AN ABSTRACT OF THE THESIS OF

Jack A. Burgess for the degree of <u>Master of Science</u> in <u>Fisheries Science</u> presented on February 12, 2001 Title: <u>Response of Trout</u>, <u>Sculpins</u>, and <u>Salamanders to</u> Experimental Manipulation of Large Wood in Cascade Mountain Streams.</u>

Signature redacted for privacy. Abstract approved: Stanley V. Gregory

Response of aquatic vertebrates to increased pool habitat complexity due to abundance of large wood was evaluated experimentally in three streams in the Cascade Mountains of Oregon. No difference in aquatic vertebrate density was detected among treatments, though there was a trend of increasing aquatic vertebrate density with increasing large wood abundance. The small change in density of aquatic vertebrate species may have been due to the overriding influence of the high habitat heterogeneity associated with cobble/boulder substrate in these streams. Large wood may have a stronger influence in simpler streams with smaller particle size, in differing environmental regimes, or at spatial scales larger than channel unit. Markrecapture estimates, catchability-based estimates, and maximum likelihood multiple removal estimates were compared in all three streams. Physical heterogeneity influenced efficiency of capture. The single pass catchability-based estimates were larger than mark-recapture estimates and maximum likelihood multiple removal estimates. Mark-recapture estimates were larger than maximum likelihood multiple removal estimates. The mark-recapture method gives more reliable and accurate estimates than maximum likelihood multiple removal method, but both methods may substantially underestimate the population. Taxon, fish length, and habitat variables influenced catchability for the population estimators examined. Probability of capture of vertebrates for the catchability-based estimator consistently decreased with increasing habitat complexity.

Understanding factors that affect the accuracy of population estimators and the impact that habitat may have on catchability will assist fisheries scientists and managers in making informed decisions regarding the selection of a population estimation method. Research on habitat restoration and habitat relationships must recognize limitations of population estimators and catchability. Recognition of the limitations of population estimators and catchability should allow resource scientists to design more reliable monitoring and evaluation of habitat restoration projects.

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Response of Trout, Sculpins, and Salamanders to

Experimental Manipulation of Large Wood in Cascade Mountain Streams

by

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APPROVED:

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Dean of 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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Response of Trout, Sculpins, and Salamanders to Experimental Manipulation of Large Wood in Cascade Mountain Streams

INTRODUCTION

Many streams in the Pacific Northwest have been simplified by the removal of large wood to improve navigation, transport of logs to sawmills, improve migratory fish passage, and stabilize stream channels (Everest et al. 1991, Lichatowich et al. 1994, Maser and Sedell 1994, Gregory 1996, NRC 1996). Large wood is an integral component of aquatic species habitat in streams and rivers (Harmon et al. 1986, Beschta 1991, Sedell et al. 1991, Lichatowich et al. 1994).

Loss of habitat and habitat diversity have been significant factors in the decline of native fish stocks (Nehlsen et al. 1991, Bevan et al. 1994). Fisheries management has attempted to restore fish stocks through habitat restoration projects based on the ecological principle that distribution and diversity of species are controlled by structural habitat diversity (Sheldon 1968, Gorman and Karr 1978, Beschta 1991, Reeves et al. 1991, Montgomery et al. 1995, NRC 1996). Many restoration projects have been designed to restore habitat for adult salmonids with little or no experimental design or evaluation of the effects of restoration on early life history stages of salmonids, responses of other aquatic species, geomorphic or hydraulic processes, or the overall health of the ecosystem (Reeves et al. 1991, Lichatowich et al. 1994). This focus on single species and disregard for early life history stages and other aquatic species potentially contributes to the continued decline of resident and anadromous salmonids and may have placed other aquatic species in jeopardy (Reeves et al. 1991). Evaluation of restoration projects often ignores the consequences of habitat restoration for salmonids to other aquatic vertebrate and invertebrate species within the stream ecosystem (Everest et al. 1991, Reeves et al. 1991).

Restoration of aquatic habitats and salmonids requires knowledge of habitat relationships and ability to accurately estimate abundance of aquatic organisms. Aquatic vertebrate population estimators are biased by species, fish size (Larimore 1961, Mahon 1980, Buttiker 1992, Bayley 1993), and by diversity of habitat and complexity of hiding cover (Larimore 1961, Rodgers et al. 1992, Bayley 1993, Bayley and Dowling 1993). Studies have shown greater accuracy for population estimates with mark-recapture techniques than for multiple removal sampling techniques (Heggberget and Hesthagen 1979, Peterson and Cederholm 1984, Buttiker 1992, Rodgers et al. 1992). Accurate quantitative estimation of abundance of aquatic vertebrates is required to determine status of populations and responses of aquatic vertebrates to habitat complexity. If structural complexity affects catchability of fish, comparisons of reaches with different physical heterogeneity require correction of evaluation of estimates.

In 1994 the Willamette National Forest of the United States Forest Service and Oregon State University developed an experiment to evaluate stream restoration with large wood in three streams in the McKenzie River drainage in the western Cascade Mountains of Oregon. The main objective of the experiment was to evaluate the response of aquatic vertebrates to increasing large wood abundance in pool habitats. A secondary goal was to determine if large wood and other habitat features alter vertebrate catchability and test the accuracy of population estimators under these

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conditions. Chapter 2 describes the study site, methodology and analysis used to evaluate and discuss the response of aquatic vertebrates to increasing large wood abundance. Chapter 3 describes the methodology and analysis used to compare a catchability-based population estimator with the Petersen single-census markrecapture population estimator and the multiple removal population estimator and discusses the effect of increasing habitat complexity on aquatic vertebrate catchability.

RESPONSE OF TROUT, SCULPINS, AND SALAMANDERS TO EXPERIMENTAL MANIPULATION OF LARGE WOOD IN CASCADE MOUNTAIN STREAMS

Abstract

Fisheries management has attempted to restore fish stocks through habitat restoration projects based on the ecological principle that distribution and diversity of species are controlled by structural habitat diversity. Response of aquatic vertebrates to increased pool habitat complexity due to abundance of large wood was evaluated in three streams in the Cascade Mountains of Oregon. Mean loge densities per 1,000 m² of aquatic vertebrates were reference 7.5, low 7.6, medium 7.8, and high 7.7. Trout, sculpins, and salamanders were roughly each one-third of the total estimated vertebrate density. No differences in density were detected among the treatments for any species. A simple linear regression model of vertebrate density and large wood abundance revealed that vertebrate density was not statistically significantly related to large wood abundance (P = 0.56, $R^2 = 0.006$). Percent of cobble/boulder substrate was positively correlated with density in multiple linear regression models for all vertebrates and each species. A multiple linear regression model revealed that percent of cobble/boulder substrate (P < 0.0001) and mean width (P = 0.05) were statistically significantly related to aquatic vertebrate density (P < 0.0001, $R^2 = 0.41$). No significant difference in vertebrate density was detected among treatments though there was a trend of increasing vertebrate density with increasing large wood treatment. The small change in density of aquatic species may have been due to the overriding influence of the high habitat heterogeneity associated with cobble/boulder

substrate in these streams. Large wood may have a stronger influence in simpler streams with smaller particle size, in differing environmental regimes, or at spatial scales larger than channel unit.

Introduction

Many streams in the Pacific Northwest have been simplified by the removal of large wood to improve navigation, transport of logs to sawmills, improve migratory fish passage, and stabilize stream channels (Everest et al. 1991, Lichatowich et al. 1994, Maser and Sedell 1994, Gregory 1996, NRC 1996). Large wood is an integral component of aquatic species habitat in streams and rivers (Harmon et al. 1986, Beschta 1991, Sedell et al. 1991, Lichatowich et al. 1994). Structural habitat heterogeneity provided by large wood increases territories for hiding, resting, foraging or escapement for aquatic organisms (Crowder and Cooper 1982, Forward 1984, Schlosser 1988, Benke and Wallace 1990, Sedell and Beschta 1991, Nickelson et al.1992, Pearsons et al.1992, Monzyk et al. 1997). Juvenile salmonids and other aquatic vertebrates use large wood structure as refuge from extremes of low flow and high peak flows during storms, cover during low summer flows, refuge from predators, and sites of foraging (Sedell and Beschta 1991, Nickelson et al. 1992, Pearsons et al. 1992).

Local abundance of fish changes in response to quantity and placement of large wood (Saunders and Smith 1962, Burgess and Bider 1980, Shirvell 1990, Nickelson et al.1992). Habitat use increased substantially in response to increased habitat complexity provided by large wood (Saunders and Smith 1962, Shirvell 1990). Forward (1984) found that local fish abundance in pools was greater at higher indices of wood complexity. Large wood enhances fish abundance by providing cover for overwintering fish, providing cover during lower summer flows, reducing velocities during high flows, and providing refuges for fishes during disturbances such as floods (Burgess and Bider 1980, Moore and Gregory 1988, Junk et al. 1989, McMahon and Hartman 1989, Gregory et al. 1991, Nickelson et al. 1992, Pearsons et al. 1992, Quinn and Peterson 1996, Harvey et al. 1999).

Fisheries management has attempted to restore fish stocks through habitat restoration projects based on the ecological principle that distribution and diversity of species are controlled by structural habitat diversity (Sheldon 1968, Gorman and Karr 1978, Beschta 1991, Reeves et al. 1991, Montgomery et al. 1995, NRC 1996). Many of these projects have been designed to restore habitat for adult salmonids with little or no experimental design or evaluation of the effects of restoration on early life history stages of salmonids, responses of other aquatic species, geomorphic or hydraulic processes, or the overall health of the ecosystem (Reeves et al. 1991, Lichatowich et al. 1994). This focus on single species and disregard for early life history stages and other aquatic species potentially contributes to the continued decline of resident and anadromous salmonids and may have placed other aquatic species in jeopardy (Reeves et al. 1991). Evaluation of restoration projects often ignores the consequences of habitat restoration for salmonids to other aquatic vertebrate and invertebrate species within the stream ecosystem (Everest et al. 1991, Reeves et al. 1991).

Projects to place large wood in streams attempt to restore habitat for salmonids and other aquatic organisms to historic quality (Lichatowich et al. 1994, NRC 1996). Large wood placed in streams influences streambed morphology by modifying patterns of flow and stream energy (Sedell et al. 1984, Harmon et al. 1986, Sedell et al. 1988, Beschta 1991, Gregory and Wildman 1994, Montgomery et al. 1995). Various accumulations of large wood, depending on size and orientation to flow, scour pools and redistribute sediments, providing a variety of habitat types beneficial to fish and other aquatic organisms (Sedell et al. 1984, Gregory and Wildman 1994, Montgomery et al. 1995, NRC 1996, Hauer et al. 1999). Large wood placed without regard to channel hydraulics and natural stream geomorphology may have detrimental effects on fish habitat (Beschta et al. 1991, MacDonald et al. 1991, Gregory and Wildman 1994, NRC 1996). Removal of large wood from streams eliminates the nick points that cause scour, allows movement of sediment resulting in shallower pools, and an overall simplification of the bed surface reducing fish productivity (Murphy and Hall 1981, Sedell et al. 1984, Lisle 1995).

In 1994 the Willamette National Forest of the United States Forest Service and Oregon State University developed an experiment to evaluate stream restoration with large wood in the McKenzie River drainage in the western Cascade Mountains of Oregon. Our main objective was to evaluate the response of aquatic vertebrates to increasing amounts of large wood in pool habitat restoration. A secondary goal was to determine if large wood and other habitat features alter vertebrate catchability and to test the accuracy of population estimators under these conditions.

Study Site

The McKenzie River drainage is typical of the Western Cascades Province of Oregon. Basalt and andesite are the most common bedrock materials of the streams and steep rugged ridges, that range in elevation to over 1,800 m. Shallow soils at lower elevations consist of tuffs and breccias with deeper soils at higher elevations derived from andesite and lava flows (Franklin and Dyrness 1988). Douglas fir (<u>Pseudotsuga menziesii</u> (Mirb.) Franco), western hemlock (<u>Tsuga heterophylla</u> (Raf.) Sarg), and western red cedar (<u>Thuja plicata</u> D. Don) are the dominant conifers on the hillslopes and streamsides. Big-leaf maple (<u>Acer macrophyllum</u> Pursh) and red alder (<u>Alnus rubra</u> Nutt.) are the dominant riparian deciduous trees.

Lookout Creek, Tidbits Creek, and North Fork Quartz Creek are located within 4 km of each other in the McKenzie River drainage at elevations between 365 to 1,525 m. These cobble/boulder bed streams were selected for a large wood restoration study because of their similar characteristics of size, gradient, flow, vertebrate communities, and land use practices (Table 2.1).

Lookout Creek, a fifth-order stream in the H. J. Andrews Experimental Forest, is designated as a research stream by the Oregon Department of Fish and Wildlife and has been closed to recreational fishing since 1969. Tidbits Creek and North Fork Quartz Creek are third-order streams outside the H. J. Andrews Experimental Forest boundary and are subject to recreational fishing. Historical land uses in the three stream basins include clearcut logging, salvage logging, large wood removal from streams, road construction, mining, recreational camping, and research. The streams

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Table 2.1. Characteristics of streams selected for a large wood restoration experiment in the Cascade Mountains of Oregon. Stream flow (taken at lower gage on Lookout Creek), stream temperatures (taken at pool tailout at time of sampling), and dominant substrates are data from the sample period in July – August 1995 and 1996. Average width, mean gradient, and pools per km are from stream survey data of 1993 and 1994.

	Lookout Creek	Tidbits Creek	N. F. Quartz Creek	
Drainage area (ha)	6,400	2,700	1,060	
Stream Order	4 – 5	3	3	
Gradient (%)	4	3	5	
Stream flow (m ³ /s) Minimum Maximum	0.6 0.3 1.3	NA	NA	
Temperature (°C)	11	12	13	
Average width	8.5 m	5.0 m	4.5 m	
Distance surveyed 1993 survey 1996 survey	1,900 m 4,100 m	6,500 m	5,000 m	
Pools/km 1993 survey 1996 survey	10 6	9	11	
% Pools 1993 survey 1996 survey	28 23	12	12	
Wood pieces/km	168	19	89	
Dominate substrate	Cobble and Small Boulder	Cobble and Small Boulder	Cobble and Small Boulder	

experience natural disturbances, such as debris flows and large floods, which alter physical habitat and disrupt biological communities during these high flow events (Lamberti et al. 1991, Swanson et al. 1998). Human activities potentially modify the timing and magnitude of these disturbance processes.

Methods

We surveyed reaches of more than 1 km in each stream to identify a set of pools that met the design criteria as experimental units. Pools were defined as having a smooth non-turbulent surface and a point of deeper scour. Other factors for selecting pools included presence or absence of large wood and similarity in size and character to other pools in the same reach. Stream habitat was surveyed during 1993 and 1994 following protocols described by Hankin and Reeves (1988). Distances surveyed were determined by available habitat. Each selected reach had at least 12 pools that met the requirements for the experimental design (Table 2.2).

The original research planned to resurvey the streams for pools with natural deposits of large wood meeting the experimental design as replacements for any lost treatment units in case of loss of experimental units from catastrophic disturbance. In February 1996, a 4-day rain-on-snow event, of more than 27 cm of rain, triggered a major flood in the western Cascades of Oregon, impacting the three experimental reaches. In some study pools in Tidbits Creek and N. F. Quartz Creek, pool dimensions increased or decreased, flow patterns changed, and one or two logs were transported out of a pool. During the flood, sediment was deposited and maximum depth in some

Table 2.2. Geomorphic characteristics of experimental pools in three streams in the Cascade Mountains of Oregon during 1995 and 1996. LO is Lookout Creek, TB is Tidbits Creek, NFQ is North Fork Quartz Creek, W_{MEAN} is mean pool width, D_{MEAN} is mean pool depth, D_{MAX} is maximum pool depth, PA is pool area, PV is pool volume, PCSA is pool cross-section area, SUB is percentage of cobble/boulder substrate in pools.

Stream		W _{MEAN}	D _{MEAN}	D_{MAX}	PA	PV	PCSA	SUB
LO	Mean	7.8	0.39	1.1	178.5	72.8	3.1	81
	Min	3.9	0.17	0.5	37.6	6.9	0.7	35
	Max	11.5	0.57	2.0	294.0	127.0	5.1	100
TB	Mean	8.4	0.38	1.2	187.6	69.1	3.2	61
	Min	5.1	0.16	0.7	62.1	16.2	0.9	20
	Max	10.5	0.85	2.0	437.5	160.6	7.7	100
NFQ	Mean	5.2	0.23	0.7	76.5	16.9	1.2	30
	Min	3.4	0.11	0.4	26.7	4.5	0.6	0
	Max	8.7	0.38	1.0	139.8	44.9	2.1	75

pools decreased to less than 0.5 m. All other pool characteristics were unchanged, and the vertebrate community in Tidbits Creek and N. F. Quartz Creek was sampled in all pools as in 1995.

In Lookout Creek, channel migration or sediment deposition from debris flows resulted in the loss of all experimental units. In June 1996, channel structure was resurveyed to identify potential experimental pools that met the criteria for the experimental design. Twelve pools that met the experimental design with natural deposits of wood matching the four experimental levels were located in the stream section originally surveyed. Vertebrate sampling and habitat measurement protocols were the same as in 1995.

Twelve pools in each stream were sub-divided into three blocks of four pools. Treatments were randomly assigned to pools within each experimental block. Pools

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received one of four experimental treatments of wood: 1) reference pools - no large wood, 2) low wood abundance - 2 large logs, 3) medium wood abundance - 5 to10 large logs and 3 to 5 small trees or tops, and 4) high wood abundance - 10 to 15 large logs and 5 to 7 small trees or tops. Logs were placed to emulate natural distributions within the stream and then cabled to large boulders, bedrock, or live standing trees (required by U.S. Forest Service). Length and diameter (maximum and minimum) were measured for each log, and numbered tags were attached. We also estimated the percent of the volume of each log in the four hydrologic zones: Zone 1 - wetted channel at low flow, Zone 2 - active channel above low flow, Zone 3 - suspended above bankfull channel, and Zone 4 - lateral to the active channel (Robison and Beschta 1990) (Table 2.3).

Aquatic vertebrates were sampled during a 5-wk period in July - August of 1995 and 1996 by crews of 6 - 12 people with two or three direct-current electrofishers (1,000 V). In Lookout Creek and Tidbits Creek, divers were used (one with the anode, two or more assisting to dip net fish) to capture vertebrates during electroshocking. Although the first electrofishing pass was standardized for all units sampled, subsequent activities permitted three methods for abundance estimates to be obtained. First, multiple pass-removal sampling produced abundance estimates in treatment units in the lower two blocks in each stream. Second, mark-recapture sampling was conducted in conjunction with two-pass removal estimates in treatment units in the upper block of each stream. Additional passes were conducted in the multiple removal units if a two-thirds reduction in capture of number of individuals of all species was not attained. Third, the mark-recapture experiments permitted catchability models to Table 2.3. Large wood volume, area, count characteristics (mean, minimum and maximum), and percent of large wood volume in each hydrologic zone (Robison and Beschta 1990) in the experimental large wood manipulation pools of the three Cascade Mountain streams during July – August 1995 and 1996.

	Wood volume to pool surface area (m ³ /m ²)	Wood volume per pool unit (m ³ /unit)	Wood count to pool surface area (#/m ²)	Wood count per unit (#/unit)	Wood surface area to pool surface area (m^2/m^2)	Wood surface area per unit (m ² /unit)	Zone 1 (%)	Zone 2 (%)	Zone 3 (%)	Zone 4 (%)
Reference	_	_	_	_	_		_	_		_
Mean	0	0	0	0	0	0	0	0	0	0
Min	-	-	-	-	-	-				
Max	-	-	-	-	-	-				
Low	0.07	11	0.04	1	0.12	15 0	16	11	20	20
Mean	0.07	11	0.04	4	0.12	13.0	10	44	20	20
Min	0.01	2	0.01	2	0.02	6.3				
Max	0.39	78	0.12	9	0.40	70.0				
Medium										
Mean	0.19	21	0.10	12	0.29	35.0	15	33	39	17
Min	0.03	4	0.04	6	0.09	13.8				
Max	1.54	127	0.24	27	0.62	84.7				
High										
Mean	0.18	24	0.20	23	0.47	55.8	9	40	34	17
Min	0.03	5	0.05	9	0.11	19.1				
Max	0.60	75	0.41	49	1.06	132.1				

be developed based on released marked fish recaptured during a single pass. These models permitted abundance to be estimated from first pass catches of all samples. Subsequent analyses in this paper are based on abundance estimated by the third catchability-based approach. In mark-recapture units, vertebrates captured in the multiple removal sampling were marked and a single recapture pass was performed after a 24-h recovery period, as recommended by Mesa (1989). Individual pools were blocked with seines during the 24-h interval between sampling to prevent emigration or immigration.

Vertebrates captured in each pass were held in separate containers. Individuals were identified to species, measured for length to the nearest millimeter, and weighed to the nearest 0.1 g with a portable balance. Fork length was measured for salmonids and total length was measured for all other vertebrates. Vent length and total length were measured for Pacific giant salamanders (<u>Dicamptodon tenebrosus</u>). Salmonids were marked with adipose fin clips, sculpins were marked with pectoral fin clips, and salamanders were marked with toe clips prior to release into their respective pools for mark-recapture estimates.

Immediately after population sampling, we measured pool length, average width, average depth, maximum depth, and depth at pool crest (Table 2.2). Length of pools was measured from pool head to crest of the pool tail along the thalweg. Average wetted surface width was measured at three evenly spaced transects. Depth was measured at three evenly spaced points along each transect to estimate average depth. Maximum depth was measured at the deepest point of the pool, and pool crest depth was measured at the deepest point across a transect at the lower end of the pool.

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Length (1) and maximum (d_{MAX}) and minimum (d_{MIN}) diameters were measured for all pre-existing large wood and experimental additions (Table 2.3). Criteria for classification as large wood were a minimum length of 1 m and minimum diameter of 10 cm. Each piece was tagged with two aluminum tags. Large wood volume (V) was calculated by the using the equation (Nakamura and Swanson 1994): Equation 1 $V = (\pi (d_{MAX}^2 + d_{MIN}^2)^* (length))/8.$

For each log, percent of length in each of the four hydrologic zones was estimated visually (Table 2.3).

We counted and measured large boulders (> 0.5 m diameter) in each pool, and visually estimated the percent of each large boulder that was submerged and the percent of each large boulder that was embedded in the substrate (Table 2.4). Percent of dominant substrate type was estimated visually.

Populations were estimated from models predicting catchability based on the first pass (e.g., Bayley 1993), two-pass multiple-removal (Zippen 1956), and Petersen mark-recapture sampling (Ricker 1975). Estimates of catchability were modeled based on proportions of marked fish recaptured, using Generalized Linear Interactive Modeling (GLIM) (Williams 1982, Francis et al. 1993). Predicted catchability is a function of species, fish size and habitat variables. Catchability estimates were used to calculate abundance estimates for each species and all species combined. Because of the different sampling method in North Fork Quartz Creek (wading only) compared to Lookout Creek and Tidbits Creek (wading and diving), separate catchability models were constructed for North Fork Quartz Creek vertebrates.

	Large	Large	Large	Large boulder	Zone 1 wood
	boulders per	boulders per	boulder	surface area to	surface area
	unit	pool surface	surface area	pool surface	plus percent
	(#/unit)	area	per unit	area (m^2/m^2)	cobble/boulder
		(#/m ²)	(m²/unit)		substrate
					(% cover)
Reference					
Mean	40	0.30	26	0.20	51
Min	3	0.05	2	0.01	0
Max	103	0.83	74	0.59	100
Low					
Mean	31	0.22	20	0.16	77
Min	5	0.07	2	0.02	28
Max	61	0.42	45	0.46	114
Medium					
Mean	30	0.23	24	0.17	50
Min	10	0.09	3	0.04	11
Max	79	0.55	101	0.54	103
High					
Mean	44	0.31	29	0.20	65
Min	1	0.01	1	0.01	23
Max	104	0.58	60	0.46	112

Table 2.4. Characteristics of boulders and cover (sum of cobble/boulder substrate and zone 1 wood area per unit) in each treatment in the three stream reaches of the Cascade Mountains of Oregon during July – August 1995 and 1996.

Analysis

Normality assumptions for the ANOVA were checked with residual and normality plots produced with Statgraphics Plus 2.1 (Statistical Graphics Corp, copyright 1994 - 1996). A natural log (log_e) transformation of large wood volume per unit (m^3 /unit) and large wood count per unit (#/unit) improved the normality of the wood data. A square root (sqrt) transformation of boulder count per unit (#/unit) and boulder surface area per pool surface area (m^2/m^2) improved normality of the boulder data. Species richness of the catches of aquatic vertebrates differed slightly between streams. Eight species were caught but only four species were present in all three streams. Only five of these species were found in substantial numbers and were included in the analyses of the response of aquatic vertebrates to abundance of large wood. Two species of trout, cutthroat (<u>Oncorhynchus clarki</u>) and rainbow trout (<u>O</u>. <u>mykiss</u>), were combined as a single taxon. Two species of sculpins, mottled sculpin (<u>Cottus bairdi</u>) and Paiute sculpin (<u>C. beldingi</u>) were combined as a single taxon, and the Pacific giant salamander was the only species of salamander. Other aquatic vertebrate species captured were longnose dace (<u>Rhinichthys cataractae</u>), speckled dace (<u>R. osculus</u>), and tailed frog (<u>Ascaphus truei</u>).

Habitat conditions, species, and size of an individual affect the probability of capture of an individual during an electrofishing effort (Bayley 1993, Bayley and Dowling 1993, Heimbuch et al. 1997). Taxa were separated into seven length categories (\leq 34 mm, 35 – 54 mm, 55 – 79 mm, 80 – 114 mm, 115 – 154 mm, 155 – 199 mm, and \geq 200 mm) and we assumed that individuals of the same taxon within a length category were similarly vulnerable to capture for given habitat conditions (Bayley 1993). Catchability (q) models were constructed for mean length (MNL) of each length category group using taxa, fish length, and habitat variables (Table 2.5, Appendix 1).

The sampling method differed slightly in North Fork Quartz Creek (two backpack shockers, wading only) from the protocol in Lookout Creek and Tidbits Creek (three backpack shockers, wading and diving). Catchability models (Table 2.6) were constructed for each taxon and mean length group depending on the sampling

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Table 2.5. Characteristics of the 12 large wood experiment pools in each of the three Cascade Mountain streams during July – August 1995 and 1996 (mean, minimum, maximum, and standard deviation). W_{MEAN} IS mean width, D_{MEAN} is mean depth, D_{MAX} is maximum depth, PA is pool surface area, PV is pool volume, PCSA is pool cross-section area, SUB is percent of cobble and boulder substrate, and s.e. is standard deviation.

Stream	W _{MEAN}	D _{MEAN}	D _{MAX}	$PA(m^2)$	$PV(m^3)$	PCSA	SUB	
	(m)	(m)	(m)				(%)	
Lookout Creek								
Mean	7.8	0.39	1.1	178.5	72.8	3.1	81	
Min	3.8	0.17	0.5	37.6	6.9	0.7	35	
Max	11.5	0.57	2.0	294.0	127.0	5.1	100	
s.e.	2.0	0.09	0.3	83.1	37.7	1.2	20	
Tidbits Creek								
Mean	8.4	0.38	1.2	187.6	69.1	3.2	61	
Min	5.1	0.16	0.7	62.1	16.2	0.9	20	
Max	10.5	0.85	2.0	437.5	160.6	7.7	100	
s.e.	1.5	0.15	0.3	96.8	39.3	1.4	25	
North Fork Quartz Creek								
Mean	5.2	0.23	0.7	76.5	16.9	1.2	30	
Min	3.4	0.11	0.4	26.7	4.5	0.6	0	
Max	8.7	0.38	1.0	139.8	44.9	2.1	75	
s.e.	1.2	0.08	0.2	30.6	8.3	0.5	22	

method. The general catchability model predicts the proportion of a taxon present that are caught in the first pass:

Equation 2:
$$q = (1 + e^{-L})^{-1}$$

where q is catchability, the proportion of a taxon present that were caught in the first pass, e is the natural exponential, and L is a linear combination of fish length and habitat variables. The catchability prediction model for trout in Lookout Creek and Tidbits Creek for example is:

$$q = (1 + e^{(-(-0.49 + 0.025(MNL) - 0.000092(LSQ) - 0.25(CMP))})^{-1}.$$

Table 2.6. Calibrated catchability coefficients for L used to calculate species abundance estimates for the three streams in the Cascade Mountains, Oregon during July – August 1995 and 1996. LO-TB is Lookout and Tidbits creeks, NFQ is North Fork Quartz Creek, MNL is species length group mean length, SUB is substrate percentage of cobble/boulder in each pool, MAXD is maximum pool depth, LSQ is mean length squared, CMP is treatment level (1, 2, 3 or 4 with respect to reference, low, medium or high) and MNLMAXD is product of mean length and maximum depth.

	Parameter	Coefficient	Standard error	
LO-TB (24 pools)				
Trout $(n = 48)$	Constant	-0.486	0.423	
	MNL	0.0254	0.00770	
	LSQ	-0.0000916	0.0000360	
	CMP	-0.248	0.0781	
Sculpins $(n = 40)$	Constant	0.169	0.664	
	MNL	0.0239	0.00797	
	SUB	-0.0281	0.00566	
Salamanders $(n = 48)$	Constant	-5.902	1.031	
	MNL	0.0820	0.0184	
	MAXD	1.893	0.555	
	LSQ	-0.00026	0.0000828	
	MNLMAXD	-0.0206	0.00645	
NFQ (12 pools)				
Trout $(n = 16)$	Constant	0.407	0.567	
	MNL	0.00743	0.00685	
Sculpins $(n = 16)$	Constant	-0.944	0.248	
	a l	• • • • •	0.716	
Salamanders $(n = 16)$	Constant	-2.909	0.716	
	MNL	0.0140	0.00626	
	MAXD	3.667	1.066	
	SUB	-0.0613	0.0215	

The catchability prediction model for trout in Lookout Creek and Tidbits Creek: $q = (1 + e^{(-(-0.49 + 0.025(MNL) - 0.000092(LSQ) - 0.25(CMP))^{-1}})^{-1}$

Abundance estimates (N_{CAL}) were estimated from predicted catchability for each taxon and length group in each pool using the equation:

Equation 3:

$$N_{CAL} = c_1 / q$$

where c_1 is the number caught in the first-pass sampling effort and q is the catchability estimate for a mean length group for each taxon. Abundance estimates for each channel unit were summed for all taxa and length groups to estimate total vertebrate abundance. Abundance estimates were standardized to density per 1,000 m² of pool surface area. For comparison, multiple removal estimates (N_{REM}) of abundance were also calculated using equations for two-passes from Zippen (1956) and for Petersen mark-recapture (Ricker 1975). Results and discussion will focus on the N_{CAL} estimates only, but multiple removal estimates (N_{REM}) and mark-recapture estimates (N_{RECAP}) are provided in Table 2.7.

Differences in total N_{CAL} density per 1,000 m² (density) of vertebrates, density of fish (trout and sculpins), and density of each taxon were evaluated with Analysis of Variance (ANOVA), using Statgraphics Plus 2.1 (Statistical Graphics Corp, copyright 1994 - 1996). Graphical displays of residuals indicated skewed distribution in the density estimates for all species and total vertebrate abundance. A natural log (log_e) transformation of N_{CAL} improved normality for the ANOVA.

Simple regression analysis described the continuous relationship between density (\log_e) of aquatic vertebrates and specific abundance of large wood in the experimental treatment pools. Multiple regression analysis was performed on measured and estimated habitat variables to explain the variation in vertebrate density (\log_e) among the experimental treatment pools. Habitat data used in the regression

Estimator	Species	Number per pool (#/pool)	Number per m ² (#/m ²)	Number per 1,000 m ² (#/1,000 m ²)	Number per 100 m (#/100 m)	Number per pool volume (#/m ³)
NCAL	Trout					· · · · · · · · · · · · · · · · · · ·
	Mean	114	0.69	695	508	2.03
	s.e.	15	0.08	79	52	0.30
	Sculpin					
	Mean	157	0.89	887	644	2.50
	s.e.	46	0.19	193	152	0.40
	Salamander					
	Mean	154	1.02	1,017	740	3.38
	s.e.	16	0.09	87	63	0.42
	Vertebrate					
	Mean	425	3.00	2,599	1,892	8.00
	s.e.	61	0.25	255	196	0.74
N _{REM}	Trout					
	Mean	73	0.53	528	371	1.33
	s.e.	11	0.13	134	83	0.21
	Sculpin					
	Mean	74	0.40	403	302	1.16
	s.e.	15	0.06	62	53	0.15
	Salamander					
	Mean	50	0.31	313	233	0.99
	s.e.	5	0.02	20	18	0.09
	Vertebrate					
	Mean	198	1.24	1,244	906	3.98
	s.e.	26	0.16	163	112	0.67

Table 2.7. Mean and standard error (s.e.) estimates of vertebrate abundance in the experimental pools in the three Cascade Mountain streams during July - August 1995 and 1996 for single pass catchability-based abundance (N_{CAL}), two-pass removal abundance (N_{REM}), and Petersen single-census mark-recapture abundance (N_{RECAP}).

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Estimator	Species	Number per pool (#/pool)	Number per m ² (#/m ²)	Number per 1,000 m ² (#/1,000 m ²)	Number per 100 m (#/100 m)	Number per pool volume (#/m ³)
N _{RECAP}	Trout					
(n = 24)	Mean	102	0.58	576	457	1.73
	s.e.	20	0.07	72	67	0.17
	Sculpin					
	Mean	95	0.48	485	355	1.54
	s.e.	36	0.15	150	115	0.41
	Salamander					
	Mean	101	0.67	666	500	2.32
	s.e.	14	0.06	63	54	0.27
	Vertebrate					
	Mean	299	2.00	1,727	1,313	5.59
	s.e.	61	0.21	212	177	0.58
analysis are reported in Appendix 1. A correlation matrix was used to identify and exclude significantly correlated variables from the analysis.

Results

Large wood was absent from the reference pools during the sampling period of 1995 and 1996 (Table 2.3). Volume of large wood ($\log_e \text{ mean m}^3/\text{pool}$) (P < 0.001) and number of pieces of large wood ($\log_e \text{ mean } \#/\text{pool}$) (P < 0.001) were significantly different among the treatments for 1995. A multiple range test procedure of large wood volume per channel unit ($\log_e \text{ mean } m^3/\text{pool}$) indicated that none of the treatments were homogeneous in 1995. For 1996, volume of large wood per channel unit ($\log_e \text{ mean } m^3/\text{pool}$) did not differ significantly among treatments (P = 0.097, F = 2.6). Numbers of pieces of large wood per pool ($\log_e \text{ mean } \#/\text{pool}$) differed among the treatments for 1996, confirming that number of large wood pieces per pool increased with increasing treatment level (P < 0.001, F = 24.4).

Large boulders comprised 14% of the visually estimated substrate in the three streams during the experiment. Numbers and area of large boulders (sqrt #/pool and sqrt m^2/m^2) did not differ among treatments during 1995 (P = 0.64, F = 0.56 and P = 0.66, F = 0.54) or 1996 (P = 0.92, F = 0.17 and P = 0.67, F = 0.52).

Analysis of variance for vertebrate density per 1,000 m² (#/1,000 m²) revealed that density did not differ between years (P = 0.074). The estimated mean \log_e density of aquatic vertebrates in the three streams for 1995 and 1996 were reference 7.5 (n = 16, s. e. = 0.17), low 7.6 (n = 16, s. e. = 0.17), medium 7.8 (n = 16, s. e. = 0.18), and high 7.7 (n = 16, s. e. = 0.13) (Figure 2.1). Estimates of vertebrate density are

Figure 2.1. Estimates of vertebrate density per $1,000 \text{ m}^2$ (mean and standard error) in the three experimental large wood manipulation streams in the Cascade Mountains, Oregon during July – August 1995 and 1996.



provided in Table 2.7 and Appendix 2 and 3. Bartlett's test to check for equal variance detected no difference among the standard deviations for the treatments (P = 0.60). A one-way ANOVA for vertebrate density (log,) found that vertebrate density did not differ among the four treatments (P = 0.73). Fish (trout and sculpins) comprised 61% of the estimated vertebrate density, but no difference in fish density (\log_e) was detected among treatments (P = 0.62). Trout, sculpins, and salamanders were roughly each one-third of the total estimated vertebrate density. No differences in density (\log_e) were detected among the treatments for any taxon (P = 0.75, n = 16, P = 0.60, n = 14, P = 0.93, n = 16) for trout, sculpins, and salamanders, respectively. Trout were separated into two age classes, young of year trout (YOY; less than 80 mm in length) and age one and older trout (adult; 80 mm and longer). No differences in density (\log_e) were detected among the treatments for either age classification of trout (P = 0.44, and P = 0.65) for YOY and adult trout, respectively (Figure 2.2). Simple linear regression models of vertebrate density and large wood abundance and trout density and large wood abundance found that vertebrate density was not statistically significantly related to large wood abundance (P = 0.56, $R^2 = 0.006$). Trout density was statistically significantly related to large wood abundance (P = 0.02, $R^2 = 0.09$) (Figure 2.3).

Percent of cobble/boulder substrate was positively correlated with density in multiple linear regression models for all vertebrates and each taxon (Table 2.8). A multiple linear regression model revealed that percent of cobble/boulder substrate (P < 0.0001) and mean width (P = 0.05) were statistically significantly related to aquatic vertebrate density (P < 0.0001, $R^2 = 0.41$) (Figure 2.4, Table 2.8). Trout density was

Figure 2.2. Mean density $(\#/1,000m^2)$ and standard error of young of the year (YOY) and adult (one plus age) trout in the three experimental large wood manipulation streams in the Cascade Mountains, Oregon during July – August 1995 and 1996.



Figure 2.3. Relationship between trout density and large wood abundance in the three large wood restoration streams in the Cascade Mountains, Oregon during July-August 1995 and 1996. (N_{CAL} are catchability-based population estimates and YOY is young of the year trout < 80 mm)



Large wood abundance

Trout

YOY $N_{CAL} = 316 + 13.5$ (wood abundance), $R^2 = 0.06$ Adult $N_{CAL} = 248 + 13.1$ (wood abundance), $R^2 = 0.12$

Sculpin $N_{CAL} = 1,191 + 3.8$ (wood abundance), $R^2 = 0.0006$

Salamander $N_{CAL} = 1,489 + 5.4$ (wood abundance), $R^2 = 0.003$

Table 2.8. Regression coefficients used to model the variability in vertebrate density estimates for the three experimental large wood restoration streams in the Cascade Mountains, Oregon during July-August 1995 and 1996. SUB is percent of cobble/boulder substrate, MW is mean width, MD is mean depth, and WV is wood volume.

Species	Parameter	Coefficient	Standard error
All vertebrates	Constant	7.24	0.23
	MW	-0.063	0.032
	SUB	0.015	0.002
Trout	Constant	4.28	0.26
	MD	1.88	0.67
	SUB	0.02	0.003
Adult trout	Constant	3.29	0.28
	MD	2.92	0.74
	SUB	0.018	0.003
YOY trout	Constant	4.09	0.28
	SUB	0.021	0.004
Sculpin	Constant	6.33	0.34
	MW	-0.15	0.05
	SUB	0.02	0.004
Salamander	Constant	6.01	0.18
	WV	-0.011	0.004
	SUB	0.014	0.003

statistically significantly related (P < 0.0001, $R^2 = 0.56$) to percent of cobble/boulder substrate (P < 0.0001) and mean pool depth (P = 0.007) (Figure 2.5, Table 2.8). Multiple linear regression models for adult trout and YOY trout revealed that adult trout were statistically significantly related to percent of cobble/boulder substrate (P < 0.0001) and mean pool depth (P = 0.0002) (P < 0.0001, $R^2 = 0.52$) while YOY trout were statistically significantly related (P < 0.0001, $R^2 = 0.29$) only with percent Figure 2.4. Observed vertebrate density versus predicted vertebrate density from regression of mean vertebrate density (log_e) with mean width and percent cobble/boulder substrate in pools of the three large wood restoration streams in the Cascade Mountains, Oregon during July-August 1995 and 1996. (N_{CAL} are catchability-based population estimates).



Predicted vertebrate density per 1,000 m²

Figure 2.5. Observed trout density versus predicted trout density from regression of trout density (log_e) versus mean depth and percent cobble/boulder substrate in pools of the three large wood restoration streams in the Cascade Mountains, Oregon during July-August 1995 and 1996.



Predicted trout density

cobble/boulder substrate (P < 0.0001). A multiple linear regression model revealed that percent of cobble/boulder substrate (P < 0.0001) and mean width (P = 0.005) were statistically significantly related to sculpin density (P < 0.0001, R² = 0.39) (Figure 2.6, Table 2.8). Salamander density was statistically significantly related to percent cobble/boulder substrate (P < 0.0001) and large wood volume (P = 0.005) (P = 0.0001, R² = 0.27) (Figure 2.7, Table 2.8).

Discussion

Ecologists have recognized that habitat diversity and structure influence community diversity and abundance. Early studies showed that bird community diversity increases with increasing complexity of vegetation (MacArthur and MacArthur 1961, MacArthur 1964). Variation in bird species diversity reflects differences in habitat composition (MacArthur and MacArthur 1961). Highly complex and diverse habitats offer more potential niches and support more diverse assemblages and communities than structurally simpler habitats (MacArthur and MacArthur 1961, Gorman and Karr 1978, Schlosser 1988, Angermeier and Karr 1984). Other studies have found the same general relationship with mammals (Rosenzweig and Winakur 1969) and lizards (Pianka 1967). The same ecological principles, indicating that distribution and diversity of species is controlled by structural features and complexity of the habitat, have been applied to aquatic environments (Sheldon 1968, Gorman and Karr 1978). Figure 2.6. Observed sculpin density versus predicted sculpin density from regression of sculpin density (log_e) versus mean width and percent cobble/boulder substrate in pools of the three large wood restoration streams in the Cascade Mountains, Oregon during July-August 1995 and 1996.



Predicted sculpin density

Figure 2.7. Observed salamander density versus predicted salamander density from regression of salamander density (log_e) versus large wood volume and percent cobble/boulder substrate in pools of the three large wood restoration streams in the Cascade Mountains, Oregon during July-August 1995 and 1996.



Habitat complexity is a primary factor influencing fish community diversity (Saunders and Smith 1962, Burgess and Bider 1980, Shirvell 1990, Nickelson et al.1992). Habitat use by fish increases substantially in response to increased habitat complexity provided by large wood with local abundance of fish increasing in response to quantity and placement of large wood in streams (Saunders and Smith 1962, Forward 1984, Shirvell 1990). Large wood influences fish abundance by providing cover for overwintering fish, by providing cover during lower summer flows, by reducing velocities during high flows and by providing refuges for fishes during disturbances such as floods (Burgess and Bider 1980, Moore and Gregory 1988, Junk et al. 1989, McMahon and Hartman 1989, Gregory et al. 1991, Nickelson et al. 1992, Pearsons et al. 1992, Quinn and Peterson 1996, Harvey et al. 1999). Juvenile salmonids and other aquatic vertebrates use large wood structure as refuge from predators and as sites of foraging (Sedell and Beschta 1991).

Resource agencies, fisheries scientists and managers have all identified loss of habitat and habitat diversity, due to past land use and resource management policies and practices, as a significant factor in the decline of native stocks (Nehlsen et al.1991, Bevan et al. 1994, Forest Ecosystem Management Team 1993). Many native fish stocks and aquatic vertebrate species in the Pacific Northwest region of the United States have been listed under the federal Endangered Species Act (ESA) or are being considered for listing (Nehlsen et al. 1991). The ESA requires protection of native fish, wildlife, and their habitat and restoration of threatened and endangered species to viable population levels. Resource managers and fisheries scientists increasingly recognize the need for better information and further evaluation of restoration efforts so that the ultimate goal of ecological restoration can be met and streams can provide natural physical and ecological functions to support aquatic vertebrate and invertebrate communities (Gregory and Wildman 1994). Additional information and experimental studies are necessary to further understand the influence of large wood on vertebrate populations and to design better fishery restoration projects for declining aquatic vertebrate and invertebrate populations.

This study evaluated aquatic vertebrate response to large-scale manipulation of large wood abundance in pools. Although there was an apparent trend of increasing vertebrate density with increasing large wood treatment, no significant difference in vertebrate density was detected among the treatments. In large wood treatment pools, estimates of vertebrate density were higher but not significantly different than in the reference pools indicating that large wood may affect distribution and abundance of aquatic vertebrates. Similar to other habitat manipulation studies, we observed an apparent trend of increasing vertebrate density with increasing large wood abundance but this trend drops off between the medium and high treatment levels.

This pattern of increasing vertebrate density with increasing large wood abundance and then dropping off at the highest treatment was also observed in a large wood habitat manipulation study in the Oregon coast range (Fieth and Gregory 1993). Their results found that there was a general pattern of increased fish biomass in pools with increased wood complexity. They concluded that some other factor such as recruitment or food may be limiting. For Cascade Mountain streams, an explanation to this pattern may be a result of confounding factors such as larger particle size.

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Large wood is an essential component of stream morphology and biotic habitat (Murphy and Hall 1980, Harris 1987, Beschta 1991, Gregory et al. 1991, Gregory and Wildman 1994, Lichatowich et al. 1994). In many small streams morphology may be controlled by natural formations such as bedrock and large boulders, rather than large wood (Montgomery et al. 1995). Many studies on the response of fish to large wood, brush bundles, fine organic debris, riparian cover and habitat manipulation have been conducted in coastal streams (e.g., Forward 1984, Rodgers et al. 1992), which have smaller substrates than streams of the Cascade Mountains. Cobble/boulder substrate, combined with deep pools, has been found to provide complex cover for fish (Bustard and Narver 1975, McMahon and Hartman 1989). The three streams we studied in the Cascade Mountains of Oregon have a high abundance of cobble and larger substrates (Table 2.6) which may affect responses to large wood abundance. Large wood was a significant habitat component for predicting trout distributions at the reach scale in a previous study in Lookout Creek (D'Angelo et al. 1995). We hypothesize that the influence of large wood on fish and salamanders decreases with decreasing spatial scale and with increasing particle size.

There is support for this hypothesis in the findings of a stream restoration project in Quartz Creek that evaluated the changes in the geomorphic and biological attributes associated with the installation of large wood accumulations (Gregory and Wildman 1994). In the first five years following wood installation they found that fish densities were usually highest in the section below the large wood restoration site and fish densities were lowest in the section above the large wood restoration site. In the two years after the 1996 flood they found that fish densities were highest in the large

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wood restoration site compared to above and below the restoration site (Gregory and Wildman 1998). Large wood cover may have minor effects on vertebrate densities in streams with large particle size during low flow but wood may affect densities during and after major disturbances (Gregory and Wildman 1998). This could explain the higher fish densities below the restoration site. Ecological responses to contribution of wood in the stream system include direct influences on population, refuge during floods, or indirect benefits of food sources because wood provides hydraulic and particulate retention that allows aquatic organisms to process organic matter (Gregory and Wildman 1994).

The Quartz Creek restoration study focused on a continuous reach rather than replicated pool units and did not include experimental replication. Both studies found fish densities were apparently higher in wood treatments than in the reference sections indicating that wood influences vertebrate abundance, but differences were not significant. A reason for this lack of significance may be the indirect effect of large wood as well as the larger particle size of these streams. Cover provided by large wood may not be as important as food sources during the summer when vertebrate abundance was estimated. This could account for vertebrate densities dropping off at the highest level of wood abundance. Additionally, large particle substrate may act as a substitute for large wood in retention of small particles and nutrients providing a similar ecological function as large wood.

The regression models further support the hypothesis that the influence of large wood on fish and salamanders decreases with decreasing spatial scale and with increasing particle size. The regression models indicate that the small amount of variation in density of aquatic vertebrates in response to the large wood treatments may have been a result of the abundant complex cover provided by the cobble/boulder substrate. Percent of cobble/boulder substrate explained less than half of the variation in density of vertebrates.

In addition, the power of this test may have been too low to detect differences between treatments. A retrospective power analysis and sample size determination indicates that the power of the test was low (0.42), for this type of experiment, leaving a high probability of making a type II error of accepting the null hypothesis when it is false. At the 0.05 Type I significance level and a power of 0.80 (Type II error = 0.20), a sample size of 44 of each treatment level would be needed to detect an effect among the treatments. Reducing the significance level to 0.10 at a power of 0.80 would still require 32 samples of each treatment to detect a difference. These sample size estimates compare to the 16 samples used in this analysis. This large unexplained variation indicates further experiments and evaluation are needed to clarify the role of large wood in complex habitats for fish and other aquatic vertebrates.

This study is consistent with other large wood studies that also found a general increase in vertebrate density with increasing large wood abundance. Sedell et al. (1984) posed the question of how much large wood in a stream is necessary for restoration of critical habitat and recovery of viable aquatic populations. This question remains valid. Although we observed no significant influence of large wood on vertebrates in this channel unit scale large wood restoration experiment; large wood is a potentially important component of stream geomorphology and biotic habitat. High physical habitat heterogeneity associated with cobble/boulder substrates in these

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streams may override the influence of large wood at the channel unit scale. Large wood may have a stronger influence in simpler stream systems with smaller particle size or at spatial scales larger than channel unit. Large wood may also have greater influence in differing environmental regimes such as floods, seasonal flows and varying water temperatures. Structural stability provided by wood may influence ecological functions and abundance of aquatic communities in streams.

Influence of large wood on vertebrate populations may be detected by a stronger experimental design through increased replication and statistical power at larger experimental scale. The ESA and Oregon Plan for Salmon and Watersheds directives to restore and maintain fish stocks and fish habitat create a unique opportunity to evaluate habitat relationships at different spatial scales and responses of vertebrates to restoration practices. Limiting factors analysis (Everest et al. 1991) is a promising tool for making decisions that provides a framework for planning, implementing and evaluating restoration of fish habitat at the appropriate spatial and temporal scale. Large-scale large wood restoration experimental design could use a limiting factors analysis to identify factors affecting survival of aquatic biota at different life stages in order to establish where mortality may be occurring and to identify any biological bottlenecks. There is an urgent need for rigorous observational and experimental studies within the context of limiting factors analysis and basin assessments because inclusion of stringent monitoring and evaluation are critical to restoration design for detecting the influence of large wood. Monitoring and evaluation of aquatic community response to habitat rehabilitation and enhancement projects are key to assessing the effectiveness and/or success of habitat projects. This

information will assist fisheries managers in adaptive management approaches for habitat restoration projects that emphasize ecosystem health.

In many studies the response of salmonids and other aquatic vertebrate species to abundance or complexity of large wood has been significant. In this study we detected that:

- Estimates of vertebrate abundance did not statistically significantly differ among the large wood treatments.
- Large wood abundance is a statistically significant habitat factor that explains a very small proportion of the variation in trout abundance in these streams.
- The large particle size substrate in these streams is a statistically significant habitat factor for aquatic vertebrates that explains about half of the variation in vertebrate abundance estimates for these streams.

These findings suggest that large wood may not be as important to aquatic vertebrates during summer as are food sources or other resources in boulder-bedded Cascade Mountain streams. However, large wood may play a more important role as hiding cover or as refuge at different times of the year or during different environmental regimes in these types of streams.

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ESTIMATOR COMPARISON AND CATCHABILITY OF TROUT, SCULPINS, AND SALAMANDERS IN AN EXPERIMENTAL MANIPULATION OF LARGE WOOD IN CASCADE MOUNTAIN STREAMS

Abstract

Mark-recapture, multiple pass removal, and catchability-based population estimates were compared in a wood abundance restoration experiment in three streams in the Cascade Mountains of Oregon. Catchability-based single pass population estimates were larger than mark-recapture population estimates and maximum likelihood multiple removal estimates. Mark-recapture estimates were larger than maximum likelihood multiple removal estimates. The mark-recapture method gave more reliable and accurate estimates than maximum likelihood multiple removal method, but both methods may substantially underestimate the actual population as estimated by the catchability-based models. Species, fish length, and habitat variables influenced catchability. Catchability consistently decreased with increasing habitat complexity.

Introduction

Loss of habitat and habitat diversity have been significant factors in the decline of native fish stocks (Nehlsen et al. 1991, Bevan et al. 1994). Accurate quantitative estimation of abundance of aquatic vertebrates is required to determine status of populations and responses of aquatic vertebrate to habitat complexity. Restoration of aquatic habitats and salmonids requires knowledge of habitat relationships and ability to accurately estimate abundance of aquatic organisms. If structural complexity affects catchability of fish, comparisons of reaches with different physical heterogeneity require correction of evaluation of estimates. This paper compares a catchability-based estimator with a mark-recapture population estimator and the multiple removal population estimator and discusses the effect of increasing habitat complexity on aquatic vertebrate catchability.

Studies have shown greater accuracy for population estimates with markrecapture techniques than for multiple removal sampling techniques (Heggberget and Hesthagen 1979, Peterson and Cederholm 1984, Buttiker 1992, Rodgers et al. 1992). In two small streams in north Norway, mark-recapture sampling was more accurate than the removal method (Heggberget and Hesthagen 1979). The study concluded that the removal method, in which constant catchability is an assumption, underestimated abundance because catchability of fish was lower after the first electrofishing pass. Mark-recapture estimates were more accurate than removal estimates in a small stream on the Olympic Peninsula of Washington (Peterson and Cederholm 1984). Markrecapture was less likely to be biased by environmental factors than the removal method. Comparison of snorkeling (direct observation), multiple removal, and markrecapture population estimation techniques in streams of Oregon's Coast Range revealed that the mark-recapture method had greater accuracy than the removal method, which had greater accuracy than snorkeling (Rodgers et al. 1992). The authors hypothesized that likelihood of capture of fish after the first removal pass decreased in large pools with greater habitat complexity and hiding cover created by large wood. They also hypothesized that greater large wood complexity reduces a divers ability to see and successfully count fish that take refuge within complex large

wood structure. Buttiker (1992) concluded that both the mark-recapture and removal methods underestimate the true population size. He also concluded that the markrecapture estimator is less likely to be negatively biased by unequal catchability than the removal estimator because of individual size selectivity or environmental factors.

Species, fish length, and habitat heterogeneity influence catchability of fish, but, removal methods and repeated observation methods assume that probability of capture of organisms is constant. Aquatic vertebrate population estimators are biased by species, fish size (Larimore 1961, Mahon 1980, Buttiker 1992, Bayley 1993), and by diversity of habitat and complexity of hiding cover (Larimore 1961, Rodgers et al. 1992, Bayley 1993, Bayley and Dowling 1993). Peterson and Cederholm (1984) found an inverse relationship between catchability of juvenile coho salmon and the amount of hiding cover in a small stream on the Olympic Peninsula of Washington. In numerous streams (Bayley and Dowling 1993) and lake enclosures (Bayley 1993) in Illinois, capture efficiency differed with fish size and was strongly affected by various habitat features. Increased catchability as fish became larger was attributed to larger fish being more vulnerable to a given voltage gradient.

The objectives of this paper are: 1) to compare catchability-based models (Bayley 1993), maximum likelihood two-pass removal (DeLury 1947, Zippen 1956) and Peterson single-census mark-recapture (Ricker 1975) population estimates and 2) to assess from catchability-based models the effect of habitat complexity associated with large wood on aquatic vertebrate catchability.

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Study Site

The McKenzie River drainage is typical of the Western Cascades Province of Oregon. Basalt and andesite are the most common bedrock materials of the streams and steep rugged ridges, that range in elevation to over 1,800 m. Shallow soils at lower elevations consist of tuffs and breccias with deeper soils at higher elevations derived from andesite and lava flows (Franklin and Dyrness 1988). Douglas fir (<u>Pseudotsuga menziesii</u> (Mirb.) Franco), western hemlock (<u>Tsuga heterophylla</u> (Raf.) Sarg), and western red cedar (<u>Thuja plicata</u> D. Don) are the dominant conifers on the hillslopes and streamsides. Big-leaf maple (<u>Acer macrophyllum</u> Pursh) and red alder (<u>Alnus rubra</u> Nutt.) are the dominant riparian deciduous trees.

Lookout Creek, Tidbits Creek, and North Fork Quartz Creek are located within the McKenzie River drainage at elevations between 365 to 1,525 meters. These cobble/boulder bed streams were selected for a large wood restoration study because of their similar characteristics of size, gradient, flow, vertebrate communities, and land use practices (Table 3.1). Lookout Creek, a fifth-order stream in the H. J. Andrews Experimental Forest, is designated a research stream by the Oregon Department of Fish and Wildlife and is closed to recreational fishing. Tidbits Creek and North Fork Quartz Creek are third-order streams outside the H. J. Andrews Experimental Forest boundary and are subject to recreational fishing.

Historical land uses in the three stream basins include clear-cut logging, salvage logging, large wood removal from streams, road construction, mining, recreational camping, and research. The streams are susceptible to debris flows and large floods, which alter physical habitat and disrupt biological communities during these high flow events (Lamberti et al. 1991). Human activities potentially modify the timing and magnitude of these natural disturbance processes.

Table 3.1. Characteristics of streams selected for large wood restoration experiment in the Cascade Mountains of Oregon. Stream flow (taken at lower gage on Lookout Creek), stream temperatures (taken at pool tailout at time of sampling), and dominant substrates are data from the sample period in July – August 1995 and 1996. Average width, mean gradient, and pools per km are from stream survey data of 1993 and 1994.

	Lookout Creek	Tidbits Creek	N. F. Quartz Creek
Drainage area	6,400	2,700	1,060
(hectares)			
Stream order	4 - 5	3	3
Gradient (%)	4	3	5
Stream flow (m ³ /s)	0.6	NA	NA
Minimum	0.3		
Maximum	1.3		
Temperature (°C)	11	12	13
Average width	8.5 m	5.0 m	4.5 m
Distance surveyed			
1993-94 survey	1,900 m	6,500 m	5,000 m
1996 survey	4,100 m		
Pools/km			
1993-94 survey	10	9	11
1996 survey	6		
% Pools			
1993-94 survey	28	12	12
1996 survey	23		
Number of LW/km	168	19	89
Dominate substrate	Cobble and Small Boulder	Cobble and Small Boulder	Cobble and Small Boulder

Methods

We compared estimates of fish and salamander abundance from paired pass removal (two-pass), mark-recapture (single-census), and catchability-based models in a wood restoration experiment in Lookout Creek, Tidbits Creek, and North Fork Quartz Creek. Six to twelve people using 2 - 3 direct-current electrofishers (1000 V) sampled experimental pools during a 5-week period in July – August of 1995 and 1996. In Lookout Creek and Tidbits Creeks, 2 - 5 divers assisted in electroshocking and capturing vertebrates during sampling. Pools were blocked with seines to prevent emigration or immigration during the sampling and recovery period (DeLury 1947, Zippen 1956, Ricker 1975), which was extended to 24 h for recapture of marked fish.

Species richness of aquatic vertebrates differed slightly between streams. Eight species were caught but only four species were present in all three streams. Only five of these species were found in substantial numbers and were included in the analysis of the response of aquatic vertebrates to abundance of large wood. Two species of trout, cutthroat (<u>Oncorhynchus clarki</u>) and rainbow trout (<u>O. mykiss</u>), were combined as a single taxon. Two species of sculpins, mottled sculpin (<u>Cottus bairdi</u>) and Paiute sculpin (<u>C. beldingi</u>) were combined as a single taxon and the Pacific giant salamander (<u>Dicamptodon tenebrosus</u>) was the only species of salamander. Other aquatic vertebrate species captured but not included in the analysis were longnose dace (<u>Rhinichthys cataractae</u>), speckled dace (<u>R. osculus</u>), and tailed frog (<u>Ascaphus truei</u>).

Vertebrates captured during the removal sampling were held in separate containers for each pass. Individuals were identified to species, measured for length to the nearest millimeter, weighed to the nearest 0.1 g with a portable balance, and marked for recapture identification. Fork length was measured for salmonids and total length was measured for all other vertebrates. Vent length and total length were measured for salamanders. Trout were marked with adipose fin clips, sculpins were marked with pectoral fin clips, and salamanders were marked with toe clips prior to release into their respective pools for mark-recapture estimates.

Fish may be behaviorally affected for 6 h or longer following electroshock capture and marking, causing marked fish to be less vulnerable to electroshock recapture efforts during that time period (Mesa 1989, Buttiker 1992). We allowed a 24-h recovery period before making our recapture pass, as recommended by Mesa (1989). During the recapture sampling effort, captured vertebrates were held in buckets of water. Individuals were identified to species, measured for length to the nearest millimeter, weighed to the nearest 0.1 g with a portable balance and checked for marks before being released back into the streams.

Analysis

In each treatment, vertebrate abundance (N_{CAL}) was estimated using catchability-models based on the first pass (Bayley 1993), from maximum likelihood two-pass removal (N_{REM}) (DeLury 1947, Zippen 1956) and from single-census markrecapture (N_{RECAP}) (Ricker 1975). The maximum likelihood multiple removal population estimator assumes constant catchability between passes (DeLury 1947, Zippen 1956). Catchability is affected by biologic and geomorphic variability and catchability may vary between electrofishing efforts (Mahon 1980). For this experiment we use a taxon, fish length and habitat-corrected single pass catchability estimator to calculate population estimates using the equation:

Equation 1
$$N_{CAL} = c_1 / q$$

where c_1 is the number of fish caught in the first sampling effort and q is catchability corrected for species, fish length and habitat. Taxa were separated into seven length categories (≤ 34 mm, 35 - 54 mm, 55 - 79 mm, 80 - 114 mm, 115 - 154 mm, 155-199 mm, and ≥ 200 mm) and we assumed that individuals of the same taxon within a length category were similarly vulnerable to capture for given habitat conditions (Bayley 1993). Catchability (q_{CAL}) models were constructed for each taxon using mean length (MNL) of each length group and measured and estimated habitat variables (Table 3.2). The sampling method was different in N. F. Quartz Creek (two backpack shockers, wading only) versus Lookout Creek and Tidbits Creek (three backpack shockers, wading and diving). Catchability models (Table 3.2) were constructed for each species and mean length group depending on the sampling method. The general catchability model predicts the proportion of fish present that are caught in the first pass:

Equation 2 $q = (1 + e^{-L})^{-1}$

where q is catchability, e is the natural exponential, and L is a linear combination of species and habitat variables. The catchability equation for trout in Lookout Creek and Tidbits Creek for example is:

$$q = (1 + e^{(-(-0.486 + 0.0254(MNL) - 0.0000916(LSQ) - 0.248(CMP))^{-1}})^{-1}.$$

Table 3.2. Calibrated catchability coefficients for L used to calculate species abundance estimates for the three streams in the Cascade Mountains, Oregon during July – August 1995 and 1996. LO-TB is Lookout Creek and Tidbits Creek, NFQ is North Fork Quartz Creek, MNL is species length group mean length, SUB is substrate percentage of cobble/boulder substrate in each pool, MAXD is maximum pool depth, LSQ is mean length squared, CMP is treatment level (1, 2, 3 or 4 with respect to reference, low, medium or high) and MNLMAXD is product of mean length and maximum depth.

	Parameter	Coefficient	Standard error
LO-TB			
Trout $(n = 48)$	Constant	-0.4862	0.4229
	MNL	0.02537	0.007702
	LSQ	-0.00009158	0.00003603
	CMP	-0.2475	0.07806
Sculpins $(n = 40)$	Constant	0.1692	0.6644
	MNL	0.02390	0.007969
	SUB	-0.02810	0.005661
Salamanders $(n = 48)$	Constant	-5.902	1.031
	MNL	0.08198	0.01839
	MAXD	1.893	0.5554
	LSQ	-0.00026	0.00008276
	MNLMAXD	-0.02057	0.006447
NFQ			
Trout $(n = 16)$	Constant	0.4068	0.5663
	MNL	0.007428	0.006849
Sculpins $(n = 16)$	Constant	-0.9438	0.2479
Salamanders $(n = 16)$	Constant	-2.909	0.7159
	MNL	0.01399	0.006264
	MAXD	3.667	1.066
	SUB	-0.06129	0.02146

The catchability equation for trout in Lookout Creek and Tidbits Creek is: $q = (1 + e^{(-(-0.486 + 0.0254(MNL) - 0.0000916(LSQ) - 0.248(CMP))})^{-1}$

Results

Estimates of vertebrate mean density (\log_e) from catchability-based (N_{CAL}) (n = 24), maximum likelihood two-pass multiple removal (N_{REM}) (n = 24), and Petersen single-census mark-recapture (N_{RECAP}) (n = 24) differed significantly (ANOVA, P = 0.0001) (Figure 3.1). None of the mean densities (\log_e) calculated by the different estimators was homogeneous (Fisher's least significant difference test). Population estimates from the multiple removal method were lower than mark-recapture estimates (Figure 3.1). Both of these methods gave lower population estimates than the catchability-based single pass method. An ANOVA on mean trout densities (\log_e) for the three estimators found that the estimates of trout density did not differ significantly (P = 0.09) (Figure 3.2). Paired t-test comparisons of trout density means revealed that mean N_{CAL} trout density was not significantly larger than mean N_{RECAP} trout density (P = 0.13) but mean N_{CAL} trout density was significantly larger than mean N_{REM} trout density (P = 0.14).

Catchability-based estimates (N_{CAL}) of vertebrate density, with few exceptions, were larger than estimates for mark-recapture (N_{RECAP}) and for multiple removal (N_{REM}) (Table 3.3). In three cases N_{RECAP} estimates were larger than estimates of N_{CAL} and one case where estimates of N_{REM} were larger than estimates of N_{CAL} . Estimates for N_{REM} were larger than N_{RECAP} estimates in one case. Overall, mean N_{CAL} estimates of vertebrate density were 49% larger than mean N_{REM} estimates and 23% larger than mean N_{RECAP} estimates. Overall, mean N_{RECAP} estimates of vertebrate density were Figure 3.1. Estimates of vertebrate density per $1,000m^2$ (mean and standard error) for catchability-based (N_{CAL}), mark-recapture (N_{RECAP}), and maximum likelihood multiple removal (N_{REM}) density estimates in the mark-recapture pools of the experimental large wood manipulation streams in the Cascade Mountains, Oregon during July – August 1995 and 1996.





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Figure 3.2. Mean and standard error of trout density estimates per 1,000 m² for the three population estimators used in the mark-recapture pools of the experimental large wood manipulation streams in the Cascade Mountains, Oregon during July – August 1995 and 1996. N_{CAL} is catchability-corrected density, N_{RECAP} is mark-recapture density, and N_{REM} is maximum likelihood removal density.



Population estimator
33% larger than mean N_{REM} estimates (Table 3.3). There was no influence of

treatment effect on density ratios for all vertebrates or for trout.

Table 3.3. Ratio of vertebrate (Vert.) and trout density per 1,000 m² estimates (mean, minimum, and maximum) for each large wood treatment level and for all treatment levels combined in the mark-recapture pools of the three streams in the Cascade Mountains, Oregon during July – August 1995 and 1996. N_{CAL} is catchability corrected density, N_{REM} is multiple removal density, and N_{RECAP} is mark-recapture density.

Treatment	N _{REM} /N _{CAL}		N _{RECA}	_p /N _{CAL}	N _{REM} /N _{RECAP}		
		Vert.	Trout	Vert.	Trout	Vert.	Trout
Reference	Mean	0.48	0.72	0.72	1.03	0.67	0.72
	Minimum	0.15	0.15	0.28	0.20	0.49	0.59
	Maximum	0.65	1.23	0.88	1.74	0.78	0.82
Low	Mean	0.43	0.74	0.66	1.00	0.64	0.76
	Minimum	0.31	0.66	0.46	0.79	0.51	0.59
	Maximum	0.61	0.86	0.90	1.29	0.84	0.89
Medium	Mean	0.41	0.85	0.69	1.24	0.60	0.72
	Minimum	0.19	0.51	0.33	0.75	0.50	0.57
	Maximum	1.24	1.46	2.04	2.55	0.68	0.85
High	Mean	0.57	0.70	0.76	1.01	0.75	0.72
	Minimum	0.34	0.48	0.50	0.64	0.58	0.55
	Maximum	0.75	0.97	1.00	1.45	1.21	0.86
Overall	Mean	0.51	0.75	0.77	1.07	0.67	0.73
	Minimum	0.15	0.15	0.28	0.20	0.49	0.55
<u></u>	Maximum	1.24	1.46	2.04	2.55	1.21	0.89

Differences in abundance estimators obviously reflect implied or determined catchability. With few exceptions, the two-pass multiple removal estimator catchability (q_{REM}) was greater than catchability (q_{CAL}) for the catchability-based estimator, corrected for taxon, fish length, and habitat in all three streams (Figure 3.3).

Figure 3.3. Catchability comparison for the catchability-based model (q_{CAL}) and the maximum likelihood multiple removal method (q_{REM}) in the three large wood experimental manipulation streams in the Cascade Mountains, Oregon during July – August of 1995 and 1996.



In Lookout Creek, q_{REM} (range 0.12 – 1.00) for trout was greater than q_{CAL} (range 0.27 – 0.68) with one exception (n = 132). In Tidbits Creek, q_{REM} (range 0.64 – 1.00) for trout was always greater than q_{CAL} (n = 133, range 0.27 – 0.68). In North Fork Quartz Creek, q_{REM} (range 0.75 – 1.00) for trout was greater than q_{CAL} (range 0.66 – 0.87) with two exceptions (n = 92). In Tidbits Creek, q_{REM} for sculpins was greater than q_{CAL} with four exceptions. In Lookout Creek and North Fork Quartz Creek, q_{REM} for sculpins was always greater than q_{CAL} . For salamanders, q_{REM} was always greater than q_{CAL} in all three streams.

In Lookout Creek and Tidbits Creek, large wood abundance, fish length and length squared of individuals, percent of cobble and larger substrate, and maximum depth were significantly correlated with catchability (Table 3.2). Large wood abundance decreased q_{CAL} for trout (Figure 3.4) but showed no effect on q_{CAL} for sculpins or salamanders. Catchability increased with mean length for trout, sculpins (Figure 3.5), and salamanders (Figure 3.6), but trout q_{CAL} (Figure 3.4) and salamander q_{CAL} (Figure 3.6) decreased with squared mean length. Only q_{CAL} for salamanders increased with maximum depth (Figure 3.7). Percent cobble/boulder substrate decreased q_{CAL} for sculpins only (Figure 3.8). There was an interaction term between mean length and maximum depth that decreased q_{CAL} for salamanders.

In North Fork Quartz Creek, mean length, percent of cobble/boulder substrate, and maximum depth significantly affected catchability (Table 3.2). Catchability (q_{CAL}) increased with mean length for trout and salamanders but not sculpins (Figure 3.9). Increasing percentage of cobble/boulder substrate reduced q_{CAL} of salamanders (Figure 3.10) but maximum pool depth increased q_{CAL} of salamanders (Figure 3.11). Figure 3.4. Predicted catchability (q_{CAL}) of trout versus large wood treatment, keeping other variables that affect trout q_{CAL} constant, in Lookout Creek and Tidbits Creek in the Cascade Mountains, Oregon during July – August 1995 and 1996. LO-TB is Lookout Creek and Tidbits Creek.



Figure 3.5. Predicted catchability (q_{CAL}) of sculpins, versus mean length, keeping other variables that affect sculpin q_{CAL} constant, in Lookout Creek and Tidbits Creek in the Cascade Mountains, Oregon during July - August 1995 and 1996. LO-TB is Lookout Creek and Tidbits Creek.



Sculpin mean length (mm)

Figure 3.6. Predicted catchability (q_{CAL}) of salamanders versus mean length, keeping other variables that affect salamander q_{CAL} constant, in experimental large wood treatment pools in Lookout Creek and Tidbits Creek in the Cascade Mountains, Oregon during July – August 1995 and 1996. LO-TB is Lookout Creek and Tidbits Creek.



Salamander vent length (mm)

Figure 3.7. Predicted catchability (q_{CAL}) of trout, sculpins, and salamanders versus maximum pool depth, keeping other variables that affect q_{CAL} constant, in experimental large wood treatment pools in Lookout Creek and Tidbits Creek in the Cascade Mountains, Oregon during July – August 1995 and 1996. LO-TB is Lookout Creek and Tidbits Creek.



Figure 3.8. Predicted catchability (q_{CAL}) of trout, sculpins, and salamanders versus percent cobble/boulder substrate, keeping other variables that affect q_{CAL} constant, in experimental large wood treatment pools in Lookout Creek and Tidbits Creek in the Cascade Mountains, Oregon during July – August 1995 and 1996. LO-TB is Lookout Creek and Tidbits Creek.



Figure 3.9. Predicted catchability of trout, sculpins, and salamanders versus mean length, keeping other variables that affect q_{CAL} constant, in experimental large wood treatment pools in North Fork Quartz Creek (NFQ) in the Cascade Mountains, Oregon during July – August 1995 and 1996.



Figure 3.10. Predicted catchability (q_{CAL}) of trout, sculpins, and salamanders versus percent cobble/boulder substrate, keeping other variables that affect q_{CAL} constant, in experimental large wood treatment pools in North Fork Quartz Creek (NFQ) in the Cascade Mountains, Oregon during July – August 1995 and 1996.



Figure 3.11. Predicted catchability (q_{CAL}) of trout, sculpins, and salamanders versus maximum depth, keeping other variables that affect q_{CAL} constant, in experimental large wood treatment pools in North Fork Quartz Creek (NFQ) in the Cascade Mountains, Oregon during July – August 1995 and 1996.



Discussion

Validity of multiple removal and mark-recapture estimates depends on several assumptions. Multiple removal population estimates assume that the population is closed, there is equal probability of capture for all fish, and that the probability of capture remains constant between passes (Zippen 1956). Mark-recapture population estimates assume that the population is closed or recruitment is negligible, no marked fish lose their marks in the time between samples, marked fish and unmarked fish are randomly distributed and equally vulnerable to capture within the population, and all marked fish captured are reported (Ricker 1975).

In this study there is no independent or true population to compare the three estimators. Mark-recapture data were used for N_{CAL} model development. The assumption of equal catchability for marked and unmarked fish may be false. The population would be overestimated if marked fish have lower catchability than unmarked fish.

We found that catchability-based population estimates were larger than markrecapture estimates and maximum likelihood multiple removal population estimates. This is consistent with the findings of other studies where population estimates were corrected for species, fish length, and habitat characteristics (Bayley and Dowling 1993, Bayley 1993). We also found that mark-recapture estimates were larger than the maximum likelihood multiple removal estimates, which is consistent with studies that compared these estimators (Heggberget and Hesthagen 1979, Petersen and Cederholm 1984, Rodgers et al. 1992). These results indicate that the mark-recapture method

provides more reliable and accurate estimates than maximum likelihood multiple removal method but both methods may substantially underestimate the population.

The assumption of constant probability of capture of organisms is seldom met. Varying habitat conditions, species, and size of an individual are known to affect the probability of capture of an individual (Buttiker 1992, Bayley 1993, Bayley and Dowling 1993, Anderson 1995, Heimbuch et al. 1997). With few exceptions, our results indicate that the two-pass removal estimator catchability was greater than catchability corrected for taxon, fish length, and habitat variables. Greater catchability associated with the maximum likelihood removal estimator consistently gave negatively biased population estimates as compared to mark-recapture and catchability-based population estimates. Catchability of the catchability-based estimator consistently decreased with increasing habitat complexity. The catchabilitybased method may provide more accurate population estimates because it compensates for the assumption of constant catchability related to the maximum likelihood removal estimator. Our findings are consistent with the findings of other studies of fish populations in small streams (e.g., Buttiker 1992, Bayley 1993, Bayley and Dowling 1993, Anderson 1995, Heimbuch et al. 1997).

Mark-recapture estimation is more accurate than multiple pass removal, but both techniques may substantially underestimate the population. In studies comparing population estimates from the Petersen mark-recapture method and from multiple removal methods to known fish populations both methods underestimated the true population. The mark-recapture method underestimated the known population by as much as 20% (5 - 20%) and the multiple removal method underestimated the known

population by as much as 30% (13-30%) (Peterson and Cederholm 1984, Rodgers et al. 1992). We believe that catchability-based estimates will give a more accurate indication of the population. Additional research using known populations could verify the increased level of accuracy in the catchability-based population estimator corrected for species, fish length, and habitat.

More time and effort may be required for obtaining initial calibration data for catchability-based estimates, but once the calibration samplings are completed less time would be involved in fish sampling. Reduced fish sampling time would be less harmful to sensitive, threatened, or endangered fish populations. The catchabilitybased estimator may be a preferred approach for large-scale restoration studies or for sampling complex habitats. Less time would have to be spent sampling fish, which would allow more stream area to be sampled in a shorter period of time. The catchability-based estimator may also be more appropriate in simple and relatively homogeneous habitats because less time would be required for sampling fish and measuring habitat in these types of streams after the initial calibration data were taken. In these circumstances, the catchability-based estimator may provide more reliable information with greater sampling area and reduced fish sampling time than the multiple pass removal or mark-recapture techniques. More studies in a variety of stream habitat types are needed to test the validity of using the catchability-based estimator method in habitats other than pools.

Understanding the accuracy of the population estimator and the impact that habitat may have on catchability will assist fisheries scientists and managers in selecting methods for population estimation. Mark-recapture is currently the preferred

method for estimating salmonid abundance if a high degree of accuracy is desired or if the population estimates are in complex habitats during periods where fish may be inactive or hiding (Rodgers et al. 1992). Our findings suggest that catchability-based estimates may give an even higher degree of accuracy than mark-recapture techniques.

Regardless of which method is selected, it is important to understand the relative accuracy of the method and how this accuracy varies with habitat complexity, population size, fish species, fish size, and other factors such as water chemistry or temperature. Fisheries scientists and managers will be able to standardize population data with quantitative characterization of population estimators for different methods. Standardized data will assist in comparing population estimates from different geographic locations on varying spatial scales. Research on habitat restoration and habitat relationships must recognize limitations of population estimators and catchability. Our study is consistent with other studies that found catchability varies with habitat variability and we conclude that habitat heterogeneity affects population estimators. Future studies of relationships between fish abundance and habitat complexity must recognize the influence of habitat heterogeneity on the methods of abundance estimation and incorporate the variation in habitat into their analyses to provide valid and reliable population information. In conclusion the findings of this study are confirmed by the findings of studies that compared these population estimators or evaluated the catchability of aquatic vertebrates in varying complex habitats. Conclusions from this study include:

• Catchability-based models may provide more accurate population estimates than Petersen mark-recapture and multiple removal methods.

- Catchability increases with fish length.
- Catchability decreases with increasing habitat complexity.
- The assumption of constant catchability of the multiple removal estimator may be false which may cause negative bias in population estimates.

The assumption of constant catchability is likely false for many studies of the response of aquatic vertebrates to restoration efforts. Previous studies could reevaluate population estimates using the catchability-based modeling method to standardize evaluation of the response of aquatic vertebrates to large wood and stream restoration efforts in varying habitats, geographical locations, or spatial scale.

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SYNTHESIS CONCLUSION

The increased emphasis on habitat management and habitat restoration to reverse trends of declining native fish stocks and vertebrate species requires rigorous measures of fish abundance. This experiment evaluated the response of aquatic vertebrates to increasing complexity created by restoration of the abundance of large wood. Although there was an apparent trend of increasing vertebrate density with increasing large wood treatment, no difference in vertebrate density was detected among treatments. High physical habitat heterogeneity associated with cobble/boulder substrates in these streams may override the influence of wood at the channel unit scale. Large wood may have a stronger influence in simpler stream systems with smaller particle size or at spatial scale larger than channel unit. Large wood may also have greater influence in differing environmental regimes such as floods, seasonal flows and varying water temperatures. If large wood significantly influences vertebrate populations, stronger experimental designs with increased statistical power by replication at larger experimental scale are required.

Accurate quantitative information of aquatic vertebrates is important in determining current conditions and in understanding aquatic vertebrate response to habitat complexity. Mark-recapture, multiple pass removal, and catchability-based population estimates were compared in all three streams. The catchability-based population estimates were larger than mark-recapture estimates and maximum likelihood multiple removal estimates. Mark-recapture estimates were larger than maximum likelihood multiple removal estimates. The mark-recapture method gives more reliable and accurate estimates than maximum likelihood multiple removal

method, but both methods may substantially underestimate the actual population. Species, fish length, and habitat variables influenced catchability for the population estimators examined. Catchability of the catchability-based estimator consistently decreased with increasing habitat complexity.

Understanding the accuracy of the population estimator and the impact that habitat may have on catchability will assist fisheries scientists and managers in making informed decisions regarding the selection of a method. Recognition of the accuracy and the limitations of population estimators and catchability should provide more reliable information to design, monitor, and evaluate habitat restoration projects. Monitoring and evaluation of habitat rehabilitation and enhancement projects is essential in assessing the effectiveness and/or success of habitat projects.

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APPENDICES

Appendix 1. Characteristics of habitat units for the experimental large wood restoration pools of the three streams in the Cascade Mountains, Oregon during 1995 and 1996. (LO is Lookout Creek, TB is Tidbits Creek, NFQ is North Fork Quartz Creek, CMP is large wood treatment, W_{MEAN} is mean width, D_{MEAN} is mean depth, D_{MAX} is maximum depth, PA is pool surface area, PCSA is pool cross section area, PV is pool volume, SUB IS percent of cobble and larger substrate, %WA is percent of zone one wood surface area to pool surface area and Cover is sum of SUB and %WA to PA)

Year	Stream	Unit	СМР	W _{MEAN}	D _{MEAN}	D _{MAX}	PA (m ²)	PCSA (m ²)	PV (m ³)	SUB (%)	%WA (m ²) to PA	Cover (%)
96	LO	1017	R	11.50	0.36	1.19	239	4.1	86	50	0.0	50
96	LO	1052	R	7.28	0.39	0.92	105	2.8	41	60	0.0	60
96	LO	1113	R	7.05	0.36	0.92	144	2.5	52	60	0.0	60
95	LO	1237	R	7.65	0.50	1.05	210	3.8	104	65	0.0	65
95	LO	1259	R	6.15	0.23	0.78	60	1.4	14	95	0.0	95
95	LO	1269	R	8.33	0.34	1.07	294	2.8	100	55	0.0	55
95	TB	4008	R	8.75	0.38	0.77	296	3.3	112	30	0.0	30
96	TB	4008	R	10.40	0.38	1.27	370	3.9	141	30	0.0	30
95	TB	4019	R	7.68	0.38	1.01	97	2.9	37	70	0.0	70
96	TB	4019	R	7.95	0.36	1.22	99	2.9	35	70	0.0	70
95	TB	4041	R	8.48	0.35	0.77	120	3.0	42	100	0.0	100
96	TB	4041	R	8.40	0.34	0.75	176	2.9	60	80	0.0	60
95	NFQ	8002	R	4.75	0.38	1.00	53	1.8	20	0	0.0	0
96	NFQ	8003	R	4.60	0.25	0.72	47	1.2	12	0	0.0	0
95	NFQ	8025	R	6.30	0.20	0.65	66	1.3	13	40	0.0	40
95	NFQ	8035	R	6.15	0.33	1.03	88	2.0	29	30	0.0	30
96	NFQ	8035	R	4.95	0.25	0.62	42	1.2	11	30	0.0	30

Appendix 1 (continued)

Year	Stream	Unit	CMP	W _{MEAN}	D _{MEAN}	D _{MAX}	PA (m ²)	PCSA (m ²)	PV (m ³)	SUB (%)	%WA (m ²) to PA	Cover (%)
96	LO	1024	L	8.48	0.41	1.05	225	3.5	91	100	2.6	103
96	LO	1067	L	10.20	0.44	1.15	164	4.5	72	100	2.3	102
96	LO	1092	L	8.35	0.57	1.44	198	4.8	113	90	0.5	91
95	LO	1224	L	10.95	0.42	1.06	250	4.6	104	80	1.0	81
95	LO	1260	L	5.23	0.32	0.80	72	1.7	23	80	2.6	83
95	LO	1302	L	5.90	0.38	0.70	151	2.2	57	100	0.8	101
95	TB	3997	L	10.50	0.42	1.15	275	4.4	116	40	0.9	41
96	TB	3997	L	8.98	0.20	1.15	270	1.8	54	40	1.1	41
95	TB	4026	L	5.05	0.69	1.30	62	3.5	43	20	3.7	24
96	TB	4026	L	5.88	0.32	1.23	88	1.9	28	20	3.8	24
95	TB	4038	L	9.08	0.85	1.90	189	7.7	160	70	5.1	75
96	TB	4038	L	10.13	0.49	1.78	205	5.0	100	40	4.6	45
95	NFQ	8000	L	5.50	0.19	0.56	93	1.1	18	20	1.7	22
96	NFQ	8000	L	4.62	0.16	0.57	65	0.7	10	20	2.5	23
95	NFQ	8014	L	4.50	0.26	0.70	75	1.2	19	10	1.4	11
96	NFQ	8014	L	6.60	0.20	0.90	106	1.3	21	10	3.2	13
95	NFQ	8029	L	6.10	0.19	0.38	58	1.2	11	10	3.9	14
96	NFQ	8029	L	8.73	0.18	0.40	129	1.6	23	10	2.5	13

Appendix 1	(continued)
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Year	Stream	Unit	CMP	W _{MEAN}	D _{MEAN}	D _{MAX}	PA (m ²)	PCSA (m ²)	PV (m ³)	SUB (%)	%WA (m ²) to PA	Co (%)
96	LO	1021	Μ	7.08	0.38	0.82	105	2.7	40	100	12.1	112
96	LO	1061	Μ	7.35	0.35	0.83	279	2.6	98	100	7.4	107
96	LO	1132	Μ	7.71	0.33	1.15	82	2.6	27	70	5.5	76
95	LO	1226	Μ	7.88	0.54	1.15	235	4.3	127	100	6.6	107
95	LO	1257	М	3.88	0.17	0.48	41	0.7	7	70	2.2	72
95	LO	1299	Μ	10.00	0.51	1.43	219	5.1	111	80	5.3	85
95	TB	3999	Μ	9.30	0.43	1.05	304	4.0	132	60	2.3	62
96	TB	3999	Μ	7.00	0.21	1.15	212	1.5	45	60	0.8	61
95	TB	4021	Μ	9.20	0.48	1.98	128	4.4	62	85	6.1	91
96	TB	4021	Μ	8.13	0.28	1.35	147	2.3	42	85	3.2	88
95	TB	4032	Μ	6.85	0.37	1.20	137	2.5	51	45	4.8	50
96	TB	4032	Μ	10.45	0.50	1.30	188	5.2	94	45	2.8	48
95	NFQ	8009	Μ	4.45	0.28	0.68	49	1.3	14	20	4.9	25
96	NFQ	8009	Μ	4.65	0.17	0.87	53	0.8	9	20	2.5	23
95	NFQ	8020	Μ	6.00	0.32	0.82	140	1.9	45	25	4.4	29
96	NFQ	8020	Μ	6.15	0.11	0.73	116	0.7	13	40	4.0	44
95	NFQ	8027	Μ	5.25	0.28	0.48	89	1.5	25	35	6.9	42
96	NFQ	8027	Μ	3.35	0.21	0.43	64	0.7	14	35	19.7	55

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Year	Stream	Unit	CMP	W _{MEAN}	D _{MEAN}	D _{MAX}	PA (m ²)	PCSA (m ²)	PV (m ³)	SUB (%)	%WA (m ²) to PA	Cover (%)
96	LO	1028	Н	8.33	0.39	0.90	242	3.3	95	100	2.2	102
96	LO	1080	Н	7.28	0.42	1.45	124	3.1	53	100	5.9	106
96	LO	1085	Η	11.25	0.42	2.03	270	4.7	113	70	2.7	73
95	LO	1230	Н	7.05	0.39	1.12	273	2.8	106	35	5.7	41
95	LO	1252	Н	3.80	0.38	0.88	38	1.4	14	80	5.3	85
95	LO	1265	Н	8.73	0.37	0.92	265	3.2	98	100	5.6	106
95	TB	3995	Н	9.03	0.40	0.90	165	3.6	66	60	6.6	67
96	TB	3995	Н	5.88	0.16	0.80	102	0.9	16	60	4.0	64
95	TB	4011	Н	9.18	0.32	1.15	235	2.9	76	75	5.8	81
96	TB	4011	Н	9.88	0.17	0.90	437	1.7	76	75	3.1	78
95	TB	4034	Н	7.13	0.38	0.72	103	2.7	39	100	13.4	113
96	TB	4034	Н	9.00	0.33	0.89	98	3.0	32	100	14.1	114
95	NFQ	8005	Н	4.10	0.35	0.60	59	1.4	20	20	8.5	28
96	NFQ	8005	Н	4.25	0.14	0.59	65	0.6	9	20	7.9	28
95	NFQ	8012	Η	5.93	0.16	0.65	130	1.0	21	75	3.4	78
96	NFQ	8012	Н	5.18	0.14	0.80	100	0.7	14	75	4.4	79
95	NFQ	8031	Н	5.40	0.38	0.98	50	2.1	19	50	14.6	65
96	NFQ	8031	Н	4.35	0.17	1.00	71	0.7	12	50	20.5	71

Appendix 2. Density estimates (per 1,000 m²) for each experimental large wood restoration pool in the three Cascade Mountain streams during July-August 1995 and 1996. IDTAG is pool identification number, CMP is large wood treatment, N_{CAL} are taxon, taxon length, and habitat corrected density estimates, N_{REM} are maximum likelihood removal density estimates, and N_{RECAP} are mark-recapture density estimates. Ref is reference and Med is medium treatment.

IDTAG	CMP	N _{CA}	_L Densit	ty/1,000m ²	N _{CAL} Total	N _{RE}	_{EM} Densit	y/1,000m ²	N _{REM} Total	N _{RECAP} Density/1,000m ²			N _{RECAP} Total
					Density				Density				Density (1.000 m^2)
			·		m^2				m^{2}				/1,000111
		Trout	Sculpin	Salamander		Trout	Sculpin	Salamander		Trout	Sculpin	Salamander	
1237	Ref	1,374	2,462	1,519	5,355	1,015	1,448	398	2,860				
1259	Ref	1,684	1,965	3,329	6,978	2,389	548	487	3,424				
1269	Ref	815	1,515	1,376	3,706	614	1,289	444	2,348	806	1,608	831	3,245
1017	Ref	355	328	228	911	231	311	105	647				
1052	Ref	489	1,018	1,309	2,816	307	624	248	1,179				
1113	Ref	756	340	537	1,633	545	235	162	942	828	283	313	1,424
4008	Ref	364	148	989	1,501	266	138	284	688				
4019	Ref	465	374	433	1,272	302	219	74	594				
4041	Ref	483	0	1,409	1,892	345	0	372	717	419	0	1,097	1,516
4008	Ref	235	112	1,103	1,450	168	152	332	652				
4019	Ref	265	458	1,500	2,223	185	235	518	938				
4041	Ref	1,158	0	1,601	2,759	178	0	217	395	234	0	547	781
8002	Ref	78	745	72	895	57	255	57	369				
8035	Ref	134	503	508	1,145	103	143	265	510	175	337	438	949
8003	Ref	84	304	89	477	96	171	96	362				
8035	Ref	257	182	1,672	2,111	317	212	670	1,199	448	189	1,043	1,679

Appendix 2 (continued)

AG CMP N _{CAL} Density/1,000m ²				N _{CAL} N _{REM} Density/1,000m ² Total Density /1,000 m ²					V_{REM} N_{RECAP} Density/1,000m ² [otal ensity 1,000 m ²				
	Trout	Sculpin	Salamander		Trout	Sculpin	Salamander		Trout	Sculpin	Salamander		
Low	918	2,032	1,154	4,104	544	1,705	313	2,563					
Low	2,364	888	1,658	4,910	1,222	374	959	2,555					
Low	1,082	4,025	1,495	6,602	713	1,017	477	2,207	856	2,686	946	4,487	
Low	564	1,289	519	2,372	359	415	167	941					
Low	724	509	643	1,876	441	200	235	876					
Low	1,457	785	1,109	3,351	965	413	314	1,692	1,205	480	431	2,116	
Low	313	115	346	774	133	364	204	700					
Low	468	214	194	876	332	177	129	638					
Low	954	0	1,104	2,058	675	0	461	1,136	761	0	1,083	1,843	
Low	343	569	2,649	3,561	96	240	277	613					
Low	218	182	483	883	172	213	142	527					
Low	272	0	2,639	2,911	197	0	682	879	333	0	1,160	1,493	
Low	64	1,340	241	1,645	43	493	526	1,062					
Low	442	353	713	1,508	379	121	338	837	472	201	569	1,242	
Low	63	274	470	807	46	311	376	733					
Low	96	319	835	1,250	78	134	202	414	124	139	309	572	
	CMP Low Low Low Low Low Low Low Low Low Low	CMP Nc./ Low 918 Low 2,364 Low 1,082 Low 1,082 Low 564 Low 724 Low 1,457 Low 313 Low 468 Low 954 Low 343 Low 218 Low 64 Low 64 Low 63 Low 63	CMPNCAL DensitLow9182,032Low2,364888Low1,0824,025Low1,0824,025Low5641,289Low724509Low1,457785Low313115Low468214Low9540Low343569Low218182Low641,340Low64253Low63274Low96319	$\begin{array}{c ccccccccccccccccccccccccccccccccccc$	$\begin{array}{c ccccccccccccccccccccccccccccccccccc$	$\begin{array}{c c c c c c c c c c c c c c c c c c c $	CMP N _{CAL} Density/1,000m ² N _{CAL} Total Total Density /1,000 m ² N _{REM} Densit Total Density /1,000 m ² Low 918 2,032 1,154 4,104 544 1,705 Low 2,364 888 1,658 4,910 1,222 374 Low 1,082 4,025 1,495 6,602 713 1,017 Low 564 1,289 519 2,372 359 415 Low 724 509 643 1,876 441 200 Low 313 115 346 774 133 364 Low 313 115 346 774 133 364 Low 468 214 194 876 322 177 Low 954 0 1,104 2,058 675 0 Low 343 569 2,649 3,561 96 240 Low 218 182 483 883 172 213 <td>CMP N_{CAL} Density/1,000m² N_{CAL} Total Density /1,000 m² N_{REM} Density/1,000m² Trout Sculpin Salamander Trout Sculpin Salamander Trout Sculpin Salamander Low 918 2,032 1,154 4,104 544 1,705 313 Low 2,364 888 1,658 4,910 1,222 374 959 Low 1,082 4,025 1,495 6,602 713 1,017 477 Low 564 1,289 519 2,372 359 415 167 Low 724 509 643 1,876 441 200 235 Low 1,457 785 1,109 3,351 965 413 314 Low 313 115 346 774 133 364 204 Low 343 569 2,649 3,561 96 240 277 Low 218 182 483 883 172 213 142</td> <td>CMP N_{CAL} Density/1,000m² N_{CAL} Total Density/1,000 m² N_{REM} Density/1,000m² Total Density/1,000 m² N_{REM} Total Total Density/1,000 m² Trout Sculpin Salamander Trout Sculpin Salamander Trout Sculpin Salamander Sculpin Salamander Low 918 2,032 1,154 4,104 544 1,705 313 2,563 Low 2,364 888 1,658 4,910 1,222 374 959 2,555 Low 1,082 4,025 1,495 6,602 713 1,017 477 2,207 Low 564 1,289 519 2,372 359 415 167 941 Low 724 509 643 1,876 441 200 235 876 Low 1,457 785 1,109 3,351 965 413 314 1,692 Low 343 569 2,649 3,561 96 240 277 613 Low 343 569 2,649 <t< td=""><td>CMP N_{CAL} Density/1,000m² N_{CAL} Total Density/1,000 m² N_{REM} Total Density/1,000 m² N_{REM} Total Density/1,000 m² N</td><td>CMP N_{CAL} Density/1,000m² N_{REM} Total Total Density/1,000 m² N_{REM} Density/1,000m² Total Density N_{REM} Total Total Density N_{REM} Total Total Density N_{REM} Density/1,000m² N_{REM} Total Total Density N_{REM} Density/1,000m² N_{REM} Total Total N_{REM} Density/1,000m² Low 2,364 888 1,658 4,910 1,222 374 959 2,555 2,666 Low 1,457 785 1,109 3,351 965 413 314 1,692 1,205 480 <t< td=""><td>$\begin{array}{cccccccccccccccccccccccccccccccccccc$</td></t<></td></t<></td>	CMP N _{CAL} Density/1,000m ² N _{CAL} Total Density /1,000 m ² N _{REM} Density/1,000m ² Trout Sculpin Salamander Trout Sculpin Salamander Trout Sculpin Salamander Low 918 2,032 1,154 4,104 544 1,705 313 Low 2,364 888 1,658 4,910 1,222 374 959 Low 1,082 4,025 1,495 6,602 713 1,017 477 Low 564 1,289 519 2,372 359 415 167 Low 724 509 643 1,876 441 200 235 Low 1,457 785 1,109 3,351 965 413 314 Low 313 115 346 774 133 364 204 Low 343 569 2,649 3,561 96 240 277 Low 218 182 483 883 172 213 142	CMP N _{CAL} Density/1,000m ² N _{CAL} Total Density/1,000 m ² N _{REM} Density/1,000m ² Total Density/1,000 m ² N _{REM} Total Total Density/1,000 m ² Trout Sculpin Salamander Trout Sculpin Salamander Trout Sculpin Salamander Sculpin Salamander Low 918 2,032 1,154 4,104 544 1,705 313 2,563 Low 2,364 888 1,658 4,910 1,222 374 959 2,555 Low 1,082 4,025 1,495 6,602 713 1,017 477 2,207 Low 564 1,289 519 2,372 359 415 167 941 Low 724 509 643 1,876 441 200 235 876 Low 1,457 785 1,109 3,351 965 413 314 1,692 Low 343 569 2,649 3,561 96 240 277 613 Low 343 569 2,649 <t< td=""><td>CMP N_{CAL} Density/1,000m² N_{CAL} Total Density/1,000 m² N_{REM} Total Density/1,000 m² N_{REM} Total Density/1,000 m² N</td><td>CMP N_{CAL} Density/1,000m² N_{REM} Total Total Density/1,000 m² N_{REM} Density/1,000m² Total Density N_{REM} Total Total Density N_{REM} Total Total Density N_{REM} Density/1,000m² N_{REM} Total Total Density N_{REM} Density/1,000m² N_{REM} Total Total N_{REM} Density/1,000m² Low 2,364 888 1,658 4,910 1,222 374 959 2,555 2,666 Low 1,457 785 1,109 3,351 965 413 314 1,692 1,205 480 <t< td=""><td>$\begin{array}{cccccccccccccccccccccccccccccccccccc$</td></t<></td></t<>	CMP N _{CAL} Density/1,000m ² N _{CAL} Total Density/1,000 m ² N _{REM} Total Density/1,000 m ² N	CMP N _{CAL} Density/1,000m ² N _{REM} Total Total Density/1,000 m ² N _{REM} Density/1,000m ² Total Density N _{REM} Total Total Density N _{REM} Total Total Density N _{REM} Density/1,000m ² N _{REM} Total Total Density N _{REM} Density/1,000m ² N _{REM} Total Total N _{REM} Density/1,000m ² Low 2,364 888 1,658 4,910 1,222 374 959 2,555 2,666 Low 1,457 785 1,109 3,351 965 413 314 1,692 1,205 480 <t< td=""><td>$\begin{array}{cccccccccccccccccccccccccccccccccccc$</td></t<>	$ \begin{array}{cccccccccccccccccccccccccccccccccccc$	

Appendix 2 (continued)

IDTAG	CMP	N _{CA}	_L Densit	y/1,000m ²	N _{CAL} Total Density /1,000 m ²	N _{RI}	EM Densit	y/1,000m ²	N _{REM} Total Density /1,000 m ²	N _{REC}	N _{RECAP} Total Density/ 1,000m ²		
		Trout	Sculpin	Salamander		Trout	Sculpin	Salamander		Trout	Sculpin	Salamander	
1226	Med	1,333	11,492	834	13,659	742	2684	261	3687				
1257	Med	2,869	923	1,057	4,849	1,449	548	657	2,654				
1299	Med	1,311	833	992	3,136	848	436	367	1,651	1,104	797	727	2,628
1021	Med	707	984	746	2,437	400	332	230	962				
1061	Med	1,579	914	1,028	3,521	899	333	300	1,532				
1132	Med	502	76	384	962	731	133	243	1,107	1,283	313	370	1,967
3999	Med	671	328	858	1,857	384	247	283	914				
4021	Med	579	688	1,379	2,646	282	255	328	864				
4032	Med	565	0	194	759	423	0	81	504	495	0	360	856
3999	Med	468	671	886	2,025	231	533	328	1,092				
4021	Med	272	792	1,472	2,536	181	321	366	868				
4032	Med	270	0	670	940	138	0	245	384	202	0	382	584
8009	Med	158	729	645	1,532	123	227	255	605				
8027	Med	313	785	3,168	4,266	311	292	363	966	364	534	1,178	2,076
8009	Med	234	734	553	1,521	216	323	323	863				
8027	Med	86	637	2,630	3,353	62	268	252	582	109	450	543	1,102

Appendix 2 (continued)

IDTAG	CMP	N _C	AL Densit	y/1,000m ²	N _{CAL} Total	CAL N _{REM} Density/1,000m ²				N _{RECAP} Density/1,000m ²			N _{RECAP} Total
					Density /1,000				Density /1,000				Density/ 1,000m ²
		Trout	Sculpin	Salamander	m²	Trout	Sculpin	Salamander	m²	Trout	Soulnin	Salamandar	
1230	High	1 760	530	402	2 602	70 <i>1</i>	463	236	1 402	Hout	Scuipin	Salamanuci	
1250	High	2 310	1 467	1 029	4 806	1 302	685	230 567	1, -72				
1265	High	1 652	3 1 50	856	5 658	910	1 887	323	3 120	1 060	2 470	658	4 1 8 7
1028	High	1,786	2.305	572	4.663	622	566	219	1406	1,000	2,470	050	4,107
1080	High	1,400	821	702	2.923	670	244	255	1.169				
1085	High	893	319	444	1.656	657	254	295	1,207	825	399	433	1.657
3995	High	434	403	1,472	2,309	264	291	375	931			100	1,007
4011	High	502	727	959	2,188	233	538	294	1,066				
4034	High	589	0	1,387	1,976	391	0	531	922	575	0	907	1,482
3995	High	98	589	437	1,124	61	341	177	579				2
4011	High	189	463	1,334	1,986	90	262	282	634				
4034	High	674	0	1,285	1,959	323	0	815	1,139	457	0	527	983
8005	High	246	363	413	1,022	205	305	220	730				
8031	High	378	618	1,071	2,013	367	201	486	1,054	519	519	924	1,962
8005	High	191	659	796	1,646	156	201	251	608				
8031	High	127	441	512	1,080	101	129	88	318	183	225	211	620
Appendix 3 Vertebrate density estimates per 1,000 m² (mean, minimum, and maximum) for the catchability-based (N_{CAL}), multiple removal (N_{REM}) and mark-recapture (N_{RECAP}) population estimator methods in mark-recapture pools of the experimental large wood manipulation streams in the Cascade Mountains, Oregon during July – August 1995 and 1996.

		N _{CAL}	N _{REM}	N _{RECAP}
Reference	Mean	2,207	1,019	1,599
	Minimum	1,144	395	781
	Maximum	3,707	2,348	3,245
Low	Mean	2,947	1,194	1,959
	Minimum	1,250	414	572
	Maximum	6,602	2,207	4,487
Medium	Mean	2,236	866	1,536
	Minimum	759	384	584
	Maximum	4,266	1,651	2,628
High	Mean	2,399	1,293	1,815
	Minimum	1,080	318	620
	Maximum	5,659	3,120	4,187