        |               |        |        |                |            |
| Density <sup>1</sup>                              |         |      |        |               | +      | +      |                | +          |
| Null  | *       |      |        |               | *      | *      |                |            |

- Indicates a negative relationship, and + indicates a positive relationship

<sup>1</sup> Mean summer density of larval *D. tenebrosus* included as an explanatory variable in movement models

\* Competing null model

Salamander movement direction was predominantly upstream in the summer ( $p < 0.001$ ) and downstream overwinter ( $p < 0.001$ ) and did not differ between culvert and reference streams (summer,  $p = 0.55$ ; overwinter,  $p = 0.53$ ). Annual movement resulted in a net downstream movement for 60% of larvae and upstream movement for 40% of larvae for recaptures in both June ( $n = 90$ ) and July ( $n = 148$ ).

Larval salamanders that moved far enough to enter a culvert (>30 m) accounted for approximately 20% of overwinter movements. The number of salamanders that moved into the center reach (movements >30 m) differed between culvert and reference streams (logistic regression,  $p < 0.001$ ,  $n = 274$ ). Salamanders were 2.5 times (95% CI, 1.2 to 5.1 times) more likely to move into the center reach on reference streams than arch streams and 4 times (95% CI, 1.7 to 15 times) more likely in reference than pipe streams.

Annual movement ( $df = 107$ ,  $F = 4.49$ ,  $p = 0.03$ ,  $R^2 = 0.04$ ) and direction ( $df = 107$ ,  $F = 4.87$ ,  $p = 0.02$ ,  $R^2 = 0.04$ ) were not associated with salamander size (size range 26 to 120 mm SVL). Smaller salamanders moved longer distances and in a more downstream direction over the year than larger salamanders, however, SVL accounted for only about 4% of the variation ( $R^2 = 0.04$ ) in movement distance and direction.

### Habitat Associations with Movement and Density

Large substrates were the only habitat feature associated with larval salamander density and movement. The best approximating a priori model for habitat associations with larval density varied by month and was not associated with the presence of a culvert (Table 2.3). In June, the null model provided the best fit to larval density and in July and August, the presence of large substrates showed the strongest association with higher larval densities, with no competing models.

The relationship between habitat characteristics and average movement differed by season. In summer, average movement

distances were negatively associated with larger substrates, with no competing models. Overwinter and over the annual cycle, movement distances were not associated with any of the habitat variables (Table 2.3).

The two models that best explained the frequency of long distance movements overwinter were culvert presence and larval density. Culvert presence alone best explained the frequency of longer movements over the annual cycle, with no competing models (Table 2.3). Both overwinter and over the annual cycle, culvert presence was associated with fewer long distance movements. Low larval densities were associated with fewer long distance movements. The sample size for long movements was inadequate for analysis over the summer season. There were more fine sediments/m<sup>2</sup> in

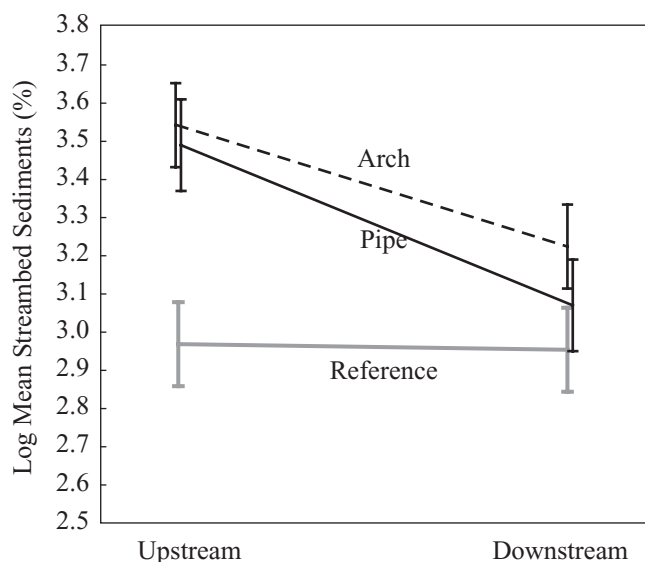


Figure 2.5. Mean estimates of streambed fine sediments/m<sup>2</sup> in upstream and downstream sections on nine culvert (arch, pipe) and five without culvert (reference) streams in the Oregon Coast Range, summer 2002.

Table 2.4. Average larval density ratios and culvert passage. The larval density ratio on each stream refers to the average density of larval *D. tenebrosus* upstream and downstream of culverts (outside) to the average density of larvae found inside of culverts (inside). Culvert passage refers to the number of individual larvae that passed from one side of the culvert to the other. Seasons are designated as summer passage (s) or winter passage (w). Partial passage is defined as small-scale movements within the culvert ( $2\text{ m} \leq \text{partial passage} \leq \text{culvert length}$ ). Sites are arch culvert (A) or pipe culvert (P).

| Stream Site  | Density ratio (outside/inside culvert) | Upstream Culvert passage (partial passage) | Downstream Culvert passage (partial passage) |
|--------------|--|--|--|
| Bearpen (A)  | 5.8                                    | 0 (3)                                      | 0 (5)  |
| Cherry (A)   | 2.5                                    | 0 (10)                                     | 2 s (14)                                     |
| Firecamp (A) | 1.8                                    | 1 s (10)                                   | 2 s (13)                                     |
| Vaughn (A)   | 1.1                                    | 1 w (2)                                    | 1 w (4)                                      |
| Yankee (A)   | 3.3                                    | 0 (3)                                      | 2 s (5)                                      |
| Axe (P)      | 8.5                                    | 0 (0)                                      | 2 w (0)                                      |
| Honcho (P)   | 7.0                                    | 0 (0)                                      | 3 s (0)                                      |
| Johns (P)    | 21.6                                   | 0 (0)                                      | 2 w (0)                                      |
| Weekly (P)   | 14.0                                   | 0 (0)                                      | 0 (0)  |

culvert streams than in reference streams (Figure 2.5;  $F_{1,11} = 9.57$ ;  $p = 0.01$ ). In culvert streams there was more of a tendency for the amount of fine sediment to decrease from upstream (above culvert) to downstream (below culvert) sections than in reference streams ( $F_{2,11} = 3.97$ ;  $p = 0.07$ ; Figure 2.5).

### Culvert Use

The density of salamanders found inside and outside of culverts varied by culvert type and the density of salamanders inside of culverts was less than in adjacent reaches ( $F_{1,7} = 20.14$ ,  $p = 0.0028$ ; Table 2.4). There was no difference in the overall density of salamanders between reference and culvert streams ( $F_{1,7} = 4.15$ ,  $p = 0.08$ ). There was, however, an interaction between salamander density inside culverts and in adjacent sections by culvert type ( $F_{1,7} = 9.2$ ,  $p = 0.01$ ). The density of salamanders was higher in arch culverts than in pipe culverts ( $p = 0.04$ ) and densities were higher in adjacent reaches than inside pipe culverts ( $p = 0.003$ ). The density of salamanders in arch culverts was no different than adjacent stream reaches ( $p = 0.72$ ; Table 2.4). The density of salamanders was from 3.1 to 18.6 times greater in arch culverts than in pipe culverts.

Occasionally, in some streams, larval *D. tenebrosus* were captured and recaptured in the same culvert. Of 79 culvert 'residents', only four were found in a pipe culvert. Additionally, all 286 captures of larvae in culverts were associated with substrate. In culverts where substrate comprised only a portion of the culvert bottom (four pipe culverts, one arch culvert), salamanders were found only where substrate was present.

Complete culvert passage by larval *D. tenebrosus*, from one side of a culvert to the other, occurred in a downstream direction in both pipe and arch culverts, in seven of nine culvert study sites, by 14 salamanders. Complete upstream passage was recorded by only two salamanders through two arch culverts. No upstream passage was detected through pipe culverts. Although complete upstream passage occurred in only two arch culverts, there was small-scale movement ( $2\text{ m} \leq \text{partial passage} \leq \text{culvert length}$ ; Table 2.4) by larval salamanders in all arch culverts but not in pipe culverts.

We assessed fish passage potential of study culverts using FishXing software and evaluated commonalities between these results and larval *D. tenebrosus* culvert passage. FishXing can only assess the potential for fish passage because salamander swimming capabilities are not known. Fish passage could not be assessed for two culverts and these were removed from the analysis. The Axe Creek culvert

(pipe culvert) was replaced before fish passage could be assessed and the Cherry Creek culvert (arch culvert) had baffles, which FishXing can not model accurately. According to FishXing models, the three pipe culverts were a barrier to juvenile salmonids and resident trout and two of the three were a barrier to adult salmonids (Figure 2.6). Arch culverts were not a barrier to either species or lifestage; however, the percent of flows that were passable by each varied by culvert. Culverts that were not modeled as passable by juvenile salmonids and resident trout also were passed by larval *D. tenebrosus* in our study (Figure 2.6)

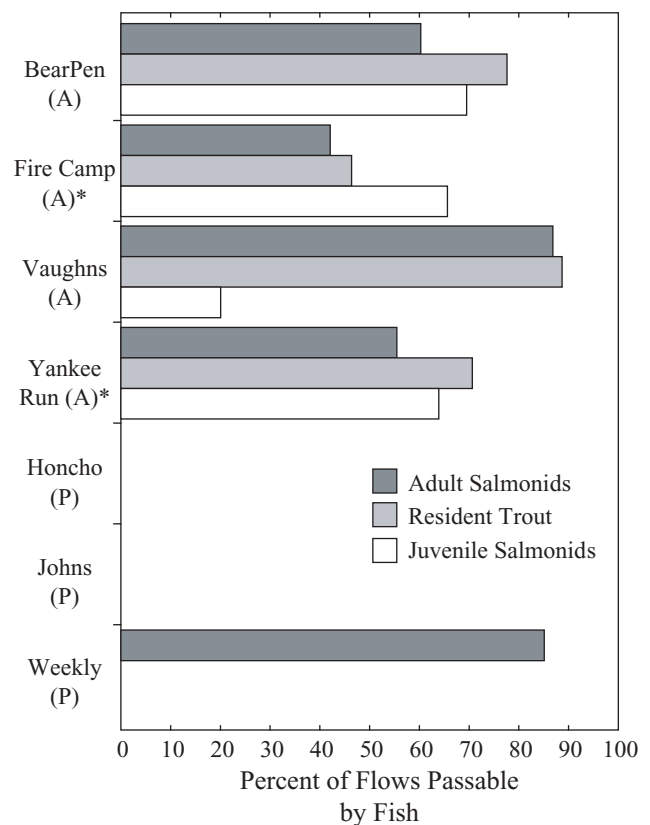


Figure 2.6. Percent of flows passable on culvert study sites in the Oregon Coast Range by fish assessment results on flows within study area range. \* Streams with complete upstream larval salamander passage.

## DISCUSSION

The majority of larval *D. tenebrosus* had high site fidelity and limited movement, which did not differ with culvert presence. Many salamanders moved short distances and did not encounter the culvert within the study reaches. A smaller proportion of the population (20%), however, was moving distances in which culvert passage was possible and these movements were truncated in culvert reaches. Our findings suggest that larval *D. tenebrosus* that are more mobile may not be moving into culverts, and that the frequency of culvert use and passage depends on culvert type.

Movement patterns of larval *D. tenebrosus* indicated two movement types: stationary and mobile individuals. Ferguson (2000) recorded a similar pattern for larval *D. tenebrosus* in British Columbia, in which a sub-group of larvae was moving longer distances than the rest of the population. It is uncertain whether these individuals are genetically predisposed to longer distance movement, or if salamander movement behavior changes episodically with external factors.

Although proportionately small, the mobile component of the larval population may be an important means of accessing resources when larval densities are high. Eggs of *D. tenebrosus* are laid in clutches of 100 or more (Nussbaum 1969) and hatching larvae occupy a small area. Despite the associated risks of predation, heavy competition for resources may induce some larvae to travel further to adequate food (Anholt and Werner 1999). If larval growth is density dependent (Petranka and Sih 1986; Petranka 1984; Wilbur 1980), dispersal may pay off for individuals that are able to encounter new habitats (Anholt and Werner 1999). Larval salamanders that are established in defaunated stream reaches can grow faster and may have higher survival due to a decrease in conspecific aggression and competition for food (Petranka and Sih 1986). We found a relationship between higher mean densities of larval *D. tenebrosus* and a greater frequency of long distance movements over the winter which supports the notion of density-induced movement.

In addition, we found that in the summer larval *D. tenebrosus* were moving more frequently in streams with fewer large substrates. Larger larval *D. tenebrosus* are associated with the use of larger substrates (Bury et al. 1991) and larvae may need to actively seek out larger cover objects as they grow. Stream reaches made up mostly of gravels may serve as 'nurseries' for first year larvae but provide inadequate cover for older (larger) larvae. Stream reaches with embedded substrates, due to sedimentation, may also provide inadequate habitat for larvae. The accumulation of fine sediments on culvert streams could reduce suitable microhabitats for the foraging and refugia needs of local populations of larvae. Since non-neotenic larvae do not reproduce, traits enhancing growth and survival until metamorphosis are likely selected.

Movement distances in this study are a conservative estimate. Maximum movement distances are defined by the length of the study reach (Staub et al. 1995). Individuals found in the 2003 extended survey areas had a higher mean movement distance than recaptures from the interior of the transect. Larvae captured in the extended areas, therefore, were not simply moving short distances from the ends of the original transect. Larval salamanders moving longer distances may be more likely to move out of the study area than less vagile individuals and consequently may be missed in

recapture surveys.

While larvae moved slightly upstream in the summer season, they experienced some net downstream displacement over the winter. Other studies, in the eastern United States, have observed downstream drift in salamander larvae (Bruce 1985, 1986). Bruce (1985, 1986) noted that most salamanders that drifted downstream were first-year larvae and movements upstream were by older individuals. First-year larvae may be less able to fight the current than older larvae but disperse more in an upstream direction as they grow. We found no strong association between the size of larval *D. tenebrosus* and movement distance or direction. However, the displacement of salamanders over the annual cycle (downstream for 60% and upstream for 40% of larvae) indicates that bi-directional movement prevents displacement of the entire population downstream.

The likelihood of larval *D. tenebrosus* crossing into a culvert or taking up residence there varies with culvert type. While pipe culverts are likely a complete barrier to upstream movement, arch culverts allow for some bi-directional movement (Table 2.4). Salamanders were found residing in arch culverts over multiple months which may indicate that these culverts are providing habitat. Culverts in which upstream passage occurred also had the highest densities (density inside culvert/in adjacent reaches; Table 2.4), suggesting that culverts that provide habitat also may provide passage. The availability of large substrates throughout the stream is associated with higher densities of larval *D. tenebrosus* (this study; Murphy et al. 1981; Hawkins et al. 1983; Parker 1991; Wilkins and Peterson 2000; Stoddard 2001; Rundio and Olson 2003) and this association also applies to culverts. Holomuzki (1991) found that small and large stream salamander larvae (60 mg to 350 mg; *Ambystoma barbouri*) were more susceptible to displacement in sand than coarser substrates. Larvae were able to maintain position in higher flows as substrates became coarser. The lack of substrates in pipe culverts appears to prevent larval *D. tenebrosus* from inhabiting these segments of the stream and reduces their access to upstream habitats.

Culverts where passage is limited may restrict the rate of larval recolonization. Ferguson (2000) found that recolonization of small scale extirpations by larval *D. tenebrosus* in British Columbia occurred by long-distance dispersers, rather than individuals on the periphery. If longer distance movements are impeded by pipe culverts recolonization of defaunated areas may be slower, reducing the likelihood of viable regional populations.

Reduced mobility and survival in the larval stage can potentially affect the terrestrial adult phase of this species. Reproduction in *D. tenebrosus* occurs during the terrestrial phase (or in aquatic adults). Since terrestrial adults can move overland and potentially deposit eggs freely along the stream length, decreased levels of larval movement may not affect the genetic structure of the population. However, studies of terrestrial adults have found lower levels of neutral genetic variation (microsatellite loci and amplified fragment length polymorphisms) and heterozygosity in recently clearcut sites than in second growth and old growth sites (Curtis and Taylor 2003) and reduced mobility in clearcut sites (Johnston and Frid 2002). If terrestrial *D. tenebrosus* are experiencing reduced mobility in areas of logging activity, a decrease in recolonization capacity and pre-metamorphic survival of larval *D. tenebrosus* by in-stream barriers may compound these effects of logging on reproducing

adults. Roads and timber harvest often occur in concert and such synergistic interactions between them warrant further study.

The effect of culverts on paedomorphic *D. tenebrosus* movement is uncertain. The low numbers of neotenes in this study could be due to small stream sizes (Nussbaum and Clothier 1973; Coriell 2003) and/or low detection rates. Little is known about the reproductive behavior, mate selection, or movement of neotenes. Their reliance on the stream network for movement, throughout their lives indicates they may be more vulnerable to isolation.

### Management Implications

Stream networks throughout the landscape are crisscrossed and bisected by an extensive road system. Many culverts in the U.S. Pacific Northwest, were installed in the 1980s and earlier, when land management practices on forested federal lands dictated an increase in road building. The life expectancy of a culvert is approximately 20 years, so that now over a million culverts are due for replacement (M. Furniss, personal communication, April 20, 2003). Current assessment and replacement of barrier culverts is estimated to take decades (US GAO 2001). The U.S. federal Northwest Forest Plan's Aquatic Conservation Strategy maintains the objective of restoring "connectivity within and between watersheds" which must provide "unobstructed routes to areas critical for fulfilling the life history requirements" of aquatic species (USDA and USDI 1994). Therefore, when these culverts are replaced managers may need to consider a wide range of aquatic organisms.

Currently, there is some overlap in the types of culverts that pass juvenile salmonids and larval *D. tenebrosus*. Unlike larval *D. tenebrosus*, the swimming performance (prolonged and burst speeds) and jumping capabilities of salmonids are well-known and can be compared with known velocities and outlet drops in culverts to determine their passage success (Toepfer et al. 1999). The same culverts that were not passable by juvenile salmonids in assessment models (USDA 1999) also were not passed by larval *D. tenebrosus* (Figure 2.6) which suggests similar culvert features may be limiting passage for both organisms. Therefore, current assessment criteria may need only minor adjustments to include this species in culvert passage design.

Although the physical movement capabilities of larval *D. tenebrosus* are not known, it is clear that the presence of stream substrates in a culvert improves habitat use and passage. It is difficult to discern the relative importance of substrate and outlet drop for passage because these features often occur in concert. Larval *D. tenebrosus* are not known to jump and outlet drop may be an initial barrier, while the absence of bottom substrates would further restrict upstream movement. Culvert replacements that simulate natural stream bottoms, slopes and widths would provide both habitat and passage opportunities for larval *D. tenebrosus*.

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## CHAPTER 3

# Survival and Growth of Larval Coastal Giant Salamander (*Dicamptodon tenebrosus*) in Streams in the Oregon Coast Range

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### INTRODUCTION

For amphibians with complex life histories, populations may be regulated by mortality in each life history stage, egg to adult (Wilbur 1980). Selection pressures on each stage vary as larvae and adults of the same species may occupy different habitats. For many aquatic-breeding animals, life history stages exist as though independent, yet aquatic conditions during the larval stage can influence adult morphology and fitness. In pond-breeding amphibians, larval conditions can affect size at metamorphosis (Wilbur and Collins 1973; Wilbur 1980), rates of metamorphosis (Shrode 1972), adult fecundity (Scott 1994) and adult fitness (Semlitsch et al. 1988). Conditions that affect larval growth and survival can affect population structure, through both the larval and adult stages of their life history.

Few studies have presented rates of amphibian larval growth and survival in natural populations and data are particularly sparse for stream-breeding amphibians. The coastal giant salamander, *Dicamptodon tenebrosus*, breeds in streams and is a dominant member of stream community assemblages throughout the Pacific Northwest (Hawkins et al. 1983; Corn and Bury 1989; Parker 1994). Primary predators of larval *D. tenebrosus* are conspecifics and larger salmonids (Parker 1993a). Some life history variation by life stage is known for *D. tenebrosus*, for example larval stage lengths can vary with latitude (Ferguson 1998). The lotic larval period for *D. tenebrosus* in Oregon is estimated to be two to three years at which point larvae either metamorphose into terrestrial adults or become paedomorphic aquatic adults (Nussbaum and Clothier 1973). Environmental conditions, including those affecting growth and survival, may drive morphological adaptations of the larval and adult forms of this species.

Both natural and anthropogenic disturbance can alter in-stream habitats (Waters 1995). Locally, culverts may influence a variety of physical stream processes such as suspended sediment load transport and water velocity and culverts may affect in-stream organism movement (Chapter 1; Warren and Pardew 1998), but effects of culverts on the survival and growth of larval stream salamanders is not known.

Environmental conditions also may affect amphibian sampling efficiency. Stream amphibians are difficult to sample (Richardson and Neill 1998) and many studies rely on simple return rates (the proportion of marked animals released on one occasion and

recaptured in the next occasion) to estimate survival. Use of return rates for estimating survival does not account for the probability of recapture (the likelihood that a salamander will be recaptured or resighted in a given capture occasion, if it is still alive and in the sample area; White and Burnham 1999), and can result in negatively biased survival estimates if capture rates of detectability are < 1.0 (Martin et al. 1995; Lebreton et al. 1993).

The purpose of this study was to estimate the variation in growth and survival that occur during the larval stage of *D. tenebrosus*. We used mark-recapture to assess the rates of apparent survival and growth for two different larval age classes (first-year and second/third-year), in winter and summer seasons and in the presence of culverts. By estimating the capture probability of larval *D. tenebrosus* we attempted to provide unbiased estimates of survival.

### METHODS

We conducted our study in the central Oregon Coast Range on private timber lands and U.S. federal lands administered by the Coos Bay District of the Bureau of Land Management (BLM; Figure 2.1). The study area lies in the Coast Range physiographic province, which is characterized by mild temperatures that range between 4.4 and 15.0 degrees C and precipitation that falls mainly as rain between the months of October and March (USDI 2002). The forested slopes consist primarily of western hemlock (*Tsuga heterophylla*) and Douglas-fir (*Pseudotsuga menziesii*) and riparian areas are dominated by red alder (*Alnus rubra*; Franklin and Dyrness 1973). Road densities in the study area (3.9 km of road/km<sup>2</sup>), associated primarily with forest management activities, are comparable to stream densities (2.9 km of streams/km<sup>2</sup>; USDI 1998; USDI 2001).

We restricted our site selection criteria to small, rocky, low gradient, perennial stream reaches in the study area in which larval *D. tenebrosus* were known to occur. We applied this selection criteria to a database of known culvert sites from the Coos Bay BLM and mapped road/stream intersections (n=81). Study sites with a culvert (culvert site, n=9) and without a culvert (reference site, n=5) that matched the stream criteria above were selected for surveys.

Larval *D. tenebrosus* surveys were conducted in the summers of 2002 and 2003 on reaches approximately 80 m in length for both culvert and reference sites. We designated the sampling areas on culvert sites such that a culvert was located at the center of the reach.

Each stream was visited on five capture occasions (June, July, August 2002, and June, July 2003). We moved in an upstream direction and captured larval *D. tenebrosus* in small nets by systematically searching all wetted stream substrates in stream and culvert sections. For a detailed description of study site layout and sampling methods, see Chapter 1.

Captured larvae were measured (snout-vent length, SVL) and individually marked with visible fluorescent elastomer (Northwest Marine Technology, Inc.<sup>1</sup>) at three body locations and released to their original capture site (Chapter 1). We had no known mortality from our handling. Marking occurred on only the first two of five capture occasions.

## Analysis

To determine the apparent survival and recapture probabilities of larval *D. tenebrosus* we fit Cormack-Jolly-Seber (CJS) open population models to the mark-recapture data. Survival estimates in CJS models do not distinguish between death and permanent emigration and are therefore minimum estimates of true survival (Lebreton et al. 1993). However, movement distances for larvae were generally small throughout the study (80% of movements < 30 m; Chapter 1) and suggested low emigration rates.

Apparent annual survival and recapture probabilities were estimated using Cormack-Jolly-Seber models in program MARK (White and Burnham 1999) for larval *D. tenebrosus* in the Oregon Coast Range. Analysis structure consisted of five capture occasions and four groups based on age class and stream type: reference stream first-year; reference stream second/third year; culvert stream first-year; culvert stream second/third years. Time intervals between capture occasions were unequal with two intervals (one month) in the summer 2002, one interval overwinter (ten months) and a single interval (one month) in summer 2003. Using MARK, we examined whether there were differences in survival or recapture probabilities that were associated with season (summer, winter), age class (first or second/third year) or culvert presence (culvert or reference stream).

We fit a fully parameterized global model that included a salamander age/culvert interaction with time effects and tested the goodness-of-fit of this model to the assumptions of the CJS model. We used the combined  $\chi^2$  values and degrees of freedom (df) from Test 2 and Test 3 from program RELEASE (Burnham et al. 1987) to estimate over-dispersion ( $\hat{c} = \chi^2/df$ ; White 2002) and test goodness-of-fit (Lebreton et al. 1992).

Before beginning the analysis, we formulated an a priori list of candidate models that reflected hypotheses concerning the effects of stream type, age and season on salamander survival. We used model selection methods based on the Akaike Information Criterion corrected for small sample size (AICc), with Akaike weights and the degree to which 95% confidence intervals for slope coefficients ( $\beta$ ) overlapped zero to evaluate the strength of evidence for competing models and specific effects (Burnham and Anderson 2002). Survival and capture probabilities were modeled as a function of age class, culvert presence, and time. We first modeled capture rates, varying survival by time only and then used the “best” capture rate model

to proceed with survival modeling (number of candidate models = 20). Time effects on survival and capture probabilities were modeled in two ways: standard CJS time dependent models (time) in which all capture occasions and survival intervals were separately estimated; and seasonal models (season) in which survival intervals were grouped according to season (one-month summer intervals coded separately from the 10-month overwinter interval). Capture probabilities, which are occasions rather than intervals, however, were not modeled by season because all capture occasions occurred in the summer. In the same analysis, we compared larval *D. tenebrosus* survival and capture probabilities between culvert and reference streams. Due to model uncertainty, competing models were considered those within 2 AICc units ( $\Delta AICc = 2$ ) of the top model.

We assigned larval salamanders to age classes based on earlier studies and the mean size of second-year recaptures in this study. Larval salamander size at first capture was used to assign age classes. The exact size at which first-year larvae become second-year larvae varies by region and study. Previous studies suggest first-year larvae range in SVL from 35 to 51 mm (36–61 mm, Kessel and Kessel 1943; 35–57 mm, Nussbaum and Clothier 1973). We used these estimates to assign first-year larvae to preliminary groups in this study, and then used the size of those individuals recaptured after a year to determine the transition between first- and second-year age classes. Salamanders that appear in streams after hatching are presumed to be first-year larvae and our lower size limit was determined by the smallest size of salamanders in this study. We combined second- and third-year larvae because it was difficult to distinguish these two age classes using size data. Paedomorphs (aquatic adults) were determined from size estimates of previous studies (Nussbaum 1976).

Salamander age class is treated as a group variable because animals remain in their initial age class for more than one interval. Most larval salamanders grew into the next age class over the winter ( $n = 2,154$ ). Larval salamanders that grew into the next age class over the summer ( $n=30$ ), however, may differ from those occupying a distinct age class. We ran the age analysis with and without these individuals to see if their inclusion changed results. The number of these individuals was low and model results were not altered, so we included them in the analysis, using their size at first capture. Larval salamanders that grew into the next age class overwinter occupied a subsequent age class in the last two capture occasions and the last survival interval. We adjusted the parameters in program MARK to account for this “aging” effect.

We used growth as the response variable in a linear regression model (PROC GLM; SAS Institute 1999<sup>1</sup>) to determine if growth was associated with size of salamander at initial capture (SVL) or culvert presence. Average monthly growth for individual salamanders captured in June and recaptured in August was used for the summer analysis. Salamanders captured in August 2002 and recaptured in June 2003 were used for the overwinter average monthly growth analysis. To determine annual growth in relation to size of salamander, we used growth of salamanders captured in June 2002 and recaptured in June 2003. We examined both linear and quadratic relationships between age and growth of salamanders. In order to compare salamander growth between culvert and reference streams, we established that growth patterns (i.e., smaller larvae grew more than larger larvae) were similar for all streams. We then

<sup>1</sup>The use of trade or firm names is for reader information and does not imply endorsement by the U.S. Department of Agriculture of any product or service.

Table 3.1. The nine top models (and null model) of survival and recapture of larval *D. tenebrosus* as determined by QAICc. Bold models are  $\leq \Delta 2$  QAICc from the top model. phi = survival and p = capture probability.

| Model                                       | QAICc           | Delta QAICc  | QAICc weights | Number of parameters | QDeviance     |
|---|-----------------|--------------|---------------|----------------------|---------------|
| <b>phi (age+season) p(age*time)</b>         | <b>4220.295</b> | <b>0.000</b> | <b>0.324</b>  | <b>11</b>            | <b>83.627</b> |
| <b>phi (age+culvert+season) p(age*time)</b> | <b>4221.025</b> | <b>0.729</b> | <b>0.225</b>  | <b>12</b>            | <b>82.344</b> |
| <b>phi (age*season) p(age*time)</b>         | <b>4221.574</b> | <b>1.278</b> | <b>0.171</b>  | <b>12</b>            | <b>82.893</b> |
| phi (age*time) p(age*time)                  | 4222.665        | 2.370        | 0.099         | 14                   | 79.956        |
| phi (age+time) p(age*time)                  | 4223.266        | 2.970        | 0.073         | 13                   | 82.571        |
| phi (age+culvert+time) p(age*time)          | 4223.787        | 3.491        | 0.056         | 14                   | 81.077        |
| phi (age+season) p(age+time)                | 4224.763        | 4.468        | 0.034         | 8                    | 94.127        |
| phi (age+season) p(age+culvert*time)        | 4227.039        | 6.743        | 0.011         | 18                   | 76.259        |
| phi (age) p(age*time)                       | 4229.033        | 8.737        | 0.004         | 10                   | 94.377        |
| {phi (.) p(.)}                              | 4273.698        | 53.402       | 0             | 2                    | 155.097       |

compared growth between culvert and reference streams using a mixed effects ANOVA (PROC MIXED, SAS Institute 1999).

## RESULTS

A total of 2,215 larval *D. tenebrosus* were individually marked (1,334 in June 2002; 881 in July 2002) across fourteen stream sites. Of those larvae marked, 1,200 (54%) were recaptured at least once during the study. First-year larvae transitioned into second-year larvae at approximately 54 mm SVL ( $\bar{x} = 54$  mm SE = 0.04, n = 49). First-year salamanders in this study were 29 to 53 mm (n = 651) second- and third-year salamanders were 54 to 99 mm (n = 525) and aquatic adults (n = 27) were > 100 mm. Low frequency of aquatic adult recaptures (5 recaptures/31 marked), however, precluded their inclusion in the analysis.

The program RELEASE revealed some overdispersion in the data, which we subsequently examined using the chi-square tests and recapture matrix to determine in which capture occasion the overdispersion occurred. Overdispersion or “extra binomial variation” in the data often indicates a lack of independence or individual heterogeneity and occurs when the sampling variance is greater than the theoretical variance (Burnham and Anderson 1998). The expected number of recaptures was greater than observed for the overwinter capture occasion but not for the other capture occasions, indicating low detection in June of 2003. Overdispersion, due in part to one capture occasion with poor detection, was accounted for using a variance inflation factor ( $\hat{c} = 1.6$ ) so we used QAICc to generalize model selection results (Burnham and Anderson 2002).

The best approximating model suggested an additive age and seasonal effect on apparent survival and an interactive age and time effect on capture probability (Table 3.1). The seasonal model was better than the standard CJS time-dependent model for predicting apparent survival ( $\Delta$ QAICc = 2.97). Therefore, apparent survival differed by age class of larvae between summer and overwinter seasons ( $\beta$  age = 0.49, 95% CI = -0.75 and -0.24;  $\beta$  season = 0.59, 95% CI = 0.27 and 0.91). All four competing models had a time and age effect.

Capture probabilities were dependent on age class and time (Table 3.1). In all competing models, the relationship between age class and time was interactive, rather than additive. Monthly capture probabilities were generally higher for first-year larvae than second/

third-year larvae (first-year larvae 0.60, SE = 0.02; 0.64, SE = 0.03; 0.39, SE = 0.05; 0.73, SE = 0.09; second/third-year larvae 0.41, SE = 0.04; 0.46, SE = 0.03; 0.47, SE = 0.07; 0.58, SE = 0.09). Capture probability was not associated with the presence of a culvert ( $\Delta$ QAICc = 6.74).

First-year salamander larvae had a lower apparent survival than second/third-year larvae over the annual cycle. The estimate of monthly apparent survival in the summer for first-year larvae was 0.77 (SE = 0.02), and 0.85 (SE = 0.02) for second/third-year larvae. Monthly overwinter apparent survival was higher than monthly summer apparent survival for both age classes (first-year larvae: 0.86, SE = 0.01; second/third-year larvae: 0.91, SE = 0.01). Given that most of the covariances were near 0, we estimated standard errors of annual apparent survival using Goodman's Formula (Goodman 1960), assuming independence between variables. Annual apparent survival for first-year larvae was therefore 0.13 (SE = 0.03) and 0.28 (SE = 0.08) for second/third-year larvae.

Model selection results indicated some support for a culvert effect on survival which was negative; however, the 95% confidence intervals on the regression coefficients overlapped 0 ( $\beta = 0.09$ , 95% CI = -0.03 and 0.21) so this effect was weak.

Annual growth rates varied by size with smaller salamanders growing faster than larger salamanders (df = 132, F = 183.6, p < 0.0001, R<sup>2</sup> = 0.74; Figure 3.1). This quadratic relationship was evident over the annual cycle. Monthly growth rates appeared to be more variable in the summer (generally high) than in the winter (Figure 3.2). There was no difference in growth rates between reference and culvert streams (F<sub>2,122</sub> = 1.41, p = 0.24). Metamorphosis occurred between the sizes 53 and 81 mm with 23% occurring after the first year and 77% occurring after the second and third year (Figure 3.3).

## DISCUSSION

High selection pressure early in the larval period affects survival to metamorphosis. Like many amphibian species that produce numerous young, apparent survival for first-year *D. tenebrosus* larvae was lower than for subsequent age classes (Wilbur 1980). Nussbaum and Clothier (1973) estimated first-year survival to be 43%, based on the ratio of first-to second-year larvae in the population. Similarly, research in British Columbia indicated a 30-35% annual mean

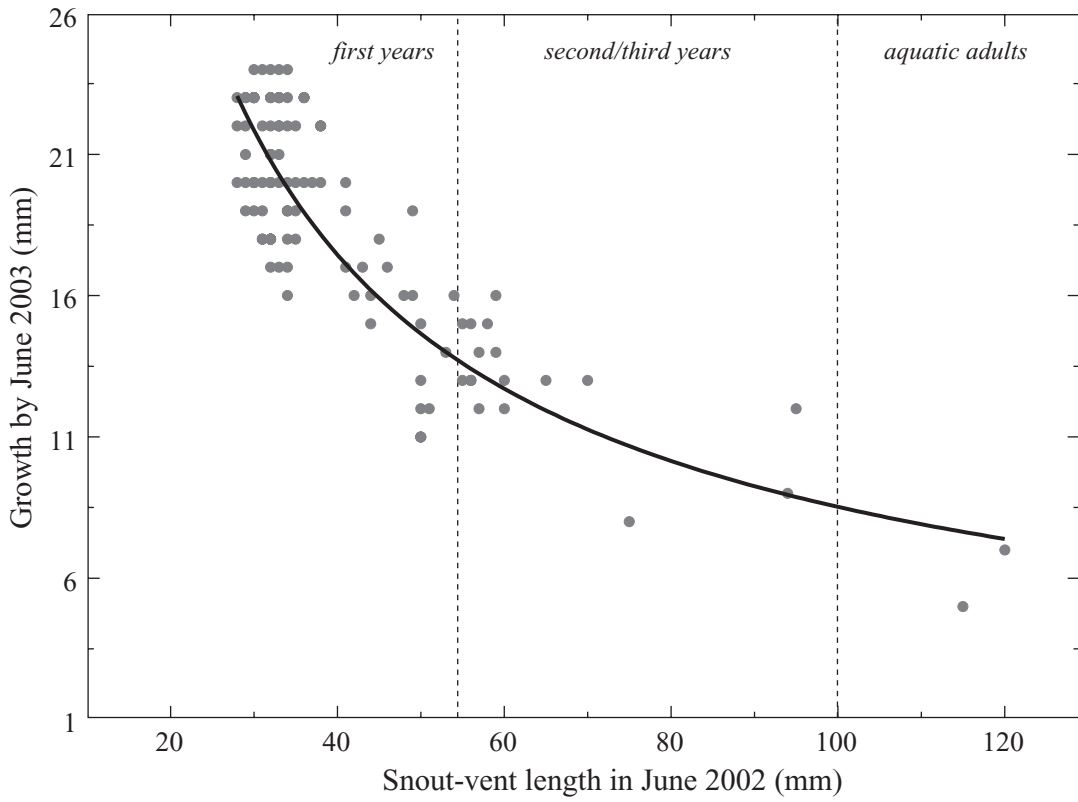


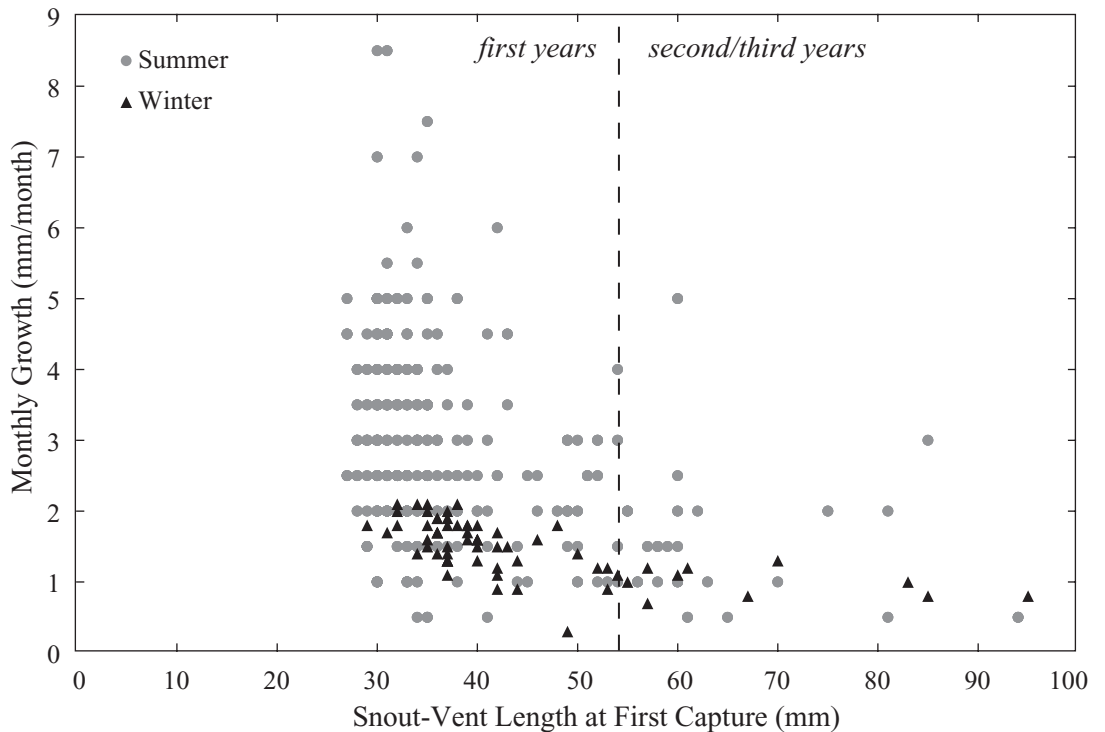
Figure 3.1. Annual growth (June 2002 to June 2003) by size at first capture in streams in the Oregon Coast Range. Dashed lines demarcate approximate size at which metamorphosis occurred in this study.

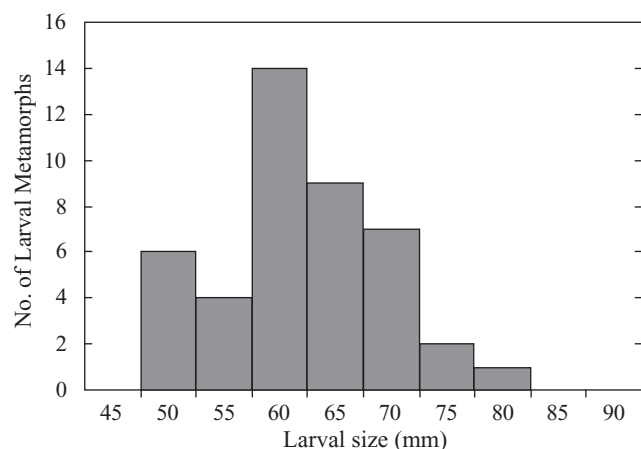
survival rate for all larval ages (Ferguson 1998). Our apparent annual survival estimates for first-year larvae were much lower (first-years: 13 %; second/third-years: 28%), perhaps due to differences in methodology, demography or environmental conditions.

Larval survival during the second/third year is likely even higher than presently reported given we did not quantify disappearance from the stream due to metamorphosis. First-year larval *D. tenebrosus* are prey for juvenile salmonids but may grow large enough by their

second year to attain a size refuge from their gape-limited predators (Parker 1993a). In addition, second- and third-year larvae are able to exploit larger prey items than first years (Parker 1994) thereby increasing their access to potential food resources. More than twice as many larval salamanders metamorphosed after the second year than after the first year (Figure 3.3), indicating that the aquatic environment may provide continued benefits for larvae that survive their first year.

Figure 3.2. Monthly growth in summer and winter 2002-2003 of larval *D. tenebrosus* in fourteen study streams in the Oregon Coast Range.





**Figure 3.3.** Snout-vent length of larval *D. tenebrosus* at onset of metamorphosis from fourteen study streams in the Oregon Coast Range.

Growth rates were highest for first-year larvae (Figure 3.1) but are also the most variable compared to older age classes. The variability in growth rates may result from variation in stream conditions. Laboratory and field studies have demonstrated that larval salamander growth can be influenced by environmental factors such as temperature and food resources (Petranka 1984), larval density (Wilbur 1980; Scott 1990; Buskirk and Smith 1991), and the presence of predators (Figiel and Semlitsch 1990; Beachy 1997). We found that growth rates appeared higher in summer (Figure 3.2), indicating that the majority of first-year annual growth occurred during their first few months. High growth coincided with low apparent survival in the summer months. Within seasons, apparent survival was lower in the summer months. This low summer survival was most likely a result of mortality and/or emigration rather than metamorphosis given that both age classes were affected and metamorphosis for first-year salamanders was low (Figure 3.3). Coupled with lower survival rates over the summer due potentially to higher predation and stream drying (Nussbaum and Clothier 1973), the first season for larval *D. tenebrosus* appears to be a time of intense selection.

Differential growth rates during the larval period may affect the life history path (aquatic or terrestrial) of an individual. Rapid growth rates may delay metamorphosis in order to capitalize on favorable stream conditions and the reverse may be true for slow growth rates (Werner 1986). Coriell (2003) set up a feeding experiment with two populations of second-year larval *D. tenebrosus* from medium sized streams and found that the group that was fed less had significantly higher rates of metamorphosis. In addition, larvae from small and large streams had different rates of metamorphosis when held under the same conditions, indicating that life history path may be determined before the second year.

The capture probabilities for larval *D. tenebrosus* were relatively high (mean for first-years 59%, second/third-years 48%) given that salamanders were hand captured in moving water. These are some of the first data to quantify capture probabilities for larval stream salamanders so comparisons to other stream habitats are not possible. Bailey et al. (2004) found terrestrial salamander capture probabilities to be between 0.20 (SE= 0.04) and 0.35 (SE=0.03) due to less time spent on the surface. Capture probabilities in this study may indicate high site fidelity (Chapter 1) and time mostly spent above

ground in the stream channel. Despite their smaller size, first year salamanders had a higher capture probability than second- and third-year salamanders throughout the summer. Older age classes may be better able to secure refugia and therefore evade detection.

The availability of in-stream habitat takes on critical importance for larval *D. tenebrosus* given the relatively long larval period. We found a weak culvert effect on survival for both age classes. There was no culvert effect on capture probability, however, which indicates that lower survival on culvert streams was not due to poor detection. Sedimentation can alter available microhabitats by filling in interstitial spaces and effectively reducing the number of large substrates available for cover and foraging. Lower apparent survival on streams with culverts could be due to higher levels of fine sediment in these streams (Chapter 1) or other local conditions such as food availability or predation. Growth rates were unaffected by the presence of a culvert, which could indicate that mechanisms other than growth were affecting survival on culvert streams. Although seasonal demographic rates can be estimated for these populations, a long-term study may be needed to address variation in survival and growth between years and further investigate the effect of culverts on survival.

Growth in terrestrial adults after metamorphosis has not been determined, although the growth rates for paedomorphic adults were low (Figure 3.1). Species with little post-metamorphic growth may exhibit a greater correlation between larval quality and adult fitness (Semlitsch 1987). Maintenance of high quality larval habitat may be critical for providing conditions that foster early growth and survival.

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*J.P. Sagar, 2004, Movement and Demography of Larval Coastal Giant Salamanders (Dicamptodon tenebrosus) in Streams with Culverts in the Oregon Coast Range, M.S. thesis, Oregon State University, Corvallis, Oregon.*

## CHAPTER 4

### Summary of Findings

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The fragmentation of river and stream networks by barriers can have negative impacts on the movement and survival of aquatic species (Peter 1998). Many species depend on connectivity of the stream corridor in order to capitalize on shifting habitats and resources (Fagan 2002). The potential for road-crossing stream culverts to block or filter biological passage is demonstrated by migratory salmonids that must travel through stream networks to reproduce (Baker and Votapka 1990). The movement of resident species, however, also may be affected by the presence of culverts (Wofford 2003). The coastal giant salamander, *Dicamptodon tenebrosus*, has a complex life history with a multi-year aquatic larval stage. Culverts may present a barrier to this weak-swimming stream obligate. Larvae are top predators in headwater systems (e.g., Rundio 2002) and culvert barriers that effect their movement and survival could have cascading effects through aquatic faunal communities.

We investigated the effect of culverts on the movement and survival of larval *D. tenebrosus* using mark-recapture techniques. Our study objectives were to: compare movement in culvert reaches with movement in reference reaches, between two different types of culverts and; to present estimates of survival for larval age classes in culvert and reference streams. The following are the main findings of our research, implications for management and a discussion of the potential implications of barrier culverts on other species.

#### **Movement**

An understanding of in-stream movement distances by larval *D. tenebrosus* will allow an evaluation of potential effects on populations by barriers created by culverts. Although movement was minimal for the majority of salamanders during the course of this two-year study, a minority of movement distances (20%) were longer and enabled us to assess the potential for culvert passage. Monthly movement rates did not differ by season (~1.5 m/month). Mean movement distances are similar to those found in British Columbia (Ferguson 1998), however, larger populations in this study enabled us to estimate the frequency of longer range movements. These are the first data on instream movement for larval coastal giant salamanders in the center of their range and the first to indicate a larger-scale use of stream networks.

Movement direction determines whether larvae drift or actively move upstream. There was a directionality component to salamander movement and it differed by season. In the summer season, larval *D. tenebrosus* moved more upstream and over the winter season they moved more downstream. Over the annual cycle, 60% of larvae were displaced downstream and 40% were displaced upstream. There was no association between salamander size and movement distance and direction. The direction of movement, with regard to stream flow direction, has not previously been studied in stream amphibians in the Pacific Northwest.

#### **Culvert Passage and Use**

This is the first study to investigate culvert passage by larval salamanders and examine use and passage between culvert types. Although the scope of inference for these findings is limited to culvert sites within the study area, our results suggest effects that likely extend more widely in this species range.

Mobile individuals within the population are limited in their ability to move through reaches of stream with culverts. There was no difference in larval mean movement distances on culvert versus reference streams, however, the potential for moving longer distances was greater in reaches without a culvert than in those with a culvert.

In comparison to pipe culverts, arch culverts were able to achieve greater connectivity for larval *D. tenebrosus* between stream reaches. Larval *D. tenebrosus* moving in an upstream direction may be more affected by culverts than those moving downstream. Downstream culvert passage by larvae occurred through both pipe culverts and arch culverts while upstream passage occurred only through arch culverts. Partial upstream passage was also design-specific and only occurred in arch culverts.

Arch culverts supported greater densities of larval *D. tenebrosus* than pipe culverts. Larval *D. tenebrosus* occupied arch culverts both as transients and residents and were found to inhabit stream reaches and culvert reaches in similar densities. The presence of substrate was associated with salamander use in arch culverts.

## Habitat Associations with Movement and Density

The abundance of large substrates was the only habitat feature associated with mean movement and density of larval *D. tenebrosus*. This finding is similar to other studies that have found higher densities of larval *D. tenebrosus* in habitats with abundant large streambed substrates (Murphy et al. 1981; Hawkins et al. 1983; Wilkins and Peterson 2000; Parker 1991; Rundio and Olson 2003). In the late summer, abundant large substrates were associated with higher densities of larvae and lower average movement distances. Greater mean movements on streams with smaller substrates may be linked to a need to find larger substrates for cover as body size increases. Longer movements by larval *D. tenebrosus* through the stream reach were associated with the absence of a culvert, indicating a possible barrier effect. Additional results include an association between high larval density and greater frequency of long distance movements and a higher percentage of streambed fine sediments on streams with culverts.

### Larval survival

Apparent survival of larval *D. tenebrosus* was associated with age of larvae, season and the presence of a culvert. Annual apparent survival was higher for second/third-year larvae than first-year larvae and survival was higher for both age classes in the winter than in the summer. Survival was higher for larvae on streams without culverts although culvert presence had a weaker effect on survival than both age and season. A study in Oregon used the ratio of first-year to second-year larvae in the population to estimate larval *D. tenebrosus* survival and survival estimates were higher (43%; Nussbaum and Clothier 1973) than those in this study (first-years: 13 %; second/third-years: 28%). Estimates of survival in British Columbia, using mark-recapture methods, also were higher but did not differentiate between age classes of larvae (Ferguson 1998). This is the first study to estimate survival by age class in the center of larval *D. tenebrosus*' range.

## MANAGEMENT IMPLICATIONS

Culvert replacement is currently being conducted on National Forest and Bureau of Land Management lands across the U.S., and culvert assessment criteria for passage have not yet been established for non-fish aquatic organisms. This study indicates that pipe culverts are not providing habitat for larvae and are likely a barrier to upstream movement. Low first-year larval survival indicates there is high selection pressure early in the larval phase and loss of stream habitat could have negative consequences.

In fish-bearing streams, passage criteria for juvenile salmonids loosely corresponds with larval *D. tenebrosus* passage, although more rigorous testing of larval physical capabilities is needed. Substrate presence and heterogeneity that simulates the natural stream channel may be important in providing passage for larval *D. tenebrosus* and should be considered key in culvert replacement. Fine sediment deposits upstream of culverts may decrease larval habitat. Culvert replacements that simulate both the natural stream bed and hydraulic conditions would help provide both habitat and passage opportunities for larval *D. tenebrosus*.

## Species Implications

The reduction of movement and loss of habitat by larval *D. tenebrosus* in culvert reaches has implications both for the adult stage of this species and other aquatic organisms. Pre-metamorphic survival was apparently low (Chapter 3) and small decreases have the potential to alter the number of larvae making it into the terrestrial adult population. Variation in larval recruitment would exert strong influence on terrestrial adult population structure.

In addition, culvert and road installation frequently occur in concert with upland forest management, and summed threats to this species must account for both terrestrial and aquatic habitat alterations. A study in British Columbia found that terrestrial *D. tenebrosus* had reduced mobility (Johnston and Frid 2002) and lower levels of neutral genetic variation (microsatellite loci and amplified fragment length polymorphisms) and heterozygosity in recently clearcut sites than in second growth and old growth sites (Curtis and Taylor 2003). The spatial scales used by entire populations of *D. tenebrosus* are unknown, yet across their life cycle, entire watersheds may be used. Watershed-scale studies of *D. tenebrosus* populations relative to the effects of multiple land use patterns are warranted.

There are three related *Dicamptodon* species in the Pacific Northwest and since they share many morphological and ecological characteristics they may be similarly affected by culverts. Little is known about the movement patterns of each species. Cope's giant salamander (*Dicamptodon copei*) is a near-obligate paedomorph (Jones et al. 2004). Cope's giant salamanders spend multiple generations in stream networks and may be particularly vulnerable to population subdivision by barrier culverts. The Idaho giant salamander (*Dicamptodon aterrimus*), California giant salamander (*Dicamptodon ensatus*), and *D. copei* have smaller distributions (Jones et al. 2004) than *D. tenebrosus* and the loss of potential habitat for larvae due to barrier culverts could effect these populations.

While the effect of culverts on larval *D. tenebrosus* may have implications for other species, whether a culvert acts as a barrier can depend on the species and the flow conditions at the barrier (Warren and Pardew 1998; Peter 1998). For this reason, culverts can act as a biological filter, allowing passage of certain species at certain times of the year. Barrier culverts, and especially multiple culverts on one stream, could alter the composition of biotic communities and the local biodiversity in these systems. Preliminary data from this study (Appendix B and C) suggest that gaps in the distribution of aquatic organisms exist at some types of culverts. For stream obligate species, barriers may subdivide populations and impede or prevent recolonization after disturbance, increasing extinction risk due to fragmentation (Lacy 1987). Within several decades, fragmentation and isolation by culverts can reduce genetic diversity in isolated populations of resident species (Wofford 2003).

Many stream-associated amphibians are intolerant of low moisture conditions and use the stream margins as a movement corridor (Gibbs 1998). Culverts that are narrower than the channel width and do not have stream margins may force these animals to cross via the road. Road conditions may promote faster rates of desiccation and introduce traffic related mortality (deMaynadier and Hunter 2000). From preliminary research in this study (Appendix B) some stream-associated species do use stream margins in culverts, where they exist. However, little is known about the frequency of this occurrence. Culverts that are wide enough to allow

stream meandering may improve both hydraulic and biological connectivity.

Strategies for culvert remediation that target a particular species and do not accommodate a wide range of aquatic organisms, life stages and ecosystem processes may not provide long term benefits. Research investigation into the use of culverts by stream-associated amphibians (Dunn's salamanders, *Plethodon dunni*), as well as use by other aquatic species (torrent salamander, *Rhyacotriton* spp.; crayfish, *Pacifastacus* spp.; tailed frog larvae, *Ascaphus* spp.) would facilitate an ecosystem perspective of culvert effects on stream communities.

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## Appendix A. Program MARK analysis results.

Full table of apparent survival and recapture probabilities for MARK analysis for two age classes (first-year; second-/third-year), two seasons (winter; summer), and two stream classes (with culvert; without culvert).

| Model                                      | QAICc    | Delta QAICc | QAICc weights | Number of parameters | QDeviance |
|--|----------|-------------|---------------|----------------------|-----------|
| phi (age+season) p(age*time)               | 4220.295 | 0.000       | 0.324         | 11                   | 83.627    |
| phi (age+culvert+season) p(age*time)       | 4221.025 | 0.729       | 0.225         | 12                   | 82.344    |
| phi (age*season) p(age*time)               | 4221.574 | 1.278       | 0.171         | 12                   | 82.893    |
| phi (age*time) p(age*time)                 | 4222.665 | 2.370       | 0.099         | 14                   | 79.956    |
| phi (age+time) p(age*time)                 | 4223.266 | 2.970       | 0.073         | 13                   | 82.571    |
| phi (age+culvert+time) p(age*time)         | 4223.787 | 3.491       | 0.056         | 14                   | 81.077    |
| phi (age+season) p(age+time)               | 4224.763 | 4.468       | 0.034         | 8                    | 94.127    |
| phi (age+season) p(age+culvert*time)       | 4227.039 | 6.743       | 0.011         | 18                   | 76.259    |
| phi (age) p(age*time)                      | 4229.033 | 8.737       | 0.004         | 10                   | 94.377    |
| phi (season) p(age*time)                   | 4234.380 | 14.085      | 0             | 10                   | 99.724    |
| phi (time) p(age*t)                        | 4234.567 | 14.272      | 0             | 11                   | 97.899    |
| phi (age) p(age*year)                      | 4239.966 | 19.670      | 0             | 6                    | 113.346   |
| phi (age+season) p(time)                   | 4241.951 | 21.656      | 0             | 7                    | 113.324   |
| phi (age*culvert*time) p(age*culvert*time) | 4243.308 | 23.013      | 0             | 32                   | 64.145    |
| phi (culvert) p(age*t)                     | 4247.052 | 26.757      | 0             | 9                    | 114.407   |
| phi (time) p(age)                          | 4253.564 | 33.269      | 0             | 5                    | 128.951   |
| phi (time) p(time)                         | 4254.338 | 34.042      | 0             | 7                    | 125.711   |
| phi (time) p(.)                            | 4257.858 | 37.562      | 0             | 4                    | 135.250   |
| phi (time) p(culvert)                      | 4259.148 | 38.852      | 0             | 5                    | 134.534   |
| phi (.) p(.)                               | 4273.698 | 53.402      | 0             | 2                    | 155.097   |

Appendix B. Aquatic Species Assemblages in Culverts and Adjacent Reaches

**Introduction**

In addition to coastal giant salamanders (*Dicamptodon tenebrosus*), many other aquatic species inhabit Pacific Northwest streams. I was not able to address the potential for culvert passage for each of these species. However, I present here summary data on species densities in reference, culvert and adjacent reaches. Our objectives were to describe incidence of culvert use by novel species and to provide comparisons between aquatic organism density in culverts and their density in adjacent stream reaches by culvert type.

**Methods**

We divided study streams into 5 m sections and noted occurrence of tailed frog tadpoles (*Ascaphus truei*), crayfish (*Pacifastacus* spp.), Dunn's salamander (*Plethodon dunni*), red-legged frog (*Rana aurora*), sculpin (*Cottus* spp.) and salmonids (*Oncorhynchus* spp.) that were encountered within each section for three stream visits in 2002 (June, July, August). The density of stream-obligate species (*A. truei*, *Pacifastacus* spp., *Cottus* spp. and *Oncorhynchus* spp.) can be

estimated because the stream was searched across the wetted width (mean abundance/wetted search area). We did not search stream banks, however, and stream-associated species (*P. dunni*, *R. aurora*) were found incidentally. For these species we simply note their presence in stream and culvert sections.

**Results and Discussion**

Both stream-associated and aquatic organisms were found in culverts. There appeared to be greater use of arch culverts than pipe culverts, although this comparison was not quantified (Table B.1; Table B.2). One stream-associated species (*P. dunni*) was found in all of the culverts with dry stream margins, indicating that they do use these areas. Pipe culverts appear to fragment the distribution of all five taxa examined. However, more research is needed to definitively determine the effect of culverts on the movement and distribution of aquatic species. Summary data, such as these, on a larger scale could augment our knowledge of aquatic community distributions in relation to culverts.

**Table B.1. Density (no./m<sup>2</sup>) of aquatic organisms in reference, culvert, and adjacent stream reaches.**

| Reach type | Stream    | Tailed Frog |         | Crayfish |         | Salmonid |         |
|------------|-----------|-------------|---------|----------|---------|----------|---------|
|            |           | stream      | culvert | stream   | culvert | stream   | culvert |
| Reference  | Alder     | 2.7         |         | 0.6      |         | 4        |         |
|            | Cherry    | 1.5         |         | 0        |         | 1.7      |         |
|            | Firecamp  | 1.4         |         | 1.8      |         | 3.9      |         |
|            | Honcho    | 0.17        |         | 0.68     |         | 2.7      |         |
|            | Weatherly | 0           |         | 0.48     |         | 3.2      |         |
| Arch       | Bearpen   | 1.25        | 0.1     | 0        | 0       | 1.68     | 0.6     |
|            | Cherry    | 1.05        | 0.81    | 0.03     | 0.13    | 0.75     | 0.4     |
|            | Firecamp  | 0.08        | 0.04    | 0.41     | 0.4     | 2.01     | 1.16    |
|            | Vaughn    | 0.06        | 0       | 1.03     | 0.3     | 0.63     | 0.53    |
|            | Yankee    | 0.01        | 0.05    | 0.2      | 0.52    | 1.96     | 0.23    |
| Pipe       | Axe       | 0.88        | 0       | 0.23     | 0       | 2.81     | 0.59    |
|            | Honcho    | 0.4         | 0       | 0        | 0       | 0.26     | 0       |
|            | Johns     | 0.26        | 0       | 0        | 0       | 0.2      | 0       |
|            | Weekly    | 0.08        | 0       | 0        | 0       | 0.2      | 0.3     |

| Reach type | Stream   | Dunn's Salamander |         | Red-legged Frog |         |
|------------|----------|-------------------|---------|-----------------|---------|
|            |          | stream            | culvert | stream          | culvert |
| Arch       | Bearpen  | 0                 | 1       | 0               | 0       |
|            | Cherry   | 1                 | 1       | 0               | 0       |
|            | Firecamp | 0                 | 1       | 1               | 1       |
|            | Vaughn   | 1                 | 0       | 0               | 0       |
|            | Yankee   | 1                 | 1       | 1               | 0       |
| Pipe       | Axe      | 1                 | 0       | 1               | 0       |
|            | Honcho   | 1                 | 0       | 0               | 0       |
|            | Johns    | 1                 | 0       | 1               | 0       |
|            | Weekly   | 1                 | 0       | 0               | 0       |

**Table B.2. Presence of riparian associated species in culverts and adjacent stream reaches.**

Appendix C. Density of the Stream Mollusk, *Juga* spp., in Reference Streams, Culverts, and Adjacent Reaches**Introduction**

The stream mollusk, *Juga* spp., plays a prominent ecological role in small streams both as a consumer and prey species. Eleven species of *Juga* are found in the western United States and they are most common and widely distributed in streams west of the Cascade Range in the US Pacific Northwest. *Juga silicula* is restricted to streams and small rivers and *Juga plicifera* occurs in large rivers (Burch 1982). *Juga silicula* is one of the most abundant macroinvertebrates in streams and rivers west of the Cascade Range, comprising up to 90% of the invertebrate standing crop biomass in small lowland streams (Hawkins and Furnish 1987). Due to its generalist and opportunistic feeding habits it is able to inhabit a variety of habitats. *Juga* spp. live for five to seven years and reach reproductive maturity after three years (Hawkins and Furnish 1987). *Juga* spp. play a major role in leaf processing (Warren et al. 1960). A population of *J. silicula* was capable of processing 35% of the allochthonous inputs to a stream in Oak Creek, Oregon (Warren et al. 1960). In addition, they are a food source for the coastal giant salamander, *Dicamptodon tenebrosus*, and reticulate sculpin (*Cottus perplexus*; Esselstyn and Wildman 1997; Warren et al. 1960). *Juga* comprised 68% of the prey ingested by *D. tenebrosus* and 41% ingested by *C. perplexus* in Berry Creek, Oregon (Warren et al. 1960). In areas where *Juga* were abundant, they were the most frequent prey item in *D. tenebrosus* stomachs (60%; Esselstyn and Wildman 1997).

High population densities and food limitations may stimulate dispersal of snails (Furnish 1990). In an Oregon stream, Furnish (1990) found that snails made upstream movements of 15 cm a day in low densities and 49 cm a day in high densities. The maximum distance upstream by an individual was 15 m. Movements by *Juga silicula* increased in summer and with increasing temperatures (Furnish 1990).

Culverts that act as barriers may affect *Juga* spp. population structure. Dillon (1998) found significant genetic differences between

populations of aquatic snails at study sites above and below a culvert in Naked Creek, North Carolina. He determined that upstream movements of a freshwater snail (*Goniobasis proxima*) were blocked by a perched culvert in Naked Creek, North Carolina (Dillon 1988). Our objective was to examine the distribution of *Juga* spp. in culvert reaches by visibly assessing trends in density of *Juga* spp. between culverts and adjacent stream reaches.

**Methods**

In June 2002 I sampled for the stream mollusk *Juga* spp. from 14 study streams (Chapter 1). I divided each stream into 5 m sections and then divided the section into a grid of 1 m<sup>2</sup> plots. I then selected two consecutive numbers from a random number table: the first and second numbers determined the x-axis and y-axis locations on the grid. If one of the numbers fell out of the grid I selected a third number. A 1 m<sup>2</sup> square made from pvc piping was placed on the grid location and all visible *Juga* spp. were counted within the plot. Where riffles obscured the plot area, a plexi-glass view box was used. There was one plot for each 5 m section through stream and culvert reaches on all fourteen streams.

**Results and discussion**

The mean density of *Juga* spp. varied widely between streams (Table C.1). Mean mollusk density tended to decline in some culverts, notably pipe culverts (Table C.1). In addition, mean mollusk densities were consistently higher upstream of arch culverts. More research is needed to understand if distribution gaps along the stream and in culverts also describe a barrier to movement for *Juga* spp. These preliminary data suggest pipe culverts are significant barriers to this species. Genetic testing of snails upstream and downstream of culverts could highlight potential differences, if population subdivision due to culverts exists.

Table C.1. *Juga* spp. density (no./m<sup>2</sup>) on randomly selected plots on thirteen streams in the Oregon Coast Range.

| Reach type | Stream    | <i>Juga</i> Density (no./m <sup>2</sup> ) |                  |          |
|------------|-----------|---|------------------|----------|
|            |           | downstream                                | center (culvert) | upstream |
| Reference  | Alder     | 34  | 79               | 58       |
|            | Cherry    | 5   | 5                | 9        |
|            | Firecamp  | 13  | 12               | 26       |
|            | Honcho    | 14  | 10               | 17       |
|            | Weatherly | 12  | 13               | 14       |
| Arch       | Bearpen   | 6   | 16               | 17       |
|            | Cherry    | 2   | 1                | 6        |
|            | Firecamp  | 4   | 5                | 29       |
|            | Yankee    | 99  | 12               | 128      |
| Pipe       | Axe       | 72  | 0                | 116      |
|            | Honcho    | 4   | 0                | 21       |
|            | Johns     | 31  | 7                | 49       |
|            | Weekly    | 14  | 0                | 2        |

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