DEMOGRAPHY, DISPERSAL AND COLONISATION OF LARVAE OF PACIFIC GIANT SALAMANDERS (*DICAMPTODON TENEBROSUS*, GOOD) AT THE NORTHERN EXTENT OF THEIR RANGE

by

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Hons. B.Sc., The University of Toronto 1995

A THESIS SUMBITTED IN PARTIAL FULFILMENT OF
THE REQUIREMENTS FOR THE DEGREE OF

MASTER OF SCIENCE

in

THE FACULTY OF GRADUATE STUDIES

Department of Zoology

We accept this thesis as conforming
to the required standard

THE UNIVERSITY OF BRITISH COLUMBIA

November 1998

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Date Dec 1/98

DE-6 (2/88)

Abstract

The Pacific Giant Salamander, (*Dicamptodon tenebrosus* Good) is red-listed in British Columbia, the northern extent of the species' range. Little is known about the demography of these populations and their ability to recover from disturbance by recolonisation. I conducted a field experiment to measure the colonising ability of larval Pacific Giant Salamanders at 4 streams within the Chilliwack Valley of British Columbia. I also estimated basic survival, growth and dispersal rates for these larvae. These rates were compared to others from Oregon where this species is not considered threatened.

Mark-recapture in 120 m reaches in four streams in 1996 and 1997 revealed (a) lower larval densities, (b) lower annual growth rates and (c) similar annual survival of these larvae in comparison to those in similar Oregon streams. Due to slower growth rates, I hypothesise the the larval period in British Columbia is 2-3 times longer than in Oregon.

To study colonisation, larvae were removed from a 25-40 m section within each 120 m reach and the recolonisation of each section was monitored for 13 months. Depleted reaches were repopulated slowly by larval dispersal and more quickly by adult reproduction. Few larvae moved more than 4 m. Full recolonisation of these reaches was predicted to take 6-42 months. Provided terrestrial adults are available, local reproduction appears to be a more effective means of repopulating an area than larval immigration.

Larval dispersal was not influenced by larval density, biomass, substrate, wetted width, depth, or pool-riffle composition. Logging-induced habitat shifts may thus have little consequence to larval dispersal as movement was uniformly low through a variety of micro-habitats.

Although logging and other disturbances may increase the rate of local extinction of *D. tenebrosus* in British Columbia, these populations are not unusually susceptible to disturbance. Despite having lower density and growth rates than in other parts of their range, larvae in British Columbia exist within the survival and growth bounds of other non-threatened stream-dwelling salamanders. More importantly, recruitment can facilitate rapid recovery from small-scale disturbances. Conservation efforts should focus on terrestrial as well as aquatic habitat and dispersal routes.

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Acknowledgments

I cannot imagine a more supportive, insightful and helpful supervisor than I found in Dr. William Neill. I thank him for our many hours of discussion regarding my thesis and the wonders of nature in general, his patience and belief in me when I encountered challenges with my work, and his sense of humour. It has truly been a pleasure to work with Dr. Neill and his advice has been invaluable. I would also like to thank my committee members Dr. Jamie Smith and Dr. John Richardson. Their careful review of my research has been instrumental in shaping my initially rough tangle of ideas into coherency. I greatly appreciate their help. I would also like to thank Dr. Dan Haydon for his statistical advice.

I was very privileged to have an excellent team of dedicated field assistants: Diane Casimir, Leonardo Frid, Mark Krause, Shelagh Parken, Alex Skrepnik, and Carolynn Stephenson. Many thanks to them for their hard work and unflagging pursuit of salamanders in rain or shine. A very special thanks goes to Karl Mallory for his advice on site selection, capturing techniques, and assistance with field supplies and housing. Additional thanks go to the many other volunteers who came out to Chilliwack for a few days to help with my field work.

This project would not have been possible without the generous financial support of Forest Renewal B.C. and the World Wildlife Fund of Canada. I would also like to thank N.S.E.R.C. who provided personal financial support through a PGS A scholarship.

I must also thank the many people whose friendship and sense of humour kept me on track. Special thanks go to Christine, Anne, Bea, Christianne, Krista, Stephanie, Michelle, Tony, David C. and Wendy for "dragging" me for a beer, keeping me company at the Railway Club, and enduring Braveheart a record 10 times.

Finally, I would like to each and every one of the 600+ Pacific Giant Salamanders that had to endure my handling throughout the course of this experiment. I sincerely hope the information I gained through this endeavour will prove useful to the maintenance of this elusive and beautiful creature within the Chilliwack Valley.

For Irene and Tom,

Dulcius ex Asperis

Chapter 1: General Introduction

In 1989, the Pacific Giant Salamander (*Dicamptodon tenebrosus* Good) was declared vulnerable by the Committee on the Status of Endangered Wildlife in Canada (COSEWIC). This species is red-listed and classified as "at risk" by the provincial government of British Columbia. Despite this designation of the highest level of risk (British Columbia Ministry of Environment, Lands & Parks 1993), the true status of this species in Canada and the extent to which it is threatened are unknown. Much of the evidence supporting *'D. tenebrosus'* listing comes from observation of perceived threats such as logging (Haycock 1991), and the assumption that being on the margin of the species' range makes populations in British Columbia inherently more vulnerable to extirpation. This assumption is based on field evidence from other taxa that shows peripheral populations have a greater probability of local extinction (Lomolino & Channel 1995, Nathan et al. 1996) than those in the centre due to lower population densities (Hengeveld 1990, Lawton 1993), lower survival (Randall 1982, Rogers & Randolph 1986), and lower fecundity (Caughley et al. 1986) . While these factors may warrant concern, there has been no thorough demographic examination of *D. tenebrosus* populations in British Columbia to demonstrate that they are truly imperilled.

The scientific criteria required to assess whether a species is at risk are not well defined. Many different schemes of assessment have been proposed (Ayensu 1981, Mace 1991, Spellerberg 1992, Primack 1993, Caughley & Gunn 1996), but no standard methodology has been adopted. It is generally agreed however, that evaluation of requires knowledge of local demography, the impact of human activities and the general ability of the species to respond to disturbance (Soulé & Kohn 1989, Primack 1993, Ellis & Seal 1995). Using these issues as a

guide, several key questions can be formulated to assess whether *D. tenebrosus* populations in British Columbia merit special conservation attention:

a) Local Demography

- Are population densities significantly reduced in regions where the species is considered threatened in comparison to areas where they are not?
- Are populations declining in regions where they are considered threatened?
- Are vital demographic rates such as survival, fecundity and/or growth significantly lower in regions where the species is considered threatened in comparison to areas where it is not?
- Are *D. tenebrosus*' vital demographic rates uncharacteristically low in comparison to other non-threatened stream dwelling salamanders?

b) Impact of human activities

- Are population densities, survival, fecundity and/or growth rates reduced in regions that have been logged, the primary form of human disturbance in *D. tenebrosus'* range?
- Do the specific habitat changes caused by logging compromise *D. tenebrosus'* dispersal and recolonisation ability?

c) General ability to recover from disturbance

- How quickly can *D. tenebrosus* recolonise sites of local extinctions?

Some of these questions are addressed in this thesis. In a two year study such as this one, long term population trends cannot be assessed. However, basic life history information and seasonal demographic rates can be estimated. This information is a crucial first step for identifying whether these allegedly vulnerable populations behave differently from those in Oregon, Washington and California where the species is not a major conservation concern. These basic rates can also be compared to those in other, non-threatened stream-dwelling salamanders to reveal whether this salamander is intrinsically less viable than other species. Such fragility would indicate an increased susceptibility to extinction, even in the absence of disturbance.

To obtain reliable demographic estimates, I repeatedly sampled a few populations (5) instead of less intensively sampling a large number of sites. This study is the first to produce robust estimates of larval density, survival, growth, dispersal and colonising ability for several populations of *D. tenebrosus*. Many of these parameters such as survival and growth have never before been rigorously estimated for *D. tenebrosus* in British Columbia. Others such as colonising ability have never been measured for this species anywhere in its range.

In addition to the estimation of basic vital rates, I examined if the more recently logged sites displayed distinct demographic properties. Although not rigorous, this qualitative analysis may generate preliminary hypotheses of how habitat influences larval persistence.

This species' general ability to recover from disturbance, a final indicator of vulnerability, was studied experimentally. In British Columbia, logging is presumed to increase the frequency of local extinction (Farr 1989, Haycock 1991), yet almost nothing is known of *Dicamptodon's* ability to recover by colonisation. I simulated point extinctions within larval populations and monitored the speed of recolonisation. I also studied larval dispersal in differing stream micro-habitats to determine if recolonisation is habitat-dependent.

I) Natural History

Pacific Giant Salamanders are an important component of the vertebrate fauna in the forests of the Pacific Northwest. In the streams where it occurs, this salamander is often the dominant predator and can constitute up to 99% of the total vertebrate biomass (Murphy & Hall 1981). Larvae prey primarily upon benthos (Parker 1994) although large individuals can also eat Tailed Frog (*Ascaphus truei)* larvae, small fish and smaller conspecifics (Nussbaum et al. 1983). Adult salamanders consume large prey including mice, shrews and lizards (Bury 1972). With

larvae occurring at densities of up to 3 per m^2 in some Pacific Northwest streams (Kelsey 1995), they may regulate numbers of their prey species.

In British Columbia, these animals spend at least two years as aquatic larvae (Richardson & Neill 1995). Larvae reside primarily in cool, fast flowing headwater streams although some have been found in larger streams and lakes. After the larval period, *D. tenebrosus* either transform into sexually mature terrestrials or remain in streams in neotenic form. Adults can grow up to 35 cm in total length, making this species the largest semi-aquatic salamander in North America (Nussbaum et al. 1983).

II) Distribution

Pacific Giant Salamanders are found along the western coast of North America from northern California to southern British Columbia. In Canada, *D. tenebrosus* is found only in the Chilliwack River drainage basin and a few adjacent small tributaries that drain directly into the Fraser River. Within the Chilliwack Valley watershed, *D. tenebrosus* is distributed patchily with many unexplained gaps in its distribution. Survey work in Chilliwack detected *D. tenebrosus* in only 21 of 59 seemingly habitable streams (Richardson & Neill 1995). It is possible that many of these currently barren streams have experienced local extinction.

III) Role of larvae in Urodele population dynamics

My research was conducted solely on larvae of *D. tenebrosus*. While no concrete prediction of species' persistence can be drawn from the study of one life history stage, larval ecology is an essential component of population biology. Furthermore, there is reason to believe that larvae may be the only stage in recently disturbed habitats. Terrestrial adults may suffer great mortality in clearcuts due to increased desiccation and freezing in exposed habitats (Richardson

1994). Under such a scenario, depopulated areas would rely on larval propagules from undisturbed stream reaches for recolonisation. Although this hypothesis has not yet been tested, it suggests that studies of larvae are vital to judge the recovery potential of this species.

IV) Organisation of Thesis

This thesis is composed of three research chapters and a general conclusions section. The research chapters will address the following three topics: 1) *D. tenebrosus* larval demographic rates in British Columbia, 2) habitat-dispersal associations and 3) recolonising ability. In combination, these studies will provide new insights into the resilience of this species and whether it is currently compromised in British Columbia. Each chapter is based on two summers of research within the Chilliwack Valley. The major goals and hypotheses of each chapter are outlined below.

1) *Life history and demography of Pacific Giant Salamander larvae in five streams at the northern limit of its range*

The primary aim of this chapter is to provide base-line demographic information on larval *D. tenebrosus* populations in British Columbia and compare rates with those collected in more southerly, non threatened populations. I also examine the influence of forest age from 5 to 60 years on demography and the impact of larval population density on survival and growth.

2) *Determinants of Dispersal in Pacific Giant Salamander Larvae*

In this chapter, I examine the influence of abiotic and biotic factors on dispersal of *D. tenebrosus* larvae. As dispersal is the key means by which populations re-establish in disturbed

areas, a knowledge of the environmental and demographic factors that limit movement may be useful for management.

3) *Colonising Ability of Pacific Giant Salamander larvae*

In this experiment I measured how quickly artificially depleted stream reaches were recolonised by *D. tenebrosus* larvae. I tested whether larvae are capable of recovering from small disturbances within a short period of time (< 1 year). I also tested whether this recolonisation is limited by source population density, size structure and location.

4) *General Conclusions*

The general conclusions section summarises the major findings of this research. This section discusses the implications of this research to the evaluation of *D. tenebrosus*' current status and future persistence in British Columbia.

Chapter 2: Life history and demography of Pacific Giant Salamander larvae in five streams at the northern limit of its range

Introduction:

As the number of species exposed to human disturbance increases, there is a great need to assess the potential impacts on population persistence. Although no definitive criteria exist, it is widely accepted that information on local demography is vital to evaluate the viability of populations (Soulé & Kohn 1989, Caughley & Gunn 1996, Primack 1993). Basic life history information is useful both to understand habitat requirements and suggest the mechanisms that limit populations in different areas. Reductions in demographic rates such as survival, reproduction and growth between habitats can also suggest causes of decline and local extinction (Caughley & Gunn 1993). Conversely if demography is unaffected by habitat change, there is little reason for concern about the persistence of such populations under similar events.

In this chapter I present detailed demographic analyses of larval Pacific Giant Salamanders (*Dicamptodon tenebrosus*) in five sites in the Chilliwack Valley of British Columbia, the northern extent of this species' range. In British Columbia, populations of this red-listed species are thought to be limited by cool temperatures and threatened by logging (Haycock 1991). Very little demographic analysis has been conducted to support these claims. I examined larval survival, recruitment, metamorphosis and growth. My aims were to:

1) Provide base-line demographic information for larvae in British Columbia;

2) Examine the relationship between logging history and larval demographic parameters;

3) Examine the relationship between survival, growth and larval density.

1) Pacific Giant Salamander life history - a review

Given the secretive nature of *D. tenebrosus*, much of the basic life history of this animal remains unknown. What is known about this species' ecology and response to disturbance comes from studies in Washington, Oregon, and California. Very little research has been conducted in British Columbia. The following summarises what is known about *D. tenebrosus'* life history and the major questions that remain.

a) Reproduction

Whereas *D. tenebrosus* in Oregon and California are believed to have distinct breeding periods in Spring and Fall (Nussbaum et al. 1983), preliminary evidence from British Columbia suggests the timing of breeding is variable (Haycock 1991). If this is true, *D. tenebrosus* in British Columbia would be one of the few temperate amphibian species to display asynchronous breeding (Duellman & Trueb 1986). Although the timing of breeding may be variable, it is potentially concentrated in specific months or seasons. In this study, mark-recapture throughout the active seasons of 1996 and 1997 was used to test for seasonality in recruitment of *D. tenebrosus*.

Observations in aquaria and the field show that eggs take approximately 200 days to hatch (Nussbaum et al. 1983) into larvae 33-35 mm in total length (Nussbaum & Clothier 1973). Newly hatched larvae remain buried in the substrate and attached to their yolk sac for three to four months before appearing in streams at 45-51 mm in length (Nussbaum & Clothier 1973). Combining these periods, I assume that larvae are first detectable 9-11 months after they are spawned. Using this criterion, the timing of breeding in my streams was back-calculated as 9-11 months from the first appearance of small, 45-50 mm long larvae.

b) Transformation

After 2-4 years as larvae, *D. tenebrosus* either transform into terrestrial adults or remain in the stream in neotenic form (Duellman & Trueb 1986). The timing of transformation varies considerably between populations (Nussbaum & Clothier 1973), but is believed to occur between June and August. If so, the frequency of large larvae should decline over this period. I tracked changing size structure throughout the active season to pinpoint the timing of transformation in Chilliwack streams. Describing the chronology of natural abundance fluctuations in larval populations, either by recruitment or metamorphosis, will help biologists distinguish change caused by life history processes and change caused by extrinsic factors.

c) Survival

Little is known about larval survival in *D. tenebrosus* and how it varies seasonally and spatially. Scientists have identified several sources of mortality in *D. tenebrosus,* but not their net effect on survival. Chief agents of mortality in this species are thought to be cannibalism, predation, and desiccation (Nussbaum & Clothier 1973). Preliminary research in the Chilliwack region suggests that larval survival varies throughout the year. More larvae "disappear" over the summer than they do over the winter (Neill & Richardson 1998). It is unclear whether this increased summer loss rate is due to transformation or higher mortality. I attempted to separate these alternatives by correcting summer survival rates for loss due to transformation. Seasonal differences in survival were then assessed by comparing this less biased summer rate to the winter disappearance rate.

d) Growth

Working in one British Columbia stream, Haycock (1991) found that first year larvae increased between 0.5 to 3.2 mm in snout-vent length (SVL) per month during the active season. It is unclear whether these rates vary between streams, habitats and regions. I measured larval growth at four sites within the Chilliwack Valley. Mean growth at these sites was compared to estimates from larvae in Oregon, the centre of *D. tenebrosus'* range, to examine if northern populations showed signs of depressed growth

2) The Impact of Logging on Life History Parameters

Most studies of *D. tenebrosus* in the Pacific Northwest have inferred logging effects by correlating larval density to the age of the surrounding forest. Results of these studies have been mixed, with some finding reduced density in logged stands (Bury 1983, Bury & Corn 1988, Connor et al. 1988, Corn & Bury 1989, Cole et al. 1997), others finding no effect (Hawkins et al. 1983, Kelsey 1995) and still others finding increased density in logged areas (Murphy et al. 1981, Murphy & Hall 1981). Without examining demographic rates, it is difficult to interpret why abundance varies, increasing or decreasing, in logged areas.

I investigated growth and survival in different aged stands in addition to larval density to determine if they varied with forest age. Only a small number of sites were investigated in this analysis so my ability to detect habitat-specific population trends is low. However if recently logged habitat is of poorer quality to *D. tenebrosus* larvae than mature forest, I expected to find some correlation between larval demographic rates and forest practices. If logging is highly detrimental to these animals, I predicted that either larval density, survival and/or growth should increase with forest age.

Demographic analysis may also reveal whether one of the proposed benefits of living in a recently logged stream, increased growth (Murphy et al. 1981, Murphy & Hall 1981, Hawkins et al. 1983), is valid. Temperature and primary productivity of streams often rise after logging, possibly enhancing the food supply and length of growing season of *D. tenebrosus* (Murphy et al. 1981, Corn & Bury 1989). Higher growth rates could increase the fitness of larvae in clearcut streams by shortening the length of time they spend exposed to size-dependent cannibalism and predation. I tested whether forest age related to larval growth rate.

3) Biotic Regulation in *D. tenebrosus* Larval Populations

In addition to forest habitat, I also examined the influence of larval density on demography. Some studies of larval salamanders indicate survival and growth are primarily a function of population density (Kusano 1981, Petranka & Sih 1986, Buskirk & Smith 1991). It is therefore possible that larval demography is more influenced by density than forest habitat. I examined whether survival and growth decreased with increasing larval density at four sites. Although the number of sites used in this analysis is low, if strong density dependence was acting these trends should be evident.

Methods:

Site Selection

Five headwater streams in four watersheds of the Chilliwack River drainage basin were selected for study. Sites were selected both on the basis of accessibility by logging road and larval abundance. Only sites at which at least one larvae was detected within a preliminary thirty minute searching period were used. Sites differed in their logging history (Table 2.1). Four of

the five sites were used in a colonisation experiment (Chapter 4) and were sampled intensively throughout the active season in 1996 and 1997. At these sites, larvae were removed from a central portion of the stream. This manipulation should not influence this analysis as all demographic estimates were gathered from larvae living outside of the removal zone. The fifth site, Foley R, was studied only for a few months in summer 1996. As a consequence of reduced sampling frequency at this site, estimates of survival and growth were not compared to those at other sites. Abundance was calculated for this site and used in the analysis of logging history and larval density.

Mark-Recapture

A 120 m reach of stream was selected at each site. Larvae living within these reaches were routinely sampled using mark-recapture. Partial removals of 25-40 m in length were conducted on four of these five streams. Only the remaining 80 to 95 m of unmanipulated (non-cleared) reach was used in this analysis (Table 2.1) Sampling was conducted weekly (Table 2.2). With the exception of Foley R, all sites were sampled at least twenty times. This frequency of sampling ensured that the opportunity to recapture animals was high.

On each visit, the entire 120 m reach was systematically searched. All large rocks and debris were turned over and the substrate inspected for larvae. All overturned material was returned to its original position. Larvae were detected by sight or touch and captured in small dip nets. Their location was recorded to the nearest half meter and marked by tying fluorescent flagging tape to a rock. Captured larvae were held individually in 1 L plastic jars during subsequent processing.

Unmarked larvae were anaesthetised in a 0.33g L^{-1} solution of MS222 (tricaine methanesulfonate). While anaesthetised, larvae were marked either by toe clipping or the insertion of a Passively Induced Transducer (P.I.T.) tag (AVID Micro chips, MUSICC 21-23). Each tag emits a distinct electromagnetic field which can be picked up by a hand held reader (AVID Power Tracker II) and translated into a unique identity code.

Animals with a total length < 100 mm were toe clipped. A unique combination of one or two toes was removed from these animals with a scalpel. Toes that appeared to be regrowing on subsequent capture were clipped again. Larvae ≥ 100 mm were given a P.I.T. tag. To insert a tag, a small incision was made anterior to the hind leg on the animal's side. A disinfected tag was then inserted by hand (wearing medical gloves) under the first layer of skin. The wound was disinfected with antibacterial ointment and sealed with Vet Bond™, a veterinary surgical adhesive. On recapture, all larvae were examined for toe loss and scanned with a hand-held P.I.T. tag reader.

The total body and snout-vent length of each larva were recorded to the nearest millimetre. Animals were also weighed on a portable electronic balance (Ohaus Inc.) accurate to 0.1 g. Animals were returned to their initial point of capture after they had regained their swimming ability.

Larval Abundance and Density Estimation

I used a closed mark-recapture model to estimate larval density throughout this study. Closed models assume that no birth, death or dispersal into or out of the study area have occurred during the period when the mark-recapture data were collected. As such, data must be gathered over a short period of time to minimise bias due to non-closure (Pollock et al. 1990).

Mark-recapture data were split into four periods: Spring 1996, Fall 1996, Spring 1997 and Fall 1997 (Table 2.3). With the exception of Fall 1997, each period consisted of data from four mark-recapture episodes over four weeks. A four-week period was thought to be the longest span of time that would meet the assumptions of a closed population model. In Fall 1997, density was estimated on the basis of two instead of four sampling periods.

The program CAPTURE (Burnham et al. 1994) was used to calculate larval abundance during each 4 week interval (Spring 96, Fall 96, Spring 97). From inspection of capture records, it was evident that some animals were more likely to be caught than others. As a consequence, the assumption of equal probability of capture was violated. To account for this, the data were fitted to a specific model within CAPTURE (Burnham & Overton 1979) known as M(h) that compensates for heterogeneity in capture probability (Burnham & Overton 1979). This model requires more than two sampling occasions to determine the amount of variation in capture probability between animals. With only two sampling intervals, Fall 1997 abundance could not be estimated by the M(h) model. Abundance at this time was calculated using the Lincoln-Peterson method (Lincoln 1930). Chapman's Modification of the Lincoln-Peterson method was used to offset bias caused by low recapture probability (Chapman 1951) (Appendix 1). By ignoring heterogeneity in capture probabilities between individuals, this model may underestimate abundance in comparison to M(h) (Pollock et al. 1990). Larval density (individuals per m^2) was estimated at each site by dividing the estimated abundance by the area of the study reach (length of unmanipulated stream searched multiplied by the average wetted width) (Table 2.1).

Size Structure Variation: Recruitment, metamorphosis and logging impacts

Measurements of total length on first capture were pooled over all time periods and used to generate a cumulative length-frequency histogram at all five sites. I used Kolmogorov-Smirnov tests to examine if larval size-frequency distributions varied between sites with different logging history. Additionally I examined the mean body size of larvae at each site. Statistical differences in larval size between sites were evaluated using a Kruskal-Wallis test.

To investigate temporal trends in recruitment and metamorphosis, I examined how size structure changed throughout the larval active season at four sites. At each site, histograms of larval total length were computed for each month of the study period: June - September 1996, June and September 1997. Kolmogorov-Smirnov tests were used to determine whether the shape of the length distribution changed significantly through time. The data were examined for evidence of a sudden appearance of larval recruits at some point during the active season and for a sudden disappearance of large larvae due to transformation.

Larval Disappearance Rates and Survival

Open population mark-recapture models give relatively robust, unbiased estimates of disappearance rates between sampling intervals (Pollock et al. 1990). Disappearance does not necessarily reflect the amount of death, as animals may also leave the study area by dispersal. From this point forward, I will use the term "disappearance" to refer to the percentage of animals that leave the study area over a given period, while "mortality" is used only when the actual death rate is implied. I calculated and compared larval disappearance rates over one

month in the active season (mid July to mid August) and over winter (September - May) at four sites. The Program JOLLY was used to estimate these rates (Hines 1991).

I also recorded information on dispersal and transformation to assess how strongly these processes influenced summer disappearance rates. By measuring distances travelled between captures, I was able to characterise larval dispersal distances and estimate the probability of migration into or out of the study zone between sampling periods. Calculating the percentage of loss due to transformation was more difficult. From my observations in the Chilliwack area, most larvae $\geq$ 130 mm in total length showed signs of imminent transformation, i.e. considerable reduction of gill size and the appearance of marbling on the skin. Using a cut-off of 130 mm total length, I calculated the percentage of larvae large enough to be on the verge of transformation in each Spring sample. If this fraction was high, I interpreted disappearance rates from Spring to Fall as being significantly influenced by metamorphosis.

Growth

Growth between captures was defined as the change in snout-vent length (SVL). As many larvae lose part of their tail, possibly as a result of fights, SVL is a more accurate measure of skeletal growth than total body length. The difference in SVL length between first and last capture during the active season (June - September) was plotted as a function of the number of days between captures. A linear regression was used to determine the strength of this relationship. Amphibian growth is probably best described by a curvilinear rather than linear relationship, with rates slowing down with age. However I was examining size changes only over a few months of the active season and not between years. I assume linear analysis is sufficient to describe this short term growth.

To examine how age influences growth, I calculated daily growth rates for larvae < 100 mm (small) in total length and ≥ 100 mm (large). Although there is no definitive means of ageing larvae, my successive 1996-1997 mark-recapture suggests larvae 100 mm in length are at least one year old. Thus this analysis attempts to look at differences between larvae in their first year, and those older (2-4 years?). I used analysis of covariance to determine if daily growth was affected by body size. If body size strongly affected growth rate, comparisons between sites were stratified by size.

Results

Abundance and Density Estimation

Larval density in the five study streams varied between 0.46 and 1.31 larvae m^{-2} (Table 2.4). With the exception of Foley R, mean density at each site was based on four estimates of abundance. As only one measurement of density was taken at Foley R, this site was excluded from statistical analysis of between-site density differences. Mean density varied significantly between the remaining four sites but not between Spring and Fall (Two-way ANOVA, site effects: $F_{3,8} = 9.642$ $p = 0.005$, season effects: $F_{1,8} = 0.419$, $p = 0.535$). Larval density was highest in the young second growth site, but not significantly so (Table 2.5).

In the four sites monitored for two summers, larval abundance showed moderate seasonal and annual fluctuations (Figure 2.1). Spring densities in 1997 were always slightly lower than Fall 1997 estimates. Similarly in 1996, almost all Spring density estimates were equal or less than the Fall values.

Size Structure

Summed across all sampling dates, larval body length at all sites varied from 40-160 mm (Figure 2.2). Mean larval size varied significantly between sites (Table 2.6). Larval size was significantly higher in the young second growth site (Kruskal-Wallis, $\chi^2 = 29.152$, $p < 0.001$). Given that only one site was in this habitat category, this result could be due to random site variation and not to forestry treatment.

Size-structure fluctuated between months in the summer of 1996 (Figure 2.3 a,b,c,d) and 1997 (Figure 2.4). In Fall 1997, the size structure at Promontory 3a and Tamihi C-DS was significantly shifted towards small larvae in the 40-50 mm length range (Kolmogorov-Smirnov test, $p < 0.001$). A similar influx of small larvae appeared at the Promontory BH and Promontory 3a in August 1996. The proportion of larvae larger than 130 mm TL consistently declined from June to September at Promontory BH and Promontory 3a. In 1996, significant decreases in large larvae were evident as early as July (Kolmogorov-Smirnov test, $p < 0.01$). Similar decreases were seen in 1997, but as no July sample was taken in this year it is difficult to pinpoint the start of this decline.

Larval Disappearance Rates and Survival

Before summer and winter rates were compared, they were scaled to the same time period. A one-month winter disappearance rate was extrapolated from the nine month rate in the following way:

$$1 \text{ Month Winter Disappearance Rate} = (9 \text{ month Winter Disappearance Rate})^{1/9}$$

Back calculated monthly winter disappearance rates were not consistently higher or lower than monthly summer rates (Table 2.7). Summer disappearance rates did not appear to be related to

forest practices, with rates being similarly low in the oldest and youngest site (Promontory BH and Tamihi C-DS). The same is true for winter rates that had no specific association with the logging history of sites. Summer and winter disappearance rates were not clearly associated with larval density, with the two streams most similar in density (Centre HF and Promontory BH) having the most divergent rates.

On average, larval disappearance over a one month period in the summer was about 12%. As *D. tenebrosus* larvae are poor dispersers (Chapter 3), I have assumed dispersal does not significantly impact month to month disappearance rates in a 120 m reach. Transformation, however, could account for a more significant loss of individuals over the summer months. For example, in the first sampling period of 1996, 18% (34/192) of all larvae were large enough to be close to transformation and 80% of these same individuals (n = 34) were never caught again. The mean capture probability at all sites varied between 15-20% per occasion. Given that each stream was sampled an additional 15 times, these large individuals should have been recaptured at least once during the remainder of the study if they were still in the reach in larval form.

The fraction of the monthly summer disappearance due to transformation can be approximated as the percentage of larvae >130 mm in an area at the start of a summer month multiplied by their observed disappearance rate over the same one month period. Combining data from all my study sites, this value equals approximately 10% (13% of larvae > 130 mm TL x 80% disappearance rate of these larvae). The percent of larvae that actually die over a one month period in the summer can be estimated as the percentage of total disappearances minus the percentage of disappearances due to metamorphosis: 12% - 10% ≈ 2%. This value slightly underestimates mortality as it assumes all disappearance of larvae > 130 mm was due to transformation and not death. Taking this value as a lower extreme, I assume that between 2%-

5% of larvae die over a one month period in the summer, the rest of the loss being due to transformation.

As transformation does not occur in winter, winter disappearance rates are likely to be a good reflection of mortality. I thus conclude that larval mortality is lower throughout the summer (2-5% per month) than it is in winter (mean disappearance of 12% per month). Combining these estimates of summer mortality with winter disappearances rates, mean annual survival of larvae was approximated to be between 30% and 35%.

Growth

In the 4 sites where growth was studied, small larvae (< 100 mm total length) grew faster than large larvae ($\geq$ 100 mm total length) but not significantly so (ANCOVA, $F_{1, 211} = 1.485$, $p = 0.224$). Pooling across all body sizes, growth was described at all sites (Table 2.8). Mean daily larval growth rate throughout the active season was 0.06 mm (95% C.I.: 0.04 - 1.11 mm per day). Growth at the only clearcut site, Tamihi C-DS, was almost twice as fast as other sites (Figure 2.5) although the trend was not significant. Larval density did not influence variation in growth.

Discussion:

Larval Demography in British Columbia

a) Larval Density

In this study, mean larval density was 0.88 ± 0.09 individuals per square meter of stream. My study sites were chosen because they had relatively high larval densities and therefore they reflect maximum densities within the Chilliwack area.

b) Reproduction

Two sites experienced a sharp increase in young-of-the-year larvae (Promontory 3a & Tamihi C-DS) in the late active season (August - September). Using Nussbaum et al.'s (1983) developmental data as a guide, breeding at these two sites must have been concentrated in September-October of 1996 to give rise to a recruitment pulse in the Fall of 1997. At the other two sites, density increased in August and September but there was no increase in the frequency of small larvae. It is difficult to interpret this mixture of results. At both Tamihi C-DS and Promontory 3a, the increase of recruits in Fall of 1997 could have been the result of a single clutch hatching. In both cases, the appearance of hatchlings was concentrated within a 10 m reach of stream. My results could thus be explained by the existence of one female at each of the two sites laying eggs at approximately the same time, and not seasonally restrictive breeding. Direct study of adults at many different streams is needed to clarify seasonal trends in reproduction. Unfortunately radio-tracking of 20+ adult *D. tenebrosus* in the Chilliwack region by Johnston (1998) and L. Frid (pers. comm) have failed to yield any information on reproduction.

c) Transformation

The size structure throughout 1996 (Figure 9a) shows a loss of large larvae (> 130 mm TL) between June and August at both the Promontory 3a and Promontory BH site. No change in the frequency of large larvae was found at either Tamihi C-DS or Centre HF. It is possible that larvae in the latter sites were more prone to neoteny than those at Promontory 3a and BH.

Losses at the Promontory sites were most visible between June and July, suggesting that transformation may peak in the early stages of the active season.

d) Survival

After correcting the mean survival rate across all sites for transformation loss, monthly survival of larvae was found to be higher in summer than in winter. Harsh climatic conditions over the winter, including snowfall and the freezing of streams, may be responsible for reduced survival during this season. Extrapolated over a year, these mean survival rates suggest that only 30-35% of larvae survive each year. Survival throughout a 2-4 year larval period (as suggested by Duellman & Trueb (1986) for this species) could thus vary from 1-12%.

e) Growth

Larval *D. tenebrosus* in my study sites grew between 1.3 mm and 3.2 mm in SVL per month from June through September. I found no significant difference between the growth of larvae < 100 mm TL and $\geq$ 100 mm TL, and thus estimate and all subsequent values were based on the pooled set of all larvae, regardless of body size. My growth rates are similar to those reported by Haycock (1991) who found that first year larvae in one Chilliwack stream grew between 0.5 mm and 3.2 mm SVL per month (mean = 1.3 mm).

The above growth calculations are for the active season only (June - September). As rates likely slow during winter months, these estimates cannot be extrapolated to predict annual growth. At each site, a few larvae were recaptured in successive summers and their annual growth could be calculated. These individuals were not used in my growth analysis as their inclusion would have violated the assumption of linear regression that every value on the x-axis

has a measurable value of y (Zar 1984). As larvae were only sampled in summer, time (the x-axis) was a continuous variable only throughout the active season and not between years. Temporarily ignoring this statistical concern, I included annual growth information from these larvae calculated a growth rate of 7.3-10.6 mm SVL a year. Assuming the same amount of length is added every year, it could take 4-6 years for larvae in my study areas to grow from their SVL when first detectable (≈ 25 mm) to their SVL at metamorphic size (70 mm +).

Comparison of Demographic Rates with other areas in D. tenebrosus' *Range*

Given the paucity of data from other parts of *D. tenebrosus'* range, it is difficult to make robust geographic comparison between larval demography in British Columbia and demography in Washington, Oregon and California where the species is not considered threatened. What is known about this species and its closest relative, *Dicamptodon ensatus*, is presented in Table 2.9. A few general geographic trends in demography are evident, although in all instances these patterns require more replication to be confirmed. Mean density of larvae in forested streams in Oregon was 2.3 larvae per square meter (Corn & Bury 1989), almost three times the maximum density recorded in this study. The difference in larval density between Washington and British Columbia is not nearly so pronounced. The mean density of larvae reported in this study exceeded that from Washington. However the data from Washington was based on a random sampling of sites whereas data in this study was drawn from streams known to have reasonably high densities of larvae. As such it should not be concluded that abundance is generally higher in British Columbia, but rather that these areas likely do not differ greatly in larval density.

Nussbaum & Clothier (1973) estimated annual survival of first year *D. tenebrosus* larvae in one Oregon stream to be 43%, slightly greater than the 30-35% estimated in this study.

Annual survival does not appear to vary much between these regions, however the length of the larval period does. According to my analysis, larvae in my four study streams could take 4-6 years to reach metamorphic size (130 mm TL +). Larvae in two Oregon streams were estimated to grow 2-3 times faster than larvae in my study, and are believed to have a larval period of only two years (Nussbaum & Clothier 1973). Even if annual survival was the same in Oregon and British Columbia, net survival through the larval period will be lower in British Columbia. For example if annual survival was 40% in both regions, survival throughout the entire larval period would be 16% in Oregon (2 year larval period), and only 0.5-3% in British Columbia (4-6 year larval period). This difference in net larval survival may help explain why densities of *D. tenebrosus* are lower in British Columbia than in the centre of its range. However, many more populations in both British Columbia and Oregon need to be studied before any geographic trends in survival can be confirmed.

The Impact of Logging on Life History Parameters

The low number of sites used in this study makes it difficult to examine the influence of logging on *D. tenebrosus*. Although my sites differed in logging history from recently clearcut (< 5 years) to mature second growth (+ 60 years), there was almost no replication of particular forest age classes. As such, I cannot ascertain whether variation in demographic rates is due to logging effects or random site variation. However even with a small number of sites, it is useful to examine if the more recently logged sites display distinct demographic properties.

Across my five study streams, only larval growth appeared to be associated with forest practices (Table 2.10). Although not statistically significant, larval growth rate at the clearcut site was almost twice as fast as in any of the closed canopy sites. This observation is common in

fisheries research, where growth is frequently found to increase in clearcut streams (Hartman & Scrivener 1990). My results suggest this phenomenon also occurs in *D. tenebrosus* larvae.

If both larvae and adults of *D. tenebrosus* have greater fitness in clearcut streams due to increased growth however, it is unclear why these areas are sometimes found to have the lowest densities of larvae (Corn & Bury 1989, Welsh 1991, Cole et al. 1997). Further research in recently logged and unharvested areas is needed to determine whether growth enhancement is a constant feature of larvae in streams draining clearcuts. It is possible that this phenomenon occurs only under certain altitude, productivity and climatic conditions. Regional differences in these variables may explain why studies of *D. tenebrosus* throughout its range have found varied associations between logging history and larval density (Murphy et al. 1981, Murphy & Hall 1981, Bury 1983, Hawkins et al. 1983, Bury & Corn 1988, Connor et al. 1988, Corn & Bury 1989, Kelsey 1995, Cole et al. 1997).

Biotic Regulation of Dicamptodon tenebrosus *Larvae*

Population density was not correlated with individual growth or survival across my four study sites. Given that *D. tenebrosus* are aggressive and cannibalistic, the lack of a relation between density and survival is surprising, especially as density-dependent survival has been found in other stream dwelling salamanders (Shoop 1974, Petranka & Sih 1986). It is possible that cooler climatic conditions experienced by larvae living in British Columbia limit populations from attaining densities at which resources become scarce and competition/cannibalism occur.

Conclusions:

The mode of larval regulation in my study areas still remains uncertain. There is weak evidence that logging may influence larval growth but not density or annual survival. On the basis of my investigation, I propose that *D. tenebrosus* larvae living at the northern extent of their range in British Columbia are limited by regional climatic conditions. This is supported by reduced growth, density and survival (as a consequence of a longer larval period) at my sites in comparison to those from Oregon, the centre of the species' range. By elevating stream temperature, logging may enhance larval growth rates. Studies of more clearcut areas are required to confirm if growth enhancement is a universal feature of these habitats, and if so, what the long term implications of this phenomenon are on population processes.

Site	Time since harvest (yrs)	Forest Type	Mean Width of Stream (m)	Length of Study reach (m)
Centre HF	35	Young second growth	1.02	95
Foley R Creek	2	Clearcut	0.98	120
Promontory 3a	60+	Old second growth	1.88	80
Promontory BH	60+	Old second growth	1.77	80
Tamihi C-DS	5	Clearcut	1.36	95

Table 2.1: Age and category of forest surrounding streams used in demographic analysis of larval *D. tenebrosus* populations. Forest age was determined by locating each stream's U.T.M. coordinates on forest cover maps of the Chilliwack area.

Site	Period of Study	Number of times sampled
Centre HF	June 28 - September 11, 1996 May 27 - July 2, 1997 September 4 - September 11 , 1997	25
Foley R Creek	June 5 - August 9, 1996	9
Promontory 3a	June 4 - September 17, 1996 May 20 - June 23, 1997 September 2 - September 9, 1997	28
Promontory BH	June 3 - September 19, 1996 May 22 - June 25, 1997 September 3 - September 10, 1997	28
Tamihi C-DS	July 12 - September 24, 1996 May 30 - July 3, 1997 September 5 - September 12, 1997	23

Table 2.2: Duration and frequency of sampling of five sites used in demographic study. Sites were sampled once a week.

Site	Spring 1996	Fall 1996	Spring 1997	Fall 1997
Centre HF	June 28 - July 22	August 26 - September 16	June 10 - July 2	September 4-11
Foley R Creek	July 4 - July 25	---	---	---
Promontory 3a	July 3 - July 23	August 28 - September 17	June 2 - June 23	September 2-9
Promontory BH	June 24 - July 17	August 12 - September 5	June 5 - June 25	September 3-10
Tamihi C-DS	July 12 - August 1	August 29 - September 18	June 12 - July 3	September 5-12

Table 2.3: Dates of sampling for estimation of larval abundance and survival. Only one sampling period was possible at Foley R as the efficiency of capture became so low in August of 1996 that monitoring was discontinued. Larvae were still present in this site in 1997 but at very low density.

Site	Mean Larval Abundance In 120 m reach	Mean Larval Density (larvae / m^2) and standard error
Centre HF	128 ± 13	1.31 ± 0.13 (4)
Foley R	102 ± 12	0.87 (1)
Promontory 3a	69 ± 14	0.46 ± 0.09 (4)
Promontory BH	160 ± 14	1.13 ± 0.10 (4)
Tamihi C-DS	83 ± 14	0.64 ± 0.11 (4)
Mean		0.88 ± 0.09

Table 2.4: Mean larval abundance and density at the five study sites. Numbers in brackets represent the number of density estimates used to calculate the mean value.

Forest Type	n	Mean Larval Density (larvae / m^2) and standard error
Clearcut	2	0.76± 0.16
Young Second Growth	1	1.32
Old Second Growth	2	0.80± 0.47

Table 2.5: Mean larval density in streams running through different forest types. Forest type was not a significant predictor of larval density (ANOVA, $F_{2,2} = 0.948$, $p = 0.513$).

Site	Forest Type	No. of larvae	Mean Body Length	Tukey HSD Group
Centre HF	Young second growth	148	102.8 ± 32.1	c
Foley R	Clear Cut	73	80.1 ± 35.8	a
Promontory 3a	Mature second growth	133	93.4 ± 41.4	b, c
Promontory BH	Mature second growth	240	83.2 ± 30.0	a, b
Tamihi C-DS	Clear cut	140	100.8 ± 35.2	c

Table 2.6: Mean body length (± SD) of larvae at each site. Tukey's HSD test was used to compare sites. Sites that share the same HSD letter are statistically indistinguishable at p = 0.05.

Site	J-S Summer 1996 Survival Rate	J-S Winter 1996-1997 Survival Rate	Monthly Disappearance Rate in Summer	Monthly Disappearance Rate in Winter	Predicted Annual Disappearance Rate
CenHF	0.79 ± 0.10	0.62 ± 0.13	0.21	0.05	0.69
Pro3a	0.79 ± 0.20	0.52 ± 0.24	0.21	0.07	0.74
ProBH	0.92 ± 0.32	0.17 ± 0.05	0.04	0.18	0.84
Tam C	1.00 ± 0.43	0.16 ± 0.07	0	0.18	0.84
Mean	0.89 ± 0.06	0.37 ± 0.12	0.12 ± 0.05	0.12 ± 0.03	0.76 ± 0.14

Table 2.7 : Jolly-Seber (J-S) estimates of *D. tenebrosus* larval survival and disappearance rates (± SE). J-S survival estimates are for one month in the summer of 1996 and for 9 months (September - June) over the winter of 1996-1997. Disappearance rates have been scaled to reflect change over a month period in both summer and winter.

Site	Growth Equation	n	r^2	p
Centre HF	0.059(# days) + 0.627	49	0.15	0.005
Promontory 3a	0.042(# days) + 1.314	43	0.09	0.047
Promontory BH	0.054(# days) + 0.641	78	0.25	<0.001
Tamihi C-DS	0.106(# days) + 1.468	41	0.41	<0.001

Table 2.8: The relationship between change in snout-vent length and number of days between capture of *D. tenebrosus* larvae during the active season. P-values are the probabilty that the slope of the change in length vs. time relationship is indistinguishable from zero

Location	Habitat	Density (# / m^2)	Annual Survival	Monthly Growth in Active Season (May - Sept) (SVL / month)	Annual Growth (SVL/ yr)	Size at transfor -mation (mm TL)	Age at transfor -mation (yrs)
British Columbia	Forested	1.0 (3)[a]		1.3 - 1.8 mm (3)[a] 1.3 mm (1)[f]	8-9 mm (3)[a]		
			30-35 % (4)[a]			≈ 130 (4)[a]	4-6 [a]
	Logged	0.8 (2)[a]	- all larvae	3.2 mm (1)[a]	11 mm (1)[a]	133-155 (1)[f]	
Washington	Forested	0.5 (14)[b]					
	Logged	0.5 (23)[b]					
Oregon	Forested	2.3 (23)[c]		1.5- 2.2 mm (2)[d]	20- 28 mm (2)[d]		
			43% (1)[d]			92 - 166[d]	2-3[d]
	Logged	0.5 (20)[c]	- 1st year larvae				
California	Forested			*D. ensatus* 4.2 mm[e] (1)		*D. ensatus* 135 (1) [e]	*D. ensatus* 2 (1)[e]
	Logged						

Table 2.9: Demographic variables collected for larval *D. tenebrosus* and the closely related *D. ensatus* throughout their range. Subscripts represent the source of information: a) this study, b) Kelsey 1995, c) Corn & Bury 1989, d) Nussbaum & Clothier 1973, e) Kessel & Kessel 1943 & f) Haycock 1991. Where possible, data are stratified by forest type with logged sites being less than 10 years old and forested sites older than 10 years. Data presented in the middle of a box are not habitat specific.

Variable	Rank				
	Highest				**Lowest**
Summer Survival	TamC	ProBH		Cen	Pro3a
Winter Survival	Cen	Pro3a		ProBH	TamC
Mean Total Length	Cen	TamC	Pro3a	ProBH	FolR
Daily Growth Rate	Tam C	Cen		ProBH	Pro3a
Larval Density	ProBH	Cen	FolR	TamC	Pro3a
Time Since Harvest	ProBH		Cen		FolR
	Pro3a				TamC

Table 2.10: Summary table of demographic variables and their relationship to larval density and logging history. For each variable, sites are ranked from highest value to lowest (highest = left, lowest = right). Of the four demographic variables, time since harvest correlates only with daily growth rate (negative). Larval density correlates with none of the four demographic variables. ProBH = Promontory BH, Pro3a = Promontory 3a, Cen = Centre HF, FolR = Foley R and TamC = Tamihi C - DS.

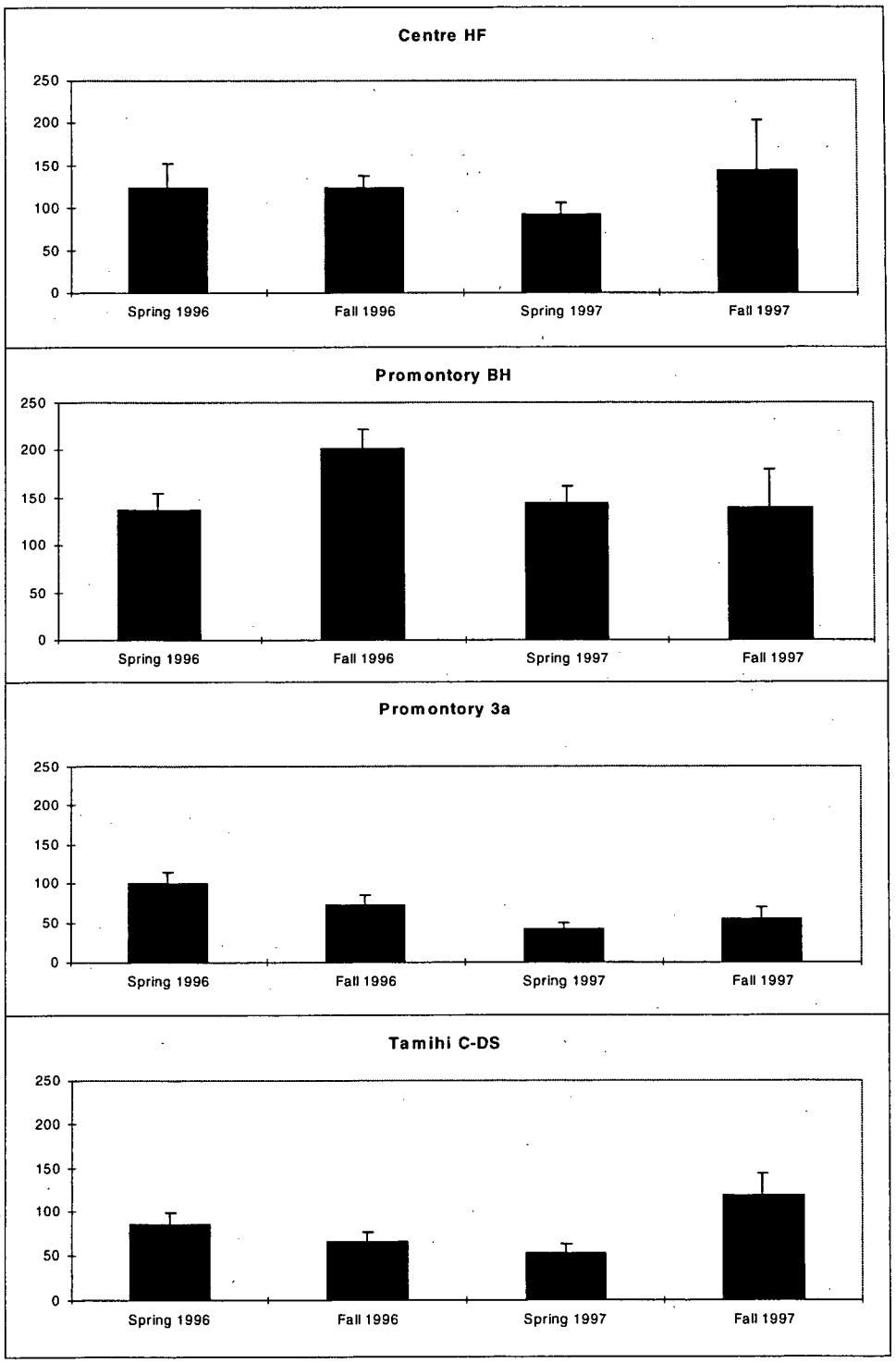
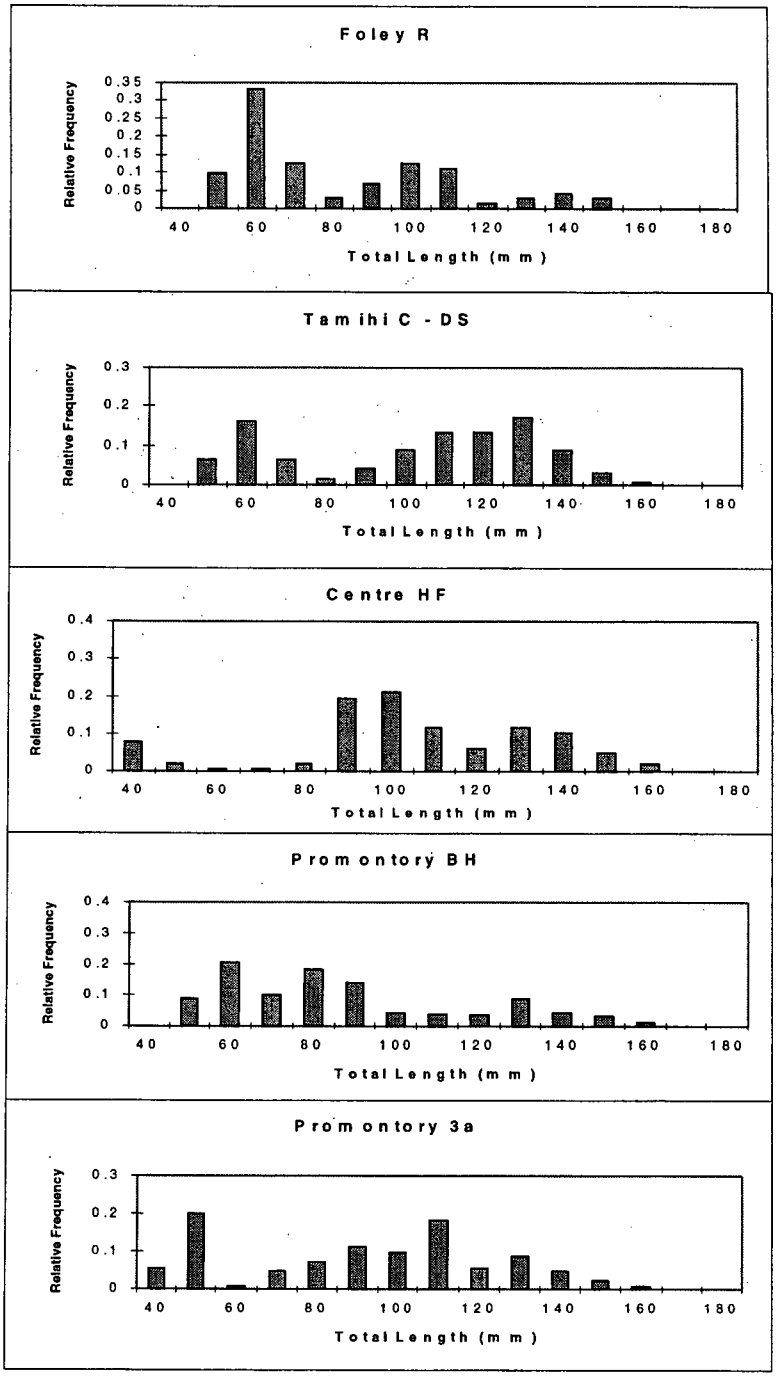


Figure 2.1: Estimated abundance of *D. tenebrosus* larvae at four study sites in 1996 and 1997. Bars represent one standard error.


Foley R
Relative Frequency
0.35
0.3
0.25
0.2
0.15
0.1
0.05
0
40 60 80 100 120 140 160 180
Total Length (mm)
Tamihi C - DS
Relative Frequency
0.3
0.2
0.1
0
40 60 80 100 120 140 160 180
Total Length (mm)
Centre HF
Relative Frequency
0.4
0.3
0.2
0.1
0
40 60 80 100 120 140 160 180
Total Length (mm)
Promontory BH
Relative Frequency
0.4
0.3
0.2
0.1
0
40 60 80 100 120 140 160 180
Total Length (mm)
Promontory 3a
Relative Frequency
0.3
0.2
0.1
0
40 60 80 100 120 140 160 180
Total Length (mm)

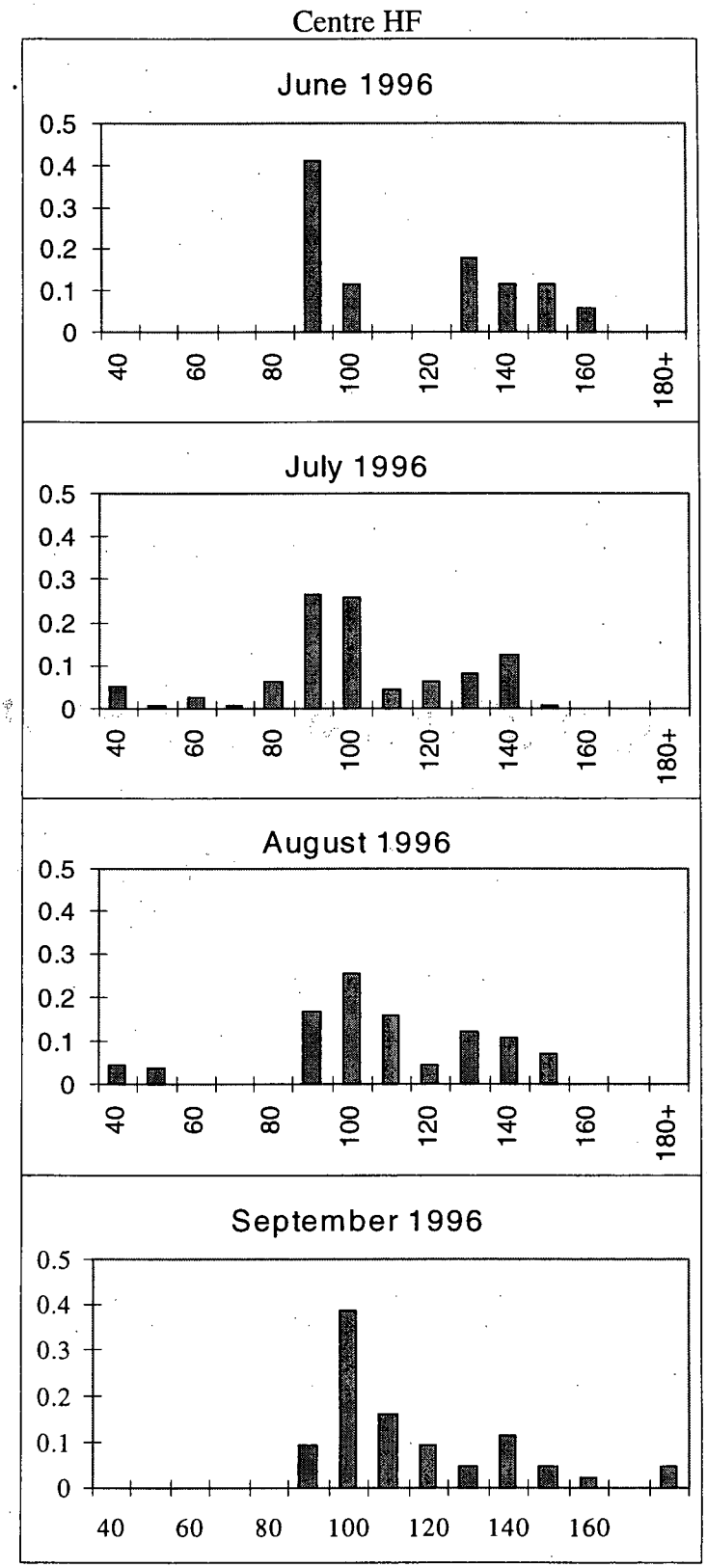


Figure 2.3a: Seasonal changes in size structure of larvae at the Centre HF site. The x-axis represents total body length (mm) and the y-axis is proportion in sample

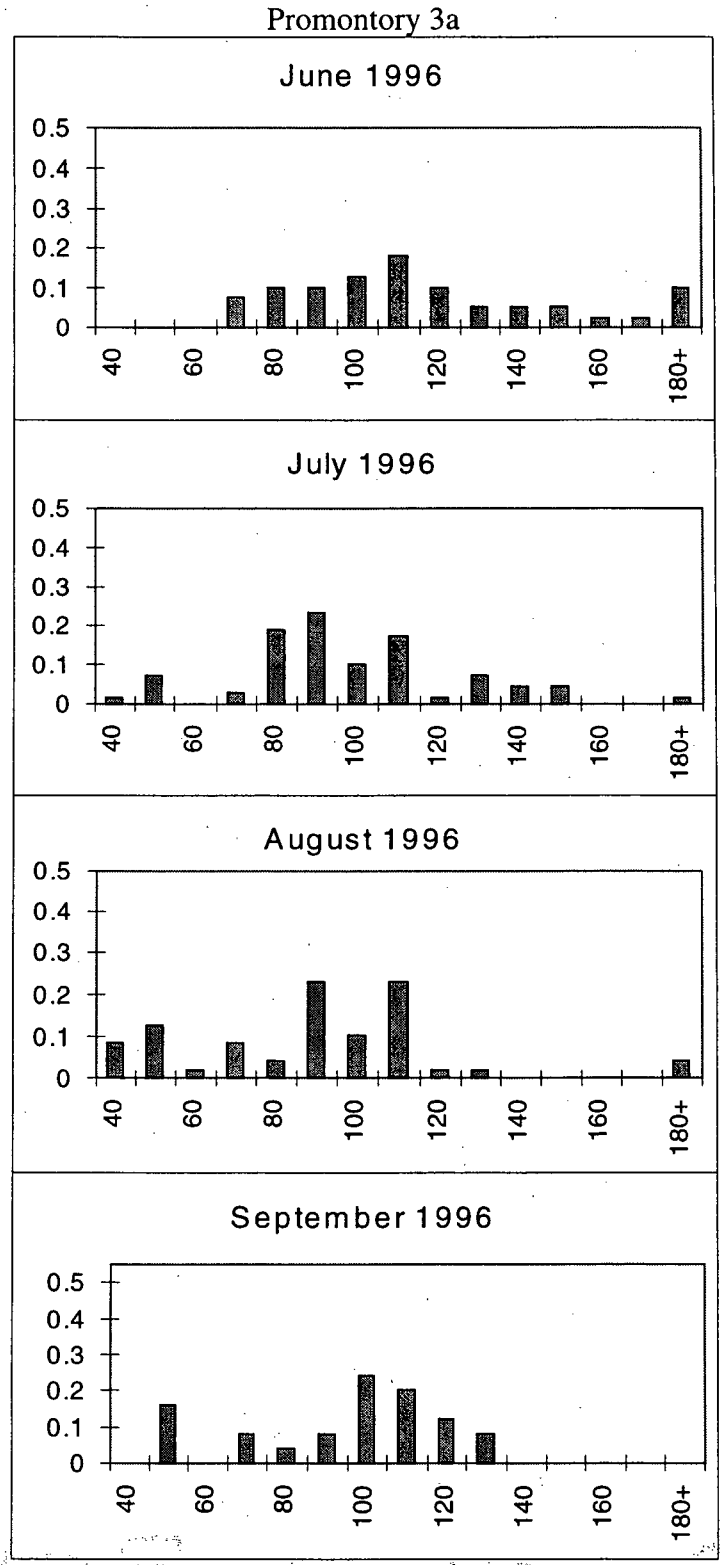


Figure 2.3b: Seasonal changes in size structure of larvae at the Promontory 3a site. Axes are the same as in Figure 2.3a.

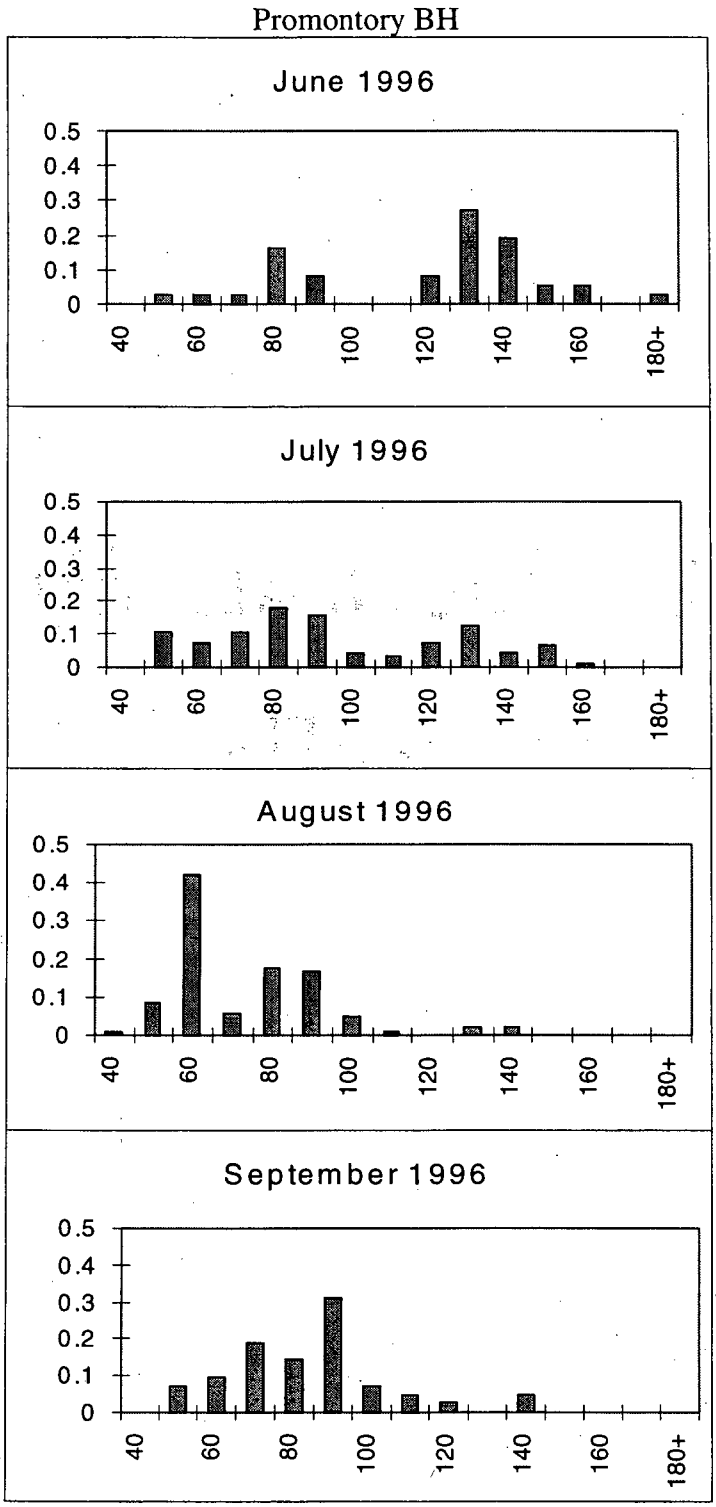


Figure 2.3c: Seasonal changes in size structure of larvae at the Promontory BH site. Axes are the same as in Figure 2.3a.

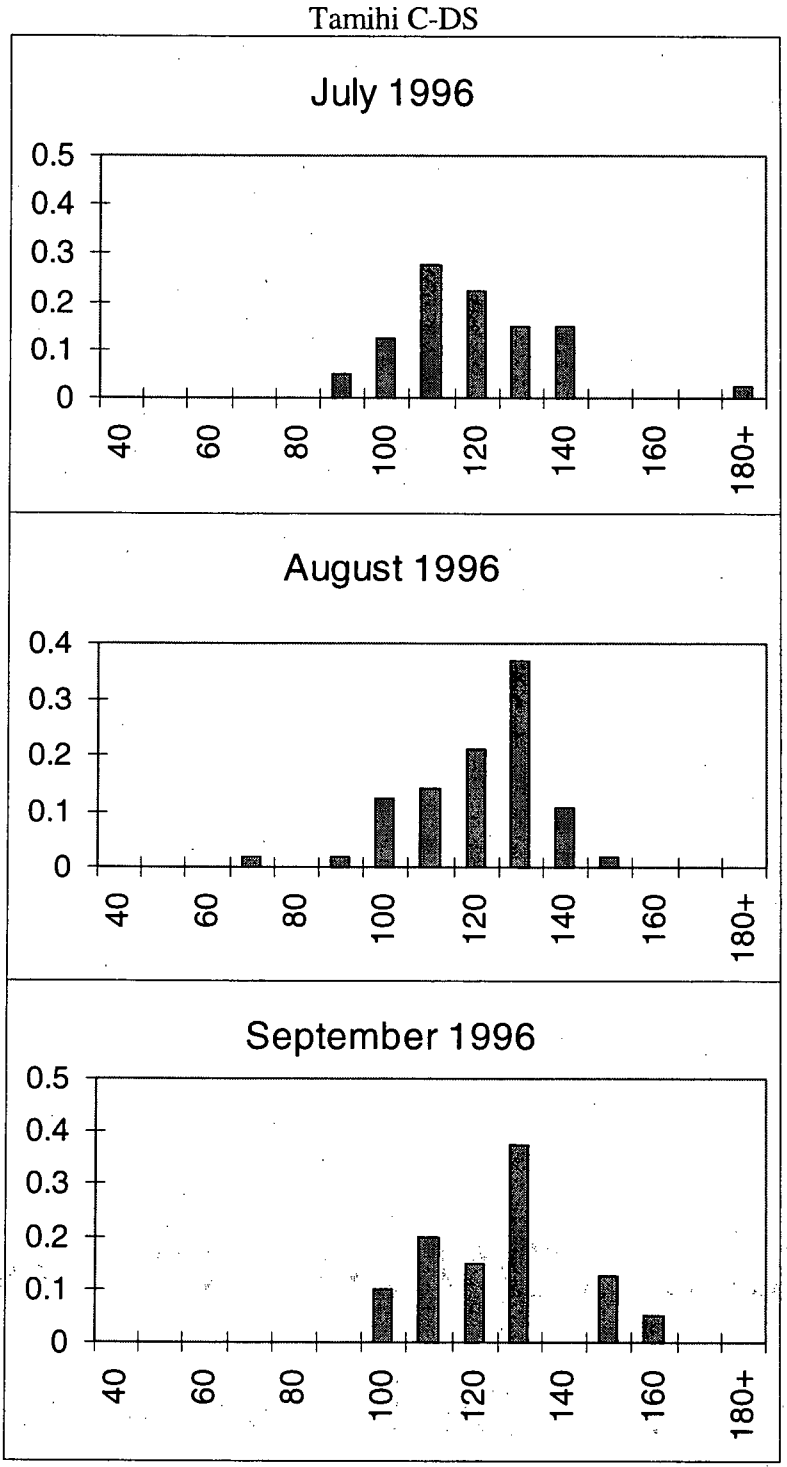


Figure 2.3d: Seasonal changes in size structure of larvae at the Tamihi C-DS site. Axes are the same as in Figure 2.3a.

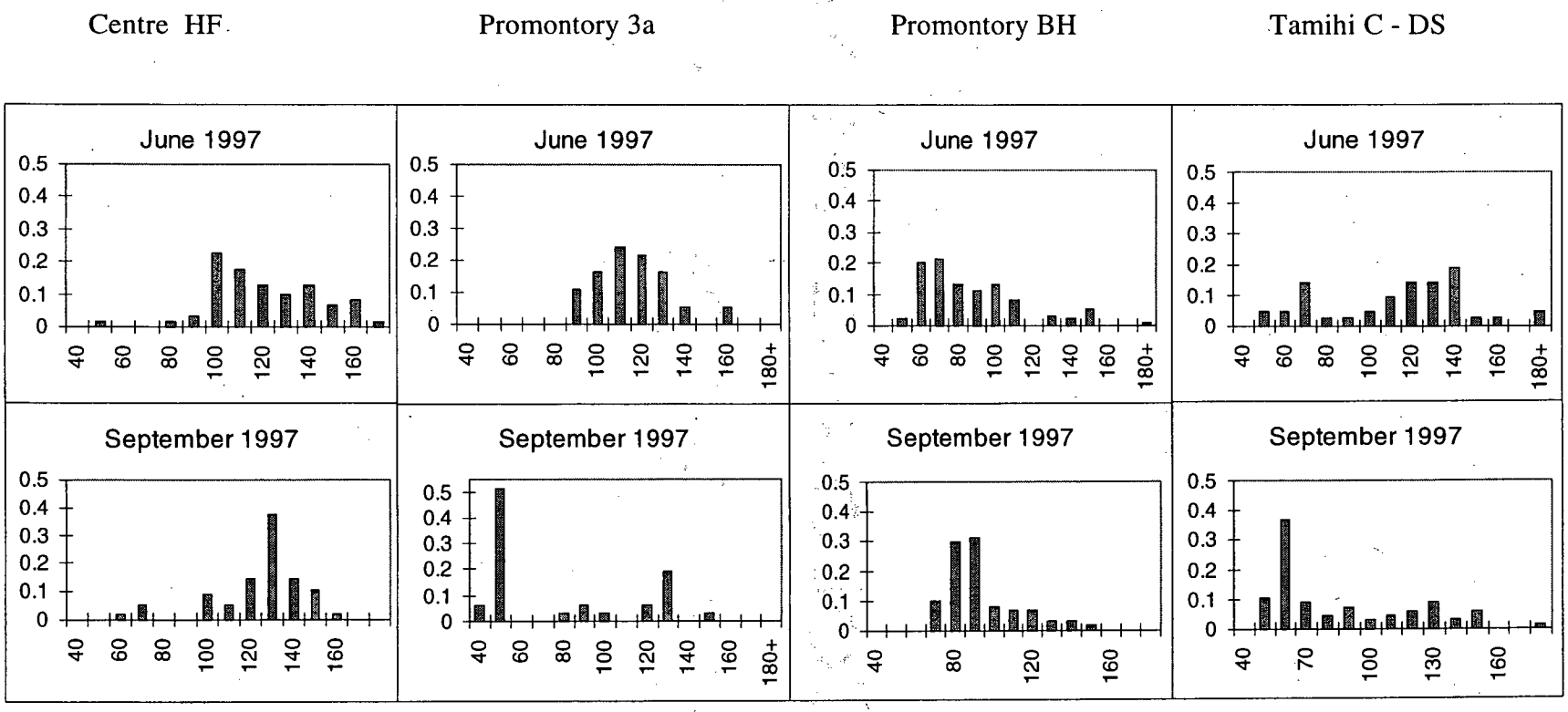


Figure 2.4: Seasonal changes in larval size structure in 4 *D. tenebrosus* populations in 1997. Axes are the same as in Figure 2.3a.

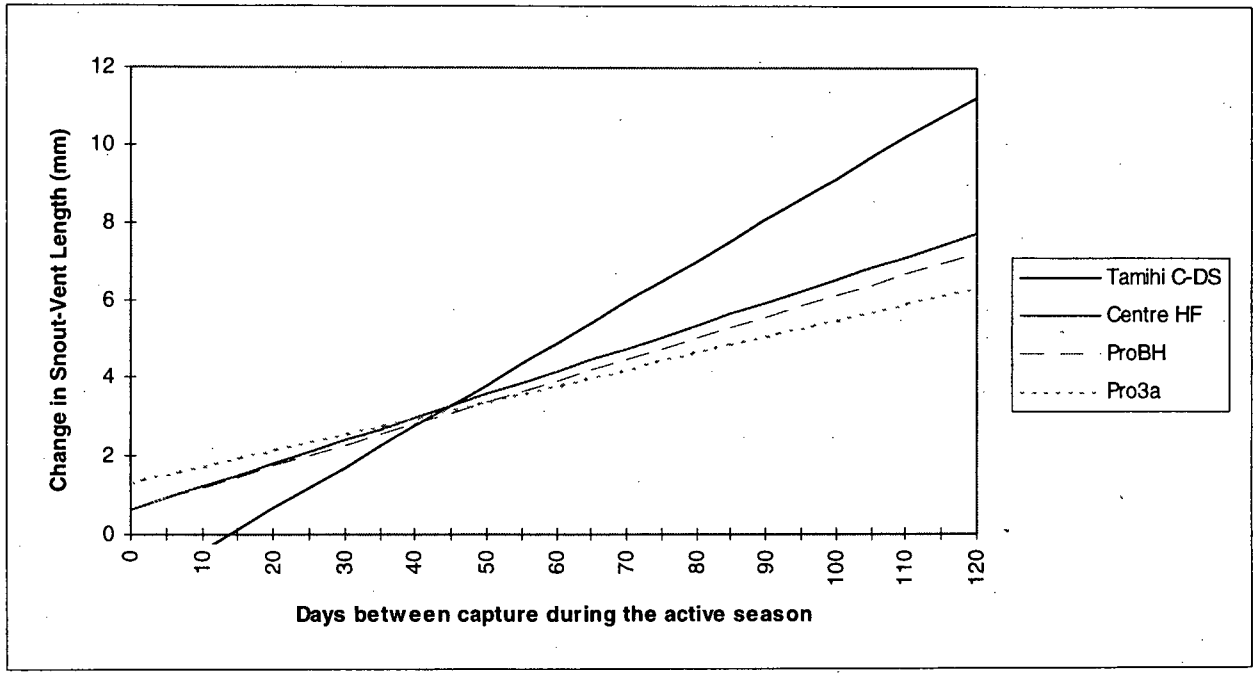


Figure 2.5: Predicted change in snout-vent length (mm) in *D. tenebrosus* larvae from four different streams. These rates apply only between June and September (active season). The slope of these relationships did not significantly differ between sites (ANCOVA, Site*growth effects $F_{3,210}$ = 0.332, p = 0.802)

Chapter 3: Determinants of Dispersal in Pacific Giant Salamander Larvae

Introduction:

The principal aim of this study was to examine the influence of abiotic and biotic factors on the dispersal and movement of *D. tenebrosus* larvae. As dispersal is a key means by which populations can re-establish in sites of local extinctions, a knowledge of the environmental and demographic factors that enhance movement may be useful for management. I studied movement by *D. tenebrosus* larvae at two different spatial scales in four streams in the Chilliwack Valley. At each scale I examined the relationships between larval dispersal, habitat, and population density. This two-tiered approach was taken to determine whether micro-habitat features (< 10 m) or the general state of the stream (mean condition in 120 m reach) were a better predictor of larval movements. In addition to addressing spatial variation, I also tested for temporal shifts in mobility in response to seasonal changes in stream temperature, water volume and abundance of pool habitat.

Some scientists have argued that habitat disturbance, specifically by logging, is particularly detrimental to Pacific Giant Salamanders as they are adapted to the historically stable, temperate rainforests of the Pacific Northwest (Welsh 1991). However very little is known about *D. tenebrosus'* ability to survive through disturbance and/or disperse in response to locally adverse conditions. In this study, I describe the median values and general range of distances *D. tenebrosus* larvae are capable of moving over two summers and examine whether dispersal is elevated in habitats with physical attributes similar to logged streams (i.e. open canopy, high silt). This information will demonstrate the capacity of larvae to respond to disturbance by dispersal.

Components of larval habitat and their potential impacts on dispersal

Almost nothing is known about the stream attributes that influence dispersal by *D. tenebrosus* and facilitate its re-entry into streams after local extirpation. In this study, I examined 13 different environmental factors that might influence larval dispersal (Table 3.2). These variables are frequently referred to in the literature as important components of stream-dwelling amphibian and fish habitat (Southerland 1986, Tumlinson et al. 1990, Walls et al. 1992, Murphy 1995, Welsh & Lind 1996, Slaney & Martin 1997). The variables fall into five categories: 1) Hydrology (stream depth, width, volume and percent pool), 2) Geomorphology (slope and substrate composition), 3) Climate (mean air and water temperature), 4) Disturbance history (time since harvest and percent canopy coverage) and 5) Food availability (average macrobenthos abundance). Possible effects of these variable on larval ecology and dispersal are discussed below.

1) Hydrology

Larval Pacific Giant Salamanders are predominantly found in pools (Haycock 1991). It is unclear whether higher abundance in pools is due to lower mortality, increased immigration, or adult preference for oviposition in these areas. Stream depth and width are also good predictors of larval salamander abundance, with abundance frequently decreasing with increasing wetted width (Richardson & Neill 1995) and increased stream depth (Southerland 1986, Tumlinson 1990). By following movement into and out of reaches of different width, depth and pool composition, I tested whether dispersal could account for abundance patterns associated with these variables.

2) Geomorphology

The abundance of stream dwelling salamanders is often correlated with substrate type (Tumlinson 1990, Welsh & Lind 1996). In Western Washington and Oregon, the abundance of *D. tenebrosus* was positively correlated with the number of substrate crevices and cover objects available (Hall et al. 1978, Murphy & Hall 1981, Connor et al. 1988). To maintain their position against a current, *D. tenebrosus* larvae must be able to grip the substrate. Gravel and pebble substrates are easier for larval salamanders to grip onto than fine sediment (Holomuzki 1991). Thus alteration of stream sediment size may change displacement rates. In the field I tracked movement rates of larvae on a variety of different substrate types. If displacement increases on silty substrates, influxes of fine sediment into streams after logging (Murphy 1995) may trigger a net loss of larvae from these reaches.

3) Climate

Larval activity is often reduced at high temperatures (Maurer & Sih 1996). In Chilliwack, *D. tenebrosus* larvae become sluggish and easy to catch at stream temperatures $\geq$ 20 C (W. Neill, pers. comm.). In this study, I compared movements by larvae at four sites differing in mean air and water temperature. If increasing temperature reduces movements, warming of streams may significantly lower dispersal between stream reaches and connected tributaries. Summer water temperatures in streams draining clear cuts in coastal Oregon were up to 10 C higher than in those under a closed canopy (Beschta et al. 1987). Even in the absence of other habitat change, increased temperature in logged streams could limit larval dispersal.

4) Food availability

The abundance of aquatic invertebrates in streams often increases for a few years after logging. Clearcut sites in Oregon had an average of 1.5 to 2.3 times as many benthic invertebrates in June and August as those in forested sites (Murphy et al., 1983). Such increases may reduce the need to make extended foraging trips in recently logged streams. I thus predicted larval salamanders should move more frequently and perhaps over greater distances in sites with low aquatic invertebrate abundance.

Density Dependent Determinants of Movement and Dispersal

In my second analysis, I investigated whether the density of resident larvae influences the number of dispersers an area produces or absorbs. If it does, the reduction or removal of one high density population could alter the flow of individuals to or from surrounding areas. As *D. tenebrosus* larvae interact aggressively and prey on smaller conspecifics (Nussbaum et al. 1983, Connor et al. 1988, Mallory 1996), I predicted that greater mortality and/or emigration should occur from high density reaches, and that movement frequency should increase within high density areas. These predictions are based on the assumption that neighbour-neighbour physical contacts increase with density, and should trigger agonistic displacements to other areas of the stream. I tested these predictions at two scales. The first prediction was tested by studying dispersal in and out of a series of 10 m reaches with differing densities, and the second by monitoring the numbers and lengths of movements made within four 120 m reaches of different density.

Body size and dispersal

A final factor that may influence larval mobility is body size. Body size determines how easily a larva can be displaced either by the stream current or other conspecifics (Bruce 1986, Mallory 1996). In a stream mesocosm experiment, larval body size was the most important determinant of displacement probability (Mallory 1996). Small larvae were routinely displaced or eaten by larger larvae in Mallory's experiment. Consequently I predicted that movement would decrease with increasing body size.

Methods:

Abiotic Determinants of Dispersal

I) *Habitat and Movement: 120 m Reach Scale*

Larval movement and habitat associations were studied at four streams differing in logging history in the summer of 1996 and 1997 (Table 3.1). At each stream a 120 m reach was chosen and thirteen measures of stream habitat were collected (Table 3.2). After appropriate statistical transformation, the mean value of each variable was computed for each site. One way analysis of variance was then employed to test for between-site differences in habitat. All percentages (i.e. % pool habitat, canopy cover and substrate composition) were arcsine square root transformed and all counts (i.e. number of benthic invertebrates in one sample) were square root transformed to better approximate a normal distribution before analysis.

Mark-recapture censuses were conducted weekly at each site from June to October 1996, and in June and September 1997 to study larval movement (see Chapter 2). All larvae were uniquely marked, either by toe clipping or a P.I.T. tag. On each visit, the location of every larva was recorded to the nearest 0.5 m. Larval dispersal within each 120 m reach was

characterised by two variables: 1) the proportion of moving and stationary larvae and 2) the cumulative length of movements. A movement was considered to be any displacement > 0.5 m from the capture point.

Information on altitude and time since harvest was taken from forest cover maps of the Chilliwack Area (1: 250000). All other variables were measured in the field. Benthic invertebrate abundance was assessed from approximately twelve samples collected at each site in July and August 1996. Samples were collected in riffles every 20 to 30 m along the study reach using a 30 cm x 30 cm Surber sampler (250 μm mesh). The substrate within the 900 cm^2 quadrat was vigorously raked for one minute. All material drifting up from the substrate was captured in the drift net and stored in 33% ethanol. In the lab, this material was sorted through a 1 mm sieve and counted under a dissecting microscope.

The percent of pool habitat in each 10 m section of the 120 m study reach was estimated visually on four occasions in the Fall of 1996 (August-September) and on six occasions in the Spring of 1997 (May-June). Pools were identified as areas of stream approximately 900 cm^2 or greater in area of still water. The percent pool habitat in the entire 120 m reach was calculated by averaging all estimates from the 12 consecutive 10 m estimates. These means were averaged over all sampling days to give a grand mean for the percent of pool habitat in each site over the course of the study.

The percent of canopy closure within each of 12 consecutive 10 m sections was estimated using a hand held densiometer with a 10 x 10 grid. As canopy coverage did not vary much throughout the study, this variable was measured only once. The slope from the start of each 10 m reach to the end was estimated using a clinometer. These twelve estimates were averaged to give the mean slope of each stream reach.

On the first day of habitat sampling, the widest point in each 10 m sampling reach was determined and marked with a wooden stake. Weekly measurements of wetted width, maximum and mean depth were taken at these points (one per 10 m reach) in August-September 1996 and June 1997. Mean depth was based on the average of six equally spaced measurements of depth taken along a transect perpendicular to the stream bank. Wetted width and depth measurements were combined to estimate the volume of water in each 10 m section using the following equation:

Vol. of Water in 10m Reach (m^3) = (Wetted Width at Point) x (Mean Depth at Point) x 10

For each sampling day, the total water of volume in the study site was calculated as the sum of volumes from all twelve 10 m reaches.

Substrate composition at each site was described in four randomly chosen 10 m reaches. Stream substrate was classified into five different categories on the basis of particle size (Table 3.3). Finally, air and water temperatures were measured at each 120 m reach on every sampling occasion.

II) Habitat and Local Dispersal: 10 m Reach Scale

Four non-contiguous 10 m segments were randomly chosen from each 120 m reach. Seven environmental variables that varied between segments were measured in each 10 m zone: percent coarse substrate (substrate $\geq$ 64 mm across the longest longitudinal axis), percent silt substrate, percent canopy coverage, percent pool habitat, slope, maximum wetted width and maximum stream depth. Measurements were taken at each reach on several occasions

throughout the summer of 1996 and 1997. All percentages were arcsine square root transformed for analysis. I used analysis of covariance to determine if there was a relationship between each habitat variable and the number of larvae moving into or out of a reach (log(x + 1) transformed) and whether this relationship varied between sites.

Seasonality and Movement: Variation in Time

Water volume, percent pool and temperature (air and water) show strong seasonal fluctuations in streams. Mean values of these variables were computed for August-September 1996 (late active season) and May-June 1997 (early active season). I examined whether seasonal changes in these variables were mirrored by corresponding differences in larval movement.

Biotic Determinants of Dispersal

I) Larval Density and Movement: 120 m Reach Scale

In this analysis I examined the association of movement frequency, movement length to larval density within the four 120 m study reaches. Mark-recapture data collected in 1996 and 1997 were used to estimate the larval density at each of the four study streams. I calculated the mean density of larvae at each site throughout two summers of study (see chapter 2 for estimation methods). I assessed whether the frequency and median length of movements made at each site increased with larval density.

II) Larval Density and Local Dispersal: 10 m Reach Scale

Four non-contiguous 10 m reaches were randomly chosen from each of the four study sites. From repeated mark-recapture sampling, the total number of resident animals living in each reach from June 1996 to September 1997 was recorded. A resident was defined as an animal that was only ever caught within the 10 m reach. Over this same period, the number of immigrants and emigrants into each zone was recorded. An immigrant was a larva initially caught outside the 10 m focal reach that subsequently dispersed into it. An emigrant was a larva initially found within the 10 m reach that dispersed out.

A *per capita* immigration rate for each 10 m reach was calculated for the 13 month period from June 1996 till September 1997 by dividing the number of larvae that moved into the zone by the size of the resident population. A *per capita* emigration rate was similarly calculated by dividing the number of larvae that left each reach by the number of residents. I used analysis of covariance to test if local immigration and emigration rates depended on resident density, and whether these relationships varied between sites. A similar analysis was used to determine if the biomass of resident larvae within a 10 m reach was related to local immigration and emigration.

Body size and dispersal

Finally I tested the hypothesis that larval dispersal is negatively related to body size. I used a linear regression to relate larval body size and distance travelled by larvae within a 120 m study reach at all sites. At the 10 m scale, I used a chi-squared test to compare the proportions of large ($\geq$ 100 mm total length) vs. small larvae ($<$ 100 mm total length) that dispersed.

Results:

Abiotic Determinants of Dispersal

I) Habitat and Movement: 120 m Reach Scale

Larvae at 3 of the 4 study sites were highly sedentary. Larvae at Centre HF had the highest probability of moving (Table 3.4). Ninety three percent of larvae moved at this site in comparison to 71-80% at the other streams. The median distance moved by Centre HF larvae, 8 m, was also greatest (Table 3.5), followed by Tamihi C-DS, Promontory BH and Promontory 3a. The distribution of distances travelled by larvae at Centre HF was significantly different from the two Promontory sites (Kolmogorov-Smirnov test, $p < 0.01$), but not from the Tamihi C-DS site (Kolmogorov-Smirnov test, $p = 0.34$).

Four habitat variables distinguished Centre HF: percent pebble, percent gravel, water volume and wetted width (Table 3.6). Centre HF had less gravel and pebble than any of the other three sites. Substrate at this site was mainly composed of sand/silt (33%) and large boulders (37.2%). Centre HF was also the narrowest stream with a mean maximum wetted width of just over 1 m (Table 3.6). Water depth was slightly but not significantly lower at this site. The total water volume contained in the 120 m reach was also significantly lower at Centre HF, likely as a result of its narrow mean wetted width.

II) Habitat and Local Dispersal: 10 m Reach Scale

None of the 7 measured microhabitat variables were related to larval dispersal in 10 m stream reaches (Tables 3.7a, b). In every case, there was a significant interaction between the slope of movement-habitat relationship and the site at which data were collected. Although

reach scale attributes may influence larval dispersal, the nature of this relationship likely varies between sites and no general prediction can be made from knowledge of the selected habitat variables alone.

Seasonality in Dispersal

Stream hydrology and temperature varied significantly between the late active season in 1996 and the early active season in 1997. At three sites, water volume in the early season was double or more of that in late season (Figure 3.1) and both wetted width and depth decreased (Figures 3.2 a & b). The amount of pool habitat also increased throughout the active season (Figure 3.3).

With the exception of Tamihi C-DS, air and water temperature changes between sampling periods in the late season 1996 and early season 1997 were modest (Figures 3.4 a & b). The mean difference in water temperature between these two periods did not exceed 3 C at any site. Mean air temperature at Tamihi C-DS fell by 8.3 C between sampling periods in the late season of 1996 and early season of 1997.

Despite large hydrological changes and moderate temperature changes, there were no differences in larval movement between early and late season. The distribution of distances travelled by larvae in the early summer was similar to that in late summer (Kolmogorov-Smirnov test, $p = 0.985$) (Figure 3.5), and the frequencies of movements were nearly identical between the two periods (Figure 3.6).

Peak flow in small headwater streams of the Chilliwack valley usually occurs with snow melt in April or May. Capture efficiency is very low at these times because of cool water temperatures (< 5 C) and poor visibility of larvae in fast flowing currents. Larval dispersal

could increase during this time in response to flow, but this possibility was not tested in this study. If larval dispersal fluctuates seasonally, it does so outside of the June - September active season.

Biotic Determinants of Dispersal

I) Larval Density and Movement

Mean larval density varied significantly over the four study sites (Figure 3.7) but this variation was not related to either measurement of movement. Larval densities at Promontory BH and Centre HF were significantly higher than the two other sites. Despite this similarity in larval density, these two streams displayed very different movement patterns. Almost all larvae at Centre HF moved at least once and when they did, half travelled at least 8 m. In contrast more than a quarter of the larvae at Promontory BH failed to move and those that did generally stayed within 2-3 m of their original point of capture. Across these four streams, there is no evidence that *D. tenebrosus'* density influenced movement.

II) Larval Density and Local Dispersal

The number of resident larvae in a 10 m reach did not significantly affect local immigration ($F_{1,11} = 1.683$, $p = 0.101$, $r^2 = 0.180$) or emigration ($F_{1,11} = 1.576$, $p = 0.235$, $r^2 = 0.153$). There were no were no interactions between site and local immigration or emigration (ANCOVA, immigration site effects: $F_{3,11} = 0.329$, $p = 0.804$; emigration site effects: $F_{3,11} = 0.199$, $p = 0.895$). There was almost an identical number of immigrants and emigrants in each reach (Figure 3.8). This correlation suggests that the tendencies to immigrate and emigrate at the 10 m scale are not independent. Larvae that immigrated into a reach were more likely to

leave it after a few months than those that were established in the area at the beginning of the experiment. From a total of 41 larval immigrants, 14 later emigrated (34% of total) whereas only 15 % of larvae in each reach at the start of the study later emigrated.

The total biomass of resident larvae had no effect on immigration (ANCOVA $F_{1,11}$ = 1.878, p = 0.198, r^2 = 0.0217) or emigration rates (ANCOVA $F_{1,11}$= 1.381, p = 0.265, r^2 = 0.155) and there were no significant site effects (immigration site effects $F_{3,11}$ = 606, p = 0.625; emigration site effects $F_{3,11}$ = 0.350, p = 0.790). As immigration and emigration rate were not related to either the density or biomass of residents in 10 m reaches of stream, it seems unlikely that biotic interactions have a strong influence on local dispersal of larvae.

Body Size and Dispersal

Larval body size was not strongly correlated to dispersal distance within a 120 m reach of stream. Body size was positively, but not significantly, correlated with cumulative distance travelled by larvae (Figure 3.9). At the 10 m scale, the proportion of large larvae ($\geq$ 100 mm total length) dispersing was significantly greater than for small larvae (χ^2 = 4.831, $p < 0.05$, 1 df). Contrary to my prediction, small larvae were slightly more sedentary than their larger conspecifics. Assuming that size is the most important predictor of larval displacement, these results suggest dispersal was not due to the involuntary displacement of small larvae by larger individuals or a strong current.

Discussion

Abiotic Determinants of Movement

Across my 3 of my 4 study sites, the rates and lengths of larval movement were similar. Only one site exhibited different movement behaviour, Centre HF, where larvae tended to move more frequently and further than at the other three streams. Centre HF differed in substrate and wetted width from the other sites, but with such little variation in movement amongst streams there is no way of correlating these habitat differences to variation in dispersal. In fact, the lack of association between these variables and movement at the 10 m scale suggests they have no effect on movement.

At the 10 m reach scale, none of the 7 measured habitat variables was associated with larval mobility in *D. tenebrosus*. This pattern suggests that the positive association between larval density and pool habitat, decreasing wetted width and some substrate classes is not created by dispersal into preferred areas. If larvae are found at higher densities in pools or narrow reaches, it is because either adults selectively oviposit and/or larvae survive better in these areas. If shifts in the habitat variables I studied affect larval demography, they do so by changing survival and not dispersal.

The lack of association between larval movement and all other measured habitat variables could also be a function of inappropriate measurement scale. Prior to this study, little was known about larval dispersal by *D. tenebrosus*. Field study of other stream dwelling larval salamanders found that they can move up to 10 m in one day (Holomuzki 1991). I thus chose to partition and describe habitat in 10 m units, assuming that larvae were capable of moving between reaches of this length in response to local conditions. However, most larvae moved less than 5 m over a season. Consequently, larvae may be capable of selecting only amongst habitats within a few

meters of their origin. Therefore I can only conclude that pool habitat, water depth and volume do not explain movement between reaches of 10 m or greater.

Density Dependent Determinants of Dispersal

Larval density had no influence on movement by *D. tenebrosus* larvae at 10 m and 120 m reach scales. This observation contradicts my original prediction of density-dependent regulation as a result of intraspecific aggression and cannibalism. Given the hostility that characterises most larval interactions in the laboratory (Mallory 1996), it is surprising that density had no impact on movement. It is possible however that my study was conducted on too large a scale to detect local effects of density. Mallory's (1996) study of larval interactions was conducted in pools and riffles a few metres in length. Results observed at the 1-5 m scale may not explain movement over larger areas. Alternatively the cannibalism and antagonism noted by Mallory may not reflect interactions in natural settings. It is also possible that density may be more important in more southerly parts of the range where larval densities and biomass are higher than in British Columbia (Murphy & Hall 1981, Kelsey 1995).

Body size and dispersal

The fact that one third of all immigrants into 10 m reaches later became emigrants suggests that a sub-section of larvae are more mobile than the rest of the population. If this is so, one might ask what differentiates a disperser from a resident. I initially expected smaller individuals to be more vulnerable to displacement by the stream current or other larvae (Bruce 1986, Mallory 1996). Contrary to this expectation, I found that large larvae were slightly more mobile than smaller individuals, perhaps because large larvae face lower risks when travelling.

Cannibalism risk decreases with body size and large larvae may be less likely to be attacked while moving than their smaller conspecifics. These results suggest that movements throughout the stream are not forced by dominant conspecifics.

Conclusions

My main conclusion is that *D. tenebrosus* larvae exhibit high site fidelity and extremely limited dispersal. Most larvae failed to move more than 5 m over 13 months. Of those that did move, ninety percent stayed within 20 meters of their original capture point. Although variation existed between sites, movement was generally conservative in time and space. The correlation between immigration and emigration at the 10 m scale suggests that although most larvae are sedentary, a small number of transient animals travel frequently throughout the stream. It is unclear why these individuals are transient. As size was a weak predictor of movement length, this behaviour cannot be ascribed to a particular age group or to dominance interactions.

Larvae seem ill-equipped to disperse in response to habitat changes. Any local and lethal impact that could not be avoided by a movement of less than 20 m would likely kill 90% of all larvae. It should be cautioned, however, that is conclusion is based on the observation of larvae within relatively stable environments. Other than my mark-recapture surveys and seasonal shifts in climate and stream flow, there were no disturbances or drastic habitat changes within each stream during this study. It is possible that larval dispersal is elevated in more rapidly changing or highly disturbed environments than used in this study.

Poor larval dispersal ability is not unique to *D. tenebrosus*. Other species of stream-dwelling salamanders exhibit similar behaviour. *Desmognathus fuscus, Desmognathus ochrophaeus* and *Ambystoma barbouri* have small home ranges of 1.44, 1, and 1 m^2

respectively (Ashton 1975, Holomuzki 1982, 1991). While larvae of *D. tenebrosus* certainly have limited dispersal capabilities, this trait does not distinguish the species.

Low dispersal of larvae does not necessarily make this species vulnerable to extinction. Recent evidence suggests that adults are not similarly limited in movement. Seasonal dispersal distances > 100 m were recorded in some radio-tracked adults in the Chilliwack drainage (Johnston 1998). However disturbances such as logging may put adults at greater risk than larvae by increasing their probability of desiccation while on land (Blaustein et al. 1994). If adult mortality is high, the site fidelity of larvae may hasten local extinction. Until the exact demographic effects of logging on both adults and larvae are known, the consequences of low larval mobility on population persistence are unknown. However this study suggests that logging-associated habitat changes such as increased silt, temperature and riffle habitat do not trigger local emigration.

Site	U.T.M. Co-ordinates	Forest Type
Centre HF	0607380 [5437289]	Young Second Growth
Promontory 3a	0587800 [5439500]	Old Second Growth
Promontory BH	0585800 [5439500]	Old Second Growth
Tamihi C-DS	0591385 [5428429]	Clearcut

Table 3.1: Name and location of four *D. tenebrosus* larvae streams used in this study. All populations were studied from June to October in 1996, and in June and September of 1997.

Food Availability	Climatic	Disturbance History	Hydrology	Geomorphology
Invertebrate Abundance	Air Temp. Water Temp.	% Canopy Closure Time since harvest	% Pool in stream Water Volume in Stream	% Boulder in Substrate % Cobble in Substrate % Gravel in Substrate % Pebble in Substrate % Silt in Substrate Slope

Table 3.2: Macrohabitat and environmental features measured at each site.

Substrate Class	Size Designation
Boulder	> 256 mm
Cobble	64 mm - 256 mm
Pebble	16 mm - 64 mm
Gravel	2 mm - 16 mm
Sand/Silt	< 2 mm

Table 3.3: Substrate definition and size classes. Size designation refers to the longest longitudinal axis of the stone.

Site	Total Number of Recaptured Larvae	% of Recaptures that moved	% of Recaptures that did not move
Centre HF	90	93	7
Promontory 3a	55	80	20
Promontory BH	94	71	29
Tamihi C - DS	54	83	17
Total	293	83	17

Table 3.4: Percentage of movers and non-movers at each site. The larvae at Centre HF were significantly more liable to move than those at all other sites (Chi-squared test, $\chi^2 = 10.348$, $p < 0.025$).

Site	Median distance moved (m)	Range (m)	n
Centre HF	8.0	0.5 - 111.5	83
Promontory 3a	1.5	0.5 - 62.5	44
Promontory BH	2.0	0.5 - 104.0	70
Tamihi C-DS	4.0	0 - 34.0	45
All sites combined	3.8	0.5 - 111.5	231

Table 3.5: Median distance moved by larvae at each site. The median cumulative distance moved at Centre HF was significantly higher than at any other site (Brown-Mood Median test, $\chi^2 = 18.42$, df = 3, $p < 0.001$).

Dependent Variable	Centre	TamC - DS	Pro3a	ProBH	p
% Larvae that never moved	7^{a}	17^{b}	20^{b}	29^{b}	0.0250^{+}
Median Distance Travelled by Larvae	8.0^{a}	4.0^{b}	1.5^{b}	2.0^{b}	0.001^{+}

Independent Variable	Centre	TamC - DS	Pro3a	ProBH	p
Age of Forest (yrs)	35	5	60+	60+	--
Altitude (m)	760	700	640	560	--
Mean # Benthic Invertebrates	50.3^{a} (2,6)	20.6^{b} (1,5)	95.5^{a} (2,6)	66.9^{a} (2,6)	0.0605
% Canopy Coverage	31.5^{a} (1,12)	0.0^{a} (1,12)	70.9^{c} (1,12)	78.3^{c} (1,12)	0.0001^{+}
% Pool Habitat	21.9 (9, 12)	23.5 (10, 12)	26.8 (9,12)	27.3 (10, 12)	0.7616
% Boulder	37.2^{b} (1,4)	26.7^{b} (1,4)	7.5^{a} (1,4)	$20.0^{a,b}$ (1,4)	0.0111^{+}
% Cobble	20.6 (1,4)	18.4 (1,4)	15.0 (1,4)	23.8 (1,4)	0.4508
% Pebble*	5.6^{c} (1,4)	13.8^{b} (1,4)	36.0^{a} (1,4)	36.0^{a} (1,4)	0.0001^{+}
% Gravel *	3.5^{a} (1,4)	13.8^{b} (1,4)	25.0^{c} (1,4)	$15.0^{b,c}$ (1,4)	0.0001^{+}
% Sand/Silt	33.0^{b} (1,4)	27.3^{b} (1,4)	16.3^{a} (1,4)	5.2^{a} (1,4)	0.0015^{+}
Mean Air Temp. (C)	15.3^{a} (18, 1)	19.2^{b} (17, 1)	13.9^{a} (23, 1)	14.1^{a} (21, 1)	0.0061^{+}
Mean Gradient of 10 m Reach*	20.3^{b} (1,12)	18.8^{b} (1,12)	12.3^{a} (1,12)	12.3^{a} (1,12)	0.0001^{+}
Mean Water Temp. (C)	$10.8^{a,b}$ (18,1)	12.0^{b} (17,1)	8.9^{a} (23,1)	9.4^{a} (21,1)	0.0002^{+}
Mean Water Depth (cm)	6.1^{a} (10,12)	13.2^{b} (10,12)	7.9^{a} (10,12)	8.3^{a} (9,12)	0.0001^{+}
Water Volume (m^3)*	5.5^{a} (10,12)	12.4^{b} (10,12)	9.0^{b} (10,12)	9.3^{b} (9, 12)	0.0045^{+}
Wetted Width*	102^{a} (10,12)	136^{b} (10,12)	188^{c} (10,12)	177^{c} (9,12)	0.0001^{+}

Table 3.6: Movement behaviour and habitat properties of four *D. tenebrosus* larvae populations. Values in brackets (x,y) represent the number of samples used in each analysis, with "x" indicating the number of times the site was visited and "y" the number of samples taken on each visit. The $^{+}$ symbol denotes which habitat variables were significantly different between sites., with different letter superscripts being significantly different from one another (Tukey's HSD test). The * symbol indicates which habitat properties distinguish the most mobile population, Centre HF, from all the others.

a) Larval Immigration and Habitat Characteristics

	Main Effects		Interaction Effects		
Variable	$F_{1,11}$	p	$F_{3,11}$	p	r^2
% Coarse Substrate*	2.554	0.138	5.105	0.019	0.735
% Canopy Cover	0.100	0.757	6.748	0.011	0.552
% Pool in Reach	1.739	0.214	8.409	0.003	0.712
% Silt in Substrate	5.600	0.037	9.338	0.002	0.727
Maximum Water Depth	0.648	0.438	5.730	0.013	0.629
Slope	1.215	0.294	6.735	0.008	0.694
Maximum Wetted Width	0.012	0.914	5.044	0.019	0.730

b) Larval Emigration and Habitat Characteristics

	Main Effects		Interaction Effects		
Variable	$F_{1,11}$	p	$F_{3,11}$	p	r^2
% Coarse Substrate	2.959	0.113	3.693	0.046	0.701
% Canopy Cover	0.700	0.419	4.292	0.039	0.418
% Pool in Reach	< 0.001	0.988	4.071	0.036	0.526
% Silt in Substrate	3.345	0.095	4.888	0.021	0.576
Maximum Water Depth	0.702	0.420	3.853	0.042	0.526
Slope	3.197	0.101	6.812	0.007	0.666
Maximum Wetted Width	0.501	0.494	3.834	0.042	0.641

Tables 3.7a & b: Analysis of covariance results from study of local movement (10 m reach scale) , habitat characteristics. and site effects. Sixteen data points were used in each ANCOVA (4 from each site). Main effect results refer to the relationship between a continuos habitat variable and the log(x+1) transformed number of immigrants and emigrants respectively. Interaction effects test the hypothesis the slope of the relationship between a habitat variable and movement is similar at all sites.

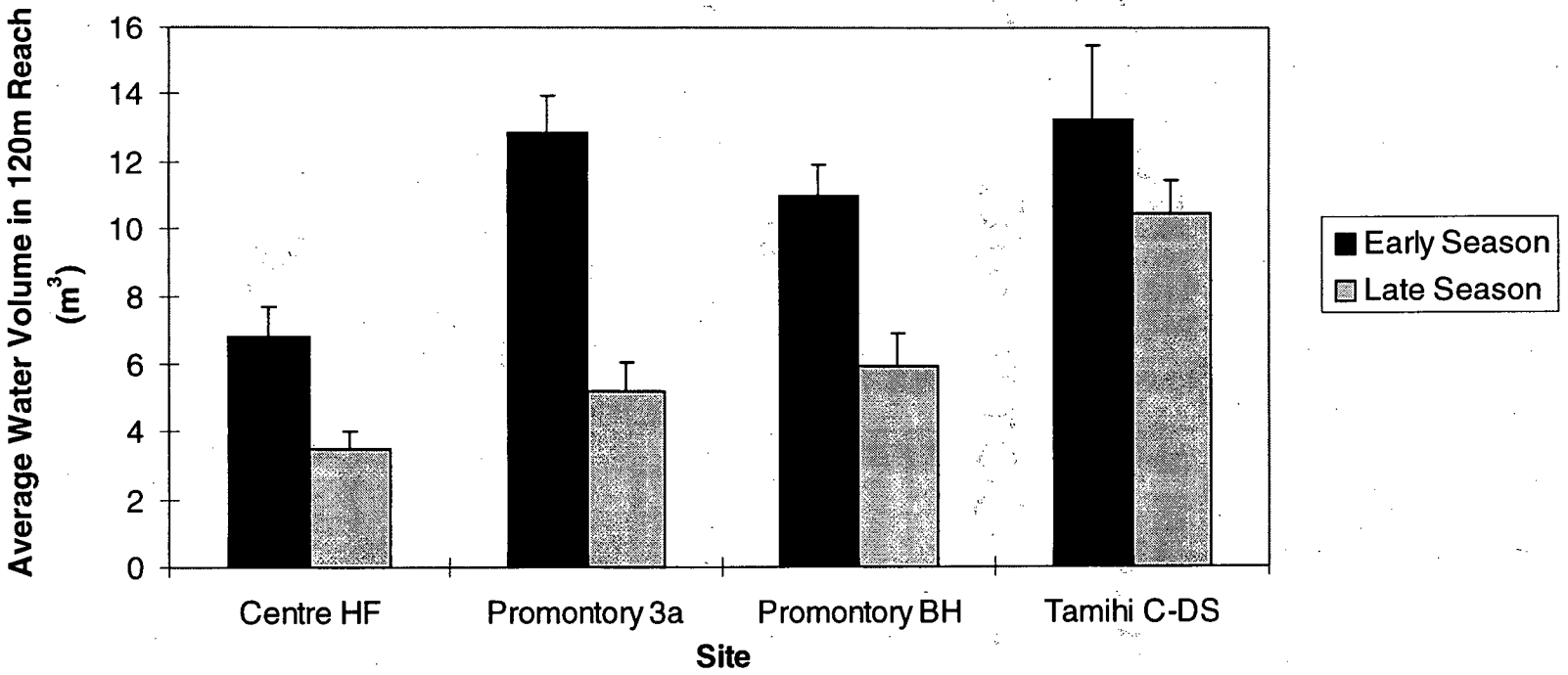
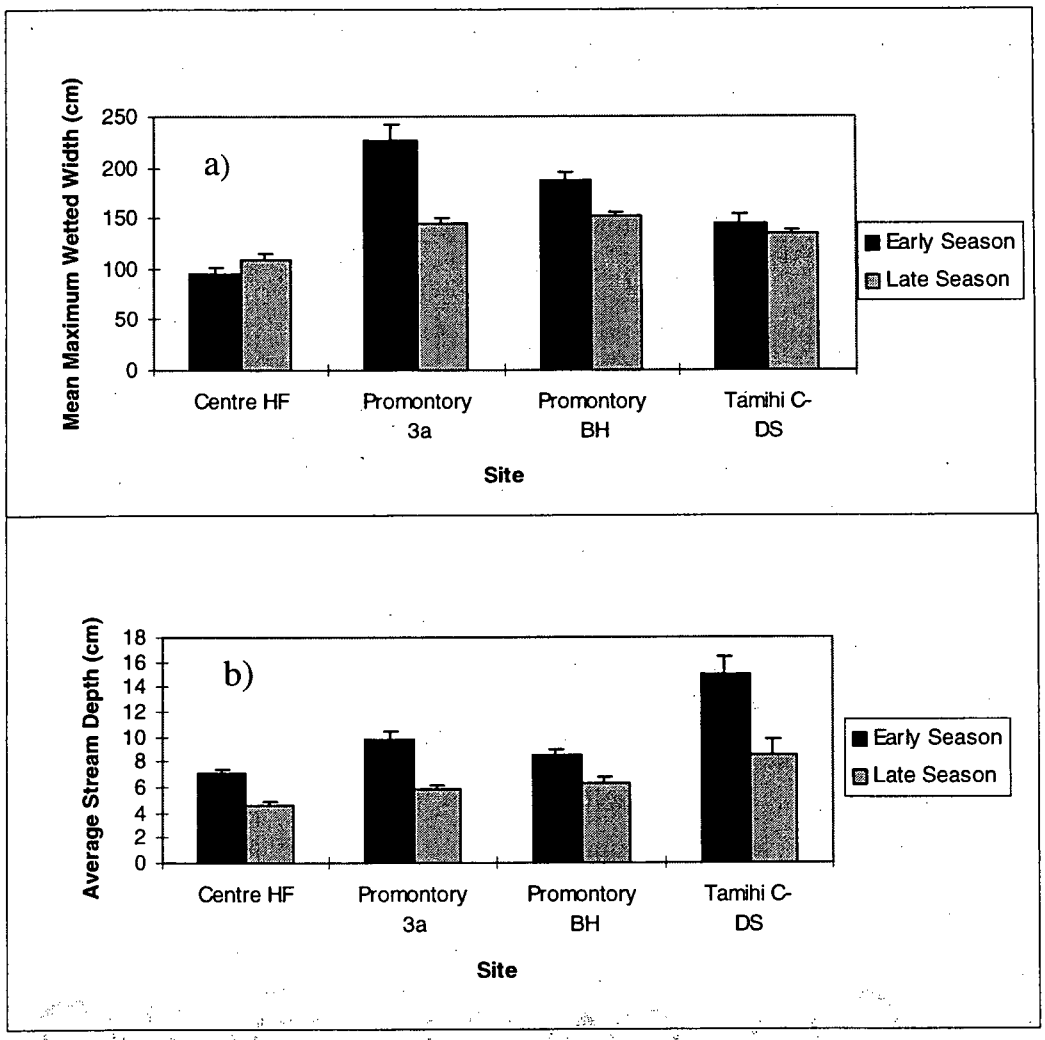


Figure 3.1: Seasonal differences in the average volume of each 120 m reach . The error bars represent one standard error. Average water volume was significantly higher in the early season at Centre HF (T-test, t = 2.814, p = 0.002, df = 8), Promontory 3a (t = 4.146, p = 0.004, df = 8) and Promontory BH (T-test, t= 3.334, p = 0.0125, df =7). N = 6 for dark bar, N = 4 for light bar.



Figures 3.2a & b: Seasonal changes in wetted width and depth in four streams containing *D. tenebrosus* larvae. Early season measurements were collected in June and July 1997. Late season measurements were taken in August and September 1996. Sample sizes as in Fig. 3.1.

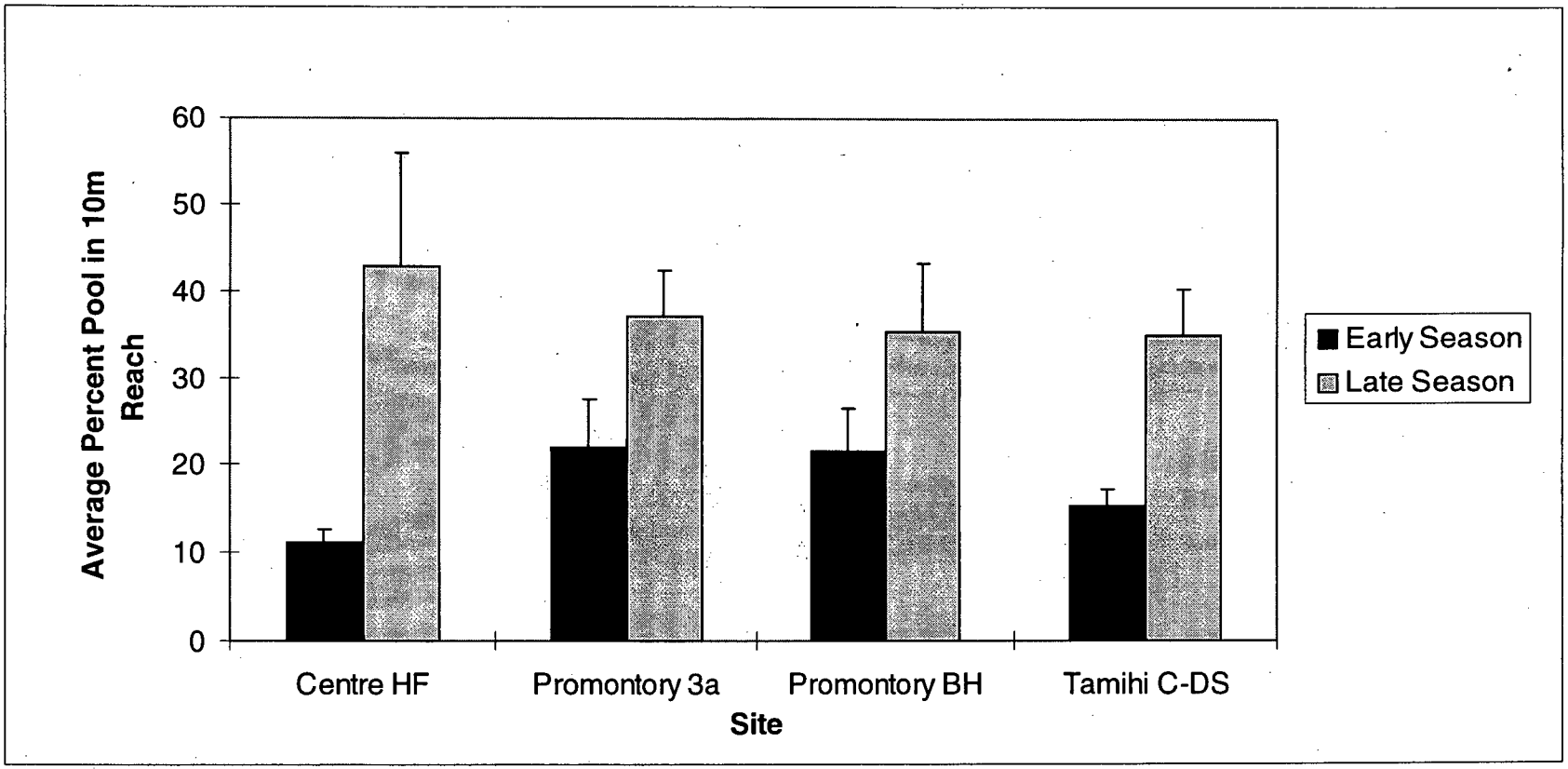


Figure 3.3: Seasonal differences in the mean percentage of pool habitat in each stream with standard errors. The transformed values of mean percentage of pool habitat were significantly different between the late season 1996 and early season 1997 at Centre HF (t-test, t = -3.924, p = 0.006, df=7) and at Tamihi C-DS (t-test, t= -4.082, p = 0.004, df = 8) . Sample sizes as in Fig. 3.1.

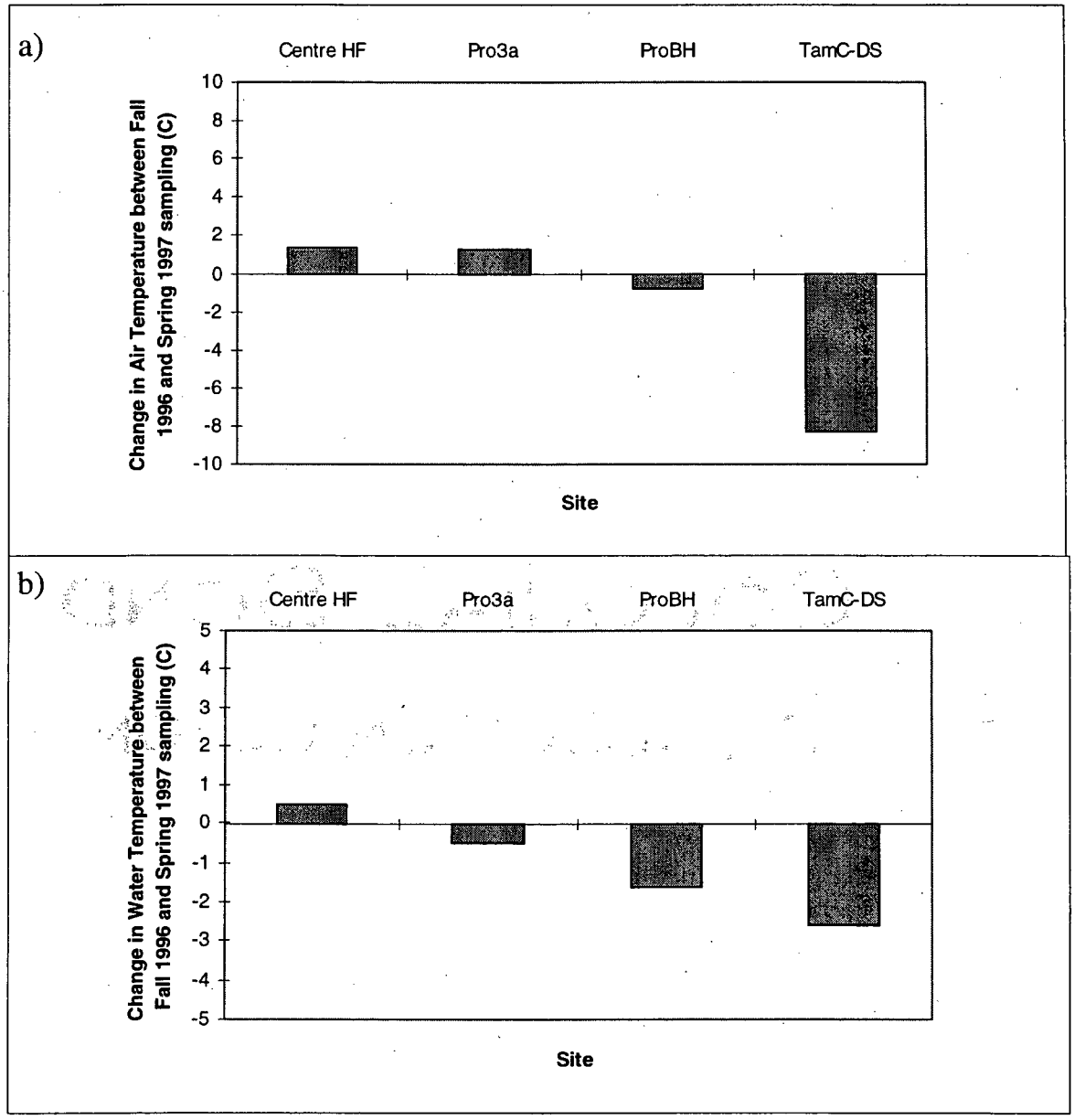


Figure 3.4a& b: Differences in the mean air and water temperature between late season 1996 and early season 1997 sampling. Each site mean was based on 8-18 observations.

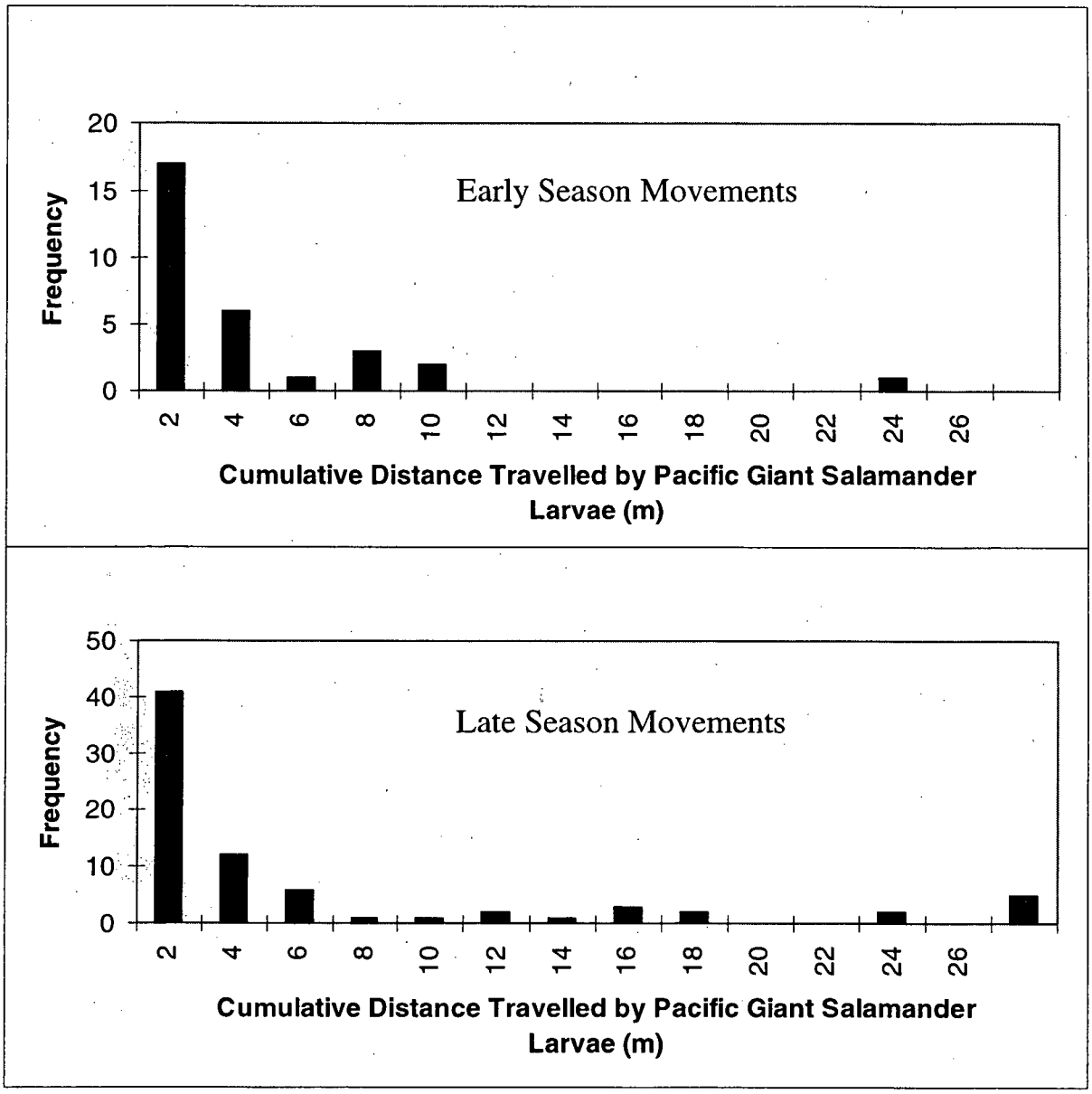


Figure 3.5: Cumulative distance travelled by *D. tenebrosus* larvae early and late in their active season. These data are pooled from all of the four streams. Early season refers to movements made in June and July 1997 (n = 30) and late season to movements made in August and September 1996 (n = 76). There was no significant difference between these two distributions (Kolmogorov-Smirnov test, p = 0.985).

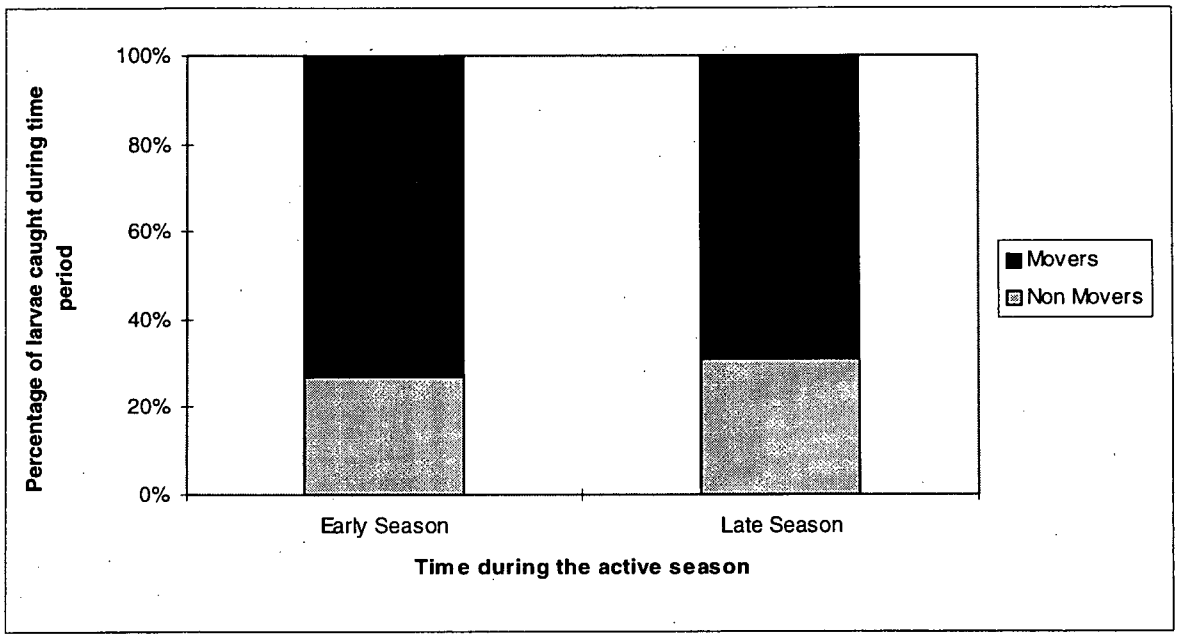


Figure 3.6: Proportion of larvae that moved (displacement greater than 0.5 m) and did not move at two different periods throughout the active season. The proportion of movers was not significantly different between these two periods.

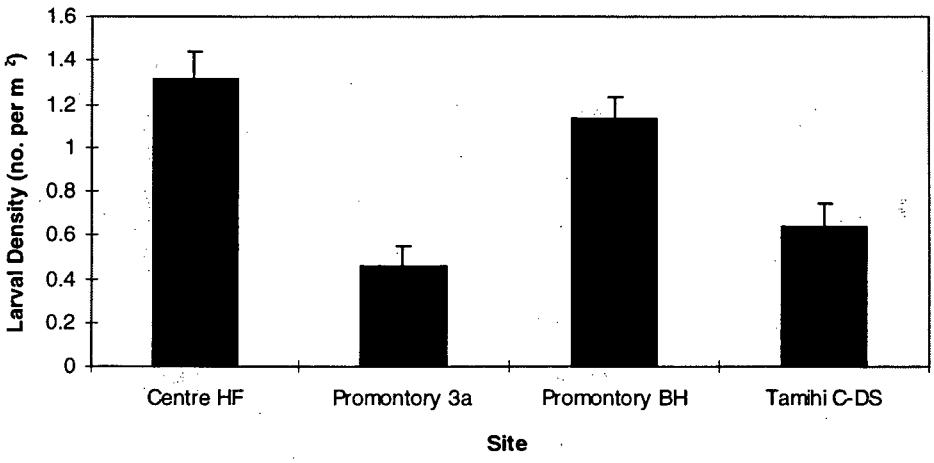


Figure 3.7: Mean larval density and standard error at four *D. tenebrosus* larvae streams.

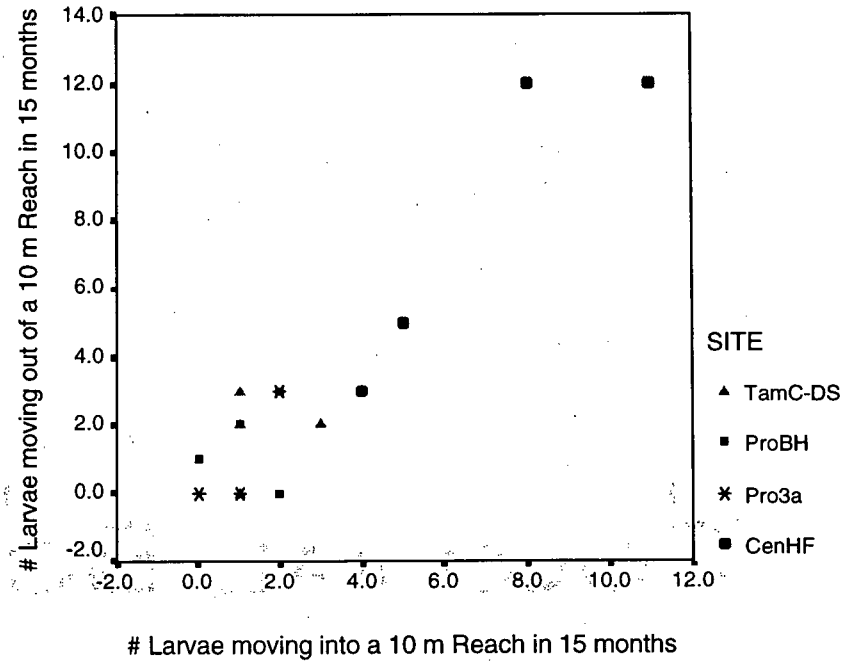


Figure 3.8: Relationship between the number of larvae moving into and out of a 10 m reach of stream during a 13 month experiment. The log (x + 1) transformed number of larvae moving into a zone was significantly related to the log (x + 1) transformed number moving out (ANCOVA, $F_{1,11} = 5.619$, $p = 0.037$). There were no site interactions (ANCOVA, site effects $F_{3,11} = 0.333$, $p = 0.802$).

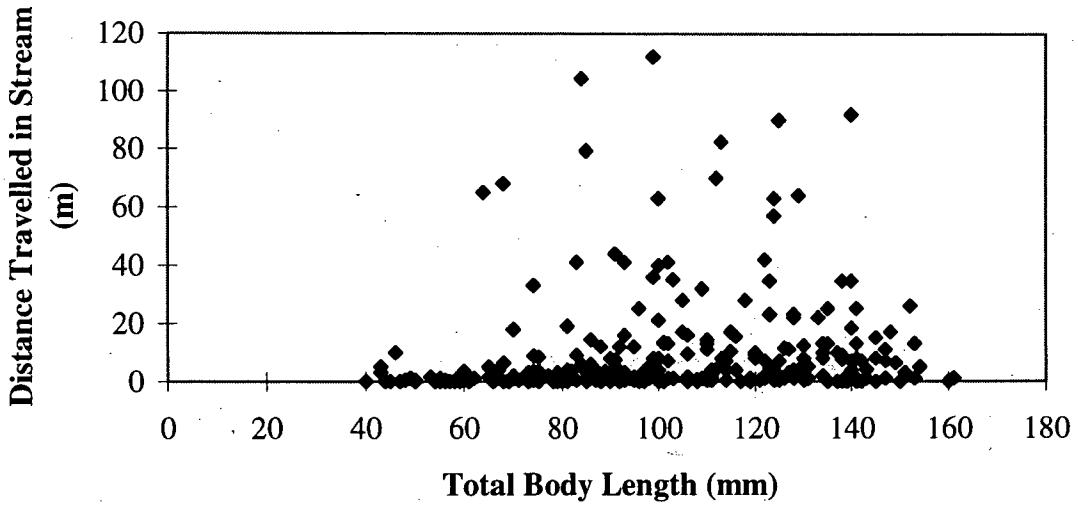


Figure 3.9: The relationship between body length and cumulative distance travelled, pooled over all sites (n = 241) . The dark line is the line of best fit between these two variables. This regression was not significant ($r^2 = 0.007$, $p = 0.192$). The relationship between these variables is described as : Distance travelled (m) = 0.061* Body length(mm) + 4.81.

Chapter 4: Colonising Ability of Pacific Giant Salamander Larvae

Introduction:

The ability of salamander populations to recover from local disturbances has been debated by conservation biologists (Petranka et al. 1993, Ash & Bruce 1994, Petranka 1994). Specifically, herpetologists have argued over whether amphibians can compensate for increased rates of habitat disturbance by rapid recolonisation. In the Pacific Northwest, habitat loss is primarily due to logging and development.

Several studies have found that population densities of aquatic salamanders are lower in streams draining through clearcuts than in undisturbed stands (Bury & Corn 1988, Connor et al. 1988, Corn & Bury 1989, Welsh 1991, Cole et al. 1997). The small population paradigm tells us that small populations are more vulnerable to local extinction than large populations (Caughley 1994). Thus by decreasing population density, logging may increase the probability of local extinction. If dispersal can facilitate rapid recolonisation of disturbed areas, an increased frequency of local extinction may have no long term affect on salamander persistence. However, if larval and adult dispersal are weak, regional extinction may ensue when entire landscapes are disturbed.

It is generally believed that amphibians are poor dispersers (Duellman & Trueb 1986, Blaustein et al. 1994) and it has even been suggested that amphibian communities are influenced more by dispersal ability than by specific habitat tolerances or competitive interactions (Cortwright 1986). A twenty year translocation study in western Indiana found that the semi-aquatic Two-Lined Salamander, *Eurycea cirrigera*, could survive in many areas outside its traditional range, but it had been excluded from those areas by poor dispersal ability (Thurow

1996). Thus even within undisturbed, tolerable habitat, dispersal may limit amphibian distribution and community composition.

Pacific Giant Salamanders and disturbance

In this study, I used experimental techniques to measure the colonising ability of larval Pacific Giant Salamanders (*Dicamptodon tenebrosus*). In Canada, this provincially red-listed species is restricted to the Chilliwack River drainage basin where it is distributed patchily. Survey work in this area detected *D. tenebrosus* in only 22 of 59 seemingly habitable streams within this area (Richardson & Neill 1995). It is possible that many of these currently barren streams experienced local extinction in the past. Logging has occurred on much of *D. tenebrosus*' Canadian range, and may increase the frequency of local extinction (Haycock 1991).

Though little is known of this species' ability to respond to local extinction by colonisation, larvae reappeared in one Washington stream only two years after it had temporarily dried (Nussbaum & Clothier 1973). It is unknown whether these animals were dispersers from nearby areas or survivors that took refuge in subsurface waters during the drought.

I tested the hypothesis that colonisation of barren stream reaches by *D. tenebrosus* is rapid (< 1 year) and is accomplished by larval dispersal. I did this by simulating reach extinctions at four stream sites. I removed larvae from 25-40 m stream sections and then monitored recolonisation of these areas for a year. As colonisation implies the establishment of animals in an unoccupied habitat, this phenomena could not be studied by monitoring immigration into populated reaches. If movements are influenced by the presence of conspecifics, as found in *D. tenebrosus* larvae in the lab by Mallory (1996), dispersal rates into

populated and depopulated reaches will vary significantly (Stenseth & Lidicker 1992). Thus to model the natural process of colonisation, experimental removals had to be conducted.

In addition to measuring the speed of recolonisation, this experiment yielded information about the relative contribution of larval dispersal and adult reproduction to the repopulation of barren areas. Both larvae and terrestrial adults are potential dispersal agents in this species. Terrestrial adults are more mobile than larvae, with some radio-tracked individuals travelling up to 305 m from their capture site between July and October (Johnston 1998). Although larvae are more limited in their dispersal capabilities, they are much more numerous than adults and can move > 50 m during the active season (Neill 1998). Consequently they may be the most efficient colonisers in stream reaches experiencing frequent, small-scale disturbances due to debris torrents or rock slides. Such disturbances are relatively common in headwater streams of the Pacific Northwest and their frequency is increased by logging (Lamberti 1991). I examined the size structure of the colonists of my removal zones to assess which life history stage, adult or larvae, had added the most individuals.

Even if larvae are not efficient colonisers, there are reasons for studying their movements. Larvae may be the only viable dispersal stage in logged habitats, because terrestrial adults may suffer high mortality in clearcuts due to an increased risk of desiccation and freezing. (Richardson 1994). Under such a scenario, depopulated areas could be recolonised only by larval propagules from undisturbed stream reaches. It has not yet been tested, however this hypothesis suggests studies of larvae are vital for judging recovery potential.

Although removal studies have been widely used to estimate dispersal rates in other taxa (Stenseth & Lidicker 1992), these methods have seldom been used on amphibians (Bruce 1995). My study is one of the first to use removal techniques to estimate colonisation in salamanders.

Removal techniques have several shortcomings (Appendix 2). In this experiment I have employed a mixture of field and statistical techniques to reduce the impact of the five most serious biases noted by Stenseth and Lidicker (1992) (Appendix 2). Although none of these corrections completely eliminates bias, they provide more accurate measures of colonisation. Because conservation decisions often rely upon the recovery potential of a species, it is essential that these estimates be as accurate as possible.

Methods:

Measuring Colonisation in the Field

The colonising ability of *D. tenebrosus* larvae was studied in four headwater streams in the Chilliwack River Valley: Centre HF, Promontory 3a, Promontory BH and Tamihi C-DS. The location and age of surrounding forest habitat at each site is detailed in Chapter 2 (Table 2.1). At each site, a 120 m long reach of stream was set aside for study. Colonisation was studied by removing all larvae from a 25-40 m central section of this study reach

1) Pre-Removal Sampling

Each 120 m reach was searched intensively each week in June and July 1996 (Table 4.1) to identify all larvae that might later act as colonists. Larvae were captured by hand and individually marked (see Chapter 2) before being returned to their location of capture. All sites were sampled between 5 to 8 times to enumerate the larval population before removals began (Table 4.1). Even after this effort, some unmarked individuals were found within the study reach suggesting not all resident larvae may have been marked or some dispersal from beyond the study reach took place.

2) Creating Removal Zones

After the initial marking period, removal zones were created in the middle of each 120 m reach. The length and area of the removal zone at each site varied between 25-40 m long and 26-75 m^2 (Table 4.2). The size of the removal zones varied because of a prior decision not to remove more than one third of the larval population at any site. This fraction was chosen to ensure that there were more than enough individuals in the adjacent reaches to fully recolonise my removal areas. In two sites, larvae were heavily clustered in the middle of the study reach and only 25 m could be cleared while at the other two sites, larvae were distributed more uniformly and the middle 40 m was cleared.

Removals were conducted on a daily basis at each site in late July and early August 1996. Mesh fences (1 mm^2) were built to obstruct dispersal into or out of the area during the removal period. All captured salamanders (larvae, neotene or adults) were taken out of the stream and housed in artificial stream channels. The number of larvae removed varied between sites (Table 4.3). Searching was stopped when no larvae were captured in the removal zone on two consecutive days. At this time the dispersal fences were removed and the reach was opened for colonisation.

3) Monitoring Colonisation

Each 120 m site, including a removal zone and up and downstream source reaches, was monitored on a weekly basis until late September 1996, when water temperature dropped below 6 C and larvae could no longer be detected. Weekly sampling resumed from June to mid July 1997 and again for two weeks in September 1997. No further removals occurred after monitoring started in 1996. The identity and location of each larva found inside and outside of

the removal zone were recorded. All newly found larvae were uniquely marked so that their future dispersal could be followed. All larvae captured within the removal zone after clearing were categorised as potential colonists.

By continuing to mark individuals in areas outside the removal zone, I estimated larval abundance in the adjacent reaches. I used the program CAPTURE to calculate larval abundance in the source areas in September 1996 and June 1997 (Burnham et al., 1994). Estimates for these periods were based on four weekly mark-recapture surveys. Population sizes in the adjacent areas were also calculated in September 1997. As only two surveys per site were conducted in this month, population size could not be estimated by CAPTURE (insufficient sampling intervals). Instead a simple Lincoln-Peterson model was used to estimate the size of the September 1997 population. Details of both this model and the CAPTURE estimate are included in Chapter 2.

Statistical Models of Colonisation

Colonisation was followed for just over a year at all sites. All colonisation rates represent the number of colonists entering the removal zone in a one year period (the exact period that each site was monitored is shown in Table 4.1). Two issues made the enumeration of colonists difficult. The first problem was that not all animals found in the removal zone after clearing were marked. It was thus unclear whether these larvae had dispersed into the zone or were residents that had not been removed. Second, many potential colonists were captured only once in the removal zone. Given the low capture probability of these animals, it is uncertain whether these individuals were transients or colonists that remained undetected in the zone. I dealt with these problems by calculating colonisation under three different models: a)

Conservative b) Liberal and c) Statistically probable. The conservative and liberal rates were calculated to establish the range of values within which the true *per annum* colonisation rate of larvae lies. The statistically probable model incorporates information on site-specific trapping efficiency and capture history to estimate a likely number of colonists. The assumptions and methods used to derive each estimate are detailed below:

a) Conservative Colonisation

Only larvae that were initially marked outside the removal zone and then captured within it were considered colonists. Unmarked animals found within the zone were considered missed residents except for several small, unmarked larvae (< 60 mm total length) found in the removal zone in September 1997. These animals were too young to have been present in the stream when the manipulations were taking place. They were considered to be colonists as their presence was most likely due to post-removal reproduction. These animals will be referred to as recruited colonists. To separate transient dispersers from true colonists, this model also required evidence that dispersing larvae had settled in the removal zone. All larvae dispersing into the zone had to be captured at least twice in the zone to be considered colonists.

b) Liberal Colonisation

Under this model, all larvae captured within the removal zone after clearing were counted as colonists. Any animal that was caught once within the removal zone, whether marked or not, was added to the coloniser pool. This method definitely overestimates colonisation as removals were not 100% successful at any site. Several larvae were found in each removal zone that had been marked prior to manipulation but had not been successfully

cleared. Although these animals were excluded from this estimate of colonisation rate, their presence indicates that at least some of the unmarked larvae found in the removal zone were missed residents.

c) Statistically Probable Colonisation

Unmarked larvae found in the removal zone after clearing were divided into two categories: those hatched before the manipulation and those that hatched after it. Any small larvae (< 60 mm total length) found in the removal zone in September 1997 were considered recruited colonists as described above.

As I could not determine the origin of the other unmarked larvae in the removal zone, I used a site-specific removal efficiency rate to infer how many were likely missed residents. To do this I compiled a list of all larvae captured in the removal zone before manipulation. I subtracted from this list the number of larvae known to have dispersed out of the zone or that I suspected to have transformed before clearing. Larvae larger than 130 mm in total length that showed signs of gill resorption or skin mottling were classified as probable transformers. I divided the number of larvae that were removed at each site by the corrected number detected before clearing to obtain a removal efficiency rate for each stream.

I used this efficiency index to calculate the number of unmarked larvae found in the removal zone that were likely missed residents. For example if the efficiency rate of a particular clearing was 75%, then 25% of larvae known to be present in the removal zone prior to manipulation were not successfully cleared. Thus if 20 unmarked larvae were later found in the removal zone, I inferred that 25% of them (5 larvae) had been present before the clearing and were not true colonists. By applying this correction, I divided the total number of unmarked

larvae into missed residents and immigrants. The number of unmarked larvae inferred to be immigrants was added to the number of marked animals known to have immigrated to calculate the total number of larvae that dispersed into the removal zone over the course of the experiment.

The number of dispersers does not necessarily equal the number of colonists as some dispersers may have later emigrated or died. For each disperser into the removal zone, I calculated its probability of remaining undetected in the area for the balance of the experiment. If this probability was greater than 50%, I assumed this animal was still within the zone. These animals were designated as colonists. If the probability of non-detection was less than 50% and I never caught it again, I assumed it had died or dispersed. The specific methodology used to estimate this probability is described in Appendix 3. A schematic diagram detailing the steps taken in the model is given in Figure 4.1.

Percent replacement of removed individuals by colonists

The number of colonists predicted under each of the three models was calculated. These numbers were divided by the number of animals initially taken out of the removal zone to estimate what percent of the removed individuals were replaced by colonists in a year.

Density Dependent Colonisation

A *per capita* colonisation rate was calculated for each site by dividing the predicted number of colonists by the total number of larvae marked in the source areas above and below the removal zone. This rate represents the proportion of larvae in an undisturbed reach that

were capable of local recolonisation. Only the number of colonists estimated under the Statistically Probable Model was used in this and all further analyses.

This *per capita* colonisation rate was also used to examine the relationship between larval density in source areas and speed of recolonisation. If density dependence was operating on dispersal, I predicted that *per capita* colonisation at each of four sites would increase with increasing density of the source population.

Origin of Colonists

The colonising group at each site was composed of two types of animals: second year or older larvae and young-of-the-year recruits. Young-of-the-year recruits were < 60 mm total body length in the second year of the experiment. These animals were the product of breeding in Fall 1996 and would not have hatched until the summer of 1997. All other colonising larvae would have been in the stream at the time of the removals and would only be found in the removal zone if they had dispersed in. By comparing the number of individuals in each category, I could infer the relative contributions of reproduction versus larval dispersal to the colonisation process.

Body Size and Colonisation

I wished to determine whether colonising larvae were a random sub-set of individuals from the source areas or a unique size class. To do this I summed the total number of known colonists (37) from all sites, including both larval colonists and adult-dispersed recruited colonists. An equal number of individuals was then randomly selected from the set of all larvae that did not colonise the removal zone during the year of monitoring (pooled across all sites, n = 619). The mean snout-vent length (SVL) of these individuals was calculated. This procedure

was repeated 1000 times to generate a distribution of the expected mean snout-vent length in a group of 37 randomly selected non-colonising larvae. I then compared the observed mean SVL of colonising larvae to this distribution. If the observed value fell within the outer five percent of values in the expected distribution, the body size of colonisers was considered significantly different from resident larvae (alpha = 0.05). A Pascal-based randomisation test program was written by Dr. D. Haydon for this and all subsequent resampling analyses.

Distance Travelled By Colonisers

Another resampling analysis was conducted to determine if larval colonisers exhibited distinct movement distances from non-colonisers. The cumulative distance travelled by all non-colonising larvae throughout the experiment was calculated, after excluding larvae that did not move. Non-movers were excluded as a comparison of individuals that by definition must move (colonisers) with those that often do not (8-25% of larvae remained stationary, Chapter 3) will yield the obvious result that colonisers are more mobile. Instead, I wished to know whether colonisation proceeded by the short-distance dispersal characteristic of most larvae (Chapter 3), or long-distance dispersal of a few atypically mobile individuals.

From the pooled data set of all non-colonising yet mobile larvae (those that moved > 0.5m, n = 213), a number of individuals equal to the number of in-stream larval colonisers (n = 7) was randomly selected 1000 times. After each selection, the mean cumulative distances travelled by the group was computed. An expected distribution of cumulative distance travelled by non-colonising larvae was generated from these values. The observed mean distance travelled by colonising larvae was compared to this distribution to determine if they were making statistically longer movements than those in the source areas.

Direction of Colonisation

A final analysis was undertaken to determine if colonisation was directionally biased. To do this I first examined the net direction of movements made by non-colonising larvae in the source areas of each stream. Each larva that made a net downstream movement over the course of the experiment was assigned a direction code of "0", and each larvae that moved upstream received a "1". Larvae that made no net movements were not included in the analysis. Direction records from all four sites were pooled into one data set (n = 213). From this data set, a number of individuals equal to the number of in-stream larval colonisers (n = 7) was randomly selected 1000 times. After each selection, the number of upstream movements in the group was calculated by summing direction codes of all individuals to produce an expected distribution of the number of upstream movements. I then summed the net direction codes of in-stream larval colonisers and compared it to the expected distribution.

Results:

The numbers of colonists at each site was calculated under 3 different colonisation models (Table 4.4). Conservative estimates of colonisation varied between 0 and 5 larvae per year. These estimates are low because at least 10 unique individuals were detected in each removal zone after disturbance. By assuming that none of the unmarked animals found in the removal zone were colonisers, this estimator excludes a significant proportion of dispersal. The liberal model predicted full replacement of removed larvae at three of four sites (Figure 4.2). The liberal estimates undoubtedly overestimated colonisation. The biggest flaw in this model is the assumption that all unmarked individuals found in the removal zone post-manipulation were

dispersers. From the efficiency index, I estimated that at least 25% of larvae initially detected in the removal zone post-clearing were missed residents. Any local recovery predictions based on this model will be optimistic. The Statistically Probable model consistently produced estimates midway between the conservative and liberal models.

Percent replacement of removed individuals by colonists

The percentage of removed individuals that were replaced by colonisation varied amongst sites (Figure 4.2). Under the Statistically Probable Model, 29 to 210% of the larvae removed from each site were replaced in one year. While Tamihi C-DS recovered fully, colonisation had replenished only 29-77% of the removed pool at the other three sites.

Per Capita Colonisation

Only a small percentage of all larvae caught within each 120 m study zone were colonists (Table 4.5). Across the three forested sites, (Centre HF, Promontory 3a and Promontory BH), the *per capita* colonisation rate was remarkably uniform, ranging between 3 to 5 percent of all captured individuals per year. In contrast, 13% percent of captures at Tamihi-C DS were colonists. As will be discussed below, the high *per capita* rate at Tamihi C-DS is likely due to locally higher recruitment at this site.

Density Dependent Colonisation

There was no relation between the *per capita* colonisation rate at a site and the mean larval density of larvae in the source reaches (Figure 4.3). A possible density association was observed when the *per capita* rate was split into two values, one for colonisation by larval

dispersal and another for colonisation by recruitment (Figures 4.4 a & b). There was a trend for colonisation by larval dispersal to increase with density. However this trend is based on differences of one or two dispersing individuals between sites and could easily be due to chance.

Origin of Colonists

The percentage of colonisation that was due to reproduction varied considerably between sites. Colonisers were primarily dispersing larvae at two sites, and primarily recruits at the remaining two (Figure 4.5). The only site to completely recover from the removal, Tamihi C-DS, was restocked entirely by recruits. At this site, sexually mature animals must have bred in the removal zones a few months after the removal had taken place. Promontory 3a was also exclusively colonised by recruits, but had only replaced 29% of its previous inhabitants by the end of the experiment.

Body Size and Colonisation

The expected distribution of mean SVLs in 37 non-colonising larvae is shown in Figure 4.6. Colonising larvae were significantly smaller than non-colonising individuals. This result is not due to greater dispersal by small larvae, but to higher recruitment in the depopulated zones. As shown in Chapter 3, body size had little influence on movement in any of the four study streams. The only weak trend observed was an increase in movement with body size, contradicting the notion that recruits are the most mobile. If the removal zones hold more recruits than the source areas, it is because more eggs were deposited and/or successfully hatched within them.

Excluding recruits from the sample, I tested whether the body size of larval colonisers was significantly different from non-colonising individuals. The mean SVL of in-stream colonisers, 53.6 mm, was not significantly different from the mean SVL of 7 randomly selected non-colonisers (expected mean = 53.4 mm, p = 0.446, Figure 4.7).

Distance Travelled By Colonisers

The expected mean distance travelled by non-colonising larvae was lower than that moved by the in-stream colonists, but not significantly so (Figure 4.8). The mean distance travelled by in-stream colonising larvae was more than twice the mean recorded in the source areas.

Direction of Colonisation

Pooling across all sites, the ratio of downstream to upstream movements was 42: 58. This slight preference for upstream movement was reflected in the randomisation tests, which predicted an average of 3.9 net upstream movements in a group of 7 dispersing larvae. In contrast with this value, six out of seven colonising larvae moved upstream into the removal zone. Although this result is not significantly different from expected (p = 0.224, Figure 4.8), it proves larvae are capable of moving upstream against the current into a new area.

Discussion

Local recovery in *D. tenebrosus* populations was variable during the first year following a disturbance. Full recovery occurred in only 1 of 4 sites with colonisation replenishing only 29-77% of removed individuals at the remaining three streams. Given the small area of these

removals and the high abundance of larvae in nearby source reaches, it is surprising that full recovery did not occur at all sites. It is unclear whether larvae lacked the ability to colonise at a faster rate or simply had no cause to move from where their initial location (i.e. no density dependence or destructive habitat change forcing movement).

Full repopulation within a year after removal was achieved only at Tamihi C-DS, the sole stream running through a recent clear cut. Mean air temperature at this site was higher than at the other three streams (Table 3.6). The mean abundance of macrobenthos at this site was less than half that of the forested sites. It is not known how or if these variables affect colonisation speed, but they did not appear to explain the variation in dispersal rates between four unmanipulated streams in Chapter 3. With no replicate clear cut sites, it is impossible to determine whether this is a habitat or site effect.

As my study is one of the first removal experiments to be conducted on amphibians, the closest taxonomic comparison I can make is to other aquatic vertebrates. Such comparisons show the recolonisation ability of *D. tenebrosus* larvae to be poor. For example, several species of fish removed from 40-100 m reaches in an Illinois stream regained 90% of their original abundance within 10 days (Peterson & Bayley 1993). Much variation, however, exists among fish species, with some predicted to recolonise within a few weeks (Larimore 1959), others a few months (Matthews 1986) and others up to a year (Gunning & Berra 1969). In almost all of these studies, the experimental reaches cleared were larger than in my experiment.

If recolonisation proceeds at the rates observed in my experiment, full numerical recovery at the three unsaturated sites should take 6-42 months (Table 4.6). I divided the total length of each depleted reach by its predicted recovery time to estimate how fast reaches experiencing similar reductions could be replenished (Table 4.6). For example, mild

disturbances that caused density reductions of 0.1 larvae m^{-2} (magnitude of my depletion at Promontory 3a) would be recolonised at a rate of 20 m per year. Alternatively, severe disturbances that caused depletions of 1.1 larvae m^{-2} (Centre HF), a value which would cause complete extirpation at many streams, would be recolonised at a slower rate of 7.1 m per year. I now use these simple predictions to estimate the time required for recolonisation in stream reaches running through a clearcut (maximum length of 400 m). If logging triggered only moderate depletions of 0.1-0.3 larvae m^{-2}, larval recolonisation of a 400 m x 1 m reach could take 8-20 years. However if logging triggered an almost full extirpation of larvae (depletion of $\geq$ 1.1 larvae m^{-2}), recolonisation of this stream reach could take more than 55 years.

Eight to fifty five years for the full recolonisation of a stream running through a cut-block agrees with other estimates for salamanders in logged habitats. Plethodontid salamanders in eastern North America were estimated to take 20-25 to 50-70 years to return to pre-harvest density in cutblocks (Ash & Bruce 1997). However other species of amphibians are faster colonisers. In Spain, an old lignite mine site was recolonised by several amphibian species within only two years of abandonment (Galan 1997). Similarly artificial ponds in a Bavarian experiment were colonised by the newt *Triturus alpestris* within a year (Joly & Grolet 1997). Variation in recovery speed is likely a result of species-specific colonisation ability, the magnitude of depletion caused by the disturbance, and dispersal barriers in the landscape.

Although the above extrapolation of my small-scale results to larger areas provides a quick comparison to other species, these calculations are not accurate enough to inform management decisions. My study provides a detailed description of larval colonisation, but there was no study of adults. I have shown that reproduction increases local density more rapidly than

larval dispersal. Thus, understanding the colonising ability of adults is pivotal to estimating the speed of recovery by *D. tenebrosus* after large disturbances.

Extrapolation of small-scale results to large areas is also risky as rates measured at one scale do not always predict behaviour at another. Thrush et al. (1997) found that colonisation speed for some benthic marine organisms decreases significantly with increasing plot size. Real disturbances often act over a much wider area than any experimental plots and must be restocked by a proportionately smaller colonist pool. As a consequence, colonisation rates measured in small areas will likely overestimate the recovery speed of large areas.

The type of disturbance applied in this experiment may also yield overly optimistic colonisation rates. Depopulation was achieved by removing individuals experimentally and not by destructive habitat change. This experiment did not explicitly consider the role of habitat on colonisation. As larvae were found in all sites prior to manipulation, the habitat was suitable to larvae. Habitat clearly affects amphibian colonisation in addition to intrinsic dispersal ability (Hecnar & McCloskey 1997, Skelly & Meir 1997). My experiment has shown only how quickly larvae can recolonise acceptable habitat. In the field, even if *D. tenebrosus* can reach a depopulated area quickly, they may avoid settling in it or die within it if the habitat is unsuitable. It is thus uncertain how much or if my rates would vary under different types of habitat change. However, the high speed of colonisation in the one clearcut site suggests logging does not necessarily deter movement.

Finally in my study, recolonisation refers only to the numerical replacement of individuals and not to biomass recovery. Pre and post-removal larval biomass could not be compared as the number of colonists was statistically inferred and not directly enumerated. As such, the precise identity of each colonist was not known and thus their total biomass could not be calculated.

This omission may optimistically bias the rate of recovery at the Tamihi C-DS. Although this site exceeded its pre-removal abundance within a year, the colonisers were primarily small individuals (< 60 mm TL). Larvae found in the removal zone of this site before clearing were generally large individuals (> 100 mm TL). The discrepancy in size between the pre and post-removal occupants of this zone suggests full biomass recovery was not achieved at this site.

Life History and Colonisation

As mentioned above, full recolonisation occurred only at Tamihi C-DS where colonists were exclusively recruits. This colonisation was likely achieved entirely by adults breeding in the removal zone. Colonisation by larval dispersal occurred at two sites, but never added as many individuals to the removal zone as reproduction. Larval dispersal never contributed more than 13 individuals to any removal zone. Adult females can carry between 85-200 eggs (Nussbaum 1969). Unless egg-to-larvae mortality is greater than 90%, one clutch of eggs could provide just as many colonists to a stream reach as local larval dispersal. Egg-to-larvae survival in *D. tenebrosus* is unknown, but was 22% in one population of the related *Ambystoma maculatum* (Shoop 1974). If this rate is similar to that in *D. tenebrosus,* one reproductive event could increase local density in depopulated areas much more effectively than larval immigration from adjacent reaches.

Although my one-year study is informative, the final outcome of the colonisation process cannot be judged from observation on this time scale. Re-establishment of *D. tenebrosus* in my removal zones will depend on the survival of larvae to sexual maturity, a process that could take 2-6 years (Chapter 2). Studying only larval colonists without consideration of their survival to sexual maturity may overestimate the speed of colonisation. Although individuals may have

higher survival and/or growth in the absence of conspecifics, it is still problematic to assume all larval colonisers will survive to adulthood. For example, one intertidal study found that defaunated areas were quickly recolonised by a polychaete worm species. Most colonising polychaetes, however, died without contributing to the long term recovery of the plots (Thrush et al. 1996). Although the number of larval colonists entering a depopulated area may be a good indicator of future occupancy, continued monitoring is required to ensure their presence leads to the long-term survival of individuals.

Size of Colonisers

The mean size of larvae within the removal zones was significantly lower than outside, reflecting that most new recruits were located in the removal zones. Recruits at Promontory 3a and Tamihi C-DS were clustered heavily in and around the removal zone and were not spread evenly throughout the rest of the stream. This may be the random outcome of a single clutch at each site being coincidentally deposited in or immediately adjacent to the removal zone. Alternatively there may be a selective advantage to being hatched in depopulated areas. In support of the latter hypothesis, Connor et al. (1988) found densities of first and second year *D. tenebrosus* larvae to be twenty times greater in stream sections in which older salamanders and fish were absent.

Recruits could be selectively concentrated in the removal zone if adults chose to lay eggs in areas of low larval density, or if hatchlings were more successful in the absence of conspecifics. The first of these scenarios, selective oviposition, has been recorded in other species of stream dwelling salamanders (Kats & Sih 1992). The second hypothesis, that hatchling survival is greater in low density areas, is also feasible for *D. tenebrosus.* Pacific Giant

Salamanders are known to prey on small conspecifics in the lab (Mallory 1996) and I observed some instances of cannibalism in the field. New recruits are the most vulnerable to intraspecific predation and conceivably may survive best in the absence of conspecifics. If this hypothesis is true, this benefit may favour dispersing adults and promote recolonisation in disturbed landscapes.

Dispersal Behaviour of Larval Colonists

Obviously larval colonisers had to move some distance to enter the removal zone, however their mean dispersal distance was twice that of mobile, non-colonising larvae. Many potential colonists were clustered just on the boundary of the removal zone (1-5 m away). Had they dispersed into the removal zone, the mean distance travelled by colonising individuals would be no different from that of non-colonisers. However colonisation did not proceed by gradual range expansions of these fringe animals but by a few long distance movements (4 - 63 m, mean = 26.1 m) by highly mobile individuals. Colonisers may have been behaviourally predisposed to movement and encountered the removal zone by chance. This idea is supported by findings in Chapter 3 that suggest in populated stream reaches, the larval population is composed of a large number of highly sedentary larvae and a small number of transient individuals.

Of the seven colonising larvae, six moved upstream into the zone. The dominant upstream direction of colonisation suggests that it was not always forced by the stream current. This contradicts previous claims that most colonisation occurs by downstream drift of larvae (Bruce 1985, 1986). Second growth forest downstream of disturbed reaches may therefore be a more important source of colonists than old growth stands located upstream. These second

growth areas may be more vulnerable to forest harvest and development than upstream sources. This activity could have more a destructive influence on *D. tenebrosus* metapopulation dynamics than the harvest of old growth.

Conclusions:

My experiment provides new insights into the response of the Pacific Giant Salamander to disturbance in British Columbia. Numerical recovery from small-scale "extirpations" occurs between 6-42 months after disturbance. Extirpations throughout streams the length of clearcuts (maximum length of 400 m) likely take significantly longer to be fully recolonised. This suggests that *D. tenebrosus* in recent clearcuts (< 5 years) are more apt to have survived through the logging event than to have recolonised after a local extirpation. Their presence suggests survival through logging is possible provided the stream remains intact.

Although depopulated areas can be restocked by both in-stream dispersal of larvae and adults, dispersal and oviposition by adults appears to be the most rapid means of recolonisation. Conservation efforts should therefore be directed primarily at adult dispersal capabilities and habitat requirements.

Finally, it is obvious from the above discussion that the measurement of colonisation in the field is complicated. Accurate estimates are hampered by biases due to small sample size, low recapture rates, and restricted spatial scales. While the colonisation rates I have provided are a potentially useful management tool, they should be used with caution. I have incorporated uncertainty into my estimates and generated a colonisation rate based on the probable number of colonists and not direct enumeration. Under different assumptions of capture detection and removal efficiency, slightly different estimates could be drawn from the same data. While I

believe my methods to be biologically realistic, other estimations are possible. For this reason I advocate the use of my conservative and liberal rates presented as limits for what is possible in the field.

Site	Timing of Removal	# Post Removal Checks			Total Time over which Colonisation was monitored (days)
		Fall 1996	Spring 1997	Fall 1997	
Centre HF	August 5-12, 1996	6	6	2	395
Promontory 3a	July 23-30, 1996	8	6	2	406
Promontory BH	July 17-30, 1996	9	6	2	414
Tamihi C - DS	August 8 -14, 1996	7	6	2	394

Table 4.1: Periods when colonisation by *D. tenebrosus* larvae was monitored.

Site	Size of Removal Zone (m)	Mean wetted width of Removal zone (m)	Total area of Removal Zone (m^2)	Location of Removal Zone
Centre HF	25	1.02	26	30m - 55m
Promontory 3a	40	1.88	75	40m - 80m
Promontory BH	40	1.77	71	40m - 80m
Tamihi C - DS	25	1.36	34	30m - 55m

Table 4.2: Size and location of removal zones within the 120 m study reach.

Site	# Larvae Detected Prior to Manipulation available for Removal	# Larvae That were Removed	Removal Efficiency (%)
Centre HF	37	28	0.757
Promontory 3a	26	8	0.400
Promontory BH	19	17	0.739
Tamihi C-DS	15	9	0.563

Table 4.3: Number of larvae detected and removed from experimental stream reaches. The number of detected larvae does not include individuals that were known to have dispersed out of the removal zone before the start of the experiment based on their locations in subsequent weekly surveys, or those on the verge of transformation. Removal efficiency is the total number removed divided by the total number detected.

Site	Conservative	Statistically Probable	Liberal
Centre HF	3	8	13
Promontory 3a	0	4	10
Promontory BH	1	13	22
Tamihi C - DS	5	18	40

Table 4.4: Numbers of *D. tenebrosus* larvae estimated to have colonised each removal zone annually under the Conservative, Statistically Probable and Liberal Models.

Site	# Unique Larvae Caught in 120 m Study Reach	% Captures that Were Colonists
Centre HF	162	4.9
Promontory 3a	133	3.0
Promontory BH	239	5.4
Tamihi C-DS	145	13.0

Table 4.5: Number of larvae captured in 120 m study area and the percentages of these that were colonisers.

Site	# Larvae Removed	Area of reach where they were removed (m^2)	Magnitude of local density reduction (larvae m^{-2})	Expected time for depleted reach to be recolonised (yrs)	Rate at which similar dens. reduction could be recolonised (m /yr)
Cen HF	28	26	1.1	3.5	7.1
Pro3a	8	75	0.1	2.0	20.0
ProBH	17	71	0.2	1.5	26.7
Tam C-DS	9	34	0.3	0.5	50.0

Table 4.6: Magnitude of local density reduction caused by experimental removal of larvae in four study reaches and the expected times for these depletions to be replenished by colonisation. This prediction of recolonisation time is based on the assumption that rates measured during the 13 months of this experiment would remain constant through time. I divided the total length of the depleted reaches by their estimated recovery time to predict the rate at which stream reaches with similar density reductions would be recolonised.

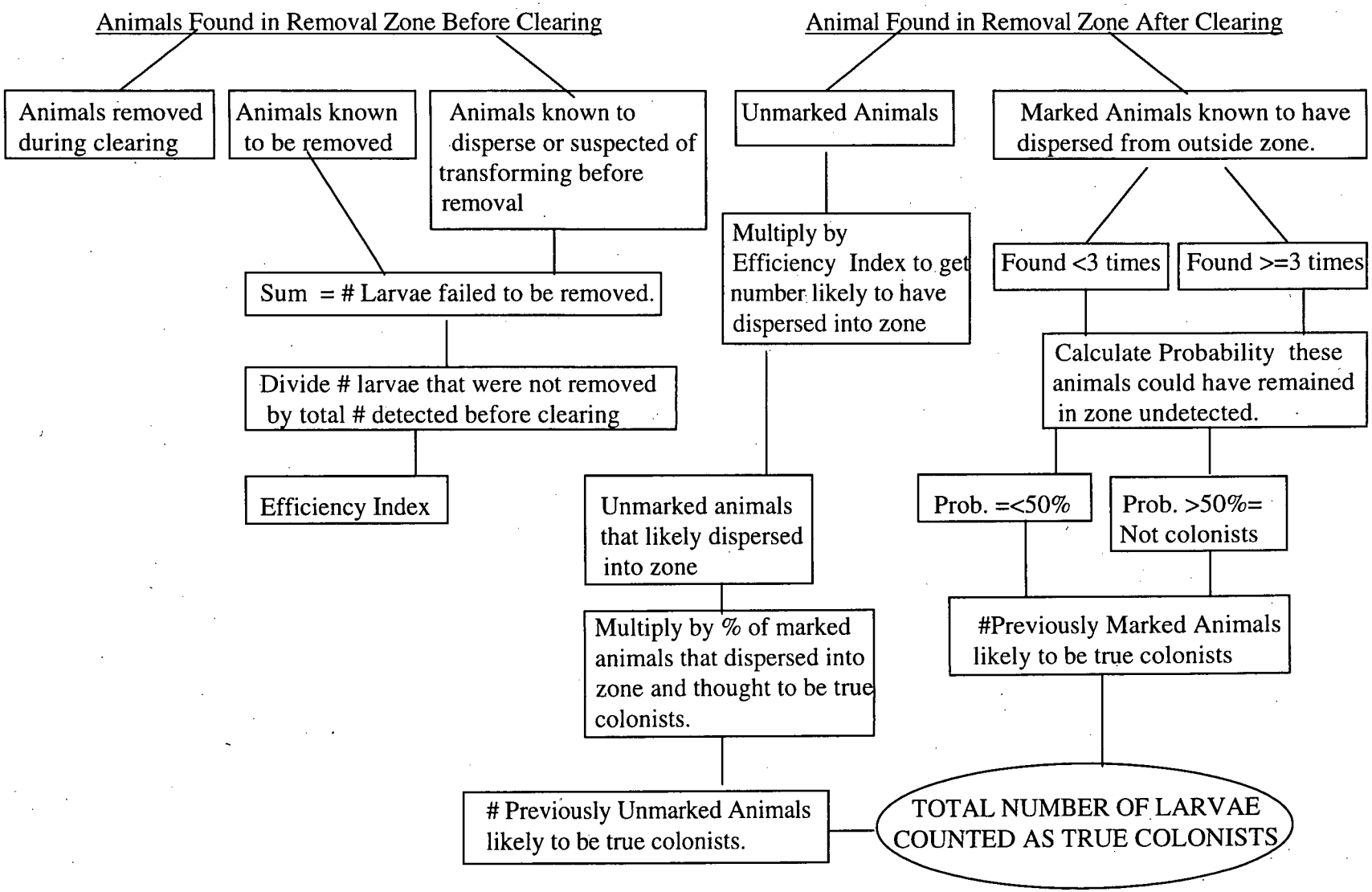


Figure 4.1: Steps taken to determine the number of larval *D. tenebrosus* colonists under the Statistically Probable Model.

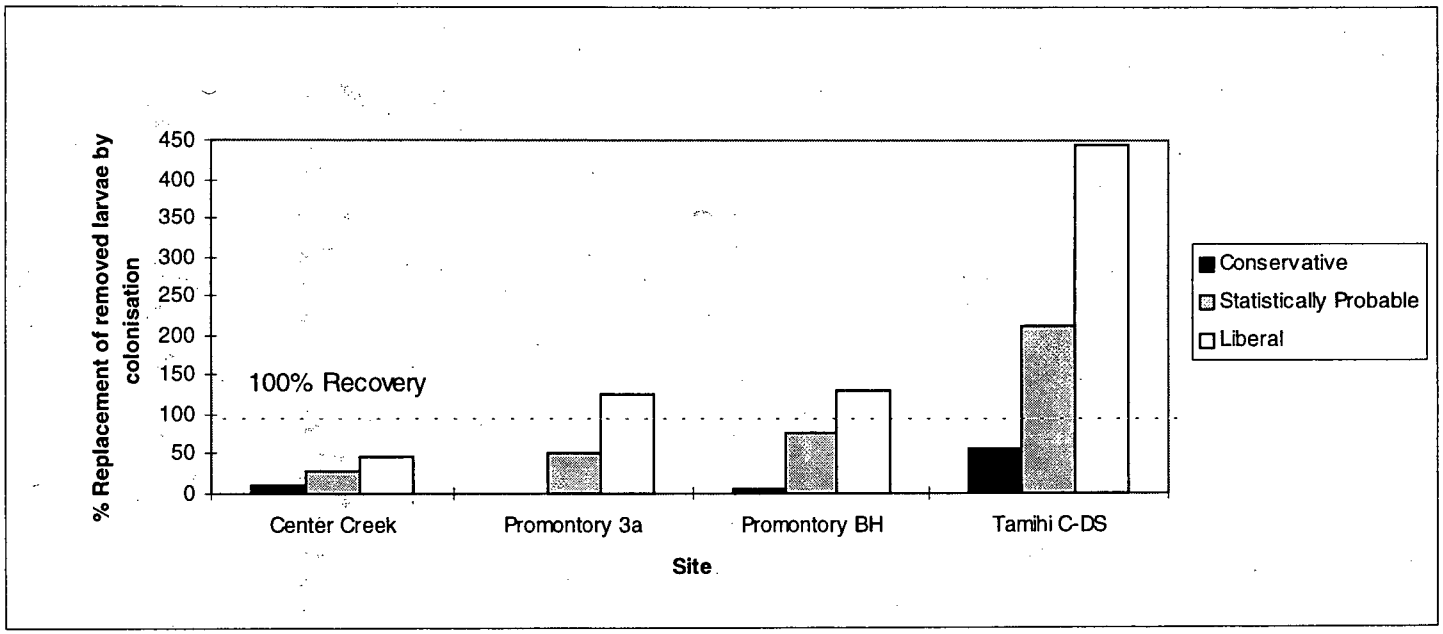


Figure 4.2: Percent recovery of artificially depleted stream reaches one year after disturbance under 3 different colonisation models. Percent recovery is the number of colonists after one year divided by the number of larvae detected in each removal zone before manipulation. Recovery values greater than 100% indicate that the pre-disturbance abundance was exceeded.

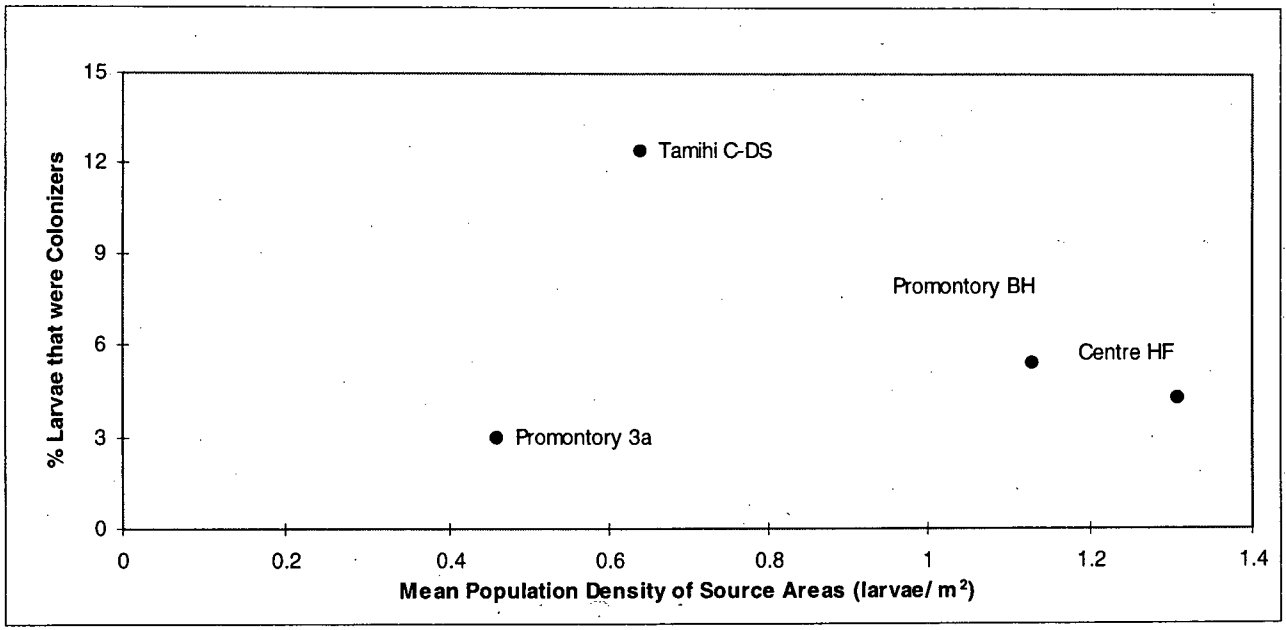
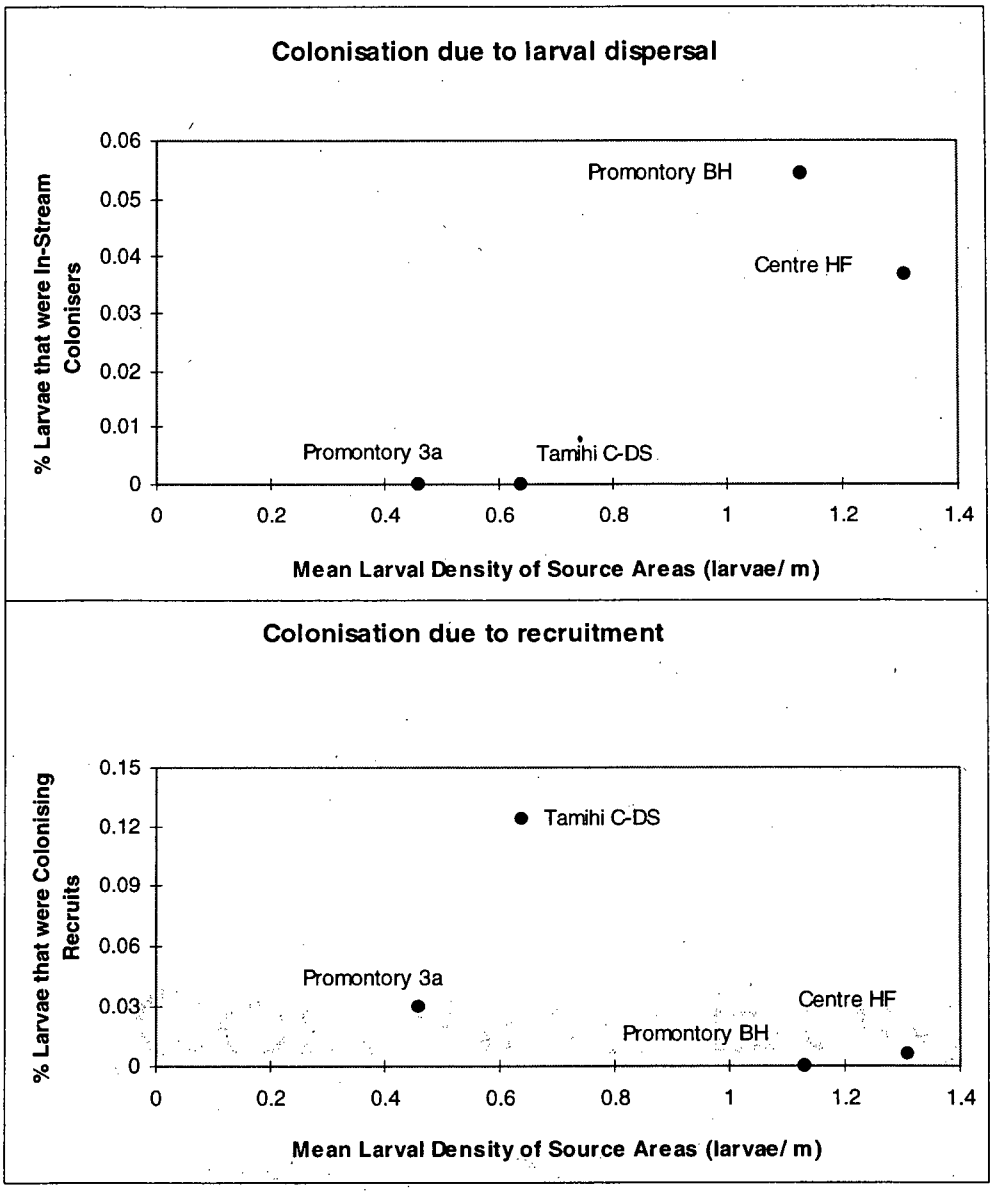


Figure 4.3: Percentage of colonisers in 120 reach as a function of mean larval density.



Figures 4.4a & b: Larval density in source areas and rate of in-stream and recruitment colonisation.

a) (Top): Percentage of in-stream colonisers in source areas as a function of mean population density. An in-stream coloniser is one that was originally captured in the source areas and then dispersed into the removal zone.

b) (Bottom): Percentage of recruits in the removal zone as a function of mean population density in the source areas.

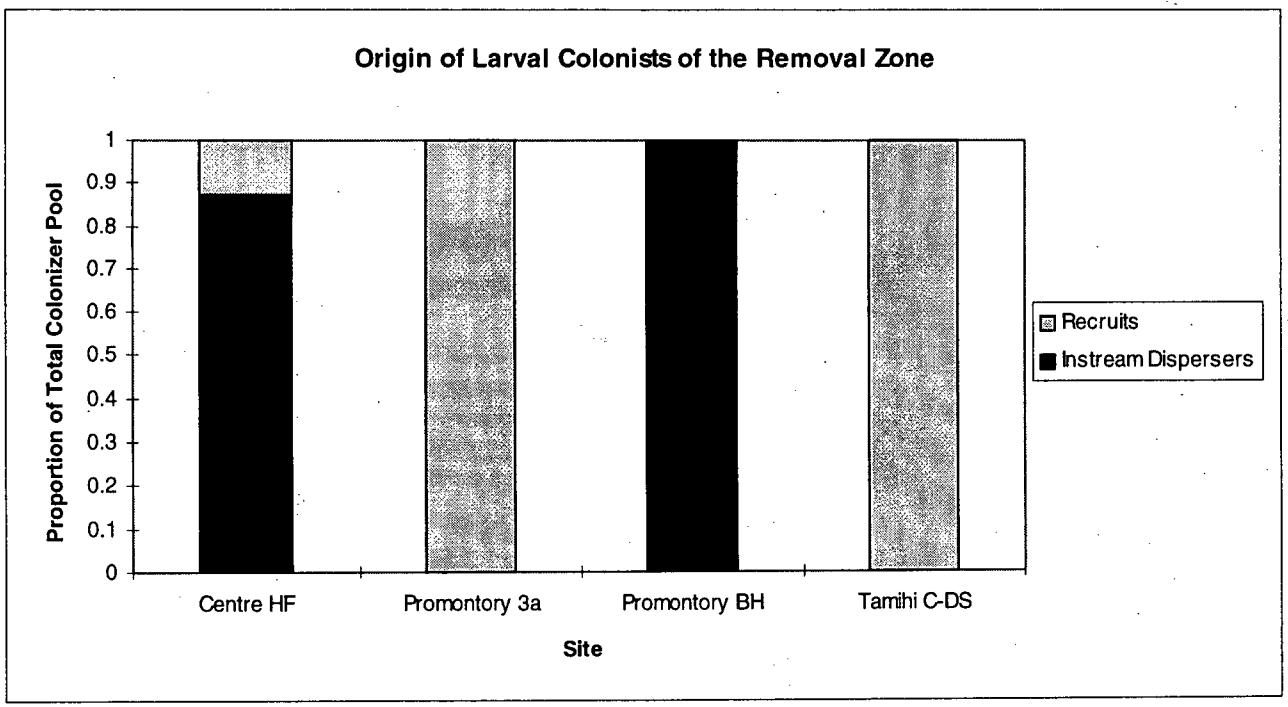


Figure 4.5: Origin of colonists that colonised the removal zone. In-stream dispersers are larvae that entered the removal zone from up or down stream. Recruits are young-of-the-year larvae that were likely deposited into the removal zone by adult dispersal and oviposition.

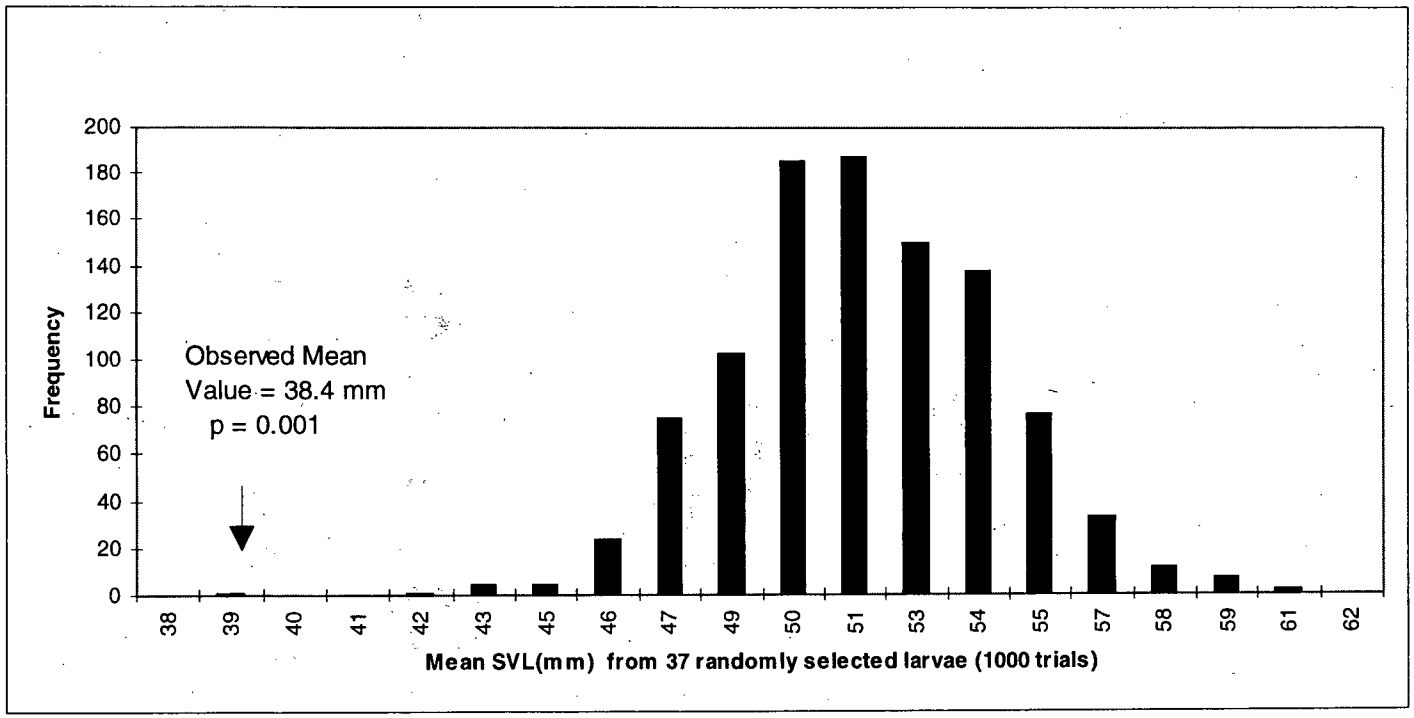


Figure 4.6: Expected distribution of mean snout-vent length (SVL) in a randomly selected group of 37 non-colonising larvae and the observed mean SVL in 37 known colonisers.

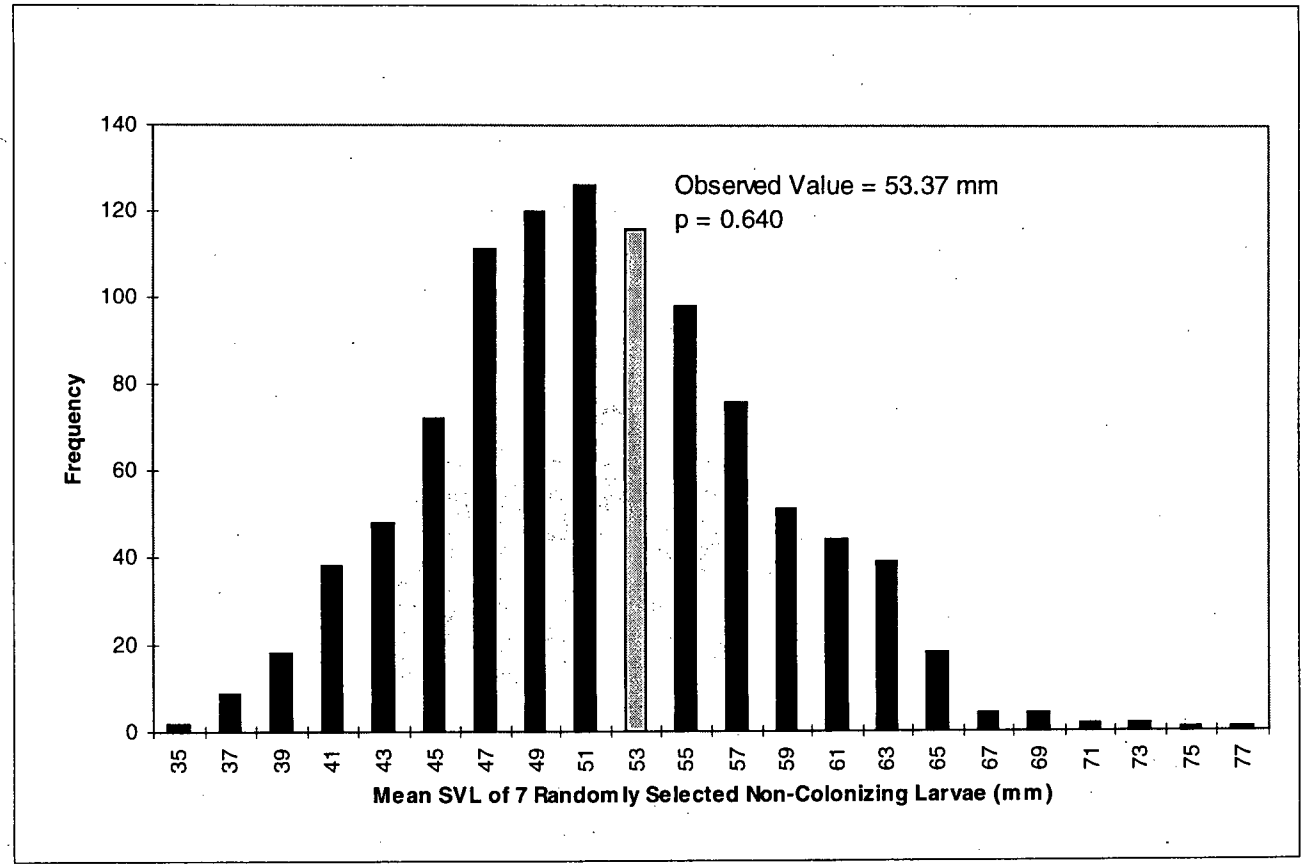


Figure 4.7: Expected distribution of mean snout-to-ventral length (SVL) in a randomly selected group of 7 non-colonising larvae and the observed mean SVL in 7 known in-stream colonisers. There is no significant difference in the mean length of larvae that actively colonised the removal zone and those that did not.

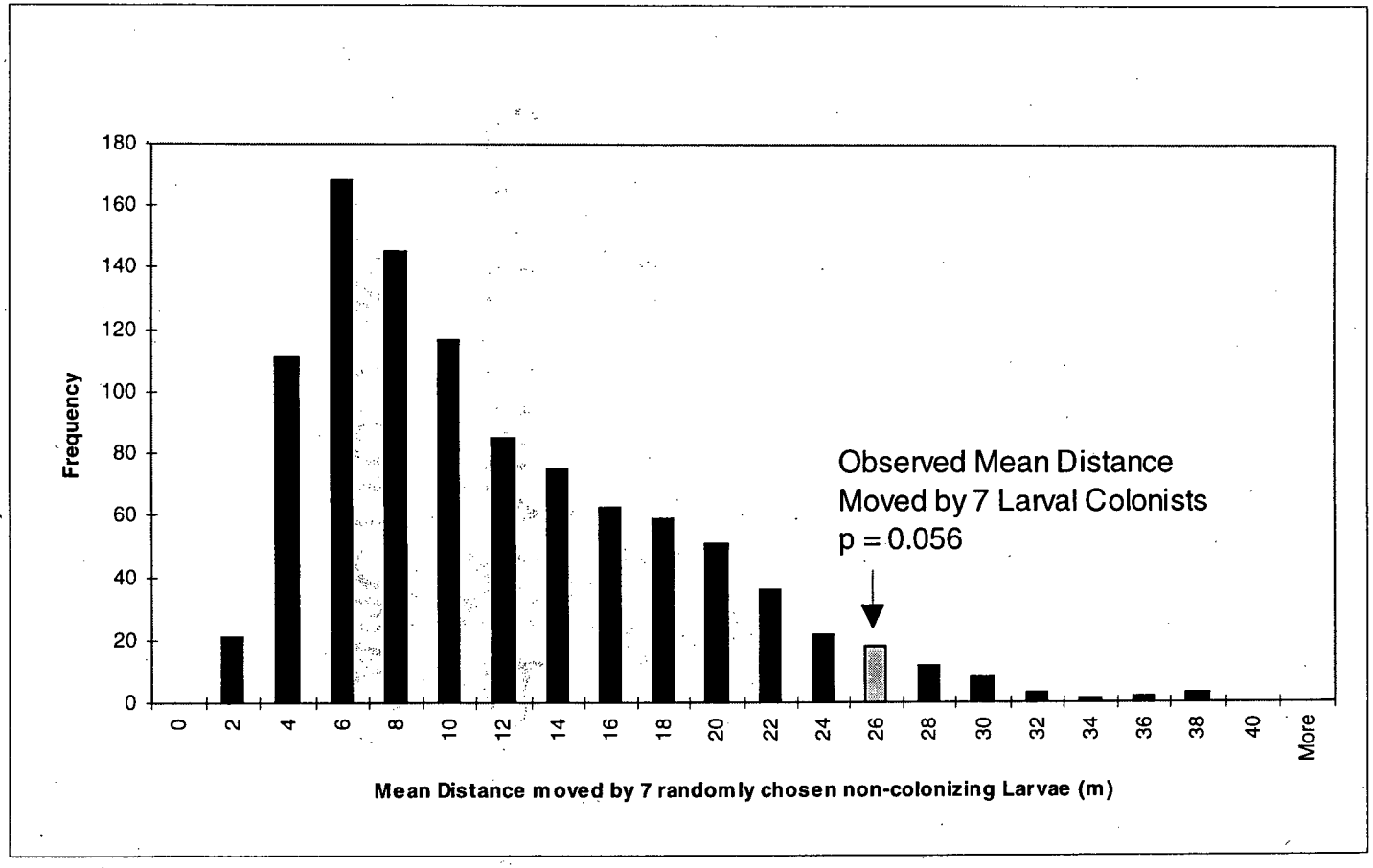


Figure 4.8: Distribution of mean cumulative distance travelled by 7 non-colonising larvae from the source areas of each site (based on 1000 trials). The mean value of this distribution, 10.7m, was lower than the mean value moved by the 7 colonising larvae : 26.1 m ($p = 0.056$).

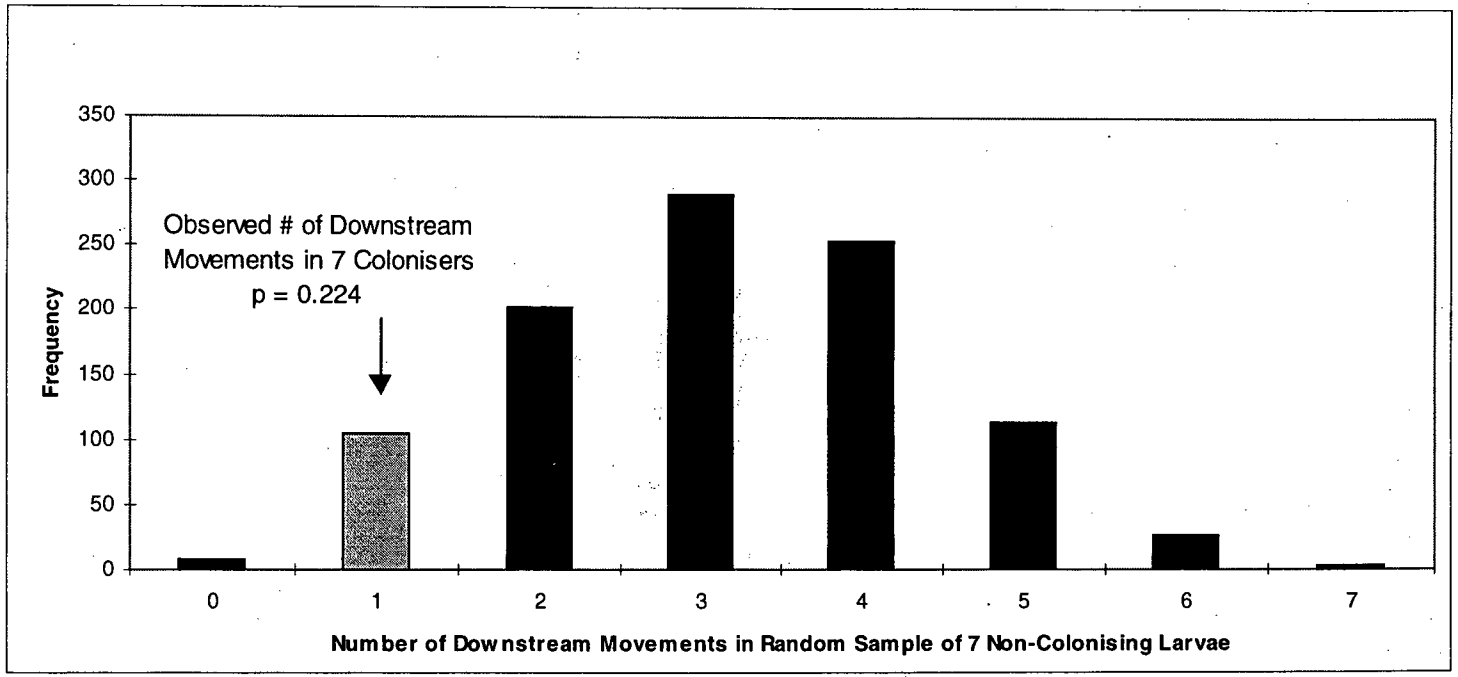


Figure 4.9: Distribution of the expected number of downstream movements in a randomly selected group of 7 non-colonising larvae (all sites pooled, based on 1000 trials). The mean of the expected distribution, 3.1 , was not significantly different from the observed number of downstream movements made in the group of 7 colonising larvae, p = 0.224.

Chapter 5: General conclusions

Two categories of risk must be addressed when evaluating a species' status: the likelihoods of stability and of persistence. Stability refers to the probability that abundance will remain constant, and persistence to the probability of extinction within a given time period (Connell & Sousa 1983). Given the difficulty of identifying 'stable' equilibria and distinguishing uncharacteristic declines from natural variation, it is often most useful to study factors which influence extinction probability and recovery potential (Connell & Sousa 1983). By examining the short-term population biology of larvae, my thesis has focused on factors that may influence *D. tenebrosus* persistence in British Columbia. Only long term monitoring of population trends will show whether this species is numerically stable in this province.

In the introductory chapter, I presented three general areas of investigation from which information on *D. tenebrosus* population viability and continued persistence can be drawn: studies of local demography, the impact of human activities, and the ability to recover from disturbance. Although I did not rigorously explore all of these issues in this thesis, my research on larval demography and colonising ability bears on each issue. After briefly reviewing my findings as they relate to these three areas, I will discuss whether the sum total of my research supports the notion that this species is at risk in British Columbia.

I. Review of major results

a) Local demography

Comparison of larval demography between threatened and non-threatened areas

I found the mean larval density in my 5 sites, 0.88 ± 0.09 m^{-2}, was just over a third of that reported in Oregon, the centre of the species' range (Corn & Bury 1989). The difference

between my density estimates and those from Western Washington, a neighbouring region where they are not endangered, is not nearly so pronounced. Kelsey (1995) calculated the mean larval density in unharvested stands in Western Washington to be 1.1 m^{-2}, only slightly greater than in this study. Lower densities in British Columbia suggests that these populations differ in one or more key demographic rates from those in Oregon.

Annual survival does not appear to vary much between these regions, however the length of the larval period does. Nussbaum & Clothier (1973) estimated annual larval survival in one Oregon stream to be 43%, only slightly higher than the 30-35% mean annual rate I estimated. According to my analysis, larvae in my four study streams could take 4-6 years to reach metamorphic size (130 mm TL +). Larvae in two Oregon streams were estimated to grow 2-3 times faster than larvae in my study, and are believed to have a larval period of only two years (Nussbaum & Clothier 1973). Even if annual survival was the same in Oregon and British Columbia, net survival through the larval period will be lower in British Columbia. For example if annual survival was 40% in both regions, survival throughout the entire larval period would be 16% in Oregon (2 year larval period), and only 0.5-3% in British Columbia (4-6 year larval period). This difference in net larval survival may help explain why densities of *D. tenebrosus* are lower in British Columbia than in the centre of its range. However, many more populations in both British Columbia and Oregon need to be studied before any geographic trends in survival can be confirmed.

Comparison of D. tenebrosus *larval demography with other salamanders*

Larval survival varies markedly between species and habitats and no typical value can be identified for stream dwelling salamanders. However it is useful to note that larval survival in *D.*

tenebrosus is similar to that in other species. I approximated annual survival of *D. tenebrosus* larvae to be 30-35% (corrected for transformation loss). Based on these rates, survival of *D. tenebrosus* through a 4-6 year larval period would be 0.5-3%. This range is similar to that of both *Ambystoma barbouri* and *Ambystoma texanum* whose survival through a 60 day larval period is 0.5-12.5% and 1-4% respectively (Petranka & Sih 1986, Holomuzki 1991). In one North Carolina stream, *Gyrinophilus porphyriticus* was found to have an annual survival of 21% (Beachy 1997), which would yield a net survival of 0.2% through its 4 year larval period. Thus survival of *D. tenebrosus* larvae in British Columbia is similar to that of other stream-dwelling species.

The growth rates I found for *D. tenebrosus* larvae are slightly lower than recorded in other temperate aquatic salamander species. I estimated *D. tenebrosus* larvae in my study streams would grow between 7.3-10.6 mm SVL per year. At similar latitudes in Alberta and Quebec, larvae of the pond dwelling *Ambystoma macrodactylum* and *Ambystoma maculatum* grow approximately 15 mm SVL although there is considerable variation (Flageole & LeClair 1992, Russell et al. 1996). Yearly increases of 12-20 mm SVL have been reported in stream dwelling *Eurycea wilderae* and *Hynobius kimurae* larvae (Beachy 1997, Misawa & Matsui 1997), but as these studies were conducted in more southern locations, comparison could be confounded by latitude effects. Although these between-species comparisons are useful, they may be confounded by differences in body size. Bigger species will likely have greater absolute growth even though their proportionate rate of increase could be lower than in small species. The species I have discussed here have slightly smaller larvae (1-2 cm) than *D. tenebrosus.*

I have shown that despite having reduced growth rates in comparison to populations in the centre of the species' range, *D. tenebrosus* in British Columbia has larval demography similar

to other stream dwelling salamanders. Annual survival and growth rates in *D. tenebrosus* larvae are comparable to those in other, non-threatened species. Although growth may not be maximal in British Columbia, larvae in these populations are not unusual with respect other stream-dwelling species.

b) The impact of human activities

The low number of sites used in this study makes it difficult to examine the influence of logging on *D. tenebrosus*. With almost no replication of forest age classes, I could not test whether variation in larval demography was due to logging or random site variation. However I found no relation between forest age and larval density across my five study sites. This neutral result has also be found by Hawkins (1983) and Kelsey (1995), but contradicts the positive association between density and forest age found by Bury (1983), Connor et al. (1988), Corn & Bury (1989), (Cole et al. 1997) and the negative association found by Murphy et al. (1981) and Murphy & Hall (1981).

I also noted that larval growth in my only clearcut site was twice as fast as in my second growth sites. From these observations, I speculate that clearcutting can reduce the density of larvae but that survivors may benefit from increased growth in disturbed habitats.

Finally I found that local larval dispersal (more than 10 m) was not influenced by any of 7 stream habitat variables including substrate type, pool-riffle composition, wetted width and depth. Dispersal was uniformly low through a wide variety of micro-habitats. Movement in my clearcut site was indistinguishable from that in my second growth sites. Blaustein et. al. (1994) suggested that anthropogenic habitat alteration exacerbates amphibian population extinction by hampering recolonisation. My results suggest that logging-induced habitat shifts in streams have

little consequence for the local dispersal of *D. tenebrosus* larvae. It is not known, however, whether these habitat changes influence the longer distance movements of larvae between confluent streams or the overland movement of terrestrial adults.

c) General ability to recover disturbance

To predict the likelihood of persistence, it is necessary to have information on a population's capacity to increase from low numbers either by recruitment or immigration (Blaustein et al. 1994). The speed of recolonisation varied between sites but was predicted to take 6-42 months to repopulate reaches of 25-40 m (26-75 m^2). Assuming the rates I observed in 13 months of study remained constant through time, moderate depletions of 0.1-0.3 larvae m^{-2} in headwater streams running through clearcuts (approximately 400 m x 1m) could take 8-20 years to be fully recolonised by larvae. Alternatively if logging caused an almost complete extirpation of larvae, full recolonisation of reaches running through a 400 m cutblock could take approximately 55 years.

The average life span of *D. tenebrosus* in the wild is not known, however similarly sized aquatic salamanders can live approximately 25 years in captivity (Duellman & Trueb 1986). If this value obtains in the field, recolonisation of stream reaches $\leq$ 400 m after moderate to severe disturbances could be achieved in one or two population turnovers. Thus provided source populations are nearby and habitat is suitable for breeding, numerical recovery can occur over short ecological time spans (less than 2 generations).

Experimentally defaunated stream reaches were repopulated both by larval dispersal and adult reproduction. Local reproduction appears to be a much more efficient means of repopulating an area than larval immigration. Only 4-5% of larvae in reaches adjacent to my

removal zones became colonists and this dispersal never contributed more than 13 individuals to any of my plots in 13 months. In contrast, clumps of 15-20 young-of-the-year, possibly all from the same clutch, were found at two sites in the summer of 1997. This suggests that in one breeding attempt, an adult female could provide an equal or greater number of colonists than supplied by neighbouring reaches with 100-200 larvae.

II. Implications for assessment of *D. tenebrosus'* status in British Columbia

Although logging and other disturbances may increase the rate of local extinction, my research suggests that *D. tenebrosus* populations in British Columbia are not unusually susceptible to disturbance. Although they are found at lower densities than in other parts of the species' range, larvae in these populations exist well within the survival and growth bounds of other non-threatened stream-dwelling salamanders. Furthermore, the combined influences of recruitment and larval recolonisation can facilitate rapid recovery from small-scale disturbances. Consequently, any argument of vulnerability must be based on the action of extrinsic factors such as logging.

In the absence of conclusive proof that logging increases local extinction rate beyond that which can be balanced by recolonisation, it is uncertain whether *D. tenebrosus* in British Columbia are truly imperilled. I caution, however, that my results are drawn from small-scale manipulations with limited replication. Their ability to describe the dynamics of all populations of *D. tenebrosus* in British Columbia and their response to disturbance is therefore limited. My colonisation rates were measured under optimal habitat conditions and in the presence of source areas containing many potential colonists. This situation is not likely to occur in the field, especially if potential disturbances such as logging occur frequently enough to diminish source

populations. To confirm my conclusions about the status of *D. tenebrosus* in British Columbia, future research should examine the colonisation of larger areas with a lower availability of potential dispersers and the colonising ability of terrestrial adults.

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Appendix 1: Chapman's Modification of the Lincoln-Peterson Method

$$N = \frac{(r + 1)(n + 1)}{(m + 1)} - 1 \qquad SE_N = \left[\frac{(r + 1)(n + 1)(r - m)(n - m}{(m + 1)^2 (m + 2)} \right]^{1/2}$$

where N = estimated population size, r = number of animals caught, marked and released in the first sample, n = the total number of animals caught in the second sample, and m = the total number of marked animals caught in the second sample (Chapman 1951).

Bias of Removal Studies	Attempted Solution in this Study
1) Low Trapability of animals prevents full removal of resident individuals.	This problem is paramount in studies that assume all animals found post-removal in the cleared zone are colonists, grossly over-inflating the dispersal rate. I could not clear all residents, but had a good estimate of the number of residents in the zone from pre-removal sampling. I used this to estimate an efficiency index for the removal. This index was used to determine what fraction of colonists were likely.
2) Distinguishing Colonisation from edge expansion	Mark-recapture was continuously conducted in the areas surrounding each removal zone. The origin of most colonists could thus be tracked to a location in the source areas. This allowed determination of the average dispersal distances made by colonists.
3) Density of Source Populations	Colonisation rates may vary with source population density. In this study, the density of each source population was repeatedly measured over the course of the experiment. As larval abundance varied considerably between sites, it was possible to examine whether colonisation was influenced by the density of the source areas.
4) Fate of Colonists	Some animals caught in the removal zone may have been transients. I used statistical techniques to determine the probability of an animal remaining in the zone given it was only captured there once.
5) Distinguishing Immigrants from Local recruits	Unmarked hatchlings found in the second year of study were considered to be recruits that had been oviposited into the removal zone and were not larval immigrants. They were still considered colonists, but categorised as the product of adult reproduction and not larval immigration.

Appendix 2: Common biases of removal studies (from Stenseth & Lidicker 1992) and attempts to correct them in this experiment.

Appendix 3 Estimating the Probability of one-time capture in the removal zone

This technique was used to estimate the probability that a larvae caught only once in the removal zone remained resident but undetected until the end of the experiment. A larvae was assumed to have colonised the removal zone on the first day it was captured in this area. Between this date and the end of the experiment there were n possible sampling occasions in which it could be recaptured given it was alive and within the study area.

The program CAPTURE was then used to estimate the mean per occasion capture probability of larvae at each site (Burnham et al. 1994). This probability was used to calculated an expected number of recaptures given the animal remained alive and in the removal zone until the end of the experiment. For example let us assume that a larvae was first caught in the removal zone in the 10 th mark-recapture after manipulation but never again in the remaining four sampling intervals Let us further assume that the mean capture probability of larvae over this time period 0.15 per occasion. The probability of the animal being present on all subsequent sampling days but not detected was calculated as follows:

$$P(\text{ never detected in 4 occasions } | \text{ present}) = (1 - 0.15)^4 = 0.52 \qquad \text{(Eqn. 1)}$$

Thus there is a 52% probability this animal remained in the zone after first capture but was not captured again. It was arbitrarily decided that any larvae with a greater than 50% probability of non-detection would be considered a colonist under the Statistically probable model.