AN ABSTRACT OF THE THESIS OF

Niels C. Leuthold for the degree of Master of Science in Fisheries Science

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Title: Comparison of Methods to Estimate Population Density of Pacific Giant Salamanders in Small Streams of the Southern Oregon Cascades.

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Stanley V. Gregory

I compared hand sampling, two-pass multiple removal sampling, mark-recapture and catchability-based population estimates for the Pacific giant salamander (*Dicamptodon tenebrosus*) at 22 sites in 11 streams of Cascade Mountains of Oregon. Mark-recapture and catchability-based population estimates were not significantly different ($p = 0.86$). Hand sampling and two-pass multiple removal population estimates were not significantly different ($p = 0.57$). However, mark-recapture and catchability-based estimates were significantly greater than two-pass multiple removal and hand sampling estimates. Hand sampling and multiple removal population estimates were frequently lower than the number of individual Pacific giant salamanders captured by all methods at a site. The catchability of each method differed between streams and within consecutive sites on the same stream. Unacknowledged differences in catchabilities among sites are

a potential source of error when using hand-sampling index counts to estimate and compare populations without correcting the estimates for the differences in Pacific giant salamander catchability. Catchability decreased significantly between the first pass of electroshocking and the subsequent recapture pass of electroshocking. This decrease was observed even though the recapture passes were performed the day after the multiple removal electroshocking. A decrease in catchability violates the assumptions of constant catchability for multiple removal population estimates and potentially explains the weaker performance of removal estimates. Hand sampling estimates did not adjust for the proportion of the population captured at each site, and this is probably the cause of their poor performance. The presumption of constant catchability in hand sampling produced biases in the population estimates, because the catchabilities were not constant. In future studies of stream amphibian abundance, catchability needs to be included in population estimation procedures to produce accurate estimates and to allow valid comparisons of population sizes between sites. Catchability models can be used to calibrate less intensive survey methods, such as hand sampling or a single pass of electroshocking, with the results from more intensive mark-recapture methods. Intensive work would be needed to do the calibrations, but afterwards a standard, more convenient method, such as electroshocking or hand sampling, can be used within the ranges of habitat values for which the calibration model is valid.

Comparison of Methods to Estimate Population Density of Pacific Giant Salamanders in Small Streams of the Southern Oregon Cascades

by
Niels C. Leuthold

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APPROVED:

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Major Professor, representing Fisheries Science

Redacted for privacy

Chair of the Department of Fisheries and Wildlife

Redacted for privacy

Dean of the Graduate School

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

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Niels C. Leuthold, Author

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CONTRIBUTION OF AUTHORS

Dr. Bruce Bury assisted greatly in the design, implementation and interpretation of this study. Dr. Peter Bayley assisted during the data analysis and interpretation, and the analysis would have suffered without his input.

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INTRODUCTION

Counts of stream amphibians have been used to examine habitat relationships, impacts of habitat alteration, and the spatial distributions of species. Accurate determination of the population sizes is crucial for comparing the abundances of animals among sites. The ability to capture individuals can vary for many reasons, including the sampling method chosen, differences in habitats, differences in the ability of observers to detect amphibians, and differences in amphibian behavior (Rosenstock et al. 2002). Differences detected in population size can be due to differences in the actual population size, differences in the catchability at each site, or a combination of the two. If catchability is not included in population estimates, it is impossible to determine the cause of observed population differences.

Accurate determination of population size is important when assessing the impacts of habitat alteration or management. Without accurate estimates of population size the impact of habitat management or a restoration plan cannot be assessed effectively. Recent reports of global amphibian declines highlight the need for accurate estimates of population sizes and trends (Wake 1991). Methods that incorporate the detectability of a species at a site into estimates of the proportion of area occupied have been developed (MacKenzie et al. 2002), and are starting to be used for pond breeding amphibians. Likewise, population estimates that include a measure of catchability, such as mark-recapture, multiple removal or quasi-likelihood catchability estimates need to be used to accurately determine the status of stream amphibian populations.

Multiple hand sampling methods for stream amphibians have been developed (Bury and Corn 1991, Diller and Wallace 1999, Dupuis and Steventon 1999, Welsh et al 1997, Welsh and Lind 2002, Wilkins and Peterson 2000), but these methods do not account for the catchability at a site or differences in catchability between sites. Accurate estimation of population size and comparison of the population sizes at multiple sites requires the inclusion of catchability. Multiple removal methods, mark-recapture methods, and quasi-likelihood catchability models incorporate catchability in their estimates of population size.

In this study, I compare the population estimates returned by hand sampling, multiple removal methods, mark-recapture methods, and quasi-likelihood catchability models. At 22 sites in the Little River Adaptive Management Area block nets were placed to minimize the immigration and emigration of Pacific giant salamanders (*Dicamptodon tenebrosus*). Sampling was first conducted by hand on 30% of available transects. Transects spanned the width of the stream and were 1 m in length in the direction of stream flow. All captured individuals were batch marked, to indicate that they were captured during hand sampling, and were released as close to the point of capture as possible. The next day two passes of removal electroshocking were performed. Captured salamanders were batch marked to indicate the pass of electroshocking on which they were captured, and were released as close to the point of capture as possible after completion of the 2 passes. One day later, a single pass of electroshocking was performed as the recapture pass. The locations of any marks were carefully recorded and the data were used to construct a capture history of each animal. Population estimates were calculated for each survey method.

Population estimates that do not account for catchability are likely to underestimate the population size. If catchability is not included in population estimates, one must assume that the catchability is constant between the sites in order to compare the populations. The assumption of equal catchability needs to be assessed prior to using methods based on index counts. The objectives of this study were to determine catchability as a function of habitat variables and sampling method, compare different methods of estimating population density, and to evaluate the assumptions of each approach.

COMPARISON OF METHODS TO ESTIMATE POPULATION DENSITY OF PACIFIC GIANT SALAMANDERS IN SMALL STREAMS OF THE SOUTHERN OREGON CASCADES

ABSTRACT

I compared hand sampling, two-pass multiple removal sampling, mark-recapture and catchability-based population estimates for the Pacific giant salamander (*Dicamptodon tenebrosus*) at 22 sites in 11 streams of Cascade Mountains of Oregon. Mark-recapture and catchability-based population estimates were not significantly different ($p = 0.86$). Hand sampling and two-pass multiple removal population estimates were not significantly different ($p = 0.57$). However, mark-recapture and catchability-based estimates were significantly greater than two-pass multiple removal and hand sampling estimates. Hand sampling and multiple removal population estimates were frequently lower than the number of individual Pacific giant salamanders captured by all methods at a site. The catchability of each method differed between streams and within consecutive sites on the same stream. Unacknowledged differences in catchabilities among sites are a potential source of error when using hand-sampling index counts to estimate and compare populations without correcting the estimates for the differences in Pacific giant salamander catchability. Catchability decreased significantly between the first pass of electroshocking and the subsequent recapture pass of electroshocking. This

decrease was observed even though the recapture passes were performed the day after the multiple removal electroshocking. A decrease in catchability violates the assumptions of constant catchability for multiple removal population estimates and potentially explains the weaker performance of removal estimates. Hand sampling estimates did not adjust for the proportion of the population captured at each site, and this is probably the cause of their poor performance. The presumption of constant catchability in hand sampling produced biases in the population estimates, because the catchabilities were not constant. In future studies of stream amphibian abundance, catchability needs to be included in population estimation procedures to produce accurate estimates and to allow valid comparisons of population sizes between sites. Catchability models can be used to calibrate less intensive survey methods, such as hand sampling or a single pass of electroshocking, with the results from more intensive mark-recapture methods. Intensive work would be needed to do the calibrations, but afterwards a standard, more convenient method, such as electroshocking or hand sampling, can be used within the ranges of habitat values for which the calibration model is valid.

INTRODUCTION

Stream amphibians in forests of the Pacific Northwest include Pacific giant salamanders (*Dicamptodon tenebrosus*), torrent salamanders (*Rhyacotriton* spp.), and the tailed frog (*Ascaphus truei*). They can be extremely abundant, yet little is known about the accuracy of survey methods to quantify stream amphibian populations. Stream amphibians can be more abundant than fish in small headwater streams and the Pacific giant salamander can account for more than 90% of the captured predator biomass in small streams (Murphy and Hall 1981, Hawkins et al. 1983, Bury et al. 1991). Thus, Pacific giant salamanders play an important role in the determination of community structure in headwater streams. Survey methods that accurately estimate population sizes of Pacific giant salamanders are important to understanding the role of these salamanders in the function of forest streams and their associated food webs.

Abundance of stream amphibians has been assessed with hand surveys of stream sections (Bury and Corn 1991, Diller and Wallace 1999, Dupuis and Steventon 1999, Welsh et al 1997, Welsh and Lind 2002, Wilkins and Peterson 2000) or by electroshocking (Murphy and Hall 1981, Hawkins et al. 1983, Burgess 2001, Roni 2002). Studies that have used electroshocking to sample for Pacific giant salamanders usually occurred while also sampling for fish (Murphy and Hall 1981, Hawkins et al. 1983, Burgess 2001, Roni 2002). Hand sampling streams for amphibians is labor intensive and sections of stream have to be sub-sampled to reduce costs and sampling effort. Electroshocking allows a whole reach of stream to be sampled in a relatively short time, and may be used to estimate salamander populations by either mark-recapture or multiple removal methods.

Hand sampling is an index count that does not adjust for proportion of the population captured at a site (Rosenstock et al. 2002, Thompson 2002). For index counts to be useful they need to be proportional to the population size, which assumes constant catchability, or catchability needs to be estimated. Therefore index counts that do not account for differences in catchability are of little value (Rosenstock et al. 2002). If catchability is constant, the percent difference in captures will be the same as the percent difference in the population densities, but population sizes will be unknown.

To look for habitat relationships or the effects of land management actions on stream biota we need to examine the effect changes in values of habitat variables have on catchability. Habitat variables are known to affect the catchability of fish (Bayley and Dowling 1993, Bayley 1993, Peterson and Cederholm 1984, Rodgers et al. 1992). Burgess (2001) found that the catchability of Pacific giant salamanders decreased with increasing habitat complexity when sampling with an electroshocker. Approaches that indirectly account for catchability have been developed though site occupancy models based on species presence data (MacKenzie et al. 2002), and may play an important role in future amphibian occupancy sampling. Unfortunately these methods cannot use count data, and abundance may be more important than presence in widely distributed species like the Pacific giant salamander.

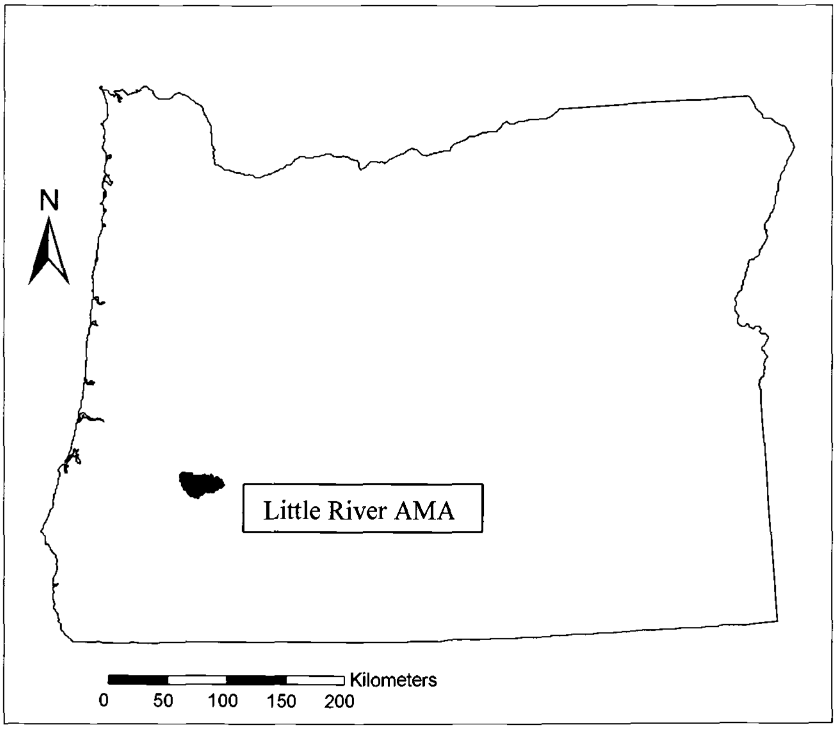
It is likely that stream amphibian catchability varies between sites. It has been argued that the assumption that catchabilities are equal is generally false and that the burden of proof should be to demonstrate that catchabilities do not change (MacKenzie and Kendall 2002). To our knowledge, no studies have determined the accuracy of hand sampling methods for estimating the population size of

Pacific giant salamanders. The objectives of this study were to determine catchability as a function of habitat variables and sampling method, compare different methods of estimating population density, and to evaluate the assumptions of each approach.

STUDY AREA

Little River Adaptive Management Area (AMA) is located in the southern Oregon Cascade Mountains approximately 29 km east of Roseburg, OR (Figure 1). Little River AMA covers 53,360 hectares and falls entirely within the larger Little River watershed. The Bureau of Land Management manages approximately 7800 hectares of Little River AMA and the U.S. Forest Service manages 25,735 hectares. The remaining 19,825 hectares in the Little River AMA are privately owned, and are mostly managed as industrial forests (U.S. Forest Service and Bureau of Land Management 1995). Elevations in Little River AMA range from 220 to 1610 m above sea level. The study area is located in a transition from the Mixed Conifer zone of southwestern Oregon and the western hemlock (*Tsuga heterophylla*) zone (Franklin and Dyrness 1988). The dominant tree species at lower elevations is Douglas-fir (*Pseudotsuga menziesii*). The Little River watershed was harvested intensively during the 1950's and 1960's and almost 60% of the watershed has been harvested (U.S. Forest Service and Bureau of Land Management 1995).

Figure 1: Map of Oregon displaying the location of Little River Adaptive Management Area.



METHODS

Sampling

We sampled 22 sites in 11 stream reaches located in the Little River Adaptive Management Area (AMA) between June and September of 2000 and 2001. Random sampling across the landscape was not feasible. Many sites that appeared appropriate on maps were not suitable for sampling when visited due to low water levels. Spatial randomness is not relevant to a study of catchability. What is important is to sample the range of representative habitats typically occupied by the species studied. We attempted to include a range of habitat conditions, such as dominant substrate size, discharge, depth, and width to represent the range of geomorphic characteristics of streams of Little River AMA (Table 1). Only sites where *Dicamptodon tenebrosus* was known to be present and fish species were absent were selected for sampling. Additionally, sampling only occurred in sites on land belonging to the Bureau of Land Management land or the U.S. Forest Service.

The downstream end of each reach was at least 50 m upstream from the nearest road crossing. Each reach was approximately 100 m long. The actual length of each reach varied because the beginning and end of reaches were determined by the end of habitat units and not by a predetermined value, but such variation is unimportant for this study. Prior to sampling we placed a 4-mm mesh block net at the downstream end of a reach. Additional 4-mm mesh block nets were placed at habitat unit boundaries when the length of the reach was between 50 m and 100 m. This process split each reach into two sites that were each approximately 50 m long, but varied in actual length.

Habitat units were sequentially mapped in the upstream direction from the downstream end of a site (see Hankin and Reeves 1988; Bisson et al. 1982). Aquatic habitat was classified as pool, riffle, step, or side-channel habitat units (Bisson et al. 1982). Adjacent habitat units had to be of a different type and each habitat unit had to be at least as long as its active channel width, with the exception of steps. We recorded the length, maximum depth, aspect and slope for each unit.

Table 1: Characteristics of the 22 sites selected for sampling in the Little River Adaptive Management Area, Oregon during June – September 2000 and June – September 2001. All data were collected at the selected sites at the time of sampling.

	Average	Min	Max	Median	SD
Stream Gradient (%)	7.0	0.8	14.5	6.6	3.5
Mean width (m)	2.6	1.2	3.7	2.7	0.7
Mean Depth (cm)	8.7	5.0	13.6	8.9	2.7
Maximum Depth (cm)	47.2	20	100	44.5	20.5
% Pool	28	0	74	28	0.2
Mean particle size (mm)	148	61	267	145	57.5
Aspect (degrees)	181	0	337	189	92.2
Water Temperature (°C)	12.7	9.0	16.5	12.3	1.9

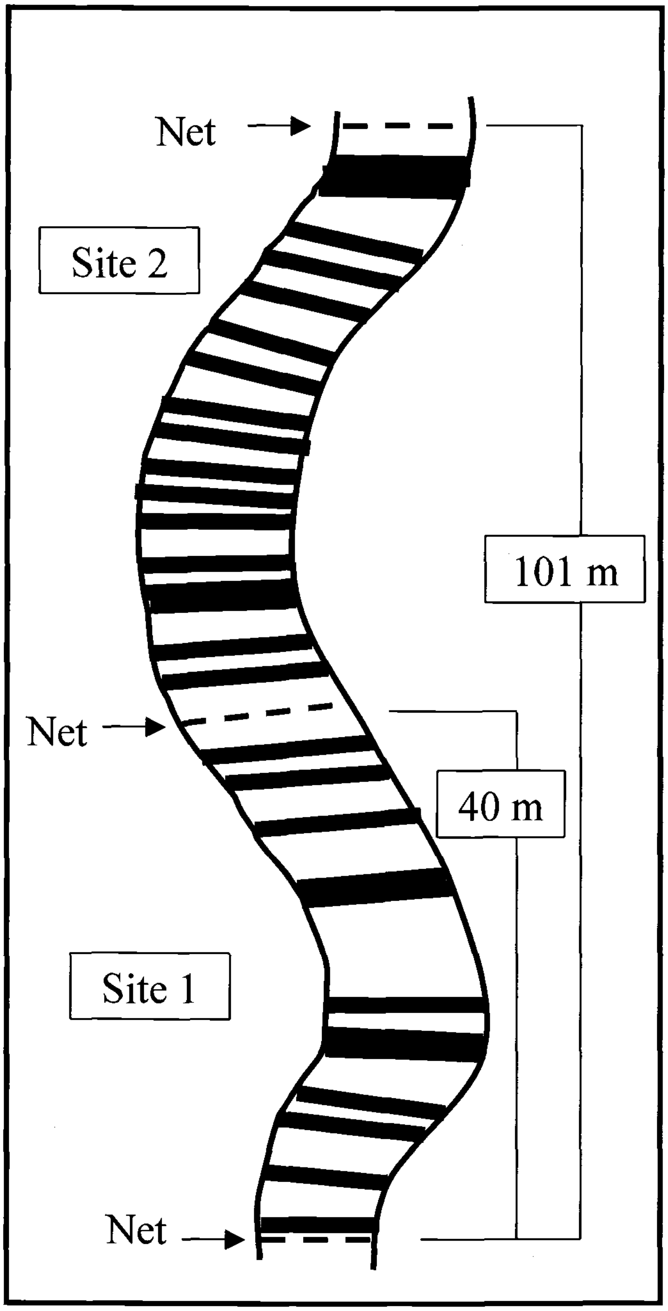
At three equally spaced locations within each unit, we measured the wetted width, active channel width, and the depth at points 25%, 50% and 75% across the wetted width.

Sampling consisted of hand sampling along randomly selected transects, two passes of removal electroshocking, and a recapture pass of electroshocking the following day. Each of the two sites in each stream reach was sampled as an independent unit. Toe clipping was used to mark *D. tenebrosus* captures for mark-recapture estimates. Individuals were batch marked to indicate if they were hand captured, captured on the first pass of removal sample or captured on the second pass of removal sampling. Each salamander could have up to two toes clipped if it was captured by hand and on one of the two passes of removal sampling. Captures of other amphibian species were recorded, but were not marked and are not used in this analysis.

Hand sampling methods were adapted from Adams and Bury (2002). We used a random number generator to select 1-m transects to hand sample. Each transect was 1 m long and spanned the width of the stream (Figure 2). At each site 30% of all possible transects were sampled, which is also the approximate percentage of the area of each site sampled. A sample of 30% of all possible transect was chosen to keep the hand sampling effort consistent between sites of differing lengths. Transects that fell in an area that was too steep to sample safely or in a pool that was too deep (>60 cm) to hand sample effectively were moved to the nearest position that could be sampled (Adams and Bury 2002).

The width of each transect was split into 0.3-m sub-transects and a rock was randomly selected and measured from each section. Average particle size was calculated from the cumulative frequency distribution for particle sizes and bedrock was treated as a zero in the calculations. At each transect we recorded, the stream width, depth at three points, dominant substrate, subdominant substrate, and the percent cover of wood, fine organic material, undercut banks, and overhanging vegetation were recorded (Adams and Bury 2002). Transects were sampled by a crew of one or two, depending on the width of the stream. If a transect was > 2 m in width, two surveyors were used during sampling. To reduce the possibility of

Figure 2: Sampling design in stream reaches sampled in Little River Adaptive Management Area, Oregon during June – September 2000 and June – September 2001. Solid black bars represent the randomly selected transect used in hand sampling. Two sites of varying length were located within each stream reach. Reaches and sites varied in length, because habitat unit boundaries were used to define the beginning and end of each site.



surveying outside a transect, we placed a meter stick along the stream to mark the upstream end of the transect. Transects were visually inspected prior to disturbing the substrate to detect any amphibians in the open (following Bury and Corn 1991). If an individual was seen in the open, it was captured prior to substrate disturbance.

We conducted a systematic search of all surfaces within the wetted channel, by starting at the downstream end of a transect and working upstream. All easily movable objects were overturned and amphibians were either washed into 4-mm mesh wire screens or they were captured by hand (Adams and Bury 2002, Bury and Corn 1991). To minimize habitat disturbance, we left objects in place that were embedded, wedged tightly or were too heavy to be moved. Objects left in place were searched by running a hand along the object and into any spaces around the object. Only the surface layer was searched and all objects were returned to their original position.

Captured amphibians were placed in resealable plastic bags with water or wet moss to be processed after a transect was completely surveyed. For each specimen captured we recorded the species, stage, snout-vent length (mm), total length (mm), mass (g), and transect location. All *D. tenebrosus* captures were marked with a toe clip to indicate that they were captured by hand. After processing, captured animals were released as close to the point of capture as possible.

Once hand sampling was completed, sites were allowed to recover overnight prior to initiation of electroshocking. We performed two passes of removal electroshocking. All electroshocking was performed with a Smith-Root Model 12-A battery-powered backpack electrofisher. A setting of 400-500 V, 30 Hz and a 12% duty cycle were used for electroshocking. Due to the small size and low water levels of the streams sampled, we used a 15.2-cm anode ring to allow greater maneuverability. The electroshocking was performed by starting at the downstream net and working systematically upstream. Once the upper net in a section was reached, the crew turned around and electroshocked quickly as they moved back to the lower net. After the downstream sweep, the lower net was carefully inspected for any amphibians that were swept into the net. During electroshocking the entire site was surveyed, while only 30% of each site was sampled by hand.

Captured individuals were processed similarly to the hand sampling protocol, except that a different toe was clipped to indicate the pass of removal sampling on which an individual was captured. All salamanders were checked for marks to see if they had been captured during hand sampling. Pacific giant salamanders were released as close to the point of capture as possible.

A single pass of electroshocking was performed the next day as the recapture pass for mark-recapture estimates. All *D. tenebrosus* captures were carefully inspected for the presence of marks. All marks were recorded to determine the capture history of any individual.

Analysis

Each of the two sites within a stream reach was sampled independently and analyzed separately, producing a sample size of 22. Any individuals captured in the lower block net during electroshocking were included as part of the capture for analysis. Population estimates of Pacific giant salamander (N_{HAND}) were calculated from the hand sampling data by calculating capture density and multiplying by the total surface area of the unit using the following formula

$$\hat{N}_{HAND} = \frac{C_{HAND}}{SA_{HAND}} * SA_{SITE}, \tag{1}$$

where C_{HAND} is the number of individual captured by hand, SA_{HAND} is the surface area searched by hand, and SA_{SITE} is the surface area of the entire site. Data from the two passes of removal sampling were used to calculate maximum likelihood estimates of the salamander population (N_{REM}) (DeLury 1947, Zippen 1956). The 2-pass maximum likelihood removal estimate can be approximated by

$$\hat{N}_{REM} = \frac{(C_1)^2}{C_1 - C_2}, \tag{2}$$

where C_1 = the number of captures on pass 1 of removal sampling and C_2 = the number of captures on pass 2 of removal sampling. Only salamanders caught during the two passes of removal electroshocking were used as marks in the calculation of the adjusted Peterson single census mark-recapture population estimate (N_{RECAP})(Ricker 1975). Using only individuals that were marked by electroshocking is more consistent with typical mark-recapture methods, where different sampling methods would not be used. The following formula was used to obtain the adjusted Peterson estimate of population size (Ricker 1975)

$$\hat{N}_{RECAP} = \frac{(M+1)(C+1)}{R+1}, \tag{3}$$

where M is the total number of marked individuals, C is the total catch on the recapture pass, and R is the number of recaptures on the recapture pass. Catchability models were fit using all of the marked individuals as the vulnerable population (N_{CATCH}). Catchability (q) is defined as

$$q = \frac{c}{v}, \tag{4}$$

where c is defined as the capture, and v is defined as the vulnerable population. The catchability on the recapture pass was modeled, and c was defined as the number of recaptures on the recapture pass and v was defined as the number of marked individuals. The catchability during the recapture pass was then modeled using habitat data.

Overdispersion occurs when the variance is greater than expected, under the given error distribution. In binomial models, overdispersion is often referred to as extra-binomial variation. Overdispersion is common in capture studies and a quasi-likelihood model was used to model catchability instead of assuming a binomial error distribution (Bayley 1993). Williams (1982) describes two methods for altering the maximum likelihood estimation by iteratively reweighted least squares to account for extra-binomial variation in a logistic regression. Williams (1982) model III was used to model extra-binomial variation because the random and fixed effects are additive on the logistic scale, aiding in the estimation of variance (Bayley 1993; Williams 1982). Capture data were separated into two groups based on snout-vent length (≤80 mm and >80 mm SVL) and the inverse of the average snout-vent length was used as a variable in each model because it was found to have greater explanatory value than untransformed length. The other variables included in the models were mean particle size, mean width, percent pool and all first-order interactions. Variables were tested for independence at the $p \leq 0.05$ level prior to including them in the model. Additional variables considered, but dropped due to high correlations or because alternate correlated variables were consider to be more influential on catchability were average depth, maximum depth, total surface area of the site, and the percentage of measured particle that were either boulders or cobble. A χ^2 drop-in-deviance test (McCullagh and Nelder 1989) was used to check for the significance of terms in a model at the $p \leq 0.05$ level. The drop in deviance is not meaningful between non-nested models, so model terms were checked for significance without changing the quasi-likelihood weighting (Bayley 1993).

The recapture pass catchability at each site was estimated as a function of habitat data measured at each site. The predicted catchability was then used to estimate the population size of unmarked individuals in the recapture pass

$$\hat{N}_{CATCH} = \frac{C_{ru}}{\hat{q}} + M , \qquad (5)$$

where C_{ru} is the catch of unmarked individuals on the recapture pass, $\hat{q}$ is the estimated catchability, and M is the total number of marked individuals. The number of marked individuals was known, so catchability estimates were only used to calculate the number of unmarked individuals.

RESULTS

We captured 1,434 Pacific giant salamanders at least once and recaptured 539 as marked individuals. Of all captures 284 occurred during hand sampling, 821 in the first pass of electroshocking, 276 during the second pass of electroshocking and 580 in the recapture pass of electroshocking (Table 2). No torrent salamanders and few tailed frogs were captured, and these species were eliminated from further analysis

At the first 2 sites sampled we were not sure if enough salamanders could be marked to obtain a reasonable mark-recapture estimate of the population size. Individual Pacific giant salamanders observed in the open outside of surveyed transects were captured and marked. The 12 salamanders marked from areas outside of transects were not used in the population estimates derived from hand sampling and were only used as marks for the catchability-based models. The inclusion of these additional marked individuals increased the number of marked individuals in the two sites by 6.6% and 5.9%. No substrate was disturbed during these opportunistic captures.

At one site the maximum likelihood removal estimate failed because the

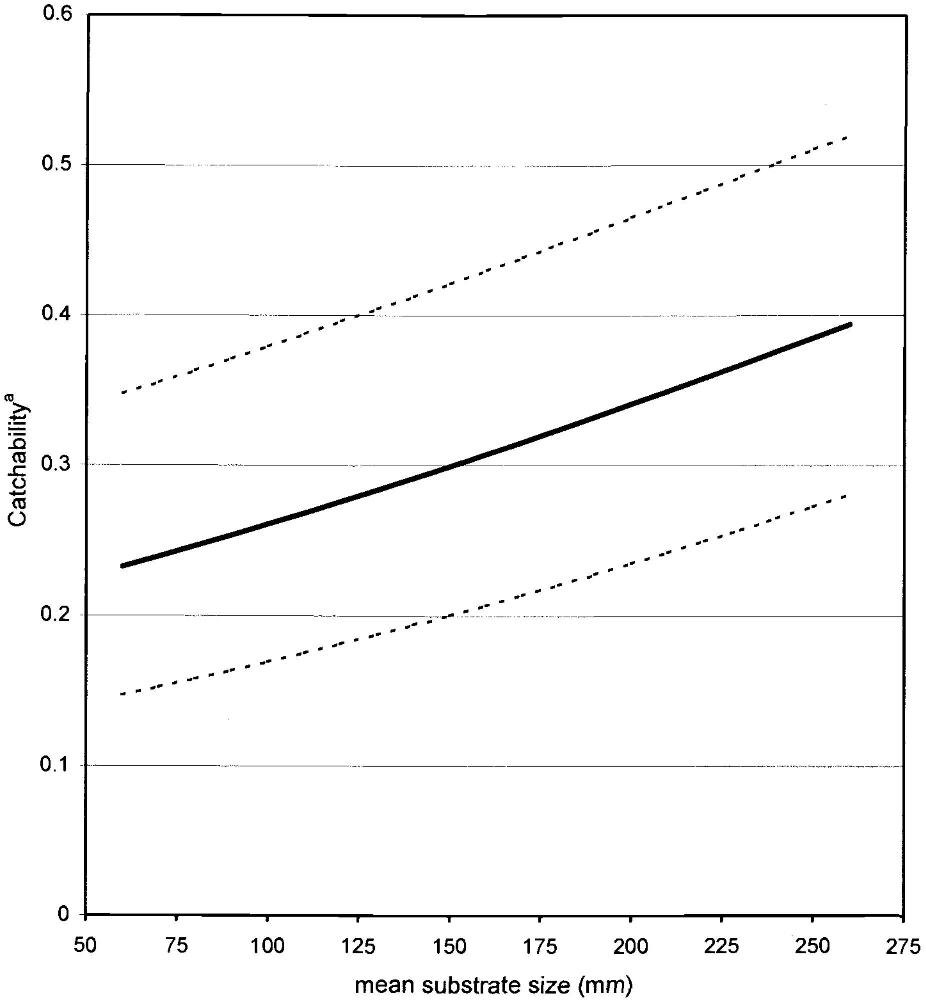
Table 2: Capture summary for Pacific giant salamanders in stream sections within Little River Adaptive Management Area, Oregon during June – September 2000 and June – September 2001. Total is the total number of captures made for all methods, including recaptures. Unique is the number of unique individuals captured for all methods. Data from the 12 salamanders caught by hand outside of a transect are not included in this summary.

	Hand	Pass1	Pass 2	Recapture Pass	Total	Unique
Average	12.9	37.3	12.6	26.4	89.1	65.2
Median	7	27.5	8.5	18.5	67	45.5
Minimum	0	5	0	1	7	5
Maximum	38	110	55	108	301	216
S.D.	12.6	31.3	13.3	26.4	79.7	57.7
Total	284	821	276	580	1961	1434

same number of individuals was captured on each pass. At another site no individuals were captured on the second pass of removal sampling and the removal estimate also failed. In both cases the multiple removal estimates are treated as null values and we did not consider them in further comparisons.

Inverse snout-vent length and untransformed SVL were not significant in the catchability model, so the data were regrouped into one size class and the analysis was repeated. The final model for catchability during the recapture pass of electroshocking included mean particle size (MPS) and mean width (MW) of each

Figure 3: Predicted recapture pass catchability (q_{CAL}) of Pacific giant salamanders versus the range of observed mean particle sizes, holding stream width constant (2.5 m), in streams of Little River Adaptive Management Area, Oregon during June – September 2000 and June – September 2001. Dashed lines represent 95% confidence interval for a population with 100 individuals.



$^{a}q_{CATCH} = (1 + \exp[-(-0.56 + 0.0038(MPS) - 0.35(MW))]\ )^{-1}$

site and was represented by:

$$q_{CAL} = (1 + \exp[-(-0.56 + 0.0038(MPS) - 0.35(MW))]\,)^{-1}. \qquad (6)$$

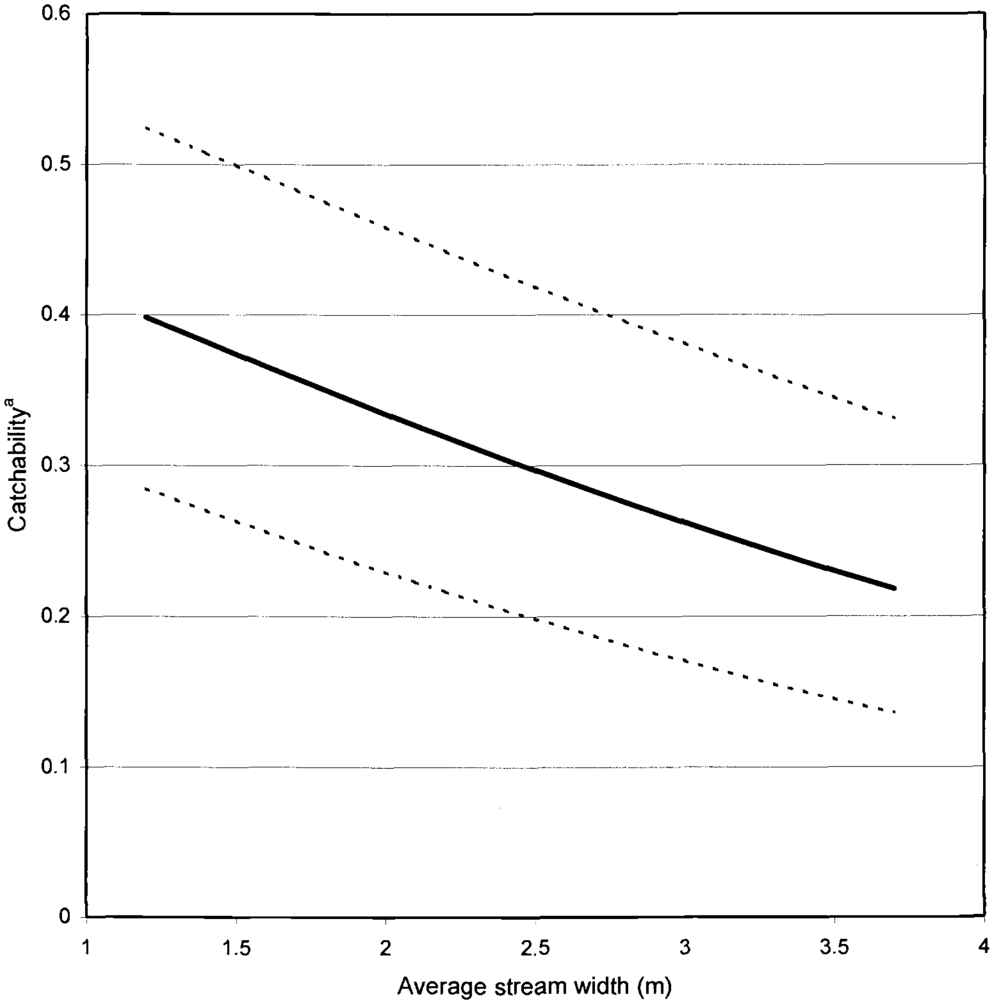
$$(SE) \qquad (0.37)\ (0.0013) \qquad (0.14)$$

The catchability model estimated an extra-binomial variance of 0.023. Holding the mean stream width constant, an increase of 50 mm in the mean particle size predicts a 1.21 times increase in the odds of capture during the recapture pass (Figure 3). If the mean particle size is held constant but the mean stream width decreases by 1.0 m, the odds of individual capture during the recapture pass is predicted to be 1.41 times greater (Figure 4).

At each site, the total number of captures ($\log_e$ transformed) on the first pass of electroshocking was significantly higher than the total number of captures ($\log_e$ transformed) on the recapture pass (ANOVA, $p \leq 0.001$). The decrease in total capture between the first pass of electroshocking and the recapture pass indicates that the catchability is not constant, because the same number of individuals was available for capture. Paired t-tests of the population estimates at each site indicated significant differences between N_{CATCH} and N_{REM} ($p \leq 0.001$, mean difference = 30.2), N_{CATCH} and N_{HAND} ($p = 0.005$, mean difference = 34.0), and N_{RECAP} and N_{HAND} ($p = 0.004$, mean difference = 34.6) in each section (Table 3). No significant differences were detected between N_{CATCH} and N_{RECAP} ($p = 0.86$, mean difference = -0.6) or N_{REM} and N_{HAND} ($p = 0.57$, mean difference = 6.1).

Estimates of N_{CATCH} and N_{RECAP} are similar in magnitude, but N_{RECAP} values were generally larger than the catchability-based estimates (Table 4). In all

Figure 4: Predicted recapture pass catchability (q_{CAL}) of Pacific giant salamanders versus the range of observed mean stream width, holding mean particle size constant (147 mm), in streams of Little River Adaptive Management Area, Oregon during June – September 2000 and June – September 2001. Dashed lines represent 95% confidence interval for a population with 100 individuals.



[a] $q_{CATCH} = (1 + \exp[-(-0.56 + 0.0038(MPS) - 0.35(MW))])^{-1}$

Table 3: Summary of population estimates for Pacific giant salamanders in stream sections within Little River Adaptive Management Area, Oregon during June – September 2000 and June – September 2001. N_{CATCH} is the catchability-based estimate of population size, N_{RECAP} is the mark-recapture estimate of population size, N_{REM} is the multiple removal estimate of population size and N_{HAND} is the estimate of population size from hand sampling.

Site	N_{CATCH}	N_{RECAP}	N_{REM} [a]	N_{HAND}
Average	86	87	64	52
Median	56	65	48	29
Minimum	5	7	6	0
Maximum	273	251	220	146
SD	76	72	54	52
Total	1898	1910	1271	1149

[a] At 2 sites the removal estimate failed. In one case equal numbers of individuals were captured on each pass and in the other case there were no captures on the recapture pass.

but 2 out of the 22 cases, the multiple removal estimates of population size, N_{REM}, were smaller than estimates of N_{CATCH} (Appendix 3). Hand sampling estimates of population size, N_{HAND}, were smaller than N_{CATCH} in all but three cases. The hand sampling population estimates, N_{HAND}, were smaller than the total number of unique individuals captured by all methods in all but five cases. There were six cases when N_{REM} was greater than or equal to the total number of individuals captured in a section. The N_{CATCH} and N_{RECAP} estimates were always greater than or equal to the number of unique individuals captured within a section.

Table 4: Summary of the ratio of population estimates for Pacific giant salamanders in sampled stream sections in Little River Adaptive Management Area, Oregon during June – September 2000 and June – September 2001. N_{CATCH} is the catchability-based estimate of population size, N_{RECAP} is the mark-recapture estimate of population size, N_{REM} is the multiple removal estimate of population size and N_{HAND} is the estimate of population size from hand sampling.

Site	N_{RECAP}/N_{CATCH}	N_{REM}/N_{CATCH} [a]	N_{HAND}/N_{CATCH}
Average	1.11	0.76	0.53
Median	1.04	0.72	0.48
Minimum	0.78	0.40	0 [b]
Maximum	2.10	1.56	1.40
S.D.	0.29	0.25	0.42

[a] At 2 sites the removal estimate failed. In one case equal numbers of individuals were captured on each pass and in the other case there were no captures on the recapture pass.

[b] 4 sites had no hand captures

In the cases where N_{REM} was larger than N_{CATCH} the population sizes were small and capturing or missing one or two individuals could greatly affect population estimates. The cases where N_{HAND} was larger than N_{CATCH}, the populations were reasonably large and errors associated with small sample size are less likely. At one of these sites, a large number of Pacific giant salamander larvae with a snout-vent length < 25 mm were captured by hand. Our data suggest that electroshocking may not capture the smallest larvae as effectively and this may have resulted in electroshocking catchability estimates that are small compared to hand sampling estimates (Figure 5).

Table 5: Summary of the catchability, q, estimates from each sampling method used for Pacific giant salamanders surveys in streams in Little River Adaptive Management Area, Oregon during June – September 2000 and June – September 2001. q_{CATCH} is the catchability estimated by the catchability models, q_{RECAP} is the estimate of catchability used in mark-recapture estimates, q_{REM} is the catchability estimate calculated during multiple removal estimates of population size and q_{HAND} is the hand sampling estimate of population size divided by the catchability-based estimate of population size (N_{CATCH}).

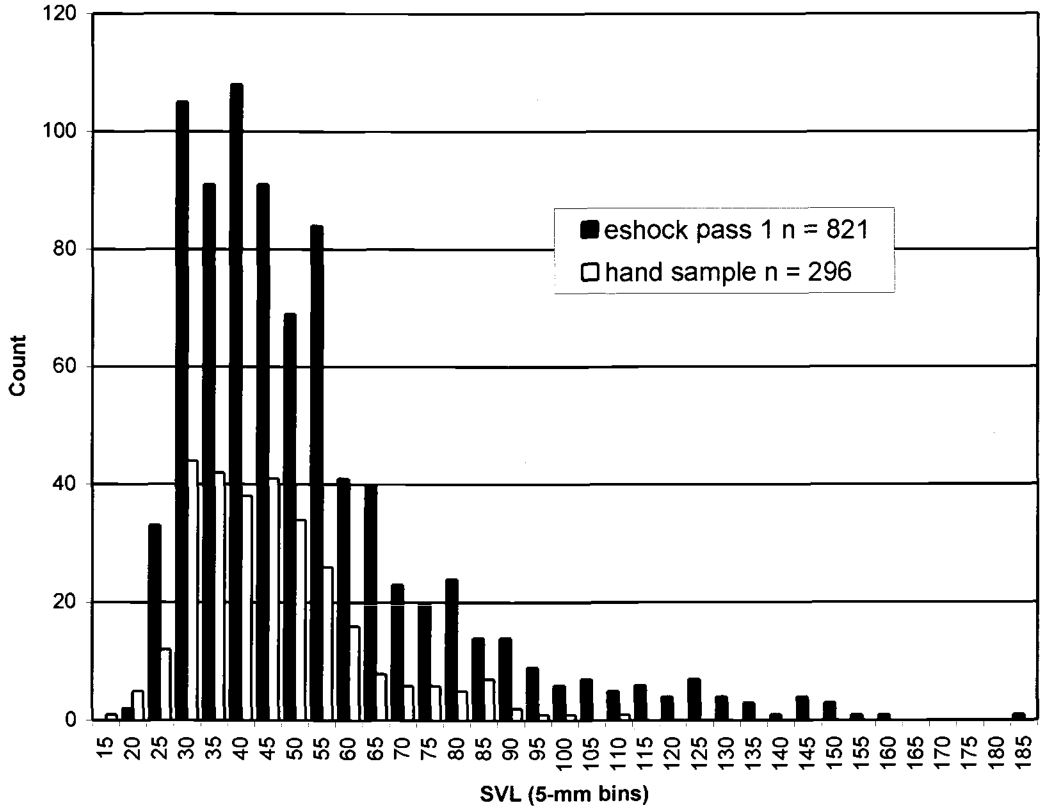
	q_{CATCH}	q_{RECAP}	q_{REM}[a]	q_{HAND}
Average	0.30	0.30	0.67	0.53
Median	0.30	0.33	0.68	0.48
Minimum	0.18	0.14	0.27	0[b]
Maximum	0.43	0.46	0.85	1.40
S.D.	0.06	0.10	0.16	0.42

[a] At two sites the removal estimate failed. In one case equal numbers of individuals were captured on each pass and in the other case there were no captures on the recapture pass. The catchability was undefined in these cases and it was not included in summary calculations.

[b] 4 sections had no hand captures.

Catchabilities (Table 5) are derived from the multiple removal and mark-recapture estimation procedures. The hand sampling catchability was calculated by dividing the N_{HAND} by N_{CATCH}. In all cases q_{REM} was greater than or equal to q_{CATCH}. The catchability estimates (q) produced by each method varied across sites and sections within sites. In four cases there were no hand captures, resulting in a catchability estimate of zero for the hand sampling. In all of these cases electroshocking captured individuals, though the total number of individual caught

Figure 5: Frequency distribution of the snout-vent length (SVL) of Pacific giant salamander captures for hand captures and a single pass of electroshocking in Little River Adaptive Management Area, Oregon during June – September 2000 and June – September 2001.



in each section was less than 15. At one site, hand sampling failed to detect any individuals in both sections.

The size distributions of Pacific giant salamanders caught by hand and caught on the first pass of electroshocking were similar (Figure 5). The first pass of electroshocking caught few individuals with a SVL less than 25 mm. Hand sampling also caught few individuals with a SVL less than 25 mm and did not capture any individuals with a SVL larger than 108 mm. On the first pass of electroshocking, 37 individuals with SVLs greater than 108 mm were captured.

The largest individual captured on the first pass of electroshocking had a SVL of 181 mm.

DISCUSSION

The true population at each section is unknown, as in all field studies, so the population estimates cannot be compared to the true population size. Determining the true population size of Pacific giant salamanders at a site is infeasible. Calibration on the basis of a known, introduced population in an uncolonized area presents problems. The handling and introduction of individuals to a new environment may cause changes in behavior that would affect catchability. Additionally, if an area is uninhabited by a species there may be important reasons that a species is not naturally found there, therefore the relevance of such an endeavor is questionable.

Our data show that the population estimates from hand sampling and multiple removal sampling frequently underestimated the population estimates derived from mark-recapture estimates and catchability modeling. Our finding that multiple removal estimates are significantly smaller than mark-recapture population estimates is consistent with data comparing these estimators in fish populations (Burgess 2001, Peterson and Cederholm 1984, Rodgers et al 1982). Burgess (2001) found a similar trend for Pacific giant salamanders in stream pools. In most cases N_{HAND} and N_{REM} were smaller than the total number of individual salamanders captured in a stream and their ratio to N_{CATCH} was not constant. Using

N_{HAND} or N_{REM} to compare populations, even for relative rather than absolute difference is problematic because these estimators do not have a consistent relationship with our best estimates of population size. Quasi-likelihood catchability models for fish have produced population estimates that are greater than mark-recapture and multiple removal population estimates (Bayley and Dowling 1993, Bayley 1993, Burgess 2001). Mark-recapture methods have underestimated the size of known fish populations by 5-20% (Rodgers et al. 1992, Peterson and Cederholm 1984). Population estimates from mark-recapture methods and catchability-based methods did not differ in this study. However, the mark-recapture and catchability-based methods are not independent, because catchability estimation uses mark-recapture. Therefore lack significant of difference between these two estimators is not surprising.

Each method makes fundamental assumptions to provide an accurate population estimate, and these assumptions are not always met. Hand sampling is an index count that assumes captures have a consistent correlation to the actual population size (Rosenstock et al. 2002, Thompson 2002), as is the index catch per unit effort from one or more electroshocking passes. The key assumption is that the catchability of Pacific giant salamanders remains constant at all sites. Three factors that affect catchability are 1) habitat variables that alter salamander behavior or alter the observer's ability to detect individuals, 2) characteristics of salamanders themselves that affect catchability, and 3) differences in observers' abilities to detect individuals (Rosenstock et al. 2002). Proper training to ensure that all crewmembers perform surveys in a similar manner can reduce differences between observers (Bury and Corn 1991). Training may be particularly important when habitat disturbance is minimized during hand sampling. Uniformity in selection of objects to be removed or not removed during surveys is needed to ensure a consistent level of effort is used during sampling.

It is difficult to estimate the differences in stream amphibian populations without knowing how habitat variables affect the results of surveys. Many studies have looked at the effect of habitat disturbance on stream amphibian abundance (i.e., Corn and Bury 1989, Welsh and Ollivier 1998), but the effect of the habitat alteration on amphibian catchability has not been quantified. Differences detected in the populations between sites may be due to actual differences in the populations or they could be due to differences in catchability. Impacts may affect amphibians in each stream differently due to interactions with other habitat variables and effects may differ between habitat units within a stream (Corn and Bury 1989, Hawkins et al. 1983, Murphy and Hall 1981). Other studies have correlated amphibian population sizes to stream habitat variables, but again these studies have not quantified the effects of habitat variables on the ability to determine population size (Adams and Bury 2002, Diller and Wallace 1999, Welsh and Lind 2002, Wilkins and Peterson 2000). Our data show that the catchability of Pacific giant salamanders differs between sites and even between two adjacent sites in the same reach. Not accounting for differences in catchability between sites makes it impossible to determine if observed differences in catches reflect real differences in populations (Bayley and Dowling 1993). Differences in catchability between sites can mask or accentuate ecological affects on existing population density, and purported trends with habitat changes can be artifacts of catchability differences.

Individual characteristics of salamanders such as size, coloration, activity level and behavior can influence how easily salamanders are detected. These characteristics may vary with age or between sites. Our results indicate that the hand survey method used did not effectively sample larger Pacific giant salamanders. This may be partly due to limiting hand sampling to shallower water and not disturbing large or embedded substrate, but it could also be due, in part, to behavioral differences between size classes.

We multiplied the estimated hand sampling density at each site by the total surface area to estimate the population size. The hand sampling population estimate assumes that the density at a subsection of belts is representative of the density across a whole reach and that this density corresponds to the population size (Bury and Corn 1989, Welsh et al. 1997). This assumption is dubious for *D. tenebrosus* because the deeper pools cannot be sampled and stream amphibian abundance may be habitat specific (Welsh et al. 1997). Basing estimates on classes of habitat units (e.g., Welsh et al. 1997) may produce more consistent population estimators, but the scale at which stream amphibians respond to instream habitat is unclear and warrants further investigation.

The hand-sampling estimate makes no effort to correct for amphibians that remain undetected and is simply an index that is assumed to have a constant relationship with the true population size. The catchability of hand sampling was not constant in our surveys making comparisons between sites invalid, unless one accounts for the differences by modeling catchability (Bayley and Dowling 1993). Most of the N_{HAND} estimates were smaller than the total number of individual salamanders captured at each section, reflecting the poor performance of hand sampling as a population estimator in our study. In three cases N_{HAND} was larger than N_{CATCH}. In one of these cases, a cluster of salamanders with a snout-vent length of less than 25 mm was captured by hand. These captures may have biased the hand sample estimate of density in the section even though it was only a small area that had a high density of individuals. The effect of hand sampling prior to electroshocking is unclear and it is possible that disturbance caused by hand sampling altered the catchability of salamanders during electroshocking. The effects of hand sampling prior to electroshocking would be particularly important if they did not affect all habitats, size classes, and individuals that were or were not captured by hand in the same manner. If there was an effect of hand sampling prior to electroshocking it is unlikely that it would affect more than a small fraction of the population. Hand sampling was only performed at a subset of the available habitat in any section, so not all of the salamanders were exposed to the same level of disturbance. From our data it is not possible to determine any impact that hand sampling may have had on subsequent electroshocking catchability.

Maximum likelihood multiple removal estimates assume population closure, equal catchability of all individuals, and constant catchability between passes (Zippen 1956). We only observed one Pacific giant salamander moving between sections and assume that using block nets kept immigration and emigration negligible over the short time period when sampling occurred. This assumption may not be valid and it is unlikely that a block net completely blocked Pacific giant salamander movement. Habitat disturbance and the handling of captured salamanders could cause individuals within a section to move. The recapture pass of electroshocking pass was started 12 or more hours after the completion of the two passes of removal sampling. The number of captures on the first pass of electroshocking ($\log_e$) was greater than the number in the recapture pass ($\log_e$), indicating a change in catchability between the passes (ANOVA, $p \leq 0.001$). The capture probability was not constant between passes and the multiple removal estimates does not meet the assumptions required for valid population estimates. It is unclear if the initial catchability and the change in catchability between passes were similar for all individuals. The decrease in catchability between passes caused the estimate of q_{REM} to be larger than it should be and resulted in underestimation of the population size (Bayley and Dowling 1993). N_{REM} was only greater than N_{CATCH} in two cases. In both instances, less than ten individuals were seen at each site and the small sample size may have caused biases in the population estimates.

The failure of the multiple removal estimates at 2 sites is problematic, if the method is to be used widely. Performing additional passes of removal sampling may reduce the number of sites where the multiple removal estimates will fail. The multiple removal estimates failed at sites where the catchability estimates of population size were less than 15 individuals (Appendix 2). Nearly all of the estimated population was captured during the 2 passes of removal sampling (Appendix 1), and it is unlikely that additional passes of removal sampling would have resulted in population estimates that would not fail. Between passes of removal electroshocking the decrease in captures was almost always greater than 50%. The average decrease in captures between passes was 64%. The few sites where the decrease in captures between passes was less than 50% always occurred at sites with small estimated populations. The large decrease in captures between the first second passes suggests limited benefit to performing additional passes of removal sampling.

Mark-recapture methods assume a closed population, marked and unmarked individuals mix randomly within the population, equal catchability of marked and unmarked individuals, and all marked individuals are correctly identified and recorded (Ricker 1975). The catchability-based estimates of population size are based on mark-recapture techniques and make the same assumptions. As in all such field experiments, it is difficult to determine if the catchability of marked and unmarked individuals are equal. If the catchability of marked individuals were lower than the catchability of unmarked individuals, the population sizes would be overestimated because the catchability of the unmarked population would be underestimated. The assumption that marked and unmarked individuals mix randomly in the population is also hard to test. Captured individuals were kept in separate containers and were released as close as possible to where they were captured. Releasing the captured salamanders near their individual capture location should keep marked individual from clumping in small areas, but the behavior of salamanders after release is unknown. It is unlikely that marked individuals were incorrectly identified. We carefully checked marked individuals prior to release to ensure the marking was readable. Pacific giant salamanders are known to be cannibalistic (Parker 1994), and we observed individuals with injuries that were likely caused by other salamanders. The injuries observed were usually missing tails sections, but on occasion we observed a damaged or missing foot. Injuries could also have been caused by shifting substrate during our hand sampling, walking in the stream, or by natural shifts in the stream substrate. Instances of a completely lost foot were rare and we feel few or no marks were missed due to such injuries.

The size of individuals can change the catchability of electroshocked fish (Anderson 1995, Büttiker 1992, Bayley 1993). Our catchability models did not find a significant effect of salamander size on catchability. In a study conducted in pools, Pacific giant salamander length affected catchability (Burgess 2001). While we suspect that salamander size affects catchability, our sample size may have been too small to detect the differences. Any effect of size on catchability may be masked by differences between habitat units. Associations between Pacific giant salamander size, substrate and habitat type may mask the effects of size on catchability.

Our results indicate that catchability increased with larger substrate. Another study found that Pacific giant salamander catchability decreased with increased percentage of cobble and boulder in the substrate of pools (Burgess 2001). This trend was interpreted as a decrease in catchability associated with an increase in habitat complexity because an increase in the percent of cobble and boulder at a site would increase the amount of interstitial space available to the salamanders. Our method of randomly choosing a surface substrate rock to measure is probably not a good measure of habitat complexity. An embedded stream may have a high number of larger particles at the surface, while sediment fills any interstitial space. Large particles account for most of the surface area and are more likely to be selected and measured. We believe that the average particle size did not provide an accurate measure of habitat complexity.

The catchability modeling indicated that catchability increased with decreasing stream width and increased with larger mean particle sizes. It is important to note that these results only apply to the range of habitat variables observed. It is unlikely that catchability will continue to increase as the stream width decreases. Electroshocking could decrease in efficiency, thus decreasing the catchability, as the stream width became very narrow. At very narrow stream widths the water generally becomes very shallow and it would probably become increasingly difficult to electroshock. Catchability models need to be calibrated to the range of habitat variables being observed or the results will be based on extrapolation, which may lead to incorrect estimates.

Concerns have been expressed about the ability of electroshocking to sample stream dwelling amphibians effectively (Corn and Bury 1989, Welsh et al. 1997). The average mass of Pacific giant salamanders captured using an electroshocker was almost 2.5 times larger (Hawkins et al. 1983) than salamanders caught in a similar study that used hand sampling (Corn and Bury 1989). The data were from different studies and geographic locations, and it was unclear if there were demographic differences between the studied populations or if electroshocking did not effectively sample smaller Pacific giant salamanders (Corn and Bury 1989).

Our data suggest that electroshocking may not effectively sample Pacific giant salamanders with snout-vent lengths less than 25 mm, but this may also be an effect of small sample size or of hand sampling prior to electroshocking. Large Pacific giant salamanders were underrepresented in our hand surveys. By limiting our hand sampling area to shallow sections, moving smaller, surface substrate items only, and sub-sampling 30% of a site, our hand surveys may have missed areas (e.g., deep pools) where larger Pacific giant salamanders were present. Pacific giant salamanders have been associated with larger substrates, which were not moved during our survey to reduce habitat disturbance (Parker 1991, Welsh and Ollivier 1998). The mean length of Pacific giant salamanders is higher in pools than in riffles, and this suggests that larger salamanders select pools over riffles (see Roni 2002). Hand sampling cannot be performed in deeper pools, potentially biasing collected salamanders toward smaller individuals present in riffles. Alternate hand sampling methods are more disruptive to stream habitat, but may increase captures, particularly of larger Pacific giant salamanders, because they move larger substrate items (e.g., Bury and Corn 1991, Welsh et al. 1997). Such methods may provide a better measure of the population size, but are more disruptive to the stream environment. Alterations in the stream habitat caused by more intensive sampling methods may have impacts on catchability that would make it problematic to resample the same sites to monitor for changes in populations. This presents an case, to a lesser degree, for the "light" touch hand sampling method that we used, and merits further investigation. Intensive hand sampling methods increase the potential adverse impacts of the sampling on the stream.

Electroshocking and hand sampling both captured lower numbers of Pacific giant salamanders with SVLs less than 25 mm than those with SVLs of 30mm. This suggests that neither method samples the smallest salamander effectively. Pacific giant salamanders with SVLs less than 25 mm are probably less available for capture due to recent hatching. In the lab, the average SVL for hatching Pacific giant salamander larvae is approximately 18 mm (Nussbaum and Clothier 1973). Hatchlings do not feed for 3 to 4 months and during this time still have a yolk sack (Nussbaum and Clothier 1973). These individuals begin feeding once they reach a SVL of approximately 24 mm (Nussbaum and Clothier 1973). Individuals that have not begun feeding may not be near the surface where they are vulnerable to captured by hand or with electroshocking. Data for individuals with a SVL less than 30 mm should probably be removed from population estimates, because they do not appear to be sampled for efficiently and may not be vulnerable to capture.

Mark-recapture and catchability-based population estimates did not differ significantly, but catchability models offer a distinct advantage. After catchability-based models are properly calibrated to relate the catch from a single sample to the actual population size, only single samples taken with the same standard protocol, but no marking would be needed in these surveys. The catchability models may incorporate significant habitat variables that can be used to more accurately predict catchability from samples at new sites where habitat variables are measured. In contrast, mark-recapture methods would require that every site be sampled at least twice, marking animals during the first survey, to provide a population estimate. The calibration procedure to provide data for the catchability models is demanding, but future standardized sampling would be less time consuming. The calibration procedure should not require more work than needed to produce an acceptable mark-recapture estimate at each site. The catchability-based models should only be used within the range of habitat conditions for which they were calibrated and occasional verifications should be done to make sure the models and standardized protocols are functioning correctly, especially when complete changes in crews occur.

To conclude, our study indicated that hand sampling and multiple removal methods did not accurately estimate population size for Pacific giant salamanders. Hand sampling assumes a constant relationship between the numbers caught by hand and the population size. This study found that the catchability is not constant and comparing populations between sites without correcting for differences in catchability is not valid. Multiple removal sampling violated the assumption of constant catchability between passes and therefore the population estimates were also invalid. Mark-recapture and the catchability-based population estimates were always greater than or equal to number of individual Pacific giant salamanders seen at each site. It was not possible to test whether the assumptions of population closure, equal catchability of marked and unmarked individuals, and random mixing of marked and unmarked individuals were valid. Violations of these assumptions may have biased the mark-recapture and catchability population estimates. Comparison between a known population and these estimates could address these questions. However, introducing a known population produces other problems and assumptions. Catchability of Pacific giant salamanders varies by habitat and that these differences need to be incorporated into population estimators to accurately compare populations at different sites and times. Methods need to be calibrated so that estimates of catchability can be used to provide unbiased population estimates.

SYNTHESIS CONCLUSION

Hand sampling and multiple removal sampling did not provide accurate estimates of Pacific giant salamander population size. Mark-recapture and catchability-based quasi-likelihood estimates of population size did not differ significantly, but were significantly larger than estimates calculated from hand sampling and multiple removal sampling. Mark-recapture estimates of population size were generally larger than the catchability-based estimates, but not significantly larger. Hand sampling captures did not have a consistent relationship with the best estimate of population size. The variation in the relationship between hand captures and the best estimate of population size indicate that hand sampling-catchability also needs to be accounted for prior to comparing any estimates derived from hand sampling.

The decline in total catch between the first pass of electroshocking and the recapture pass of electroshocking indicates that the catchability of individuals decreased between passes. The change in catchability between passes violates one of the assumptions of multiple removal sampling and suggests why the multiple removal estimator of population size performed poorly.

Our data suggest that the electroshocking catchability of Pacific giant salamanders did not differ with body size. Size has been shown to affect the electroshocking catchability of fish (Anderson 1995, Büttiker 1992, Bayley 1993). In one study, the catchability of Pacific giant salamanders in pools increased with increases in salamander size (Burgess 2001). Our study sampled both pools and riffles and it is possible that differences in habitats and particle sizes between pools and riffles masked the impact of salamander size on catchability. The sample size may have been too small to detect the effect of salamander size on electroshocking catchability.

At all sites, hand sampling was performed prior to electroshocking. The handling of captured individuals and the disturbance associated with hand sampling may have affected the subsequent catchability of Pacific giant salamanders. These effects may have been different in transects of the stream that were sampled or not sampled, and for individuals that were captured or missed in each transect.

Knowledge of the assumptions and accuracy of methods to compare the populations of Pacific giant salamanders will assist in choosing the best method. Understanding the effects of catchability on population estimates is important to making proper management decisions and will aid in the design of projects to monitor populations, and to detect and quantify the effects of habitat alterations.

This study indicates the importance of catchability when estimating Pacific giant salamander populations, and suggests that the catchability of other species of stream amphibians needs to be evaluated before comparing population estimates. Careful evaluation of stream survey methods can reduce the risk of making erroneous conclusion about the status of stream amphibian populations and their relationship to the surrounding habitat.

In other research the importance of using population estimation methods that account for catchability increasingly has been recognized. In bird sampling, several techniques have been developed that allow for an estimate of catchability in surveys (Thompson 2002). The work in bird survey methods can also be applied to other organisms. Three approaches have been used to supply population estimates that account for differences in catchability in bird surveys: 1) double sampling, 2) double-observer, and 3) distance sampling (Thompson 2002). In double sampling an index counting method is calibrated with a more intensive count at a subset of the sampling units (Cochran 1977). Traditionally the more intensive sampling method assumed perfect catchability and the sites surveyed (Thompson 2002). Bayley (2002) calibrated catchability models for fish electroshocking with data obtained by high efficiency methods such as rotenone (an icthyocide), primacord (an explosive), or pond draining. The use of high efficiency methods to calibrate less efficient methods is not required and can be relaxed if a sampling method that adjusts for catchability is used at the more intensively surveyed site is used. Burgess (2001) used mark-recapture methods to calibrate a single pass of electroshocking through quasi-likelihood catchability models. Ideally different sampling methods are used to eliminate the biases present in most sampling methods. When using calibration procedures, care must be taken to ensure the models are only being used across the range of habitat variables for which they are calibrated. Sampling in areas outside of the calibration may result in poor performance of the calibrated models.

Double-observer methods use index counts from independent observers to account for individuals present but not detected (Nichols et al. 2000). The difference in detections between observers can be used to estimate the detection probability for each observer and can be used to obtain population estimates. Such procedures assume independence of the observations between the two observers, and this can be difficult to ensure (Nichols et al. 2000). It is difficult to employ double observer methods in surveys where the action of the first observer may cause organisms to be less detectable by a second observer. In the case of stream amphibians the habitat disturbance caused by an observer looking for amphibians is likely to affect the catchability of the amphibians to a second observer. The effects of the first observer on observations made by the second observer result in a lack of independence between the observations and limit the application of this methodology.

Distance sampling methods use distances from the observer to estimate detectability (Rosenstock 2002). These methods assume that all organism in a transect are detected, the observer does not cause organisms to move, and the distance to observed organism can accurately be determined. These assumptions may be difficult to meet in the real world and require further evaluation (Thompson 2002). Additionally many of the requirements of current distance sampling methods may not be conducive to sampling for stream amphibians or other organisms. Further research would be needed to make double observer and distance sampling techniques useful for many organisms.

Multiple techniques have been developed to account for catchability in fishes. The use of multiple removal or mark-recapture techniques is common in fisheries work. For multiple removal sampling the assumption of constant catchability is probably rarely met. Mark-recapture work is labor intensive and only applies to a single site. Calibrating the results of less intensive surveys with data from mark-recapture surveys can allow accurate population estimation without intensive surveys at every site.

Any method that does not estimate the effect of catchability on abundance estimates may produce biased results. Any less intensive technique needs to be calibrated by data from a more intensive technique that incorporates an estimate of catchability. Unless the data are calibrated with the estimated catchability, we will be unable to distinguish between a difference in population size and a difference in catchability. The use of multiple surveying techniques can reduce the biases of estimates derived from a single sampling method but do not necessarily increase the accuracy or precision of estimates.

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APPENDICES

Appendix 1: Captures of Pacific giant salamanders for each method. Salamanders were sampled in streams within Little River Adaptive Management Area, Oregon during June – September 2000 and June – September 2001. Total is the total number of captures made for all methods, including recaptures. Unique is the number of unique individuals captured for all methods.

Section	Site	Hand	Pass1	Pass 2	Recapture Pass	Total	Unique
2000-01	Lower	26[a]	69	20	46	161	133
2001-01	Upper	26[b]	53	20	46	145	112
2000-02	Lower	4	43	15	24	86	71
2000-02	Upper	15	66	24	38	143	108
2000-03	Lower	7	11	8	8	34	27
2000-03	Upper	0	5	5	3	13	10
2000-04	Lower	3	9	3	6	21	16
2000-04	Upper	3	7	4	6	20	16
2001-01	Lower	1	5	3	2	11	8
2001-01	Upper	0	6	0	1	7	7
2001-02	Lower	7	20	3	13	43	29
2001-02	Upper	30	31	10	33	104	78
2001-03	Lower	23	62	9	33	127	82
2001-03	Upper	12	79	23	51	165	121
2001-04	Lower	38	62	9	39	148	90
2001-04	Upper	17	34	11	28	90	54
2001-05	Lower	0	12	2	4	18	16
2001-05	Upper	0	5	1	2	8	5

Appendix 1 (continued)

Section	Site	Hand	Pass1	Pass 2	Recapture Pass	Total	Unique
2001-06	Lower	34	85	38	66	223	161
2001-06	Upper	28	110	55	108	301	216
2001-07	Lower	4	24	7	13	48	37
2001-07	Upper	6	23	6	10	45	37

[a] 7 additional salamanders were captured outside of transects are not included in this value. These incidental captures were only used as marks in the catchability estimate.

[b] 5 additional salamanders were captured outside of transects are not included in this value. These incidental captures were only used as marks in the catchability estimate.

Appendix 2: Population estimates for Pacific giant salamanders in streams within Little River Adaptive Management Area, Oregon during June – September 2000 and June – September 2001. N_{CATCH} is the catchability-based estimate of population size, N_{RECAP} is the mark-recapture estimate of population size, N_{REM} is the multiple removal estimate of population size and N_{HAND} is the estimate of population size from hand sampling.

Section	Site	N_{CATCH}	N_{RECAP}	N_{REM}	N_{HAND}
2000-01	Lower	185.0	222.6	98.0	95.3
2000-01	Upper	184.4	144.9	85.1	114.5
2000-02	Lower	98.2	105.4	66.0	15.6
2000-02	Upper	148.4	140.4	103.7	52.6
2000-03	Lower	49.7	60.0	40.3	33.1
2000-03	Upper	14.6	14.7	NA[a]	0
2000-04	Lower	21.0	18.2	13.5	13.3
2000-04	Upper	20.0	42.0	16.3	7.8
2001-01	Lower	8.0	9.0	12.5	4.7
2001-01	Upper	9.1	14.0	NA[b]	0
2001-02	Lower	32.4	33.6	23.5	23.9
2001-02	Upper	115.1	102.0	45.8	144.8
2001-03	Lower	92.4	92.8	72.5	79.9
2001-03	Upper	149.4	148.8	111.5	51.4
2001-04	Lower	105.4	110.8	75.5	145.8
2001-04	Upper	61.8	63.5	50.3	86.3
2001-05	Lower	21.0	25.0	14.4	0

Appendix 2 (continued)

Section	Site	N_{CATCH}	N_{RECAP}	N_{REM}	N_{HAND}
2001-05	Upper	5.0	7.0	6.3	0
2001-06	Lower	205.0	193.2	153.7	145.0
2001-06	Upper	272.7	251.3	220.0	95.4
2001-07	Lower	48.0	44.8	33.9	17.1
2001-07	Upper	51.0	66.0	31.1	22.9

[a] Removal estimate failed due to equal captures on both passes.

[b] Removal estimate failed due to no captures on the second pass.

Appendix 3: Ratio of population estimates for Pacific giant salamanders in sampled streams in Little River Adaptive Management Area, Oregon during June – September 2000 and June – September 2001. N_{CATCH} is the catchability-based estimate of population size, N_{RECAP} is the mark-recapture estimate of population size, N_{REM} is the multiple removal estimate of population size and N_{HAND} is the estimate of population size from hand sampling.

Section	Site	N_{RECAP}/N_{CATCH}	N_{REM}/N_{CATCH}	N_{HAND}/N_{CATCH}
2000-01	Lower	1.20	0.53	0.52
2000-01	Upper	0.78	0.46	0.62
2000-02	Lower	1.07	0.67	0.16
2000-02	Upper	0.95	0.70	0.35
2000-03	Lower	1.20	0.81	0.67
2000-03	Upper	1.00	NA[a]	NA[a]
2000-04	Lower	0.86	0.64	0.63
2000-04	Upper	2.10	0.82	0.39
2001-01	Lower	1.12	1.56	0.58
2001-01	Upper	1.54	NA[b]	NA[b]
2001-02	Lower	1.04	0.73	0.74
2001-02	Upper	0.89	0.40	1.26
2001-03	Lower	1.01	0.78	0.87
2001-03	Upper	1.00	0.75	0.34
2001-04	Lower	1.05	0.69	1.38
2001-04	Upper	1.03	0.81	1.40
2001-05	Lower	1.19	0.69	0

Appendix 3 (continued)

Section	Site	N_{RECAP}/N_{CATCH}	N_{REM}/N_{CATCH}	N_{HAND}/N_{CATCH}
2001-05	Upper	1.40	1.25	0
2001-06	Lower	0.94	0.75	0.71
2001-06	Upper	0.92	0.81	0.35
2001-07	Lower	0.93	0.71	0.35
2001-07	Upper	1.29	0.61	0.45

[a] Removal estimate failed due to equal captures on both passes.

[b] Removal estimate failed due to no captures on the second pass.

Appendix 4: Catchability, q, estimates from each sampling method used for Pacific giant salamanders surveys in streams in Little River Adaptive Management Area, Oregon during June – September 2000 and June – September 2001. q_{CATCH} is the catchability estimated by the catchability models, q_{RECAP} is the estimate of catchability used in mark-recapture estimates, q_{REM} is the catchability estimate calculated during multiple removal estimates of population size and q_{HAND} is the hand sampling estimate of population size divided by the catchability-based estimate of population size (N_{CATCH}).

Section	Site	q_{CATCH}	q_{RECAP}	q_{REM}	q_{HAND}
2000-01	Lower	0.28	0.21	0.71	0.52
2000-01	Upper	0.23	0.32	0.62	0.62
2000-02	Lower	0.29	0.24	0.65	0.16
2000-02	Upper	0.21	0.28	0.64	0.35
2000-03	Lower	0.21	0.15	0.27	0.67
2000-03	Upper	0.18	0.27	NA[a]	0
2000-04	Lower	0.28	0.38	0.67	0.63
2000-04	Upper	0.43	0.17	0.43	0.39
2001-01	Lower	0.30	0.33	0.40	0.58
2001-01	Upper	0.33	0.14	NA[b]	0
2001-02	Lower	0.37	0.42	0.85	0.74
2001-02	Upper	0.30	0.33	0.68	1.26
2001-03	Lower	0.37	0.37	0.85	0.87
2001-03	Upper	0.33	0.35	0.71	0.34
2001-04	Lower	0.34	0.36	0.85	1.38
2001-04	Upper	0.34	0.46	0.68	1.40

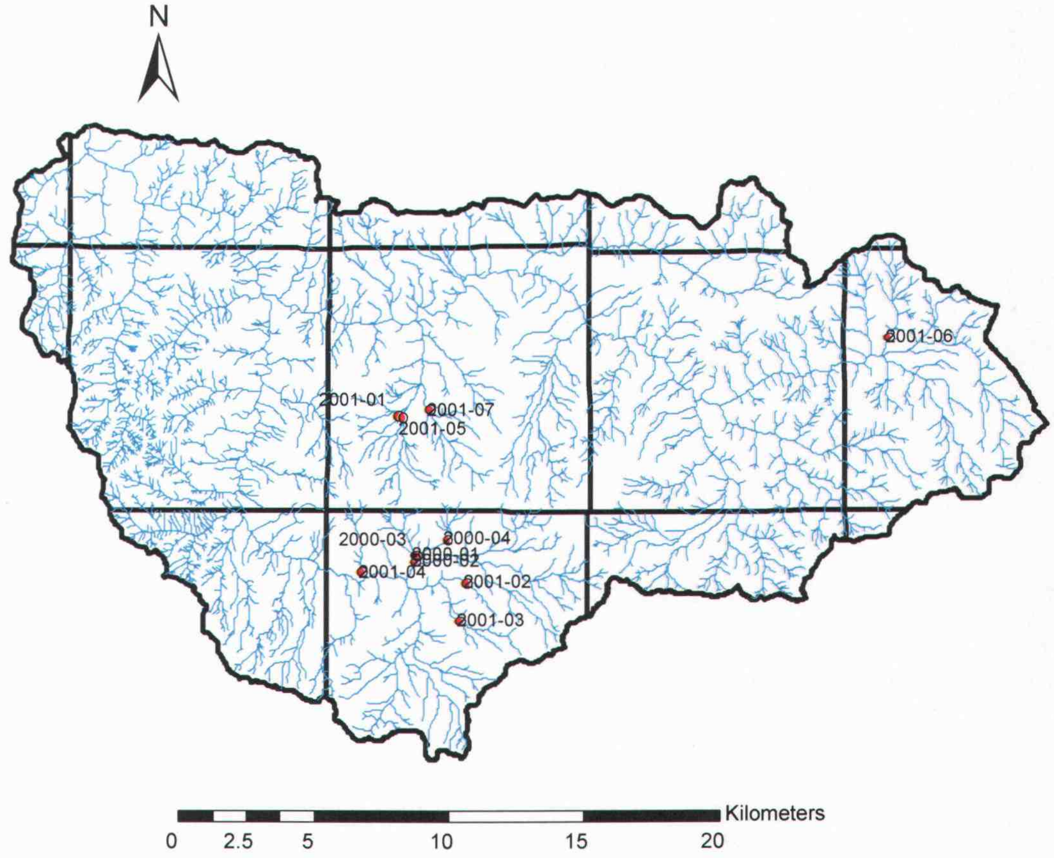
Appendix 4 (continued)

Section	Site	q_{CATCH}	q_{RECAP}	q_{REM}	q_{HAND}
2001-05	Lower	0.29	0.20	0.83	0
2001-05	Upper	0.25	0.43	0.80	0
2001-06	Lower	0.32	0.35	0.55	0.71
2001-06	Upper	0.37	0.43	0.50	0.35
2001-07	Lower	0.27	0.31	0.71	0.36
2001-07	Upper	0.26	0.17	0.74	0.45

[a] Removal estimate failed due to equal captures on both passes.

[b] Removal estimate failed due to no captures on the second pass.

Appendix 5: Map of stream segments sampled in Little River Adaptive Management Area, Oregon during June – September 2000 and June – September 2001. Two adjacent sites were sampled in each stream segment.



Appendix 6: Habitat variables for sites sampled in the Little River Adaptive Management Area, Oregon during June – September 2000 and June – September 2001. Mean particle is the mean size of all particles measured at a site. Bedrock was treated as a zero in mean particle size calculations.

Section	Site	Maximum Length (cm)	Maximum Depth (cm)	Mean Depth (cm)	Mean Width (m)	% Pool	Mean Aspect	Stream Gradient (%)	Water Temp (°C)	Mean Particle (mm)
2000-01	Lower	57.8	39	7.2	2.1	0.38	135	2.6	14.5	88.7
2000-01	Upper	55.1	100	12.3	2.7	0.42	135	7.2	12.5	78.2
2000-02	Lower	57.9	82	11.6	2.9	0.19	180	4.2	16.5	167.9
2000-02	Upper	61.7	61	11.9	3.5	0.34	180	3.2	15.0	117.7
2000-03	Lower	53.2	57	8.0	3.7	0.00	225	8.3	12.0	136.2
2000-03	Upper	44.0	44	5.6	3.5	0.18	225	5.3	11.5	61.5
2000-04	Lower	50.0	31	6.9	2.5	0.00	270	8.0	9.0	131.9
2000-04	Upper	50.8	22	5.8	1.5	0.00	270	13.0	12.0	207.5
2001-01	Lower	38.7	49	8.9	1.6	0.45	29	0.8	12.5	63.1

Appendix 6 (continued)

Section	Site	Maximum Length (cm)	Depth (cm)	Mean Depth (cm)	Mean Width (m)	% Pool	Mean Aspect	Stream Gradient (%)	Water Temp (°C)	Mean Particle (mm)
2001-01	Upper	59.8	20	5.7	1.2	0.00	23	10.1	13.0	65.9
2001-02	Lower	47.1	34	5.9	1.6	0.36	275	4.9	11.0	153.4
2001-02	Upper	54.9	25	5.0	2.1	0.13	299	6.0	13.5	117.0
2001-03	Lower	46.3	51	13.1	2.9	0.61	228	6.9	11.5	266.6
2001-03	Upper	55.8	25	10.6	2.6	0.00	338	9.0	12.0	199.6
2001-04	Lower	49.3	72	7.0	1.7	0.23	185	6.3	14.0	130.1
2001-04	Upper	44.2	26	5.5	1.8	0.09	176	14.5	15.0	133.9
2001-05	Lower	44.3	52	9.7	3.0	0.23	0	10.6	16.0	177.9
2001-05	Upper	49.5	43	10.3	3.5	0.35	29	12.3	13.0	177.9
2001-06	Lower	47.0	42	8.9	2.9	0.52	186	5.1	10.5	213.1

Appendix 6 (continued)

Section	Site	Maximum Length (cm)	Depth (cm)	Mean Depth (cm)	Mean Width (m)	% Pool	Mean Aspect	Stream Gradient (%)	Water Temp (°C)	Mean Particle (mm)
2001-06	Upper	59.8	70	13.6	2.6	0.74	200	4.1	11.0	246.9
2001-07	Lower	45.6	45	9.2	3.0	0.49	204	5.0	12.0	155.0
2001-07	Upper	49.7	49	9.9	3.2	0.42	191	6.9	11.0	162.5