

MEASURING THE EFFECTS OF INCREASING LOADS OF FINE SEDIMENT
FROM TIMBER HARVEST AND ROAD BUILDING
ON AQUATIC POPULATIONS OF *DICAMPTODON TENEBROSUS*
(PACIFIC GIANT SALAMANDER) IN CALIFORNIA'S REDWOODS.

by

Seth Pogue

A Thesis

Presented to

The Faculty of Humboldt State University

In Partial Fulfillment

of the Requirements for the Degree

Master of Arts

In Science and Natural Resources: Biology

May, 2008

MEASURING THE EFFECTS OF INCREASING LOADS OF FINE SEDIMENT
FROM TIMBER HARVEST AND ROAD BUILDING
ON AQUATIC POPULATIONS OF *DICAMPTODON TENEBROSUS*
(PACIFIC GIANT SALAMANDER) IN CALIFORNIA'S REDWOODS.

by

Seth Pogue

Approved by the Master's Thesis Committee

John Reiss, Major Professor Date

Michael Camann, Committee Member Date

Sean Craig, Committee Member Date

Michael Mesler, Committee Member Date

Michael Mesler, Graduate Coordinator Date

Chris A. Hopper, Interim Dean Date
Research, Graduate Studies

ABSTRACT

Dicamptodon tenebrosus (Pacific giant salamander) was evaluated for suitability as an indicator of aquatic habitat quality relative to increasing loads of fine sediment from timber harvest and road building. I compared three surrogates of *D. tenebrosus* population success - biomass per unit area, density, and number of age classes (dependent variables) to two measures of stream sedimentation - RSI, which measures how much of the stream bed becomes mobilized at peak flow, and D_{50} , the median bed particle diameter (independent variables) on 49 streams from three subjective disturbance categories: a control group, a moderate management group, and a high management group.

Streams impacted by sediment exhibited fewer surviving age classes, and also significantly less biomass per square meter of pool bottom. These streams were from the moderate and high management categories. Unimpacted streams (control group) exhibited the greatest number of surviving age classes and the highest biomass.

This study also presents the first quantitative analysis of *D. tenebrosus* age class structure. These animals live to be at least twelve years old.

ACKNOWLEDGEMENTS

This project was funded both by private grants and by a contract from the California Department of Forestry (CDF). Special thanks to Christopher Knopp of the North Coast Regional Water Quality Control Board, who helped lay the foundation upon which this study was conceived and carried out; Bill Trush of Humboldt State University's Institute for River Ecosystems; Pete Cafferata of CDF, Harte Welsh, Jr. and Lisa Ollivier of USDA Forest Service Pacific Southwest Research Station, to Drs. James Waters, John Reiss, Michael Camann, Michael Mesler, Sean Craig, John Sawyer, Milton Boyd, and Richard Hurley of the Department of Biological Sciences at Humboldt State University (H.S.U.), and to the H.S.U. Foundation. Thanks also to the U.S. Forest Service, the Bureau of Land Management, the National Park Service, California State Park Service, and the many private landholders, many of whom wish to remain anonymous, who allowed me to access the study stream reaches via their lands. I collected the data along with Keith Evans, Chris Grostick, Colleen Harper, Bill Lydgate, Brad Norman, Lisa Ollivier, F. Scott Riley, Chris Robinson, John Schirmer, Greg Walsh, and Jessica Watchell.

And above all else, my most profound gratitude to the late Dr. Samuel F. Pogue, whose unwavering love, support, and inspiration helped set this project - - and every other good thing in my life -- firmly on its feet.

TABLE OF CONTENTS

ABSTRACT.....	iii
ACKNOWLEDGEMENTS.....	iv
TABLE OF CONTENTS.....	v
LIST OF TABLES.....	vii
LIST OF FIGURES.....	viii
INTRODUCTION.....	1
Choosing a Vertebrate Indicator of Habitat Quality.....	3
<i>Dicamptodon</i> as the preferred amphibian indicator.....	3
<i>Dicamptodon</i> Niche and Habitat.....	5
Assumptions About Habitat Quality.....	6
MATERIALS AND METHODS.....	8
Study Area.....	8
Watershed Groups.....	8
Disturbance Category 1.....	10
Disturbance Category 2.....	11
Disturbance Category 3.....	11
Predictor Variables.....	13
RSI.....	13
D ₅₀	15
Response Variables.....	15
Biomass.....	15

Density	16
Age Classes.....	17
Multifan.....	17
Habitat Type Selection.....	19
Pool Selection Criteria	19
Pool Survey Technique.....	20
Statistical Analysis.....	21
RESULTS	23
Biomass as a function of D_{50}	23
Age Classes as a Function of D_{50}	23
Density as a Function of D_{50}	23
Biomass as a function of RSI.....	25
Age Classes as a function of RSI.....	25
Density as a Function of RSI	25
Differences between Disturbance Categories	32
Discriminant Analysis.....	38
CONCLUSIONS.....	40
Management Implications.....	44
LITERATURE CITED	48
APPENDIX A D. TENEBROSUS GROWTH AND AGE PARAMETERS	56
APPENDIX B OTHER REGRESSION SUBSETS	58

LIST OF TABLES

Table		Page
1	Regression of population variables on D_{50} and RSI	24
2	ANOVA among disturbance categories.....	33
3	MANOVA among disturbance categories	39

LIST OF FIGURES

Figure		Page
1	Locations of Study Streams	9
2	<i>D. tenebrosus</i> biomass (g/m^2) as a function of mean bed particle size (D_{50})	26
3	<i>D. tenebrosus</i> age classes as a function of mean bed particle size (D_{50})	27
4	<i>D. tenebrosus</i> density as a function of mean bed particle size (D_{50})	28
5	<i>D. tenebrosus</i> biomass (g/m^2) as a function of riffle stability (RSI)	29
6	<i>D. tenebrosus</i> age classes as a function of riffle stability (RSI)	30
7	<i>D. tenebrosus</i> density as a function of riffle stability (RSI)	31
8	Biomass across the disturbance categories	34
9	Age Classes across the disturbance categories	35
10	D_{50} across the disturbance categories	36
11	RSI across the disturbance categories.....	37

INTRODUCTION

Forest riparian and aquatic habitats in the Pacific Northwest, while naturally resilient, have been dramatically affected by clearcutting in adjacent uplands (Reeves et al. 1995, Jones and Grant 1996, Perry and Amaranthus 1997). California State regulatory agencies are mandated to administer renewable resources; this requires tools that allow accurate, repeatable quantification of the effectiveness of best management practices. Efforts to comply with this mandate of beneficial uses of water have recently generated three useful physical measurements of sedimentation: V^* , RSI, and D_{50} (Kappesser 1993, 2002; Knopp 1993, Lisle and Hilton 1992). Sedimentation has been shown to detract from a variety of beneficial uses of water quality (Lannoo 2005, Murphy and Meehan 1991, Platts et al. 1983). One of these beneficial uses is biodiversity. Therefore, this project was conceived in order to develop a quantitative biological index of downslope effects of non-point source pollution from timber harvest, road construction, and related forest use practices.

Sedimentation of aquatic ecosystems is a common effect of timber harvest and road building (Meehan 1991, Reid 1993, Waters 1995). Patch dynamics of the surrounding landscape directly affect the stream network within by influencing hydrologic patterns, microclimates, sediment loads, and energy inputs, and thus affect the incidence and abundance of the associated riparian and stream biota.

Earlier studies have established long-term detrimental effects of logging on resident forest herpetofaunas (Bury 1983, Bennet et al. 1980, Corn and Bury 1989, Murphy and Hall 1981, Pough et al 1987, Welsh and Lind 1988, 1991, and 2002). In this study, density, biomass, and age class structure of *Dicamptodon tenebrosus* was compared to the riffle's armoring and stability (as measured by RSI), and to the median particle diameter of the riffle (D_{50}), in order to quantify the impact of increasing loads of fine sediment on aquatic *D. tenebrosus* populations in California's redwoods.

The variables selected for this study are believed to reflect important aspects of stream condition. The effect of changing loads of fine sediments (as measured by RSI and D_{50}) on channel morphology, primary food production, and salmonid spawning success is well documented in controlled laboratory studies, but remain controversial in natural systems (Hicks et al., 1991; Chapman, 1988). Fining and aggradation of bedload particles is likely to adversely affect these salamanders, so the procedures developed and tested here, and the database established, will augment our knowledge of ecological processes and provide key information on how landscapes can best be managed to maintain sensitive native fauna such as amphibians. This study seeks to provide an ongoing tool for the assessment of instream conditions with respect to land uses,

for identification of factors that potentially limit biological productivity, and for identification of sensitive watersheds (Semlitsch 2000).

Choosing a Vertebrate Indicator of Habitat Quality

The vertebrates most amenable to use for assessing instream habitat quality are fish and amphibians. However, simple fish population estimators, without quantification of the relative effects of external influences, make it difficult to measure the effects of increasing sediment loads upon fish survivorship. There exists no single panacea for explaining declining numbers of anadromous fish, which may vary in response to known factors such as commercial, sport, and Indian fishing take. Therefore, fish population estimates represent a tenuous measure of stream habitat quality.

Dicamptodon as the preferred amphibian indicator

Aquatic *D. tenebrosus* was selected for this study because:

- 1) There are no well-documented external (anthropogenic) influences, such as harvesting, that are known to affect its fecundity and survival.
- 2) Amphibians are relatively long-lived compared with fish (Moyle 1976, Groot and Margolis 1991).
- 3) Larval and neotenic *Dicamptodon* stay in-stream over the course of the entire summer season. This suggests that net *Dicamptodon* pool

biomass remained stable during the sampling window for this study (H. Welsh, personal communication).

- 4) *D. tenebrosus* is northern California's most abundant aquatic amphibian and was likely to be present in most of the sampled watersheds (Murphy and Hall 1981).
- 5) The capture technique described by Parker (1991) provides highly accurate and repeatable raw population censuses of these amphibians. With most large-scale censuses, the potential exists for some individuals to go undetected. Also, there may exist a tendency to underestimate *D. tenebrosus* parameters in the control reaches (see Materials and Methods) because of greater cover availability there. This would tend to obscure the differences between the control and managed rivers, so MANOVA F-ratios below should be interpreted as minimums. It is very unlikely that any *D. tenebrosus* were actually present in the censused pools from the two rivers where no animals were found, since the binomial probability of failing to detect existing aquatic amphibians in a 10-meter -long survey of forested stream <2 m wide is 1.5×10^{-8} (Corn and Bury 1989).

Dicamptodon Niche and Habitat

Larval and paedomorphic *Dicamptodon tenebrosus* inhabit cool, cascading creeks, as well as larger, slower streams and standing water. They range from the coastal Mendocino/Sonoma County border, California, to British Columbia (Good 1989). There have been no indications of declines or increases in historical distribution, but there has probably been some fragmentation within their range resulting from habitat alterations, mostly due to forestry practices (Lannoo 2005). These salamanders play an important functional role in forest ecosystems that relates to several unique aspects of their ecology. They can comprise >95% of vertebrate predator biomass in streams, exceeding salmonids as top carnivores (Murphy and Hall 1981, Pough 1980, Wake 1991). By exploiting invertebrates too small to be used by birds and mammals, they make biomass available to larger vertebrates. Since salamanders are ectothermic, they have very low metabolic rates. This allows 40-80% conversion of ingested energy into tertiary productivity, making them both quantitatively and qualitatively important components of many forest ecosystems (Pough et al. 1987). The fact that their numbers appear to be reduced by certain anthropogenic factors could potentially affect energy flow and biomass production at all levels (Blaustein and Wake 1990, Murphy and Hall 1981, Pechmann et al. 1991, Welsh and Lind 1988).

Total length (TL) of larvae and pedomorphs ranges from 40 to 350 millimeters (Nussbaum et al. 1983, Welsh and Ollivier, unpublished data). Many of these salamanders transform to the terrestrial lifestage once TL exceeds 100 mm, while some individuals are neotenic, reaching sexual maturity while retaining larval characteristics such as external gills, tail fin, dorsoventrally flattened skull, primitive pelvic and pectoral girdle, and aquatic habitat.

Population densities of aquatic salamanders are dependent on substrate composition (Parker 1991, Davic and Orr 1987, Hawkins et al. 1983). Cobbles, boulders, and interstices provide habitat for their invertebrate food base, cover from predation, and probably from high streamflows and scour as well (Waters 1995).

Predators include weasels and river otters (Mustelidae), water shrews (Soricidae), garter snakes (*Thamnophis* sp.), salmonids, and conspecifics (Fitch, 1941; Nussbaum and Maser, 1969; Nussbaum et al., 1983; Lind and Welsh, 1990, Parker, 1993).

Assumptions About Habitat Quality

Habitat has been defined as the resources and conditions present in an area that produce occupancy, including survival and reproduction, by a given organism. Habitat quality is the ability of the environment to provide conditions appropriate for individual and population persistence (Hall et al. 1997). From

one perspective, individual organisms occupying high quality habitats produce the most progeny and maximize their lifetime reproductive success. From another perspective, the habitat with the higher carrying capacity is the higher quality habitat. That is, high quality habitat supports a larger persistent population (Johnson 2005).

All taxa, including high trophic level vertebrate carnivores such as *Dicamptodon*, evolved as a reflection of selective pressures imposed by the physical, structural and biotic elements of their ancestors' habitat. High quality habitat contains the mean mix of these elements, as expressed by the range of values measured in the control reaches. The response of *D. tenebrosus* populations to deviations from this naturally occurring range of values, as measured in the experimental reaches, is a central issue evaluated by this study. The similarity in geologic substrate, forest type, slope, and drainage area across all streams examined by this study suggests that these streams had similar amounts of available habitat before timber harvest and road building took place. If the relative amount of available habitat is a reasonable indicator of the number of mature organisms that can be supported there (Southwood 1977), then the number and biomass per unit area of mature neotenic *Dicamptodon* in these streams was probably similar as well.

MATERIALS AND METHODS

Study Area

Stream sampling took place in 51 coastal Redwood watersheds, from just above the California border in Oregon's Kalmiopsis Wilderness to the north, through Del Norte, Humboldt, and Mendocino County, and Sonoma Counties, to the southern limit of *Dicamptodon tenebrosus*' range in to the south. (Map, Figure 1.)

Watershed Groups

The streams I sampled were from the group of 60 watersheds sampled by Knopp in his 1993 study. Given constraints of time, budget, and manpower, I was able to visit 51 of the streams. Two reaches were dropped from the analysis due to sampling error. One of the rivers was sampled for *D. tenebrosus*, but not for RSI. The other was an extreme outlier because, although this river appeared uniform along all 1000 meters when sampled by Knopp (after six years of drought) in 1992, an earthquake and ten year flood returns the following winter had caused a road failure at one end of the reach. In following a strict, literal adherence to the sampling protocol (see Methods), *Dicamptodon* sampling was taken here, while RSI sampling was done at the other end of the reach, in an area essentially free from the influence of this point sediment source. Since this study was designed

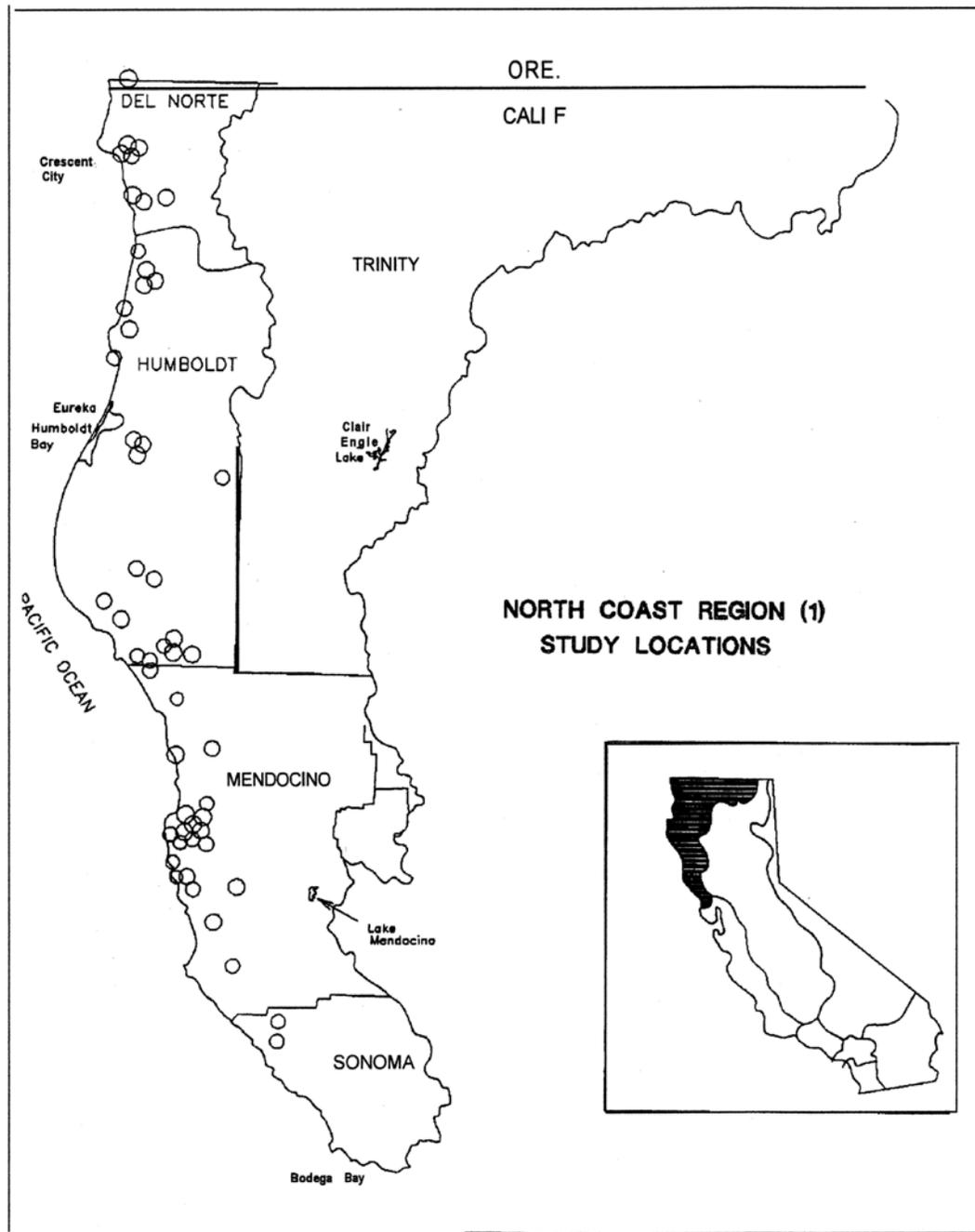


Figure 1. Locations of Study Streams

to measure the influence of *non-point* sediment impacts, and since RSI and *Dicamptodon* samples were taken from morphologically dissimilar sections of the river, this reach was dropped from the analysis.

Here is how Knopp selected the 60 streams:

Randomized samples were selectively located within 1000 meter long Rosgen B-3 type channel reaches (Rosgen 1985), with similar slope (one to four percent), and similar drainage area (two to twenty square miles).

The forty-nine streams evaluated are from the three watershed groups evaluated by Knopp in 1993 (hereafter known as disturbance categories 1, 2, and 3): a control group, containing all watersheds that satisfy the control criteria, and two experimental groups, drawn at random (from a hat by a disinterested employee of the North Coast Regional Water Quality Control Board - C. Knopp, personal communication) from a pool of 140 managed watersheds that met the criteria for stream slope, drainage area, and geology, to provide a range of potential instream habitat values to be compared to control (index) habitat conditions.

Disturbance Category 1

This is the control group ($n=17$). This category is a combination of two groups, hereinafter known as index and index (+) watersheds. Index watersheds ($n=11$), are essentially undisturbed by past or present human activity, with late

seral (old growth) forest. All known watersheds that met these criteria were sampled.

Index (+) watersheds ($n=6$), are mature-forest drainages with little or no upslope disturbance within the past 80-100 years and little evidence of residual erosion or instability due to past human activity. All known watersheds that met these criteria were sampled. As measured *Dicamptodon* and sediment variables were not significantly different between index and index (+) groups, these two groups were combined into disturbance category 1 for ANOVA, MANOVA and discriminant analysis.

Disturbance Category 2

This group ($n=16$) was comprised of watersheds with some management within the past 50 years, but with good protection of stream courses, upper- and mid-slope road locations and avoidance of unstable terrain. Timber harvest operations reflect predominantly cable systems.

Disturbance Category 3

This group ($n=16$) represents high management watersheds, drainages with recent clear-cuts, often with some protection of stream courses, but also including those exhibiting large areas of disturbed soil; unpaved, lower slope roads; inconsistent or poor stream course protection; inconsistent avoidance of

unstable terrain; and/or bulldozer "blading" of channels. Ideally, disturbances were five to ten years old.

Knopp assigned managed reaches to either disturbance category 1 or 2 based upon management histories of the watersheds, aerial photographs, and a detailed sediment budget. He writes:

"The sediment budget used in this analysis evaluated 3 separate periods for each of 60 watersheds. The intent of this budget was to develop an 'order of magnitude' resolution only. All data were derived by digitizing in roads, harvest units, stream crossings, and landslides directly from air photos and topographic maps into a CAD program. The data were separated by three (3) slope positions and in some cases by relative impact levels. No field checking was done. The analysis was done by a member of the Water Board's staff who was not familiar with the subjective analysis already underway so as to avoid bias. Once sediment sources were entered, the CAD files were simply analyzed by layers to determine the extent (of sediment input), by source, in each watershed. The results from the sediment budget were used to validate the descriptive categories. Given the results of this study, a shortcoming of the sediment budget as designed was that impacts prior to 1960 were not quantified. Given the longevity of historical impacts, future budgets should attempt to account for them."

Predictor Variables

RSI

The Riffle Stability Index (RSI) was designed to measure whether a stream channel is aggrading, in dynamic equilibrium, or degrading (Kappesser, 1993, 2002). A given RSI value represents the degree of armoring within a riffle reach relative to the size of material normally transported at bankfull flow. Increased quantities of fine particles on a streambed's surface are thought to represent a channel that is transporting a high sediment load (Platts and Megahan, 1975; Lisle, 1982). Dietrick et al. (1989) reported that the surface layer may increase its percent of fine sediments solely as a result of an increased supply of sediment, even when the particle sizes being transported remain constant. Therefore, the proportion of fines in the riffle bed compared to the largest particle the stream system is capable of transporting at bankfull flow is believed to represent the current dynamics of a channel's sediment transport process -- providing a sensitive, quantitative evaluation of whether the channel is aggrading, degrading, or in dynamic equilibrium.

Index numbers for the Franciscan geology typically range from 50 to 100, with high range numbers reflecting a riffle with a high surface fine composition and low numbers indicating a bed with few fines on its surface. For example, an RSI value of 75 indicates that 75% of the particles on the riffle bed are equal to or

smaller (finer) than the largest particle the river is capable of transporting at bankfull discharge. This indicates that the finer 75% of the bed particles were mobile at the last bankfull flow; the coarsest 25% remained stable.

The sampling technique for RSI has two components (Kappesser 1992):

- 1) Surface composition is measured with a modified Woolman pebble count. Riffle transects are established and 200 individual pebbles are measured at intervals of 300 mm along the transects to establish a geometric mean surface particle size. The particle size data is tallied by Udden-Wentworth size classes to yield a cumulative "percent finer" value for each class.
- 2) The largest material transported at bankfull discharge is determined by measuring the intermediate axis of the 30 largest cobbles on an adjacent point bar where available, or from a clear depositional bar within the riffle. These cobbles must all measure within 20% of one another. Only particles clearly mobile, as evidenced by their association with the bar form, are measured. The average of these thirty measurements produces a value which is then superimposed on the riffle bed particle size distribution, yielding a "percent finer", which is the RSI value.

This two-part process was performed on the first three suitable riffle areas encountered while walking upstream from the downstream end of each 1000 m

reach of river. Riffles sampled represent a section of stream a minimum of three channel widths long, with uniform characteristics. Riffle sections with depositional features from dammed pools or mass failures were avoided. The distance of each sampled riffle from the reach tail was recorded using a forester's hip-chain, to facilitate repeatability.

D₅₀

D₅₀ is a measurement of the median particle diameter of the riffle. That is, 50% of the riffle bed's particles are finer; 50% are coarser. As a channel's sediment load increases, D₅₀ drops, and interstitial spaces become filled with fine sediments, reducing available cover. At the same time, RSI values rise, as a higher proportion of the riffle bed becomes mobile in response to this fining.

I personally collected all RSI and D₅₀ data, measuring 33,810 bed particles on 147 riffles.

Response Variables

Biomass

Biomass was measured in grams/m² of pool bottom area of larval and neotenic salamanders. During data analysis, biomass of neonates was subtracted from the total biomass. The rationale behind this is twofold. First, biomass had to be compared to RSI in regression analysis (see statistical analysis). RSI yields a

measure of percent bedload movement during the previous winter's peak flow. Since channel shear stress is greatest at this time, streambed mobility and scour is also at a maximum. It was important to include only animals that had survived this scouring flow.

Also, ecologists often ignore newborn individuals when assessing population patterns (J. Sawyer, personal communication). The presence of neonates says little about the habitat's ability to sustain viable populations; it evinces only that an adult (possibly a terrestrial morph living outside of the stream being measured) laid eggs that hatched since the last scouring flow. Evaluating the ability of the habitat to support a cohort through the first year of life and beyond is a more accurate measurement of habitat quality. By removing neonates from the analysis, I was able to focus on only those salamanders that had survived at least one year within the habitat being evaluated. All captured terrestrial salamanders were also excluded from the analysis. This adjusted biomass was divided by pool bottom area, yielding biomass in g/m².

Density

For purposes of this study, density is defined as the total number of salamanders per square meter of pool bottom. This "head count" ignores both age and weight of captured salamanders. Neonates were excluded from this analysis.

Age Classes

This is a measure of the age class distribution of *Dicamptodon* for each reach. If habitat quality for a wildlife species is a measure of the importance of habitat type in maintaining a particular species, habitat quality should be defined in terms of the survival and production characteristics, as well as the density, of the species occupying the habitat (Van Horne 1983). One of the main purposes of this study was to determine whether age class distribution offered a quantifiable, repeatable measure of habitat condition. The computer program Multifan was used to determine the age class structure and growth rate of larval and neotenic Pacific giant salamanders.

Multifan

Until now, little was known about longevity in coastal giant salamanders (Lanoo, 2005). *D. tenebrosus* length data were analyzed using the program Multifan, which employs a robust maximum likelihood based method for estimating growth parameters (including Von Bertalanffy K) and age composition for multiple length frequency data sets (Fournier et al., 1990). The data were assigned to five sets - one for each of five months of sampling, in order to account for growth during the sampling period. The program recognized eleven age classes (Appendix A).

Although Multifan recognized salamanders larger than those in age class eleven, it could not assign any of them to a particular age class given the size of the present data set. Part of the challenge in assigning ages to animals larger than age class 11 was a length-dependent trend in standard deviations at age; that is, the standard deviation of length at age increased as age increased. The increasing variability in size at age as animals grow older is probably influenced by differences in microhabitat conditions such as food availability and temperature (Van Der Have and De Jong, 1996, Smith Gill and Bervin, 1979). There may be a genetic component as well.

As many of the animals captured were larger than Multifan's assigned length for age class 11 (92.39 to 103.50 mm snout-vent length, SVL) - any animals larger than 103.50 mm SVL were grouped together as age class 11+ for purposes of analysis. Therefore the response variable Age Classes has a range of values from 0-12.

Perhaps in the future, a modified model and/or additional data will yield several more age classes. Visual extrapolation of the age class histograms, which contain some animals >140 mm SVL, and of the Von Bertalanffy growth curve, suggest there may be twenty or more age classes [Appendix A].

Habitat Type Selection

Pools are the habitat type most amenable to efficient salamander sighting and capture using a glass-bottom viewer (or SCUBA mask) and metal mesh strainer. Also, in Rosgen type B-3 channels, pools are where salmonids spawn. Although this study does not examine relationships between any of the measured variables and salmonid survival, the database established here will be useful as a component of future studies designed to establish ties between the *Dicamptodon* and sediment parameters investigated herein and the decline of anadromous fish populations.

Pool Selection Criteria

The pool selection criteria were established by Knopp in 1993. Pools must:

- 1) Occupy at least 60% of the wetted perimeter of the channel.
- 2) Be at least four (4) times the depth of riffle crest at deepest point.
- 3) Be lateral scour pools or other pools formed as an expression of the stream's natural meandering geometry. Therefore, pools that were bedrock or woody debris controlled were excluded. Step pools, dammed pools, boulder-formed pools, and channel confluence pools were likewise avoided.

- 4) Be surveyable in an accurate manner, given time and personnel-power constraints. Therefore, pools with deeply undercut banks, giant, unmovable boulders, or depths greater than one and a half (1.5) meters were avoided.
- 5) Be representative, similar to other pools found on the reach.

Pool Survey Technique

Moving upstream from the tail of each preselected 1000 m reach of stream, the first four pools that met the criteria outlined above were thoroughly searched two to four times until all visible *Dicamptodon* were caught. We lifted every cover object larger than about 30 mm along its primary axis. When a salamander was sighted, a metal mesh spaghetti strainer was placed in front of the animal, while its tail/hindquarters was gently tapped in order to coax the animal to move into the strainer. In this way we captured over 2,100 salamanders.

Captured animals were sorted by size and placed in up to five separate buckets (in order to prevent conspecific predation), then weighed to the nearest tenth of a gram on a digital scale. Snout-vent lengths (SVL) were measured to the nearest millimeter. Cover objects were then replaced. Many cover objects that had been partially embedded prior to our search were left unimbedded, which means our sampling left a net increase in available cover in the sampled pools. Salamanders were released unharmed. Pool lengths were measured to the nearest 1/10th of a meter, and up to six (6) width measurements (more with

decreasing uniformity of pool width) were averaged to determine pool area. The distance of each sampled pool from the bottom of the reach was recorded using a forester's hip-chain, to facilitate return to the site for future monitoring.

Statistical Analysis

One purpose of this study was to establish a relationship between the two measures of channel sedimentation (predictor variables), and the three *D. tenebrosus* population viability surrogates (response variables). Therefore, univariate regressions were performed to test the null hypothesis of no correlation between predictor and response variables at $\alpha = 0.01$ (Table 1). Regressions graphics were generated using Cricket Graph version 1.3 (Computer Associates International); t-values, f-ratios, and probability levels were calculated by Number Cruncher Statistical System (NCSS) version 6.0.

Another issue evaluated by this study was whether differences in habitat condition between the three original (subjective) disturbance categories could be statistically validated. ANOVA and MANOVA comparison of the three disturbance categories using biomass, size classes, RSI, and D50 was executed on NCSS, using a strict $\alpha = .01$, to test the null hypothesis of no difference between category means.

Discriminant analysis was then performed on NCSS using biomass, age classes, RSI, and D₅₀, to test the null hypothesis of percent correct classification of

disturbance categories the same as by chance alone, with p to enter=0.10, p to exit=0.15. Cohen's Kappa statistic was utilized to test for correct classification due to chance alone (Titus et. al. 1984).

RESULTS

Dicamptodon populations are adversely affected by increasing sediment. Regressions demonstrate that as sediment levels rise, both biomass per unit area and the breadth of age class distribution decreases significantly and predictably. The number of salamanders per unit area decreases as well, although this variable is not as tightly linked to sedimentation as are the other two. (Table 1.)

Biomass as a function of D₅₀

Biomass of *D. tenebrosus* covaries with changes in D₅₀ ($r^2=.6511$, $t= 9.27$, $P < 0.0001$, Figure 1). As D₅₀ decreases, so does pool bottom biomass of these salamanders.

Age Classes as a Function of D₅₀

The number of age classes present varies along with D₅₀ ($r^2=.5686$, $t = 7.97$, $f\text{-ratio} = 60.63$, $p < 0.0001$, Figure 2). Decreasing median particle size of the bed correlates with a narrower *Dicamptodon* age class distribution.

Density as a Function of D₅₀

The median riffle particle size and numbers of *D. tenebrosus* per square meter decrease together, though this relationship is not as strong as that of biomass or age classes. ($r^2=.1879$, $t = 3.28$, $p < 0.0001$, Figure 3)

Table 1. Regression of population variables on D₅₀ and RSI

Predictor Variable	Response Variable	r-squared	t-value	Prob.
D ₅₀ '93	Biomass (g/ m ²)	.6511	9.27	<0.0001
D ₅₀ '93	Age Classes	.5686	7.97	<0.0001
D ₅₀ '93	Density	.1879	3.28	<0.0001
RSI '93	Biomass (g/ m ²)	.6681	9.26	<0.0001
RSI '93	Age Classes	.5753	7.89	<0.0001
RSI '93	Density	.2165	3.57	0.0009

Biomass as a function of RSI

Biomass of *D. tenebrosus* per square meter varies predictably with changes in RSI ($r^2 = .6681$, $t = 9.26$, $f\text{-ratio} = 92.59$, $p < 0.0001$, Figure 4). As bed mobility increases, biomass drops.

Age Classes as a function of RSI

There is a strong relationship between RSI and the number of age classes per reach ($r^2 = .5753$, $t = 7.89$, $f\text{-ratio} = 62.30$, $p < 0.0001$, Figure 5). As bed mobility increases, the number of age classes decreases.

Density as a Function of RSI

Numbers of *D. tenebrosus*/m² decrease as RSI increases, though this relationship is somewhat not as strong as that of biomass and age classes ($r^2 = .2165$, $t = 3.57$, $p = 0.0009$, Figure 6).

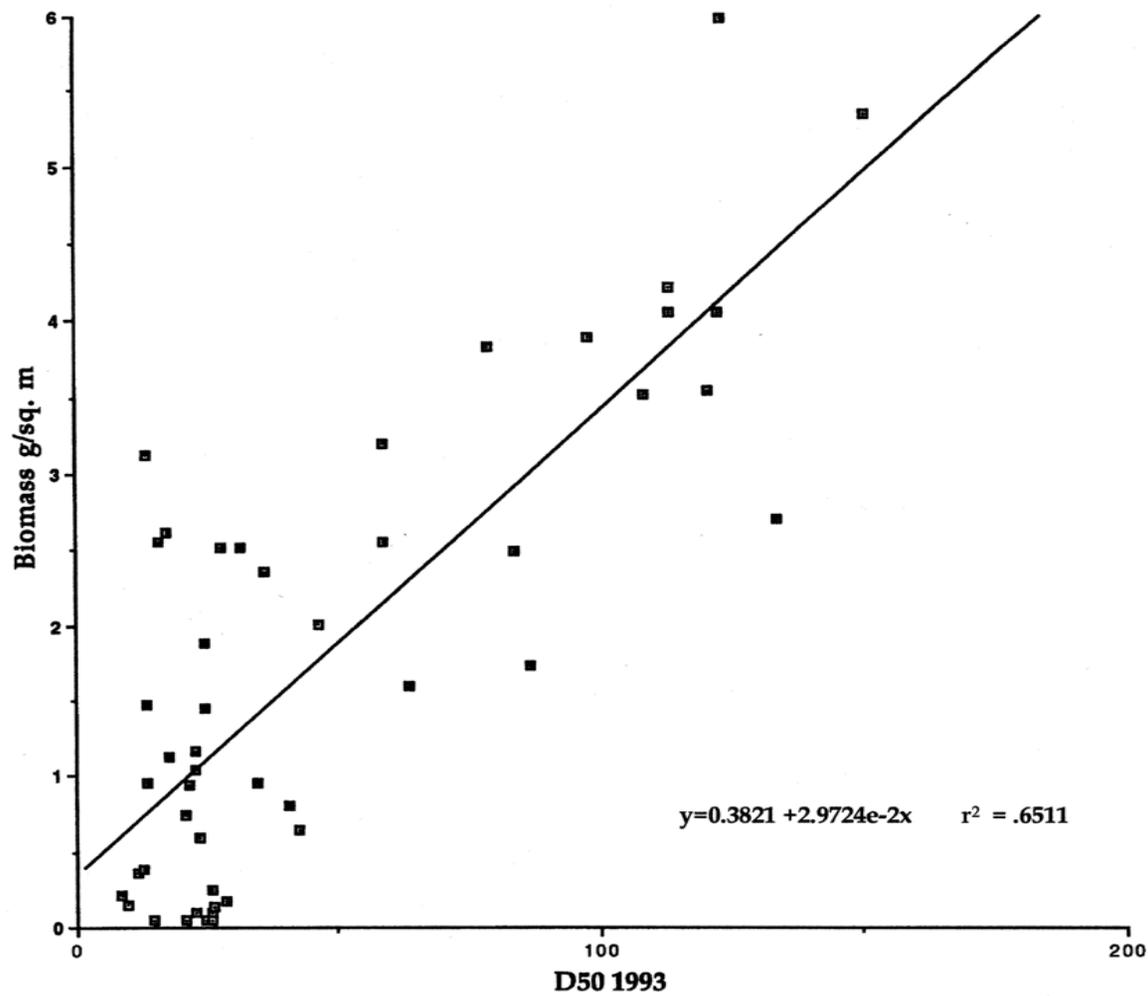


Figure 2 *D. tenebrosus* biomass (g/m²) as a function of mean bed particle size (D₅₀)

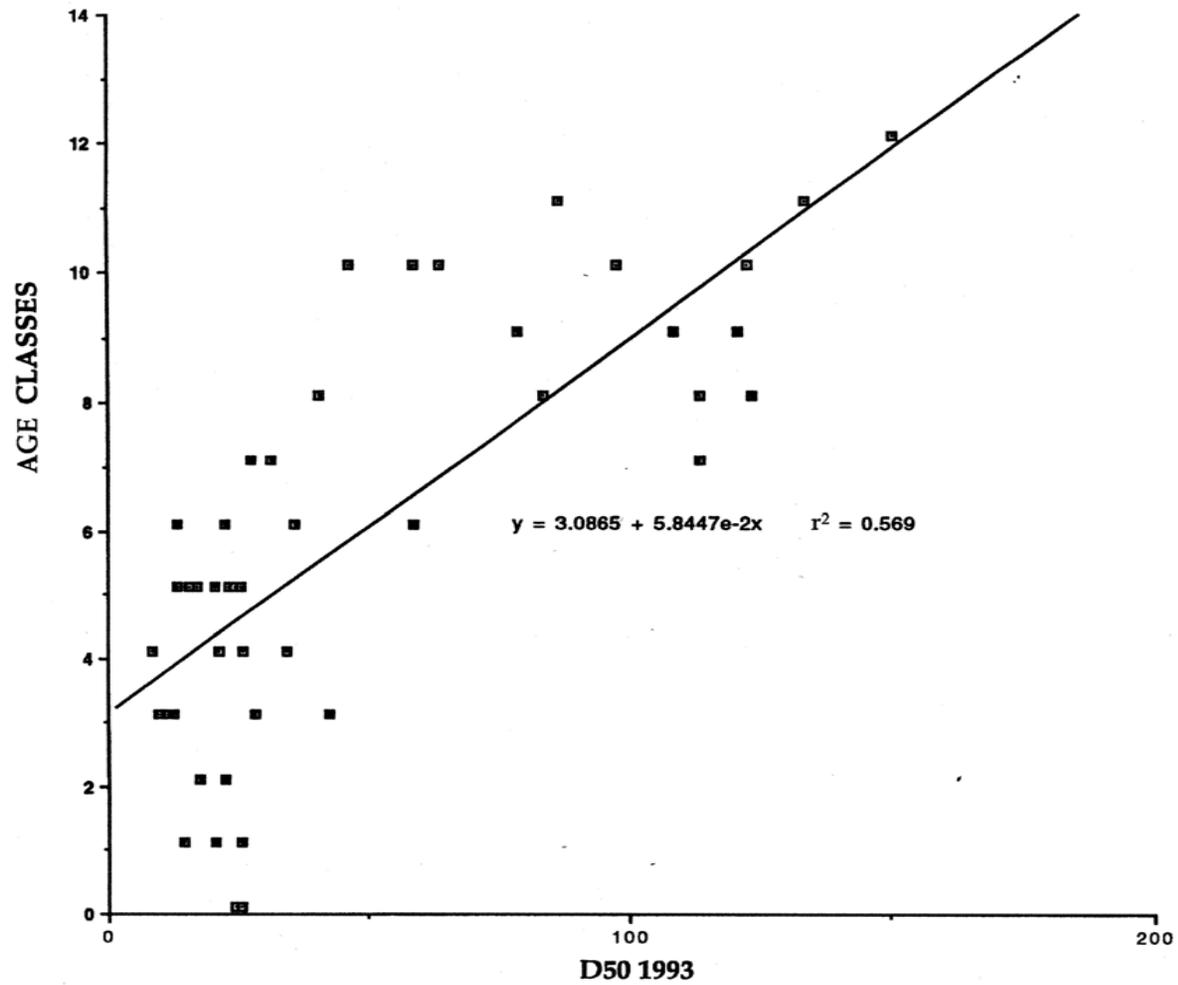


Figure 3. *D. tenebrosus* age classes as a function of mean bed particle size (D_{50})

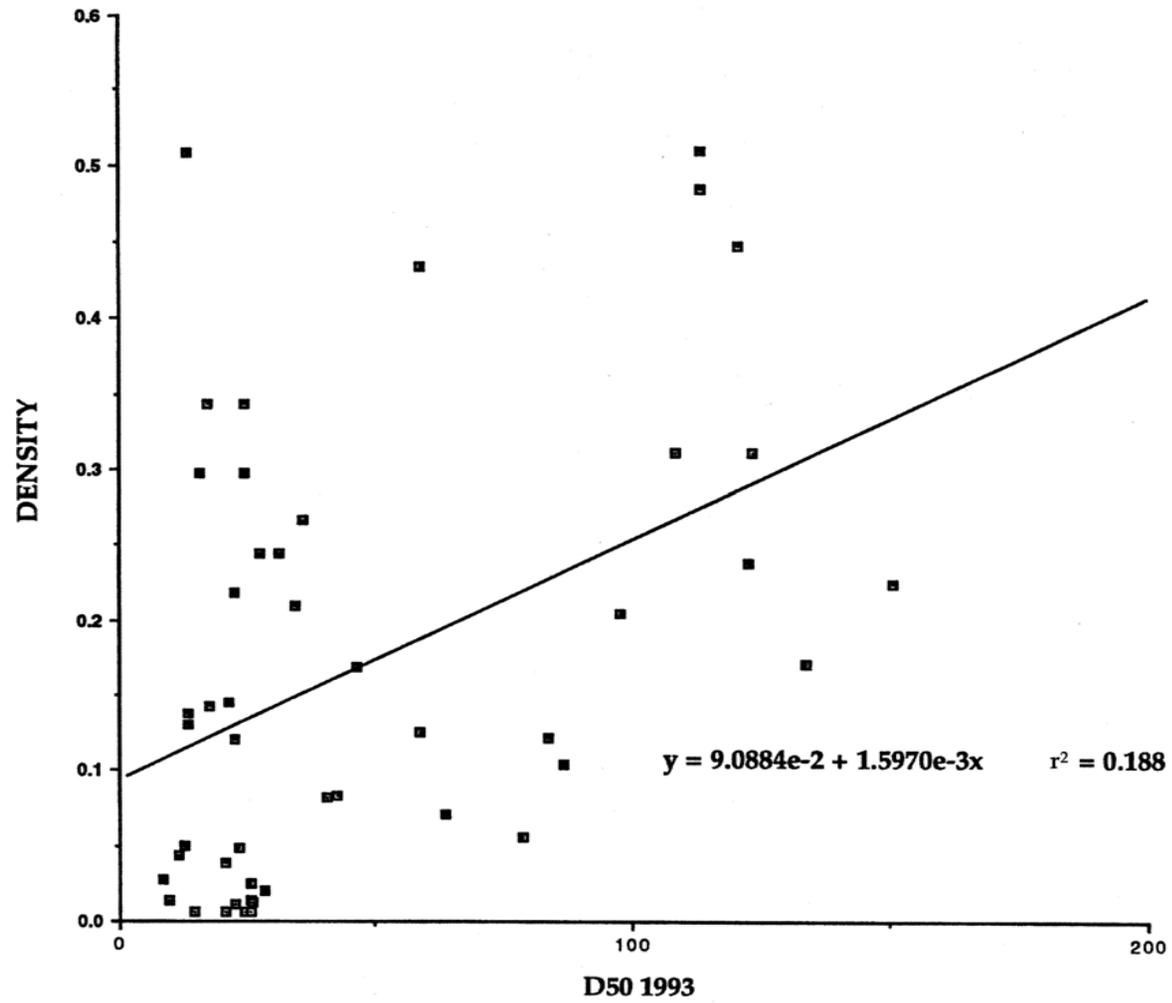


Figure 4. *D. tenbrosus* density as a function of mean bed particle size (D_{50})

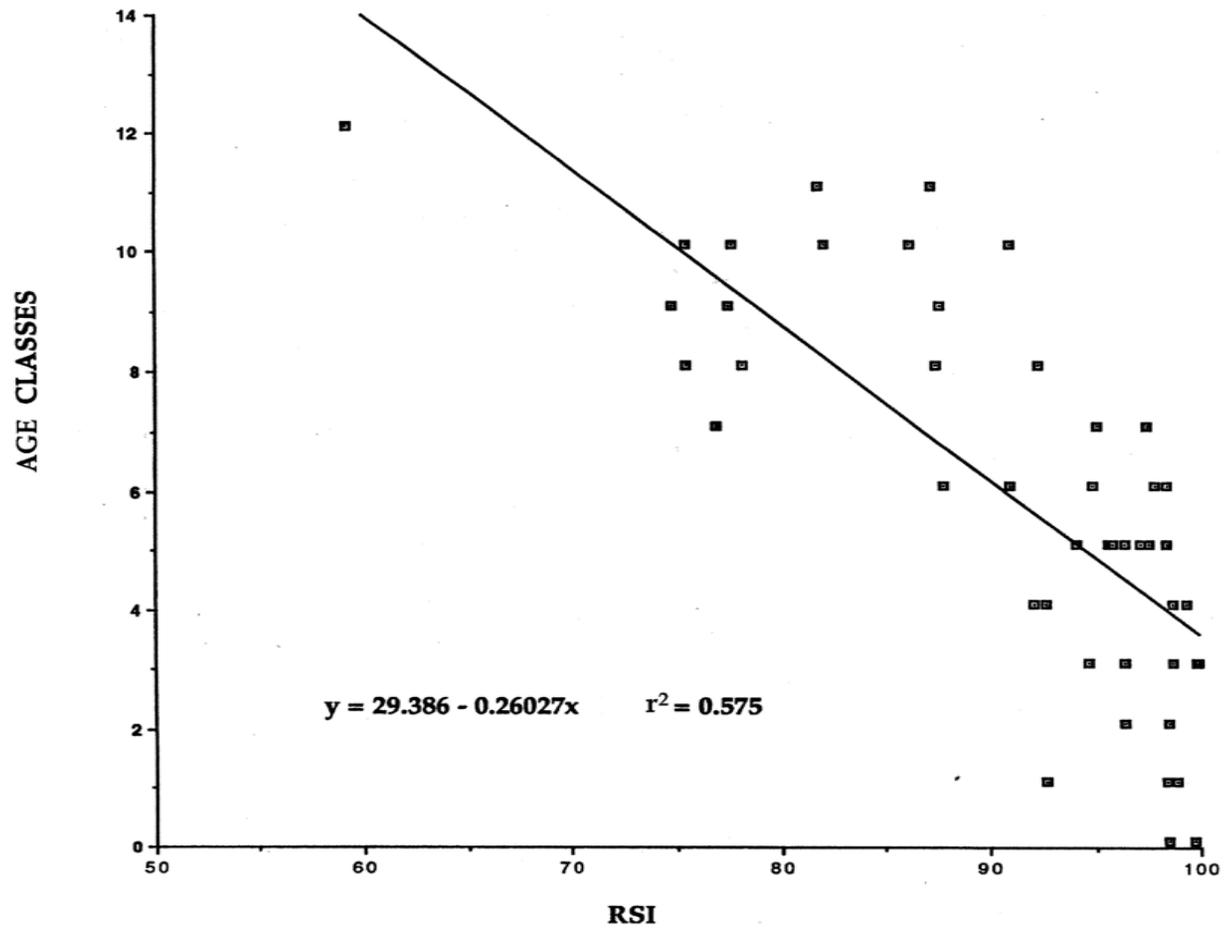


Figure 6. *D. tenebrosus* age classes as a function of riffle stability (RSI)

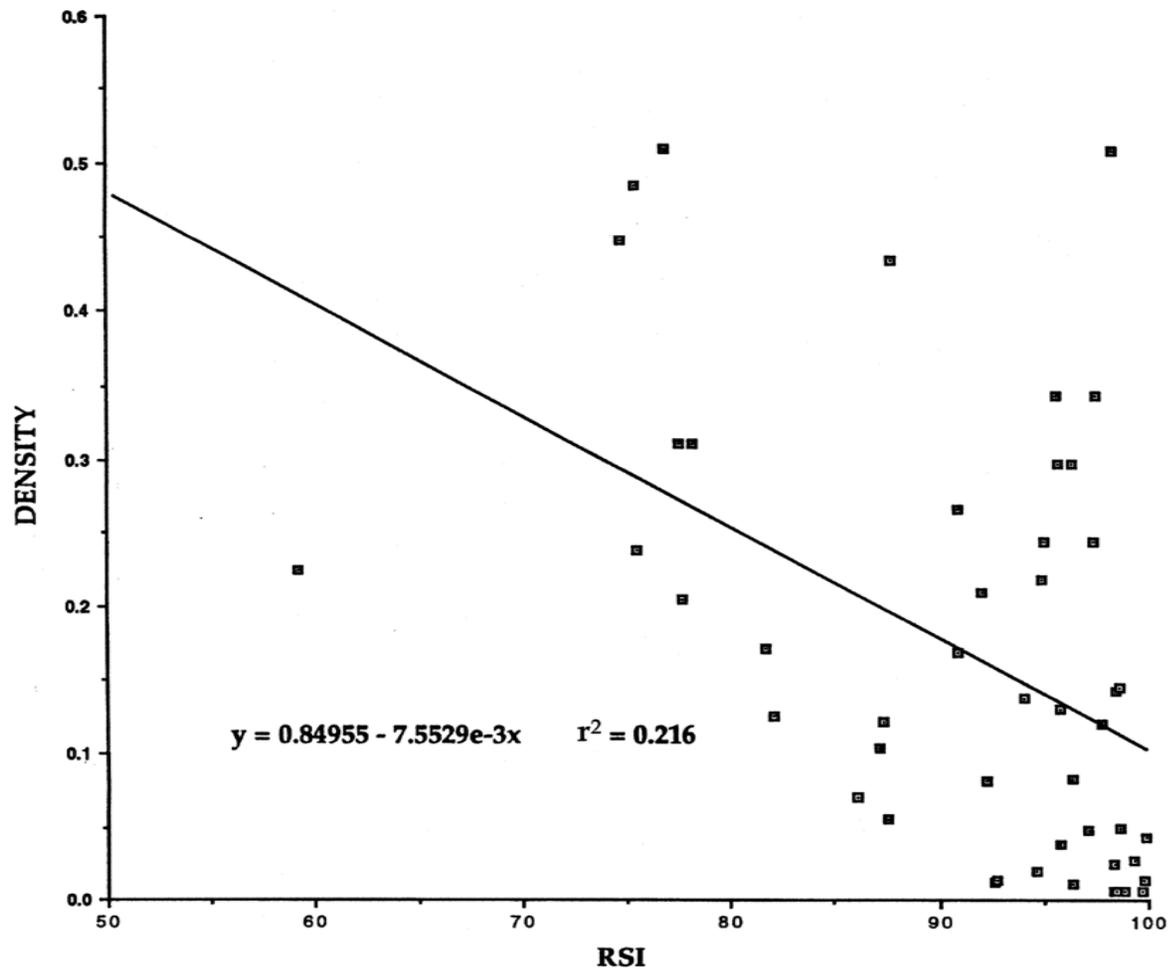


Figure 7. *D. tenbrosus* density as a function of riffle stability (RSI)

Differences between Disturbance Categories

The three disturbance categories were significantly different with respect to both the biomass and age class structure of *Dicamptodon*, and also with respect to sedimentation. (ANOVA, Table 2). There was significantly more biomass in the control streams. There was also a greater diversity along the age class hierarchy here as well, with significantly better representation of the largest neotenes (Figures 8,9).

Category 1 had the least sedimentation, while category 3 had the most. The mean streambed particle diameter was more than twice as large in category 1 (Figure 10). Riffles in category 1 exhibited the greatest stability, while those in category 3 showed the least (Figure 11).

Table 2. ANOVA among disturbance categories

Variable	DF	F-Ratio	Prob. level
Biomass/m ²	47	20.76	<0.0001
Age Classes	47	19.68	<0.0001
RSI	47	25.41	<0.0001
D ₅₀	47	27.83	<0.0001
Density	47	8.90	0.0006

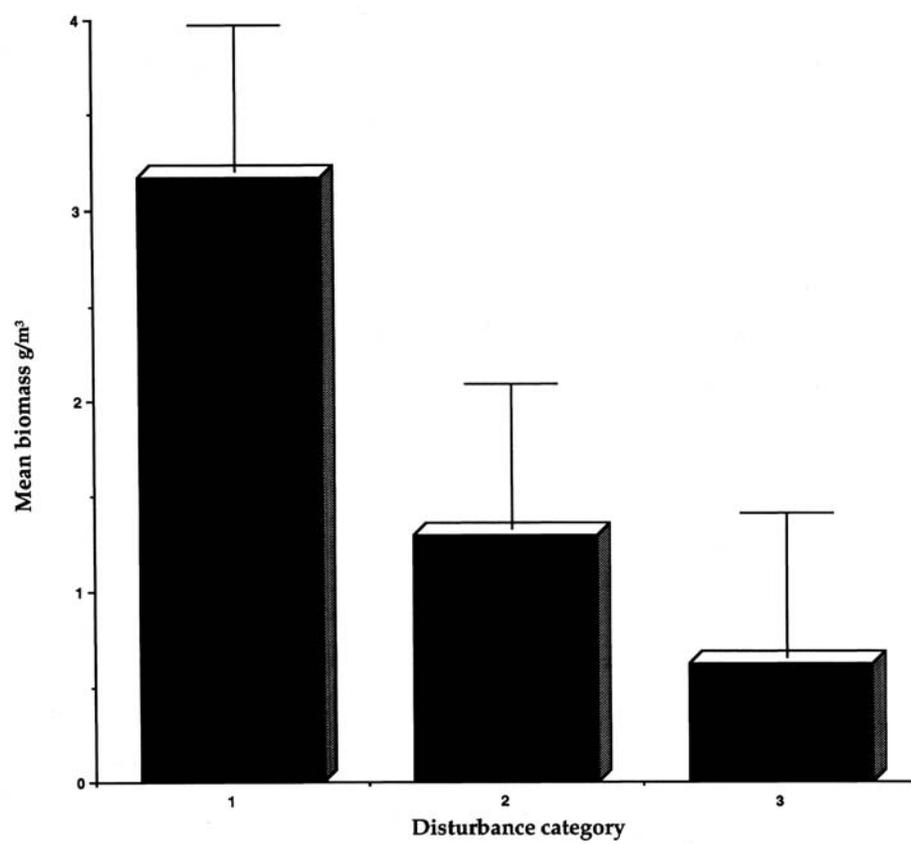


Figure 8. Biomass across the disturbance categories

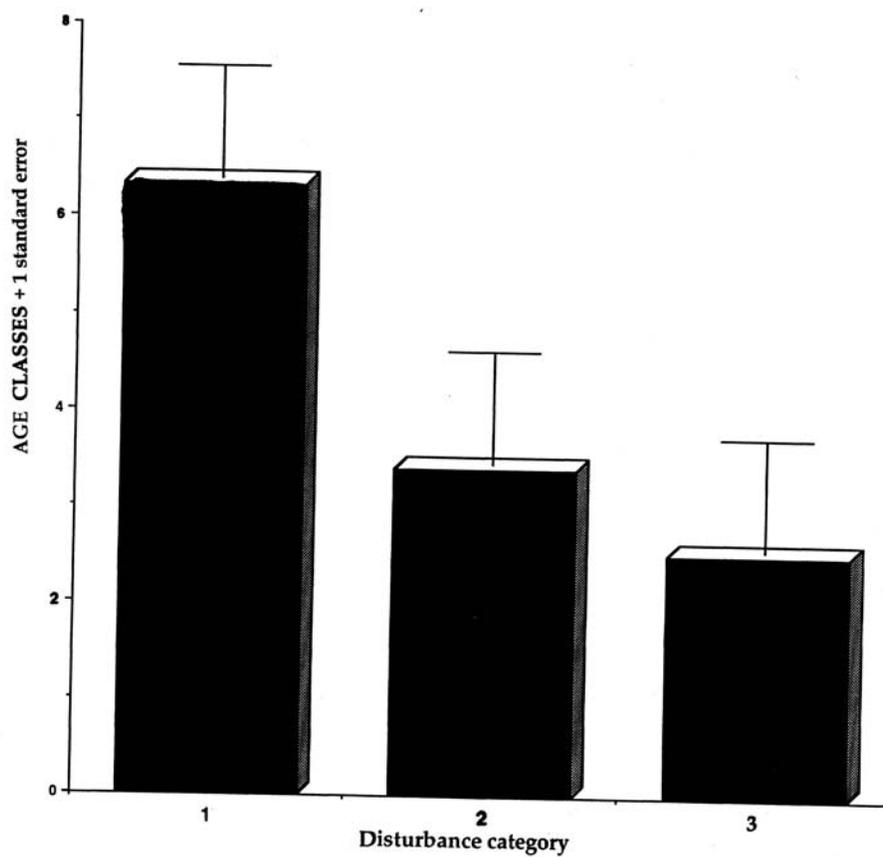


Figure 9. Age Classes across the disturbance categories

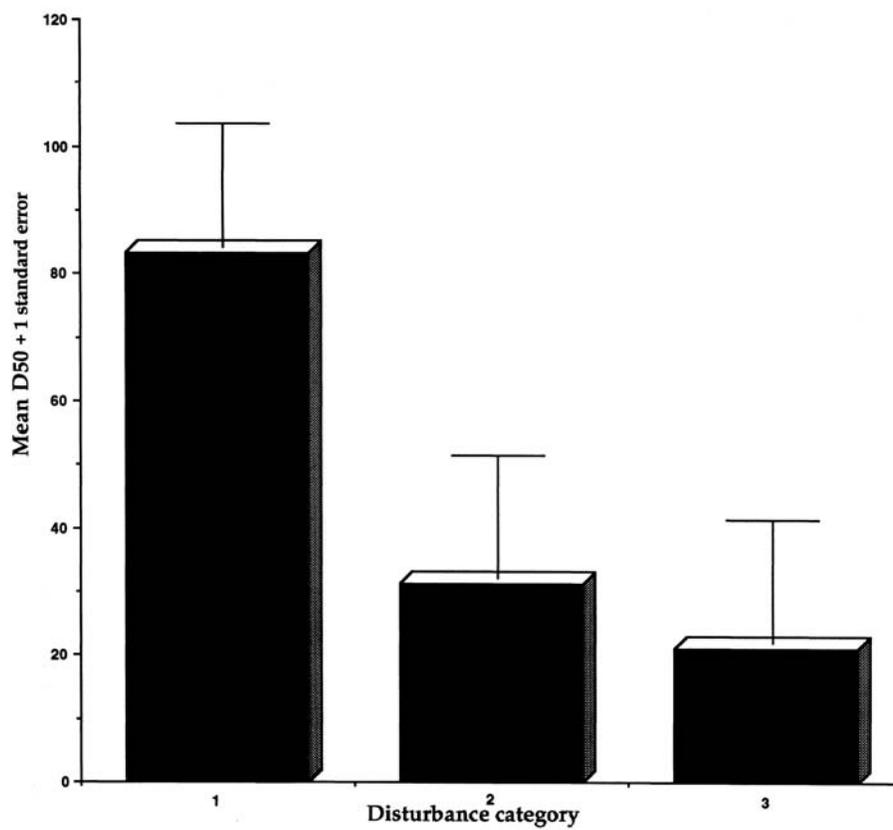


Figure 10. D_{50} across the disturbance categories

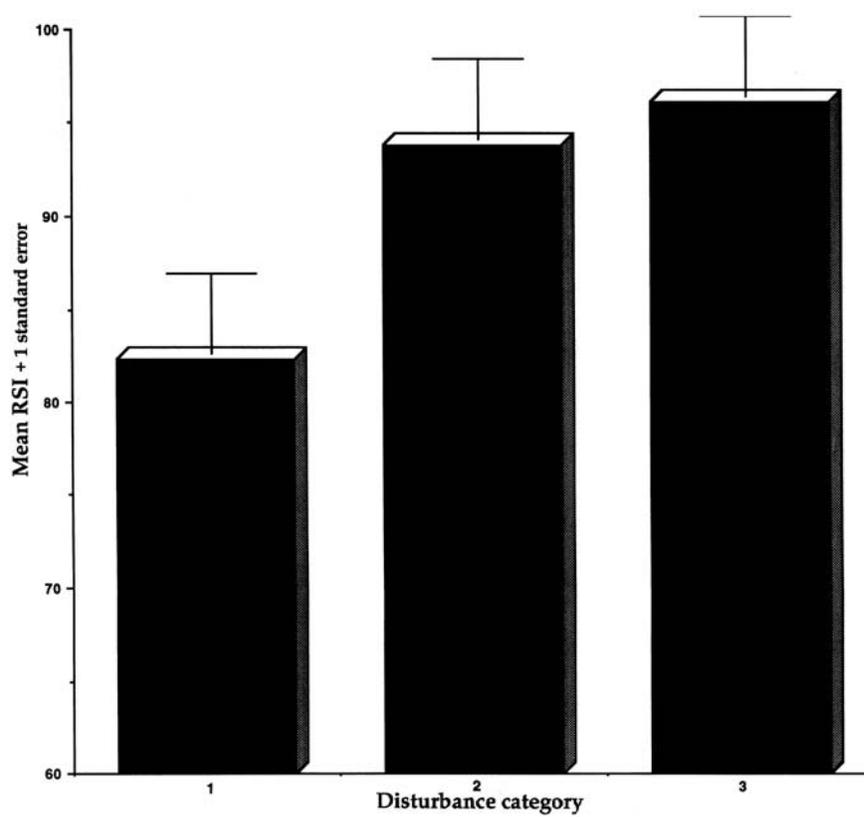


Figure 11. RSI across the disturbance categories

The variables Biomass, and Age classes, D_{50} , and RSI were screened to satisfy MANOVA assumptions, then used in a multiple analysis of variance to test whether they can be used together in order to demonstrate significant differences between the disturbance categories. All four test statistics employed demonstrate that the disturbance categories' means are significantly different. (Table 3).

Discriminant Analysis

In order to test the validity of the original (subjective) classification of streams into three disturbance categories, a discriminant analysis was employed. The analysis identified three separate groups, and classified 89.6% of the streams into the original categories. Since chance alone would correctly classify about 33.3% of three similar sized groups, the analysis provides 56.3% better classification than by chance alone.

RSI was the most significant of the five variables for discriminating between the three groups, entering the discriminant model first with overall Wilk's Lambda of 0.4697. Second, Age Classes enters the model, bringing overall Wilk's Lambda to 0.3833. The other variables added no additional predictive power.

Table 3 MANOVA among disturbance categories

Test Statistic	Value	F-Ratio	Prob. level
Wilk's Lambda	0.34792	7.30	<0.0001
Lawley-Hotelling Trace	1.59698	8.18	<0.0001
Pillai's Trace	0.74854	6.43	<0.0001
Roy's Largest Root	1.39878	15.04	<0.0001

CONCLUSIONS

The loss and degradation of habitat are among the largest threats to wildlife (Johnson 2005). Populations of stream amphibians are particularly sensitive to increased siltation because they frequent the interstitial spaces of streambeds (Bury and Corn 1988, Corn and Bury 1989). Increased siltation impacts these animals by filling rocky interstices, reducing available cover and foraging area, and has similar impacts on other substrate dwelling biota (Lisle 1989, Lisle and Lewis 1992; Lannoo 2005, Waters 1995). Use of interstices by amphibians is a characteristic shared with early life stages of both resident and anadromous fishes, as well as many stream invertebrates (Welsh and Ollivier 1998).

In the search for a vertebrate indicator of habitat quality, amphibians appear to be the best suited. Fish are often subject to seasonal movements, and their numbers can vary in response to external pressures. Amphibians, however, are highly philopatric, long-lived, and occur in relatively stable populations in undisturbed ecosystems. (Welsh and Ollivier 1998). Climate change and disease

are the only significant external factor known to affect their survival (Mendelson et al 2006, Pounds et al 2007, Romansic et al. 2006). These attributes can make amphibians a useful and reliable indicator of environmental perturbations from logging (Blaustein et al. 1994, Corn and Bury 1989). Of the amphibians on California's North Coast, Pacific giant salamanders are the most abundant. They also compensate best for habitat loss, and are therefore least affected by increased sedimentation (Welsh and Ollivier 1998). Since a stream habitat bioindicator should be responsive to the full range of potential sediment measurements, this makes them an excellent candidate.

Regressions demonstrate that total biomass of *Dicamptodon* per unit area of pool bottom decreases in a predictable and measurable fashion as sedimentation, as measured by RSI and D_{50} , increases. This suggests that the response variable Biomass can be employed as a reliable measuring tool for assessing habitat quality.

Regressions also demonstrate that the number of surviving age classes of *Dicamptodon* decreases in a predictable and measurable fashion as sedimentation increases. This suggests that the response variable Age Classes can be employed as a reliable measuring tool for assessing habitat quality.

Density, the third response variable tested by this study, has a weaker correlation to sedimentation. This is probably because density assigns equal

significance to the presence of every animal regardless of weight or age; e.g. an individual weighing five grams is assigned the same significance as one weighing a hundred and five grams, and a two year old is assigned the same significance as a ten year-old. This tends to obscure the tremendous importance that the presence of large, mature individuals plays in assessing habitat quality. Therefore Density appears to be a far less useful barometer of habitat quality.

The ANOVA results support the assumption that the three original (subjective) disturbance categories were in fact significantly different from one another with respect to the degree of impact to aquatic habitat from historic forest use practices. Streams from disturbance category 1 (control) exhibited the highest mean bed particle size, the greatest amount of available cover, and the greatest riffle stability. They also had the most *Dicamptodon* biomass and highest number of surviving age classes. Streams from disturbance category 3 (high management) exhibited the smallest mean bed particle size, the least amount of available cover, and the least riffle stability. They also had the least *Dicamptodon* biomass and the narrowest distribution of age classes. Also, ANOVA results demonstrate that D₅₀, RSI, Biomass, and Age Classes are useful stand-alone variables in assessing the degree of impact to stream habitat from timber harvest and road building.

The MANOVA results clearly demonstrate that disturbance categories 1, 2, and 3 are significantly different with respect to the degree of impact to aquatic habitat from historic timber harvest and road building. Disturbance category 3 had the poorest habitat quality, while category 1 had the best. Also, these results support the hypothesis that D₅₀, RSI, Biomass, and Age Classes can be used together to assess the degree of impact to stream habitat from timber harvest practices. The discriminant analysis employs the variables RSI and Age Classes to correctly assign 89.6% of the streams into the original (subjective) disturbance categories. Since chance alone accounts for only 33.3% correct classification, the discriminant model supports the validity of the original assignment of streams, based upon aerial photography, logging history, and sediment budget data, into disturbance categories 1, 2, and 3, further strengthening the finding that different timber harvest regimes in the three groups have led to predictable, measurable differences in sedimentation and *Dicamptodon* survival across the three groups.

There are several possible reasons why increasing loads of fine sediments have a detrimental effect on aquatic populations of *Dicamptodon*. First, as a higher percentage of the riverbed becomes mobilized during peak flow, scour increases, removing invertebrates (Platts et al., 1983). This reduces *Dicamptodon*'s food base. Scour also removes algae, a primary invertebrate food source, from stream substrates (Alabaster and Lloyd 1982). Furthermore, even a thin layer of

fine sediment can block sufficient light and inhibit the growth of algae (Newcomb and Macdonald 1991). Fine sediments also infiltrate the hyporheic zone, reducing both available habitat and dissolved oxygen for invertebrates. (Boulton et al 1977). Finally, sediments reduce available cover by burying or imbedding cobbles and boulders. *Dicamptodon* densities are a function of cover. (Davic and Orr 1987, Parker 1991). This animal must be able to hide under an object large enough to cover its whole body at once in order to avoid predation. (Lind and Welsh 1990).

Regressions of Biomass as a function of sedimentation bear this out; as sedimentation increases, biomass per square meter decreases accordingly. Regressions of Age Classes as a function of sedimentation support this finding as well; as sedimentation increases, the stream's ability to support the full range of *Dicamptodon* age classes declines in a predictable, measurable manner.

Management Implications

As sedimentation increases, there appears to be a threshold beyond which aquatic populations of *D. tenebrosus* become destabilized. Specifically, in about half (46%) of the cases where D_{50} is 26 mm or less, salamander biomass is near zero ($<0.1 \text{ g/m}^2$), and in all of the streams where salamander biomass is near zero, D_{50} is 26 mm or less. (Figure 1.) Similarly, in 43% of the reaches where RSI

is 92 or greater, their biomass is near zero ($<0.1 \text{ g/m}^2$), and in all of the streams where salamander biomass is near zero, RSI is greater than 92. (Figure 4.)

Increased sedimentation also has a detrimental effect upon *Dicamptodon's* age class structure. As interstitial spaces are filled and large cobbles and boulders become buried, it appears that the largest neotenes (SVL 100-140 mm) become less able to find suitable habitat, and they tend to be the first to disappear altogether from the stream. As sedimentation further increases, the next largest salamanders disappear, and so on. In all cases where two or fewer age classes were present ($n=7$), RSI was above 92 and D50 was below 26. Since these salamanders must survive into their third year in order to reach sexual maturity, or in order to transform into the terrestrial lifestage (Nussbaum and Clothier, 1973; Leonard et al. 1993), the presence of only these two youngest age classes suggests a profound detrimental effect on the population's continued viability.

Land managers would be well advised to take notice of streams exhibiting RSI values greater than 92, or D50 values less than 26mm. Such values may indicate a stream system that has become destabilized to the point where the watershed is no longer capable of producing sexually mature *D. tenebrosus*, and thus is unable to sustain viable populations of *Dicamptodon*. And since *Dicamptodon* is the amphibian most resistant to impacts from increasing loads of

fine sediments (Welsh and Ollivier 1998), it seems likely that in cases where a watershed can no longer sustain viable populations of *Dicamptodon*, all other stream-dwelling amphibian species may be gone as well. Therefore a RSI value of 92 or greater may indicate a watershed that is at risk of losing its stream-dwelling amphibian populations entirely. This hypothesis still needs testing.

MANOVA and Discriminant Analysis results indicate that clear-cut timber harvest and road building can significantly reduce the quality of *Dicamptodon*'s aquatic habitat. It's important to note that larval and pedomorphic *Dicamptodon* share many of the same microhabitat requirements as juvenile and fry salmon. Young salmon have the same invertebrate food base, depend on cover to avoid predation, and are negatively affected by increasing sedimentation (Cordone and Kelly, 1961; Tappel and Bjornn, 1983; Lisle, 1989; Kondolf, 2000, Gonzales, 2006). While this study does not seek to demonstrate a direct link between the two, the results established herein may allow future researchers to more clearly quantify the relationship between increased stream sedimentation from timber harvest and declining salmon populations.

This study has demonstrated that two surrogates of *D. tenebrosus* population viability - Biomass and Age Classes - provide useful tools for accurate, repeatable quantification of aquatic habitat quality. It is not this animal's sensitivity, but its toughness, that makes it well suited for use as a

biological measuring tool. Pacific giant salamanders were found in 96% of the sampled reaches, demonstrating that *D. tenebrosus* typically appears, albeit in extremely low densities, in even the most highly impacted streams. *Dicamptodon tenebrosus* is therefore responsive to the full continuum of measured values of sedimentation, as provided by RSI and D_{50} . I conclude that this animal is an extremely sensitive indicator of stream habitat stress resulting from inputs of fine sediment from timber harvest, road building, and other non-point sources.

LITERATURE CITED

- Alabaster, J. S., and R. Lloyd. 1982. Finely divided solids. J. S. Alabaster and R. Lloyd, editors. *Water quality criteria for freshwater fish*. Second edition. 1-20. Butterworth, London, UK.
- Bennett, S.H., J.W. Gibbons, and J. Glanville. 1980. Terrestrial activity, abundance, and diversity of amphibians in differently managed forest types. *Amer. Midl. Nat.* 103(2): 412-416.
- Blaustein, A.B. and D. B. Wake. 1990. Declining amphibian populations: a global phenomenon? *Trends in Ecology and Evolution* 5(7): 203-204.
- Boulton, A.J.; Scarsbrook. M.R.; Quinn, J.M.; Burrell, G.P. 1997. Land-use effects on the hyporheic ecology of five small streams near Hamilton, New Zealand. *New Zealand Journal of Marine and Freshwater Research.* 31: 609-622.
- Bury, R.B. 1983. Differences in Amphibian Populations in Logged and Old Growth Redwood Forest. *Northwest Science* 57 (3): 167-178.
- Bury, R. B. 1988. Habitat relationships and ecological importance of amphibians and reptiles. Pages 61-76 *in* K. J. Raedeke, editor. *Streamside management: riparian wildlife and forestry interactions*. College of Forest Resources, University of Washington, Seattle, Washington, USA.
- Bury, R. B., and P. S. Corn. 1988. Responses of aquatic and streamside amphibians to timber harvest: a review. Pages 165-181 *in* K. J. Raedeke, editor. *Streamside management: riparian wildlife and forestry interactions*. College of Forest Resources, University of Washington, Seattle, Washington, USA.
- Bury, R.B., and P.S. Corn. 1991. Sampling methods for amphibians in streams in the Pacific Northwest. *Gen. Tech Rep. PNW-GTR-275*. USDA Forest Service, Pacific Northwest Station, Portland, OR.
- Chapman, D.W. 1988. Critical review of variables used to define effects of fines in redds of large salmonids. *Transactions of the American Fisheries Society* 117: 1-21.

- Cordone, A.J. and Kelley. 1961. The influences of inorganic sediment on the aquatic life of streams. Reprint from California Fish and Game. 47 (2) California Department of Fish and Game, Inland Fisheries Branch. Sacramento, CA.
- Corn, P.S. and R. B. Bury. 1989. Logging in western Oregon: responses of headwater habitats and stream amphibians. *Forest Ecology and Mgmt.* 29 (1989): 39-57.
- Davic, R.D. and L.P. Orr. 1987. The relationship between rock density and salamander density in a mountain stream. *Herpetologica* 43(3): 357-361.
- Dietrich, W.E., J.W. Kirchner, H. Ikeda, and F. Iseya. 1989. Sediment supply and the development of the coarse surface layer in gravel-bedded rivers. *Nature* vol. 340: 215-217.
- Fitch, H. S. 1941. The feeding habits of California garter snakes. *Calif. Fish and Game* 27: 2-32.
- Fournier, D.A., J.R. Silbert, J. Majkowski, and J. Hampton. 1990. MULTIFAN a likelihood-based method for estimating growth parameters and age composition from multiple length frequency data sets illustrated using data for Southern Bluefin Tuna (*Thunnus maccoyii*). *Can. J. Fish Aquat. Sci.*47: 301-317.
- Gonzales, E.J. 2006. Diet and prey consumption of juvenile Coho salmon (*Oncorhynchus kisutch*) in three northern California streams. Master's thesis, Department of Fisheries, Humboldt State University, Arcata, CA
- Good, D.A. 1989. Hybridization and cryptic species in *Dicamptodon* (Caudata: Dicamptodontidae). *Evolution* 43 (4): 728-744.
- Gregory, S. V. 1997. Riparian management in the 21st Century. Pages 69-85 in K. A. Kohm and J. F. Franklin, editors. *Creating a forestry for the 21st century*. Island Press, Covelo, California, USA.
- Groot, C., and L. Margolis, editors. 1991. *Pacific salmon life histories*. University of British Columbia Press, Vancouver, British Columbia, Canada.
- Hall, L. S., P. R. Krausman, and M. L. Morrison. 1997. The habitat concept and a plea for standard terminology. *Wildlife Society Bulletin* 25:171-182.

- Hawkins, C.P., K.L. Murphy, N.H. Anderson, and M.A. Wilzbach. 1983. Density of fish and salamanders in relation to riparian canopy and physical habitats in streams of the northwestern United States. *Can. J. Fish. Aquat. Sci.* 40: 1173-1185.
- Hicks, B. J., J. D. Hall, P. A. Bisson, and J.R. Sedell. 1991. Responses of salmonids to habitat changes. *American Fisheries Society Special Publication* 19:483-518.
- Johnson, Matthew D. 2005. *Transactions of the Western section of the Wildlife Society* 41: 31-41.
- Jones, J. A., and G. E. Grant. 1996. Peak flow responses to clear-cutting and roads in small and large basins, Western Cascades, Oregon. *Water Resources Research* 32: 959-974.
- Kappesser, G. 1992. Riffle armor stability index. Version 3.1. Unpublished report, Idaho Panhandle National Forest, Coeur d'Alene, Idaho. 7 pages.
- Kappesser, G. 2002. A riffle stability index to evaluate sediment loading from streams. *Journal of the American Water Resources Association*. 38 (4) 1069-1081.
- Kondolf, G.M. 2000. Assessing Salmonid Spawning Gravel Quality. *Trans. Am. Fish. Soc.* 129:262-281.
- Knopp, C. 1992. Personal communication. North Coast Regional Water Quality Control Board. Santa Rosa, CA.
- Knopp, C. 1993. Testing Indices of Cold Water Fish Habitat. Unpublished report, Six Rivers National Forest in Cooperation with CDF and the North Coast Regional Water Quality Control Board. Santa Rosa, CA. Cooperatively sponsored by the USDA Forest Service.
- Lannoo, Michael ed. 2005. *Amphibian declines: The Conservation Status of United States Species*. Regents of the University of California.
- Leonard, W. P., H. A. Brown, L. L. C. Jones, K. R. McAllister, and R. M. Storm. 1993. *Amphibians of Washington and Oregon*. Seattle Audubon Society, Seattle, Washington, USA.

- Lisle, T.E. 1982. Effects of aggradation and degradation on riffle pool morphology in natural gravel channels, Northwest California. *Water Resources Research* 18(6): 1634-1651.
- Lisle, T. 1989. Sediment transport and resulting deposition in spawning gravels, north coastal California. *Water Resources Research* 25(6):1303-1319.
- Lisle, T and Hilton, S. 1992. The Volume of fine sediment in pools: an index of sediment supply in gravel-bed streams. *Journal of the American Water Resources Association* 28(2) 371-383.
- Lisle, T., and J. Lewis. 1992. Effects of sediment transport on survival of salmonid embryos in a natural stream: a simulation approach. *Canadian Journal of Fisheries and Aquatic Sciences* 49: 2337-2344.
- Lind, A.J. and H.H. Welsh, Jr. 1990. Predation of *Thamnophis couchii* on *Dicamptodon ensatus*. *J. Herpetology* 24(1): 104-106
- Macdonald and Pitcher. 1989. Size-frequency distribution of Pacific giant salamander larvae from streams in uncut forests in the Oregon Coast Range. in: Bury, R.B., and P.S. Corn. 1991. Sampling methods for amphibians in streams in the Pacific Northwest. Gen. Tech Rep. PNW-GTR-275. USDA Forest Service, Pacific Northwest Station, Portland, OR.
- Malanson, G. P. 1993. Riparian landscapes. Cambridge University Press, Cambridge, United Kingdom.
- Mendelson, J. R. III, K. R. Lips, R. W. Gagliardo, G. B. Rabb, J. P. Collins, J. E. Diffendorfer, P. Daszak, R. D. Ibáñez, K. C. Zippel, D. P. Lawson, K. M. Wright, S. N. Stuart, C. Gascon, H. R. da Silva, P. A. Burrowes, R. L. Joglar, E. La Marca, S. Lötters, L. H. du Preez, C. Weldon, A. Hyatt, J. V. Rodriguez-Mahecha, S. Hunt, H. Robertson, B. Lock, C. J. Raxworthy, D. R. Frost, R. C. Lacy, R. A. Alford, J. A. Campbell, G. Parra-Olea, F. Bolaños, J.J. Calvo Domingo, T. Halliday, J. B. Murphy, M. H. Wake, L. A. Coloma, S. L. Kuzmin, M. S. Price,

- K. M. Howell, M. Lau, R. Pethiyagoda, M. Boone, M. J. Lannoo, A. R. Blaustein, A. Dobson, R. A. Griffiths, M. L. Crump, D. B. Wake, E. D. Brodie Jr. 2006. Biodiversity: Confronting Amphibian Declines and Extinctions. *Science* 313 (5783): 48
- Moyle, P. B. 1976. *Inland Fishes of California*. University of California Press, Berkeley, California, USA.
- Murphy, M.L., and W.R. and Meehan. 1991. Stream ecosystems. Pp. 17-46, in: Meehan, W.R. (ed.). *Influences of forest and rangeland management on salmonid fishes and their habitats*. Amer. Fish. Soc. Special Pub. 19.
- Murphy, M. L. and J. D. Hall. 1981. Varied effects of clear-cut logging on predators and their habitat in small streams of the Cascade Mountains, Oregon. *Can. J. Fish. Aquat. Sci.* 38: 137-145.
- Naiman, R. J., R. E. Bilby, AND P. A. Bisson. 2000. Riparian ecology and management in the Pacific coastal rain forest. *BioScience* 50:996-1111.
- Newcombe, C. P., and D. D. MacDonald. 1991. Effects of suspended sediments on aquatic ecosystems. *North American Journal of Fisheries Management* 11(1):72-82.
- Nussbaum, R.A. 1983. *Dicamptodon copei*. Pp. 334.1-334.2. *Catalogue of American Amphibians and Reptiles*. Society for the Study of Amphibians and Reptiles, St. Louis, Missouri.
- Nussbaum, R.A. and G.W. Clothier. 1973. Population structure, growth, and size of larval *Dicamptodon ensatus* (Eschscholtz). *Northwest Science* 47(4): 218-227.
- Nussbaum, R.A., E.D. Brodie, and R.M. Storm. 1983. *Amphibians and reptiles of the Pacific Northwest*. University of Idaho Press, Moscow, Idaho. 332 pp.
- Parker, M.S. 1991. Relationship between cover availability and larval Pacific giant salamander density. *J. Herp.* 25(3): 355-357.
- Parker, M. S. 1993. Size-selective predation on benthic macroinvertebrates by stream-dwelling salamander larvae. *Archiv. fur Hydrobiol.* 128(4): 385-400.

- Pechmann, J.H.K., D.E. Scott, R.D. Semlitsch, J.P. Caldwell, L.J. Vitt, J.W. Gibbons. 1991. Declining amphibian populations: the problem of separating human impacts from natural fluctuations. *Science* 253: 892-895.
- Perry, D. A., and M. P. Amaranthius. 1997. Disturbance, recovery, and stability. Pages 31-56 *in* K. A. Kohm and J. F. Franklin, editors. *Creating a forestry for the 21st century*. Island Press, Covelo, California, USA.
- Platts, W.S., and W.F. Megahan, 1975. Time trends in riverbed sediment composition in salmon and steelhead spawning areas: South Fork Salmon River, Idaho. *Transactions of the North American Wildlife and Natural Resources Conference* 40:229-239.
- Platts, W.S., W.F. Megahan, and G.W. Minshall. 1983. Methods for evaluating stream, riparian, and biotic conditions. USDA Forest Service, Intermountain Forest and Range Experiment Station, GTR INT-138. 70 pp.
- Pough, H.F., E.M. Smith, D.H. Rhodes, and A. Collazo. 1987. The abundance of salamanders in forest stands with different histories of disturbances. *Forest Ecology and Mgmt.* 20 (1987): 1-9.
- Pounds, Allen J., M.R. Bustamante, L.A. Coloma, J.A. Consuegra, M.P.L. Fogden, P.N. Foster, E. La Marca, K.L. Masters, A. Merino-Viteri, R. Puschendorf, R.R. Santiago, A.G. Sanchez-Azofeifa, C.J. Still, and B.E. Young. 2007. Global warming and amphibian losses; The proximate cause of frog declines? *Nature*, Vol. 447, No. 7144. E5-E6.
- Reid, L. M. 1993. Research and cumulative watershed effects. U.S. Forest Service General Technical Report PSW-141.
- Reid, L. M., and T. Dunne. 1984. Sediment production from forest road surfaces. *Water Resources Research* 20: 1753-1761.
- Reeves, G. H., L. E. Benda, K. M. Burnett, P. A. Bison, and J. R. Sedell. 1995. A disturbance-based ecosystem approach to maintaining and restoring freshwater habitats of evolutionarily significant units of anadromous salmonids in the Pacific Northwest. *American Fisheries Society Symposium* 17: 334-349.

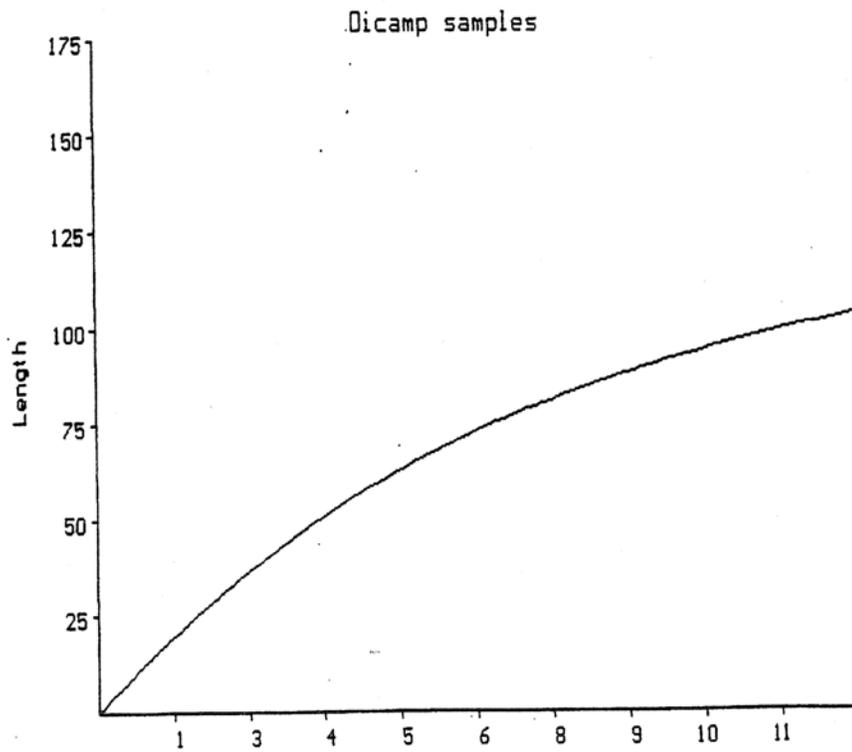
- Romansic, J.M., K.A. Diez, E.M. Higashi, A.R. Blaustein. 1996. Effects of nitrate and the pathogenic water mold *Saprolegnia* on survival of amphibian larvae. *Diseases of Aquatic Organisms* 68: 235-243
- Rosgen, D. L. 1985. A stream classification system. Paper presented at the symposium, *Riparian Ecosystems and their Management: Reconciling Conflicting Uses*. April 16-18, Tucson, AZ.
- Sawyer, J., 1992. Personal communication. Humboldt State University Dep't. of Biological Sciences, Arcata, CA 95521
- Schlosser, J. 1991. Stream fish ecology: a landscape perspective. *BioScience* 41: 704-712
- Semlitsch, R. D. 2000. Principles of management of aquatic-breeding amphibians. *Journal of Wildlife Management* 64:615-631.
- Smith-Gill, S.J. and Berven, K.A. 1979. Predicting amphibian metamorphosis. *American Naturalist* 113: 563-585.
- Southwood, T. R. E. 1977. Habitat, the templet for ecological strategies? *Journal of Animal Ecology* 46: 337-365.
- Tappel, P.D., and T.C. Bjornn. 1983. A new method of relating size of spawning gravel to salmonid embryo survival. *North American Journal of Fisheries Management* 3:123-135.
- Titus, K., J.A. Mosher, and B.K. Williams. 1984. Chance-corrected classification for use in discriminant analysis: ecological applications. *Amer. Midl. Nat.* 111(1): 1-7.
- Van Der Have, T.M. and De Jong, G. 1996. *Journal of Theoretical Biology* 183: 329-340
- Van Horne, B. 1983. Density as a misleading indicator of habitat quality. *Journal of Wildlife Management*. 47(4): 893-901.
- Wake, D. B. 1991. Declining amphibian populations. *Science* 253: 860.
- Waters, T. F 1995. *Sediment in streams: sources, biological effects and control*. American Fisheries Society Monograph 7. Bethesda, Maryland, USA.

- Welsh, H.H. Jr. and A.J. Lind. 1988. Old-growth forests and the distribution of the terrestrial herpetofauna. Pp. 439-458 in: Szaro, R.C., Severson, K.E., and Patton, D.R. tech. coords. Management of amphibians, reptiles, and small mammals in North America. USDA Forest Service Gen. Tech. Rpt RM-166. Rocky Mountain Experiment Station, Fort Collins, Colorado.
- Welsh, H.H. Jr., and L.M. Ollivier. 1992. Final report to the California Dep't of Transportation. Redwood National Park Bypass project.
- Welsh, H.H. 1993. Personal communication.
- Welsh, H.H. Jr and L.M. Ollivier, 1998. Stream amphibians as indicators of ecosystem stress; a case study from California's redwoods. *Ecological Applications* 8(4): 1118-1132.
- Welsh Jr, Hart H.; Lind, Amy J. 2002. Multiscale habitat relationships of stream amphibians in the Klamath-Siskiyou region of California and Oregon. *Journal of Wildlife Management*, Vol. 66(3): 581-602.
- Zwick, P. 1992. Stream habitat fragmentation - a threat to biodiversity. *Biodiversity and Conservation* 1:80-97.

APPENDIX A

D. TENEBROSUS GROWTH AND AGE PARAMETERS

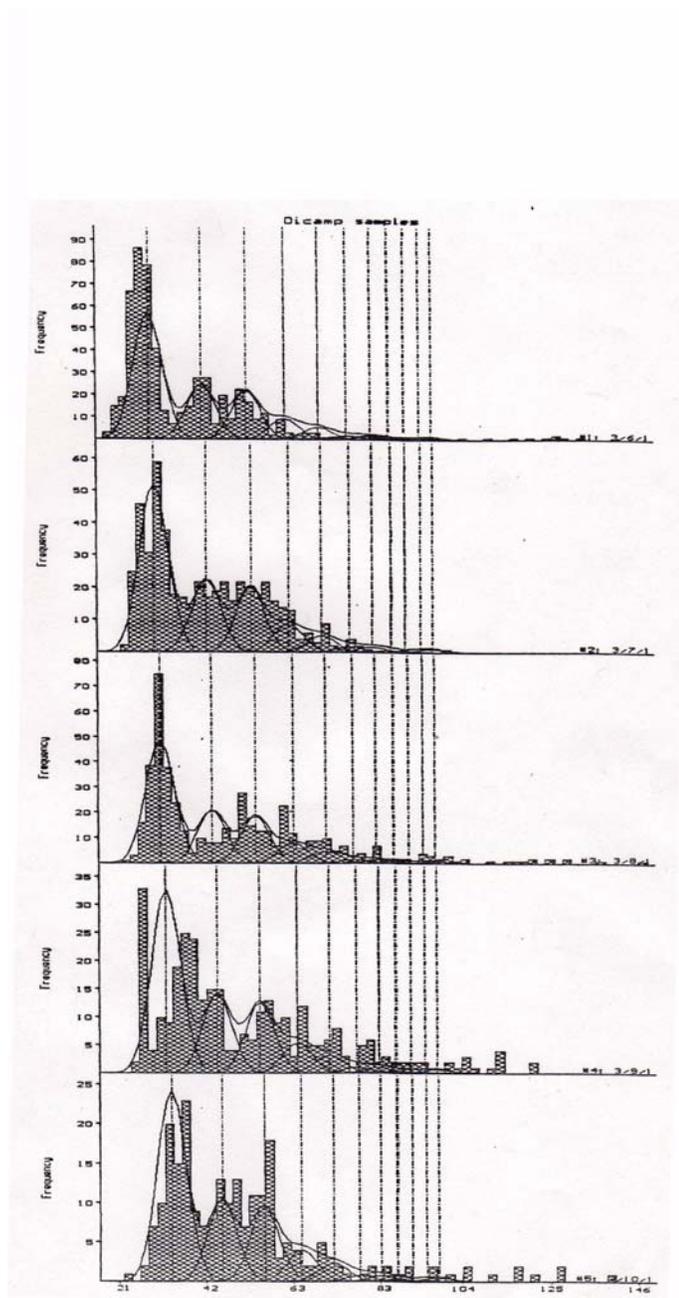
Von Bertalanffy Growth Curve



MEAN LENGTH AT AGE (mm):

Age	1	2	3	4	5	6	7	8	9	10	11
Length	22.86	36.29	47.84	57.78	66.34	73.70	80.04	85.50	90.20	94.24	97.72
S.D.	3.13	3.44	3.74	4.01	4.26	4.49	4.70	4.88	5.05	5.20	5.3

Age Class Histograms



APPENDIX B

OTHER REGRESSION SUBSETS

Table 4. Regression subsets peripheral to this study

Table 4					
Predictor variable	Response variable	r-squared	F-ratio	t	Prob.
D ₅₀ 1993	RSI '93	.8902	372.79	19.31	<0.0001
RSI '92	RSI '93	.422	29.20	5.4	<0.0001
Biomass	Age Classes	.5618	60.25	7.76	<0.0001
Biomass	Density	.5427	56.96	7.55	<0.0001
Density	Age classes	.1883	10.9	3.3	0.0018
RSI '92	D ₅₀ '93	.4147	28.34	5.32	<0.0001
D ₅₀ '92	RSI '93	.4389	31.29	5.59	<0.0001
D ₅₀ '92	D ₅₀ '93	.3481	21.36	4.62	<0.0001

RSI as a function of D_{50}

These two measures of sedimentation are tightly linked to one another ($r^2 = .89$, $t = -19.31$, $f\text{-ratio} = 372.79$, $p < .00001$; fig 8).

For any given degree of shear stress, small particles move downstream more easily than large ones. For example, a bed composed of sand is more easily mobilized than a cobble/boulder substrate. As sediment loads increase, bed particle size (D_{50}) decreases (Platts and Megahan 1975, Lisle 1982, Dietrick et. al. 1989). The channel is then capable of transporting a larger subset of the particles, so the RSI value rises.

During Knopp's 1992 data gathering, part of the test was to determine if RSI measurements performed by different members of the nine-man crew on different river reaches were consistent. At the same time, some crewmembers did not understand the cobble selection method for the "thirty count" measurements; therefore measurements were not performed in an entirely consistent manner across the reaches. Even if all crewmembers had thoroughly understood this methodology, the inherent subjectivity of the "thirty count" might have still led to inconsistencies. Still, Knopp's r^2 value for D_{50} compared to RSI is .6133. This suggests that RSI measurements taken by different individuals still provide some resolution.

The next step was to test RSI's reliability using the same person for the "thirty count" across the same rivers. I performed all RSI measurements myself for this study (1993), allowing any error due to the subjective nature of the "thirty count" to drop out when all reaches are compared, and also when RSI 93 is compared to D_{50} . In this study, the r^2 value for D_{50} compared to RSI ('93) is .8902. The high correlation between these two physical estimators suggests that collection of riverbed data ($n=33,810$, or $690/\text{reach} \times 49$ reaches) for this study was performed in a precise and consistent manner.

It also suggests that the RSI "thirty count" should be performed by the same person when RSI is to be used for comparative purposes.

Multicollinearity is a nearly perfect correlation between two predictor variables. This leaves, fundamentally, only one variable. However, there is probably not close enough correlation to evidence multicollinearity between RSI and D_{50} .

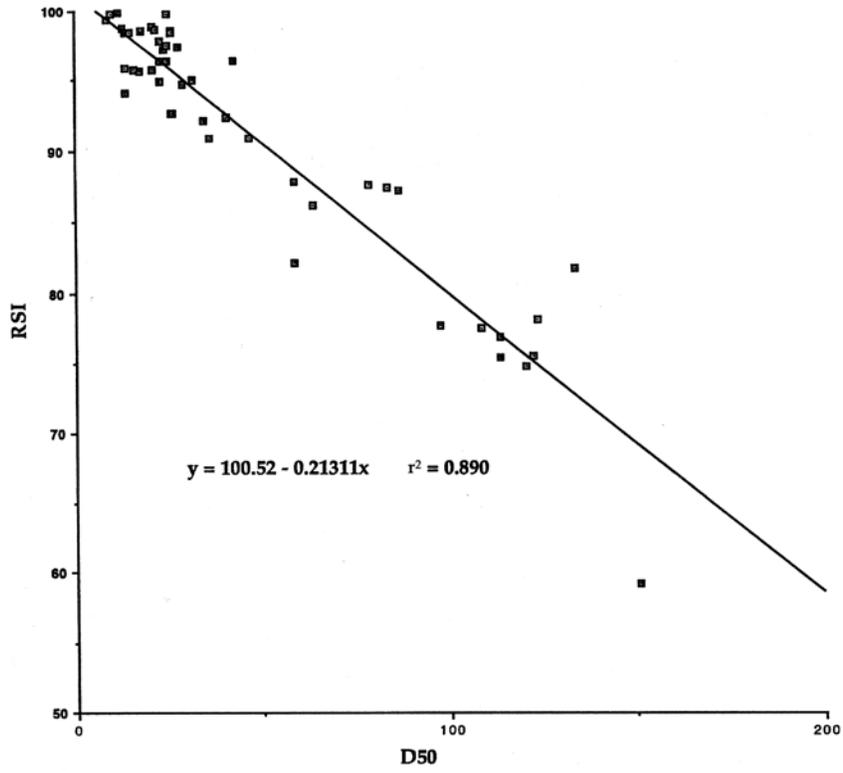


Figure 8. RSI as a function of D50

RSI 1992 vs. RSI 1993

RSI measurements taken by Knopp on these same reaches in 1992 covary with RSI values I measured in 1993 ($r^2 = .422$, Figure 9).

The 1992 RSI values were measured after six years of drought. An earthquake followed in southern Humboldt County; then a winter of flooding in the Mattole Valley, Mendocino, and Sonoma counties. The corresponding increase in point and non-point source sediment input is likely responsible for the global increase in RSI values for 1993.

It seems likely that regression of RSI measurements taken from two winters with similar flood return intervals would yield a higher r-squared value. Knopp and I were very fortunate to for the opportunity to perform these RSI measurements first after a drought, and again after a flood: it provided baseline quantification of the full natural range of values which are likely to be encountered as winter flows wax and wane in response to meteorological cycles.