AN ABSTRACT OF THE THESIS OF

Patrick J. Connolly for the degree of Doctor of Philosophy in Fisheries Science presented on January 23, 1996. Title: Resident Cutthroat Trout in the Central Coast Range of Oregon: Logging Effects, Habitat Associations, and Sampling Protocols.

Abstract Approved: ______________________

James D. Hall

Populations of coastal cutthroat trout, *Oncorhynchus clarki clarki*, were sampled in 16 headwater streams from logged (20-30 and 40-60 years ago) and unlogged (stand age 125-150 years) basins. Basins logged 20-30 years ago supported the widest range of mean biomass of age 1+ or older cutthroat trout (g/m^2) and the widest range in frequency of large woody debris (number of pieces/100 m) and pools (number/100 m), including the lowest and highest levels of these variables encountered in the study.

Stream gradient and geology of the substrate were important stream characteristics that influenced the age structure of cutthroat trout in pools. Biomass of young-of-year (YOY) cutthroat trout (g/m^2) was directly related to stream gradient and inversely related to the biomass (g/pool) of age 1+ or older cutthroat trout, especially in pools of sandstone streams. High use of pools without adult cutthroat trout by YOY suggests that when older cutthroat trout abandon pools, either by movement or mortality, important rearing opportunities are created for YOY.

I used the population size and variance estimators of Seber and LeCren (1967) and Zippin (1956) to develop tables for use in the field that list acceptable ranges of observed catch from two and three removal passes. The ranges of acceptable values were based on an estimate for coefficient of variation (CV) and, for data from three passes, the values were based on results of a chi-square test for the assumption of equal catchability. Because the full multi-termed version of Zippin's (1956) estimator of variance (i.e., with Stirling's second-order approximation) was found to be more conservative than the use of his large-sample estimator when population size was less than 200, I used the full multi-

termed version to derive estimates of CV. Because the distributions of population estimates derived from removal data are typically not normal, I discuss the use of two other confidence intervals that do not depend on the assumption of normality, those based on the log-normal distribution or a profile likelihood ratio.

Resident Cutthroat Trout in the Central Coast Range of Oregon: Logging Effects, Habitat Associations, and Sampling Protocols

by

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

Patrick J. Connolly, Author

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Resident Cutthroat Trout in the Central Coast Range of Oregon: Logging Effects, Habitat Associations, and Sampling Protocols

CHAPTER 1

Introduction

Overview of Study

Coastal cutthroat trout, *Oncorhynchus clarki clarki*, are a common part of the fish fauna throughout their distribution: Prince William Sound, Alaska to Eel River, California (Behnke 1992). This species has been relatively neglected compared with the more valued and more studied salmonid species of Pacific salmon, *O.* spp., and steelhead, *O. mykiss*, that largely overlap the distribution of coastal cutthroat trout (Giger 1972, Trotter 1987). Because the coastal cutthroat trout has historically been such a persistent part of the fish fauna of Oregon and the Pacific Northwest and because recent declines in some populations have been noted (Trotter 1989, Johnson et al. 1994), I felt that work to understand the ecology of this species was an important endeavor.

In Chapter 2, I present findings from my investigation of the status of cutthroat trout populations in basins that were logged 20-60 years ago and in basins that had not been logged. For this investigation, I searched for streams where populations existed above barriers. The cutthroat trout was the only salmonid present and often the only fish species present in stream reaches above barriers. The only other fish species present was the reticulate sculpin, *Cottus perplexus*, which was present in about half of the streams I selected for study.

I considered the small streams as experimental units having the advantage of lacking some of the key unknowns that researchers must account for when working with larger systems. Because small basins are located near ridge tops, effects from logging in small basins are not so readily masked by cumulative affects that mount downstream (Coats and Miller 1981, Ryan and Grant 1991). By restricting my investigation to the portions of small streams above anadromous and potadromous fish barriers, the need to account for some portion of the cutthroat trout's life history outside the basin was eliminated (Pella and Myren 1974, Hall et al. 1987). The need to account for the effect of interactions with other salmonid species (Glova 1984, Mitchell 1988) was eliminated by conducting my study on streams that had only one species of salmonid.

While I was sampling to assess the density of cutthroat trout in streams, I observed that pools with adult cutthroat trout often lacked young-of-year cutthroat trout, and pools without adults often had numerous young-of-year. These observations served as the foundation for the development of hypotheses about the presence and effects of age-class interactions that I address in Chapter 3.

My earliest attempts to assess the number of cutthroat trout in habitat units suggested to me how important each fish caught was to the accuracy and precision of the estimate. If adult cutthroat trout were present in a unit, they would often number only one or two. Any effort that fell short of capturing all of these larger fish strongly influenced the final estimate of biomass in a unit. In response to this situation, I used a pass-removal methodology that required continuation of sampling until no age 1+ or older cutthroat trout were caught on the last pass-removal effort. To investigate the consequences of conducting fewer pass-removal efforts on the accuracy and precision of estimates when fish populations were small, I examined aspects of the commonly used pass-removal estimators of Seber and LeCren (1967) and Zippin (1956). I present the findings of this investigation in Chapter 4.

In the final chapter, Chapter 5, I record the major conclusions from chapters 2-4, and some of the management implications for resident populations of cutthroat trout. Results from my studies highlight some of the relationships between population levels and forest management activities.

Description of the Life History of Cutthroat Trout

In this section I present a brief overview of what we know about cutthroat trout that live in small streams of the Pacific Northwest. While the following account is not exhaustive of the literature available, my intention is to provide the reader with a general background of pertinent aspects of the life history of coastal cutthroat trout.

Trotter (1989) states that peak spawning in Oregon waters occurs in February. In the Alsea system of the central Coast Range of Oregon, cutthroat trout generally spawn during December-February, but spawning may extend into April (Moring and Lantz 1975). In an Oregon Cascade stream, cutthroat trout were found to spawn in February-April (Moore and Gregory 1988). Spawning was observed to take place as late as June in a headwater stream in the Olympic Peninsula (Mitchell 1988). After emergence, fry remain close to spawning areas (Moore and Gregory 1988).

As cutthroat trout grow, the habitat they utilize changes (Moore and Gregory 1988, Trotter 1989). Age 0+ cutthroat trout are often associated with the lateral margins of a stream in slow water (Bustard and Narver 1975, Moore and Gregory 1988). Age 1+ or older cutthroat trout are largely associated with pools (Bisson et al. 1988, House 1995). Bisson et al. (1982) observed that cutthroat trout of all ages generally preferred cover provided by woody debris in both pool and riffle habitats. Adult resident cutthroat trout typically have a highly restricted home range, and will often reside in the same pool from year to year (Heggenes et al. 1991a).

Stream systems with anadromous cutthroat trout populations often have resident populations as well (Johnston 1982). Michael's (1983) attempt to determine the contribution to the sea-run population of resident cutthroat trout produced above natural barriers fell short of providing conclusive evidence. In general, the degree and significance of gene flow between sympatric populations of anadromous and resident cutthroat trout are unknown (Johnston 1982).

Below barriers, cutthroat trout are often found with coho salmon, *O. kisutch*, and steelhead. Young-of-year cutthroat trout have typically been found to be the most negatively affected in the interactions with young-of-year coho salmon or steelhead. The social dominance of juvenile coho is related to their earlier emergence and larger size relative to cutthroat trout of the same brood year (Glova 1984). Evidence suggests that habitat partitioning of available food and space occurs between cutthroat trout and coho salmon (Lowry 1966, Bisson et al. 1982, Glova 1984). Glova (1987) reported that juvenile cutthroat trout preferred pools but that they were displaced to riffle areas by juvenile coho salmon. He further found that negative interactions were less intense in streams with higher gradients combined with ample habitat of higher water velocities. Bisson et al. (1982) found that age 1+ and 2+ cutthroat trout preferred backwater pools but avoided these areas when coho were present. Bustard and Narver (1975) investigated winter habitat use and found juvenile cutthroat trout to utilize both bank and rubble cover equally whereas bank cover was more important than rubble cover to juvenile coho salmon.

Microhabitats of cutthroat trout and steelhead were regarded as similar by Hartman and Gill (1968). Mitchell (1988) reported that the highest potential for interaction between cutthroat trout and steelhead occurs between smaller fish (<10 cm) and decreases as individuals grow and seek differential habitats. He concluded that a broad spatial segregation is maintained between the two species by differences in migratory behavior and spawning preferences.

In streams above barrier falls, coastal cutthroat trout are often the only fish species present (Glova 1987, Heggenes et al. 1991b). The presence of coastal cutthroat trout above barrier falls has been attributed to the older ancestral age and time of invasion of cutthroat trout versus other native species (Mitchell 1988). Northcote (1992) argues that these isolated populations of cutthroat trout warrant our attention and protection because they represent important sources of genetic diversity.

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CHAPTER 2

Status of Resident Cutthroat Trout in Basins Logged 20-60 Years Ago in the Central Coast Range of Oregon

Patrick J. Connolly

Abstract

Populations of cutthroat trout, *Oncorhynchus clarki clarki*, were sampled in 16 headwater streams from logged basins (20-30 and 40-60 years ago) and from basins that had not been logged (125-150 year-old, post-wildfire stands). The cutthroat trout was the only fish species in 9 of the 16 streams and was found with the reticulate sculpin, *Cottus perplexus*, in the remaining streams. Basins logged 20-30 years ago supported the widest range of mean biomass of age 1+ or older cutthroat trout (g/m^2) and the widest range in frequency of LWD (number of pieces/100 m) and pools (number/100 m), including the lowest and highest levels of these variables encountered in the study.

Three streams within the group of basins logged 20-30 years ago were cleaned of LWD at the time of logging. Within a geologic stream type (basalt or sandstone), the level of biomass of age 1+ or older cutthroat trout was consistently higher in streams that were not cleaned of LWD than in streams that were cleaned of LWD. These three streams had lower levels of LWD and lower number of pools than the other streams within this class of basins.

The one variable that best explained the variation of biomass of age 1+ or older cutthroat trout among all streams was LWD. Pools had a higher biomass of these trout than any other habitat type, especially in sandstone streams. Lower levels of mean biomass were found in basalt streams that had sculpin than in basalt streams that did not have sculpin. Populations of reticulate sculpin were absent from sandstone streams with gradients higher than 4%, but they were present in some basalt streams with gradients as high as 7%.

Although all 16 streams were highly shaded by mostly closed canopies of overstory trees during the summer, the five streams with shading by conifers >35% had low biomass of age 1+ or older cutthroat trout (<1.2 g/m^2). Because some streams that were highly shaded with deciduous trees had high levels of biomass of these trout ($\geq$1.2 g/m^2), I speculate that the availability of light before leaf-out of a deciduous canopy has a positive influence on populations of age 1+ or older cutthroat trout.

Introduction

Coastal cutthroat trout, *Oncorhynchus clarki clarki*, has historically been a persistent part of the fish fauna of western Oregon and the Pacific Northwest. This study was undertaken largely in response to the recent declines that have been noted for some coastal cutthroat trout populations (Trotter 1989, Johnson et al. 1994). Both decreases and increases have been noted for abundance of salmonid populations after forests were clearcut without prescription for streamside leave areas (Hicks et al. 1991a). In the central Coast Range of Oregon where the present study was undertaken, studies of basins that were clearcut up to 25 years ago indicate that populations of adult cutthroat trout have been and continue to be negatively affected by logging (Moring and Lantz 1975, Hall et al. 1987, Schwartz 1991). Before this study, little was known about the status of cutthroat trout populations in basins of the central Coast Range of Oregon that were logged more than 25 years ago.

Resident cutthroat trout are often the only salmonid species, and sometimes the only fish species, occupying first- and second-order streams in the central Oregon Coast Range. The reticulate sculpin, *Cottus perplexus*, is a common non-salmonid species in headwater streams of the central Coast Range of Oregon and can account for a significant part of the total biomass of fish in these streams (Krohn 1968). Interactions with anadromous salmonids below barriers have often been found to be negative for coastal cutthroat trout, affecting their distribution (Hartman and Gill 1968, Hartman and Brown 1987), age structure (Bisson and Sedell 1984, Glova 1987), and habitat use (Johnston 1982; Glova 1984, 1987; Bisson et al. 1988). Because anadromous salmonid populations may be affected by downstream and ocean conditions, studies of streams with resident cutthroat trout as the only salmonid allow more direct assessment of the influence of habitat quality and role of disturbance on abundance of cutthroat trout populations.

The objective of this study was to characterize the status of populations of age 1+ or older resident cutthroat trout in basins that had not been logged and in basins where logging occurred 20-60 years ago. Basins that were logged 20 or more years ago were logged before the adoption of Oregon's Forest Practice Act in 1972 and were generally subjected to more aggressive logging practices than those allowed today (Bisson et al. 1992). Much of the logging that will occur in western Oregon in the near future will be within these once-logged systems. Reeves et al. (1995) suggested that the current practices of harvesting forests at intervals of 40-80 years may not allow habitat conditions to recover sufficiently from a previous disturbance such as logging. To predict a basin's current trajectory of change in its productivity (decreasing, steady, or increasing) and to assess the stability of a basin's populations of cutthroat trout, it is necessary to assess if influences from the first logging event remain.

Until recently, prescriptions for stream and streamside treatments were developed from experience with harvesting previously unharvested stands (Hall et al. 1987). The most recent forest practice rules for western Oregon were developed in recognition of second-growth forests as a unique portion of the forested landscape (Oregon Department of Forestry 1994). Because of the increasing prevalence of previously logged forests in the Coast Range and because of the lack of studies on fish within basins of older second-growth forests, I developed a study that specifically addressed use of these once-logged second-growth systems by resident cutthroat trout.

Study Area

All 16 streams that I chose for sampling were first- and second-order streams that drained the west side of the Coast Range. Streams ranged from tributaries of the Siletz River basin in the north to the Big Creek basin in the south (Figure 2.1). Watersheds ranged from 0.5 to 3.5 km^2, and stream gradients ranged from 2 to 8% (Table 2.1). Because many of the streams were unnamed, I assigned a two-letter code to them (Appendix Table 2.1). Seven streams had substrates that were exclusively sandstone and the remaining nine streams had substrates that were all, or part (>40%), basalt.

Seven of the 16 basins had been logged 20-30 years ago, five had been logged 40-60 years ago, and four had been logged very little (<20%) or not at all. Hillslopes of the logged basins varied from replanted conifers to unplanted mixes of conifer and deciduous

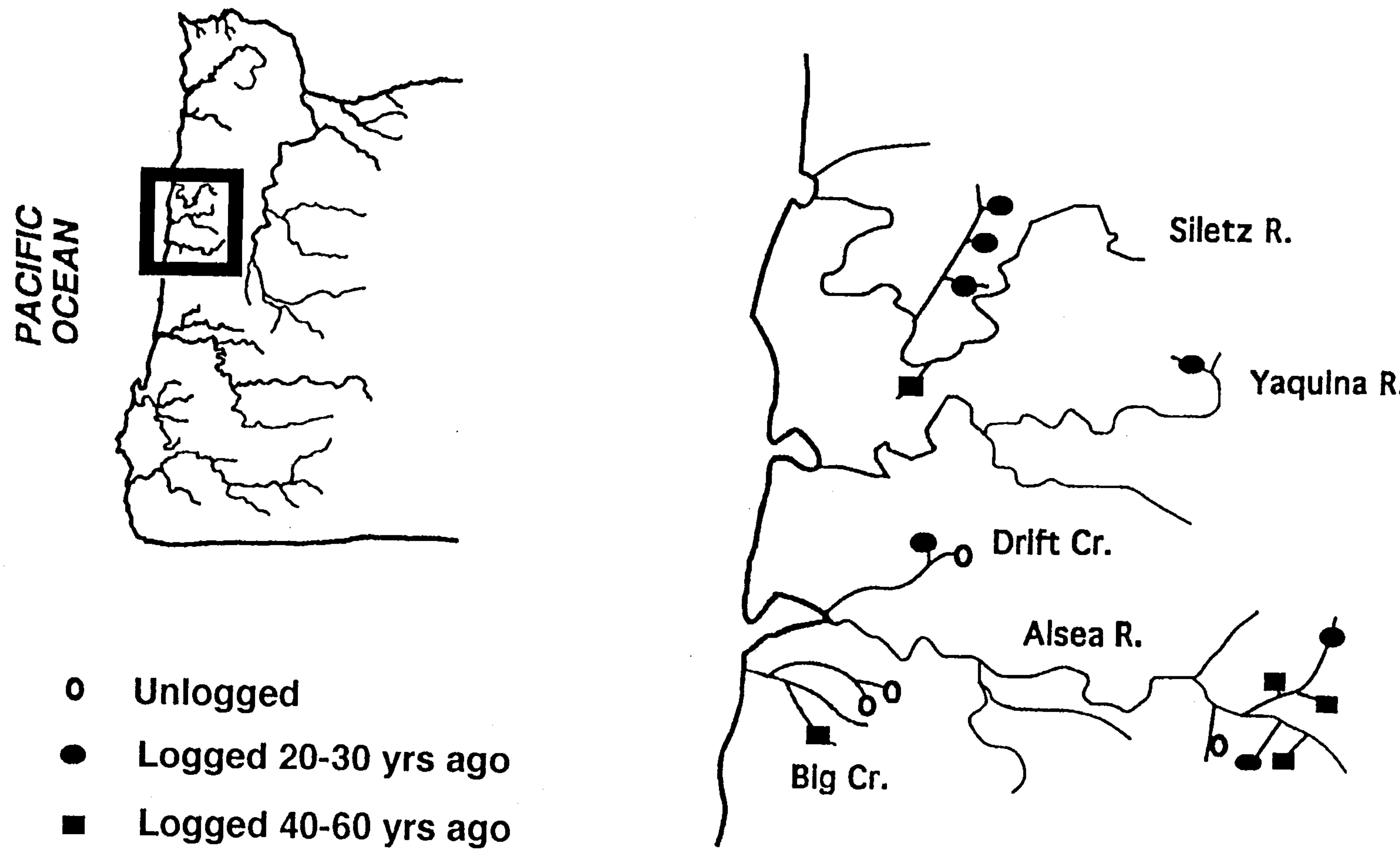


Figure 2.1. Location of sites sampled during 1991-1993.

Table 2.1. Forest management and geomorphic characteristics of 16 streams sampled in 1991-1993.

Forest management and stream code[a]	Drainage area (km^2)	Stream gradient (%)	Geology	Length of study reach (m)	Wetted area of study reach (m^2)	Pools (no./100 m)
Unlogged						
GR	0.89	4.4	sandstone	209.5	205.6	3.8
DE	1.43	5.5	mixed[c]	246.5	511.1	2.8
DW	1.15	7.1	mixed	233.2	455.6	2.6
TB	3.39	3.1	mixed	434.4	979.5	4.4
Logged						
20-30 years						
CD[b]	1.43	3.7	sandstone	491.2	754.0	2.2
WL[b]	3.47	3.2	mixed	476.0	1132.3	2.3
EE[b]	1.29	5.5	basalt	195.6	344.8	1.5
NB	0.53	4.9	sandstone	197.6	197.9	10.0
PM	1.52	3.1	sandstone	213.3	347.1	4.7
ST	0.87	5.1	basalt	144.4	221.3	7.6
LS	0.89	5.7	mixed	258.8	594.9	5.0
40-60 years						
PE	1.23	2.6	sandstone	580.7	654.1	5.0
SF	1.33	5.2	mixed	343.7	554.2	2.5
CM	2.02	7.8	mixed	293.6	779.2	4.9
LT	1.38	2.6	sandstone	255.2	452.6	7.8
PW	1.92	2.2	sandstone	471.6	652.9	6.1

[a] See Appendix Table 2.1 for location and further identification of streams.
[b] Stream was cleaned of large woody debris at time of logging.
[c] Mixed = basalt and sandstone, with at least 40% basalt substrate.

tree species. Trees within riparian areas of the logged basins were mostly deciduous, primarily red alder (*Alnus rubra*), with varying amounts of conifers. Forest stands that had not been logged were representative of the fire history that dominates the central coast region of Oregon (Juday 1977). Hillslopes of the basins that had not been logged were primarily post-fire regenerated conifer stands that were 125-150 years old with occasional older, remnant trees present. Trees within riparian areas of these unlogged basins were mostly conifer species with varying amounts of deciduous species.

I used aerial photos to identify basins that were at least 80% uncut (which I termed "unlogged") and to identify logged basins that were at least 80% cut within a five-year period. Basins were surveyed by vehicle and on foot to ensure that any cut areas in the largely unlogged basins, and any uncut areas in logged basins, were well away from the stream. No streams in the logged basins were left with riparian buffers at the time of harvest.

All streams were located above barrier waterfalls to ensure that no anadromous salmonids had access, thus all cutthroat trout were resident fish. The downstream start for sampling was located at the first habitat unit above the barrier or located further upstream depending on the consistency of forest management or stream flow. The upstream limit for sampling was determined by the upstream distribution of cutthroat trout or by abrupt increase in stream gradient or decrease in stream flow.

Methods

Habitat Surveys

I conducted habitat surveys on streams during the summer low-flow period of late June through September during 1991-1993. Following Bisson et al. (1982), I classified each habitat unit into basic habitat types (i.e., pools, glides, cascades, riffles, and steps). In addition, I classified habitat types as "pockets" when they had pool characteristics with maximum depths <20 cm . I measured each unit: length and width for all habitat units and maximum and mean depth for pools.

Surveys included collection of data on large woody debris (LWD), canopy shade, and substrate size. I defined LWD as downed wood with length >1 m, with diameter >30 cm, and with at least part of the piece within the active channel of the stream and within 2 m above the wetted surface. I identified each piece of LWD as either conifer or non-conifer.

To assess stream shading, I observed the forest canopy within a cone projected upward from the center of the habitat unit defined by a 20° angle at its base. Total amount of shading from conifer and deciduous trees within the area defined by this cone was subjectively determined. To determine the percentage of the total stream that was shaded, I calculated a weighted average shade over all habitat units, with length of the habitat unit as the weighting factor.

I assessed the geology of a stream by visually estimating the percentages of stream substrates that were sandstone and basalt throughout the study reach of the stream. I evaluated size of substrate within the wetted portion of each habitat unit, and assessed the percentage of mineral substrate within the following size classes: bedrock, boulder (>300 mm), cobble (101-300 mm), gravel (2-100 mm), sand and silt (<2 mm). A sixth class, organic debris, was used to describe the percentage of stream bottom covered by sticks, leaves, and other small organic material.

I used an Abney level and sighting pole to determine the gradient of each stream. An upstream reading and a downstream reading were taken from each placement of the sighting pole throughout the length of the stream reach. A calibration reading was performed at the beginning and end of each reach. If these calibration readings were not within 0.25% of each other, the level was adjusted and the reach was re-surveyed.

Fish Sampling

Stream habitat types served as strata for sampling of age 1+ or older cutthroat trout. Fish sampling was conducted within 2 to 5 d after a habitat survey. The general plan that I followed was to sample 50-100% of pools and at least three units of the other habitat types except steps. Because steps were characterized by steep gradients and shallow depths, the cutthroat trout population was assumed to be zero in these units. When habitat types were represented by three or fewer units, I sampled all of the units for fish. When habitat types were represented by more than three units, I used simple random (in 1991) or systematic (in 1992 and 1993) sampling techniques (Schaeffer et al. 1990) to determine which habitat units within the habitat types to sample for fish.

To census cutthroat trout within habitat units, I used a backpack electrofisher and the pass-removal method (Zippin 1956, Bohlin et al. 1989). When needed, I placed block nets at one or both ends of a habitat unit to prevent fish from escaping or entering the unit once sampling began. Removal passes were continued until no age 1+ or older cutthroat trout was caught on the last pass. At least two removal passes were conducted on each habitat unit selected for sampling. Fork length was recorded for each cutthroat trout captured. For the few cases when a weight was not obtained, a site-specific, weight-length relationship (Ricker 1975, equation 9.2) was developed and a weight was assigned to the fish based on its length.

Because age 1+ or older cutthroat trout were not caught on the last removal pass, I considered the total number of age 1+ or older cutthroat trout caught in a unit as the total population in that unit. Sampling variance for the population estimate was assumed to be zero at the habitat unit level. I derived estimates of the total population in a stream, and the associated variances, by using formulas for stratified random sampling following Schaeffer et al. (1990, equations 5.4 and 5.5). The number of cutthroat per linear meter was derived by dividing the estimated total population size by the total length of the stream reach. The biomass per unit area (g/m^2) was derived by dividing the estimated total biomass by the total surface area of the reach.

During the sampling for cutthroat trout, I also watched for the presence of sculpin. If no sculpin were seen while sampling for cutthroat trout, I considered sculpin to be absent from the reach.

Because the study encompassed three years for collection of data, I repeated sampling for three of the streams to gauge the annual variation in population size. Two of these streams, CM and SF, were sampled during each of the three years, and one stream, NB, was sampled only during 1991 and 1993. Extremely low water in NB during summer 1992 caused 11% of the stream bed to be dry by mid-August, and much of the surface water to be stagnant. To avoid stress and injury to the fish, I did not sample NB in 1992. I calculated the mean values across years for measures of the fish population and size of habitat types for the streams sampled during more than one year, and I used these mean values as data in subsequent analyses.

Analyses and Statistical Tests

Estimates of biomass of age 1+ or older cutthroat trout were compared among years (1991-93) by ANOVA with blocking for the variability among the three streams that were sampled during more than one year. When a year and stream effect were included in a two-way ANOVA and a year effect in a one-way ANOVA, the year effect was not consistent enough to significantly explain the variation in biomass of cutthroat trout ($p=0.821$ and $p=0.921$, respectively). Because within-stream differences in biomass were small relative to the among-stream differences (Figure 2.2, Appendix Figure 2.1), I concluded that year-to-year variability within the 16 streams was unlikely to be a confounding factor in other analyses.

I conducted a test for homogeneity of variance (Levene's Test, see Snedecor and Cochran 1980) and one-way analysis of variance (ANOVA) tests to compare biological and physical characteristics among basins. Three classes of basins were defined based on their differential forest management: 1) unlogged (n=4), 2) logged 20-30 years ago (n=7), and 3) logged 40-60 years ago (n=5). Following the ANOVA tests, I ran multiple

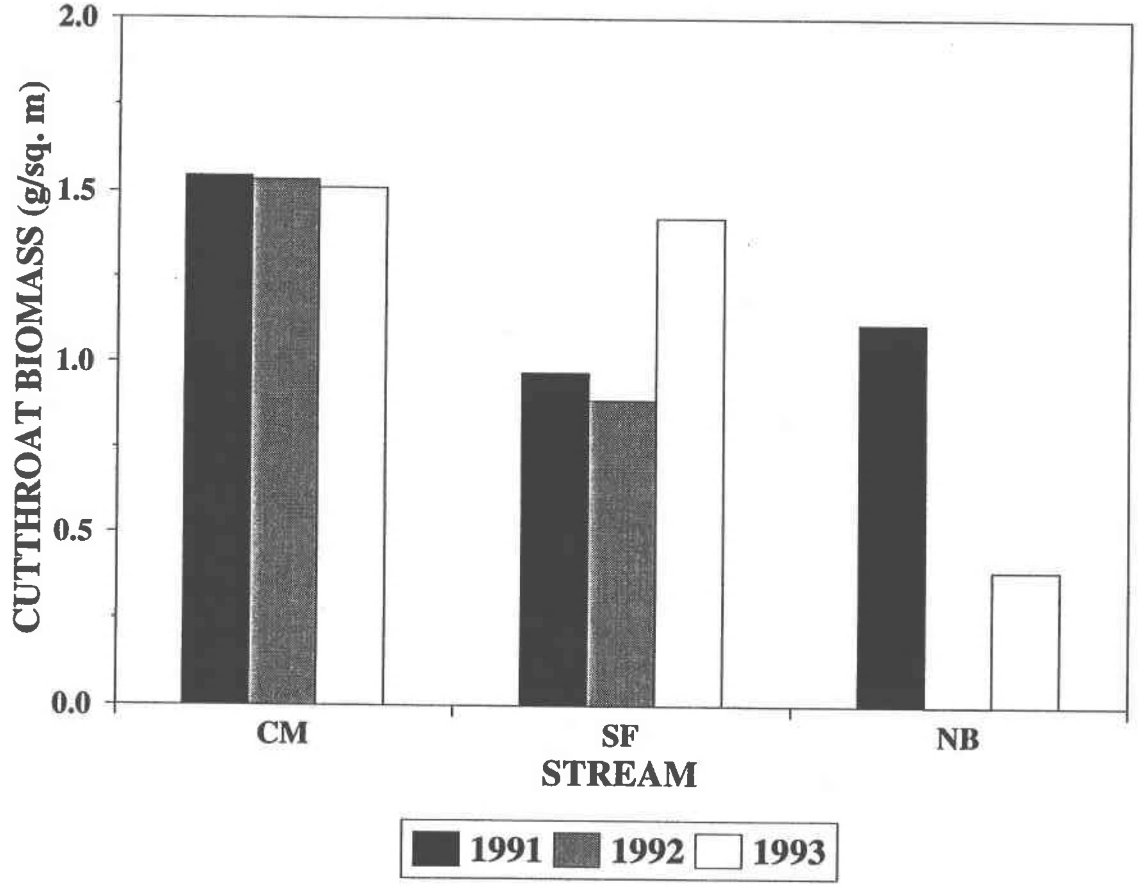


Figure 2.2. Annual variation in biomass of age 1+ or older cutthroat trout in three streams of the central Coast Range of Oregon, 1991-1993. NB was not sampled in 1992. CM=Coleman Creek, SF=South Fork, and NB=Needle Branch.

comparison tests, Tukey's *W* studentized range test (Ott 1977), as calculated by the GLM procedure in version 6.03 of SAS (see SAS Institute Incorporated 1988).

I used STATGRAPHICS (version 6.0) to conduct stepwise (forward) linear regression analysis to find the best one-, two-, and three-variable model to explain the variation found in the biomass (g/m^2) of cutthroat trout among the 16 streams (Neter et al. 1989, see Statistical Graphics Corporation 1989). Variables used in the analyses included: LWD (number/100 m), total canopy shading (%), conifer shading (%), presence or absence of sculpin, stream gradient (%), basin size (km^2), frequency of pools (number/100 m), total volume of pools (m^3), total area of pools (m^2), frequency of boulders (number/100 m), percentage of substrate coverage by size (boulder, cobble, and sand or smaller), and geology. Geology was considered to be of two types: basalt (with or without sandstone) and sandstone. I constructed a series of scatter plots to visually assess the relationships between important dependent and independent variables in the models (Appendix Figure 2.2).

To test the assumption of normality for ANOVA and regression analyses, I used the UNIVARIATE procedure within version 6.03 of SAS (see SAS Institute Incorporated 1982) to produce residual and normal probability plots and to run a test for adherence to the assumption of normality, Shapiro-Wilk's W. When needed, data transformations were conducted in attempts to improve the distribution of residuals. A log transformation for the variables of biomass of cutthroat trout (g/m^2) and of frequency of LWD (number of pieces/100 m) was found to consistently improve normality.

I used nonparametric, Mann-Whitney *U* tests (Hollander and Wolfe 1973), as calculated by the NPARWAY1 procedure in version 6.03 of SAS (see SAS Institute Incorporated 1988), to test for differences of characteristics between basalt and sandstone streams. The characteristics available for comparing these geologic types of streams included the variables listed above for regression analysis as well as the percentage of stream area within habitat types.

I used Vanderploeg and Scavia's (1979) electivity index, E*, to evaluate the distribution of cutthroat trout among habitat types. Potential values of this index range between -1 and 1. I interpreted values of zero or close to zero to represent a distribution of number of cutthroat trout that was proportional with the availability of the habitat type. I interpreted strongly negative values to represent low use of a habitat type and strongly positive values to represent high use of a habitat type.

Results

Effects of Stand Age and Forest Management

Basins logged 20-30 years ago supported the widest range of mean biomass of age 1+ or older cutthroat trout (g/m^2) and the widest range in the frequency of LWD (number of pieces/100 m) and pools (number/100 m), including the lowest and highest levels of these three variables encountered in the study (Figure 2.3). Results of Levene's Tests indicated that the variance of these three variables was not homogeneous among the three classes of basins: unlogged, logged 20-30 years ago, and logged 40-60 years ago ($p<0.025$, Tables 2.2 and 2.3).

In summer, all streams were highly shaded, but the amount of stream shaded differed among the three classes of basins. Basins that had not been logged had streams with less shading by deciduous trees than basins logged 20-30 or 40-60 years ago (Tukey's, $p<0.05$; Table 2.3). Basins logged 20-30 years ago had the lowest mean percentage of shading by conifers, but the only class of basins with significantly higher conifer shading was the unlogged group of basins (Tukey's, $p<0.05$).

The three streams with the highest biomass (>2.8 g/m^2) had levels of LWD >38 pieces/100 m and levels of shading by conifers <35% (Table 2.2). When I evenly divided the total number of streams based on levels of LWD and biomass of cutthroat trout, and then classified the streams based on level of conifer shading, all eight streams that had estimated biomass over 1.2 g/m^2 had less than 35% shading by conifers (Table 2.4). Only three of the eleven streams with less than 35% conifer shading had an estimated

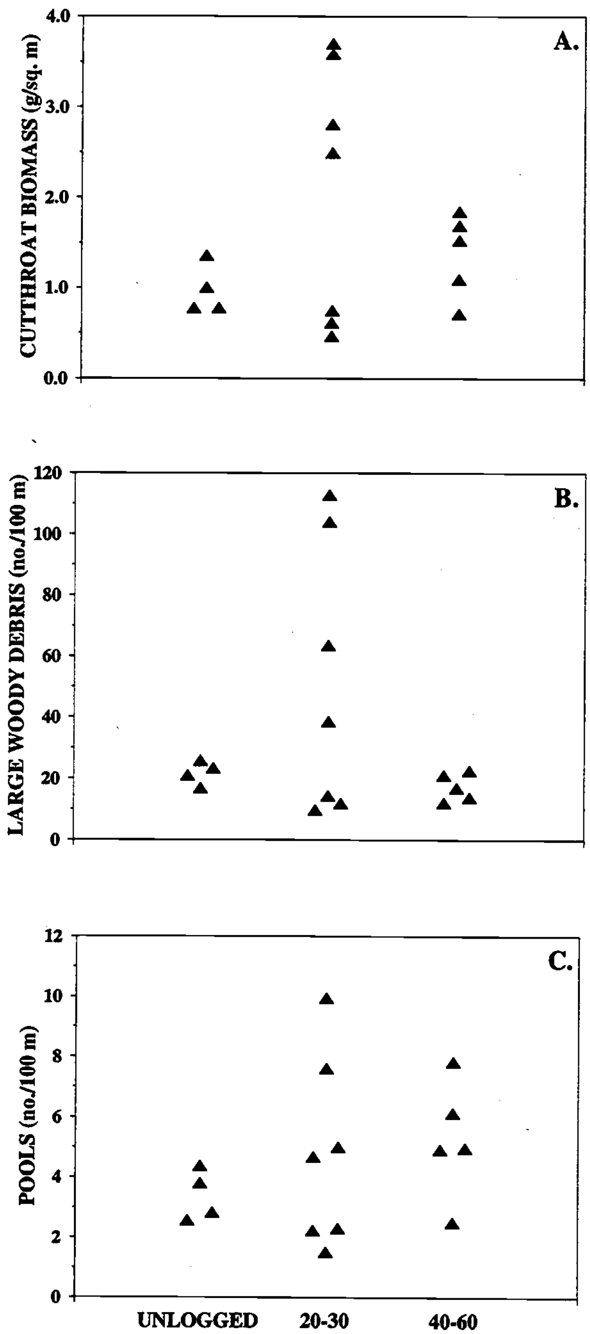


Figure 2.3. Characteristics of 16 coastal streams of the central Coast Range of Oregon classified by type of forest management activities within their basins, 1991-93. Graphs depict: A) biomass of age 1+ or older cutthroat trout, B) large woody debris (length >1 m, diameter >30 cm), and C) number of pools. The x-axis labels of 20-30 and 40-60 indicate years since logged.

Table 2.2. Biological and physical features of 16 streams sampled in 1991-1993.

Forest management and stream code	Age ≥1+ cutthroat biomass g/m²	SE	Age ≥1+ cutthroat density no./100m	SE	Mean weight of cutthroat (g)	Number LWD[a] per 100 m (% conifer)	Percentage shading by conifers (total)	Reticulate sculpin
Unlogged								
GR	0.78	0.04	7.2	0.6	10.6	25.8 (80)	36 (66)	absent
DE	0.78	0.31	12.0	5.0	13.1	23.5 (100)	79 (79)	present
DW	1.01	0.35	13.5	4.4	14.5	21.0 (100)	74 (74)	present
TB	1.36	0.31	17.1	3.4	17.9	16.8 (67)	31 (44)	absent
Logged								
20-30 years								
CD[b]	0.48	0.08	5.8	1.0	12.7	12.0 (81)	0 (78)	present
WL[b]	0.60	0.13	10.0	1.8	14.2	9.9 (98)	8 (92)	present
EE[b]	2.50	0.63	46.7	11.2	9.4	14.6 (100)	15 (93)	absent
NB[c]	0.75	0.36	6.6	1.6	14.4	63.8 (100)	28 (94)	absent
PM	2.81	0.26	16.4	1.3	28.0	104.1 (99)	31 (97)	present
ST	3.59	0.53	51.5	7.3	10.7	112.9 (97)	0 (86)	absent
LS	3.70	0.18	49.8	3.0	17.1	38.6 (100)	2 (57)	absent
40-60 years								
PE	0.72	0.12	5.6	1.1	14.4	17.1 (93)	47 (86)	present
SF[c]	1.09	0.17	11.7	1.7	15.3	14.0 (90)	44 (81)	present
CM[c]	1.53	0.01	19.1	1.4	20.1	12.3 (100)	27 (82)	absent
LT	1.69	0.07	14.5	0.9	20.7	22.7 (88)	16 (75)	present
PW	1.85	0.21	21.3	2.9	12.0	21.2 (97)	11 (83)	present

[a] LWD=large woody debris with length >1 m and diameter >30 cm.
[b] Stream was cleaned of large woody debris at time of logging.
[c] Means and standard errors over two (NB) or three (SF, CM) years are reported for the biological features.

Table 2.3. Results of one-way ANOVA tests and Levene's Test for homogeneity of variance among basins within three classes of forest management. The basin classes are: 1=unlogged (n=4), 2=logged 20-30 years ago (n=7), and 3= logged 40-60 years ago (n=5). For the multiple comparison tests, the basin classes are arranged so that lowest to highest values are read from left to right. Classes of basins that are underlined with a solid line are not significantly different at an alpha level of 0.05, and classes of basins that are underlined with a dotted line are not significantly different at an alpha level of 0.10.

Dependent variable	P-value of ANOVA test (df=2,13)	Tukey's multiple comparison test	P-value of Levene's Test
Cutthroat trout biomass (g/m^2)[a]	0.239	1 3 2	<0.001
LWD (no./100 m)[b]	0.282	3 1 2	<0.001
Pools (no./100 m)	0.507	1 3 2	0.024
Conifer tree shading (%)	0.006	2 3 1	0.839
Deciduous tree shading (%)	0.001	1 3 2	0.699
Total shading by trees (%)	0.076	1 3 2	0.122
Stream gradient (%)	0.723	1 3 2	0.422

[a] Age 1+ or older.

[b] LWD=large woody debris with length >1 m, diameter >30 cm. The data were log transformed.

Table 2.4. Classification of 16 streams by three factors: level of large woody debris, percentage of conifer shading, and biomass of age 1+ or older cutthroat trout[a]. Streams were sampled at low flow during 1991-93.

Number of large woody debris pieces[b] per 100 m	Percentage conifer shading	Number of streams with cutthroat biomass (g/m^2)	
		≤ 1.2	> 1.2
≤ 21	≤ 35	2	3
	> 35	3	0
> 21	≤ 35	1	5
	> 35	2	0

[a] Values chosen for pieces of large woody debris and biomass of cutthroat trout were values that evenly divided the total number of streams.
[b] Pieces with length >1 m and diameter >30 cm.

biomass less than 1.2 g/m^2. All five streams with conifer shading that exceeded 35% had a biomass of cutthroat trout less than 1.2 g/m^2.

The variable that explained the most variation in biomass of age 1+ or older cutthroat trout among all streams was LWD (r^2=0.356, p=0.015). LWD also explained the most variation in biomass of age 1+ or older cutthroat trout when basalt (r^2=0.556, p=0.021) and sandstone (r^2=0.359, p=0.155) streams were analyzed as separate groups. The best two-variable models for the combined and separate groups of streams as well as the best three-variable model for the combined groups were derived (Appendix Tables 2.2 and 2.3), but the results were largely confounding because of the sparsity of data within potentially important indicator variables such as geology and sampling year (Appendix Figures 2.1 and 2.2).

Three streams within the class of basins that were logged 20-30 years ago had large accumulations of LWD stacked on terraces above the stream channel. These accumulations indicated that the streams had been cleaned of LWD, a common practice associated with logging during this time period. These three streams had lower levels of LWD and lower number of pools than the other streams within this class of basins (Table 2.1). When streams within basins logged 20-30 years ago were grouped by geologic type (basalt or sandstone), the level of biomass of age 1+ or older cutthroat trout was consistently higher in streams that were not cleaned of LWD than in streams that were cleaned of LWD (Figure 2.4). Because the sample size was low and other effects may be confounding the pattern observed (e.g., stream gradient, presence of sculpin), performing a statistical test for the difference in biomass between these two groups of streams was not considered appropriate.

Effects of Geomorphology

Differences in the distribution of habitat types between basalt and sandstone streams were evident. Pools within sandstone streams accounted for about twice the percentage of surface area than did pools within basalt streams (Table 2.5). The

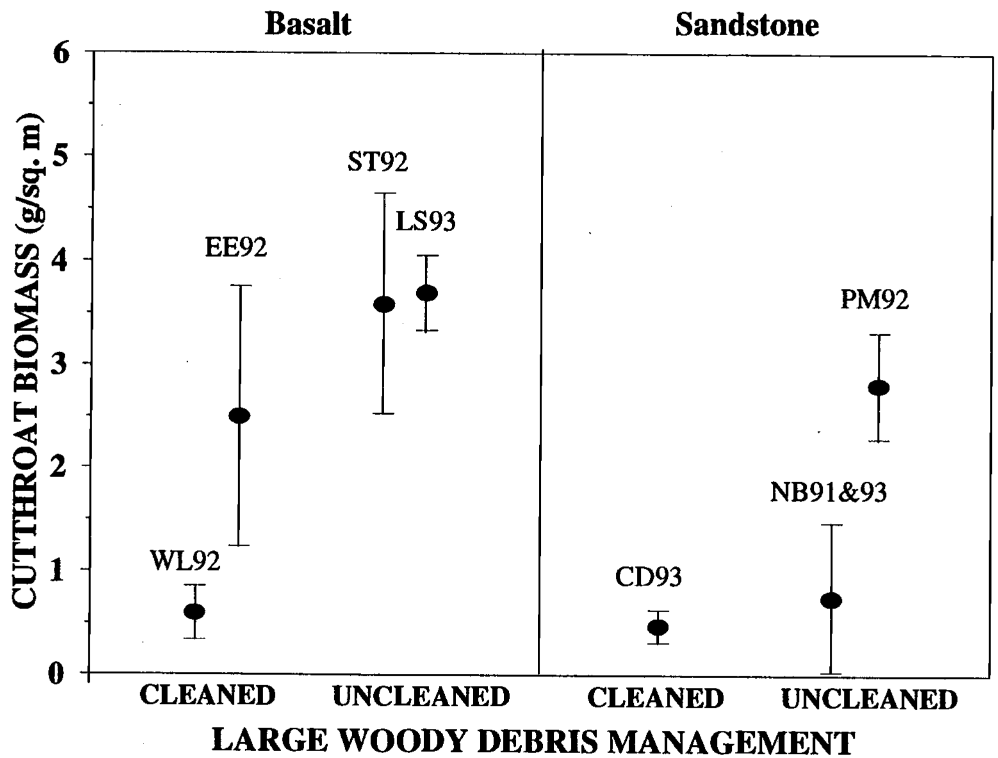


Figure 2.4. Biomass of age 1+ or older cutthroat trout in streams within basins that were logged 20-30 years ago. Streams have been classified by management of large woody debris (cleaned, uncleaned) at time of logging. Error bars represent approximate 95% confidence intervals (±2*SE). Streams are labeled with code names (see Appendix Table 2.1) followed by the year(s) sampled.

Table 2.5. Distribution of habitat types and of number and biomass of age 1+ or older cutthroat trout among habitat types in basalt (n=9) and sandstone streams (n=7).

Factor	Basalt					Sandstone					P-value of test[c]
	Mean	SE	Median	Low	High	Mean	SE	Median	Low	High	
Total stream area (%)											
Pools	15.6	3.8	11.6	4.9	40.6	33.8	6.3	32.6	9.6	55.4	0.034
Pockets[a]	1.8	0.8	0.2	0.0	6.2	9.0	5.0	3.4	0.0	35.5	0.283
Glides	10.7	1.5	11.3	2.0	18.4	11.6	2.2	12.7	5.2	21.4	0.999
Cascades and riffles	70.1	4.6	74.9	36.1	82.1	41.9	8.3	42.9	7.7	74.2	0.011
Steps[b]	1.9	0.8	0.7	0.1	7.9	3.7	1.5	2.4	0.9	12.2	0.138
Total cutthroat trout population (%)											
Pools	46.0	7.2	44.3	15.2	75.8	83.6	6.6	82.8	52.3	100.0	
Pockets	3.1	2.0	0.0	0.0	17.7	6.5	3.8	2.2	0.0	27.3	
Glides	18.3	4.7	12.1	3.1	41.4	4.3	4.3	0.0	0.0	30.2	
Cascades and riffles	32.6	5.5	27.9	9.4	59.5	5.6	2.9	0.0	0.0	17.2	
Total cutthroat trout biomass (%)											
Pools	48.1	6.4	44.3	21.3	73.8	85.8	7.1	87.5	47.1	100.0	
Pockets	3.1	1.8	0.0	0.0	16.8	6.4	3.6	0.8	0.0	20.5	
Glides	19.5	5.7	15.1	1.6	50.3	3.6	3.6	0.0	0.0	25.3	
Cascades and riffles	29.3	5.4	27.3	11.0	60.4	4.2	2.1	0.0	0.0	12.5	

[a] Pockets had pool characteristics but had maximum depths <20 cm.

[b] Steps were gradient breaks between habitat units and were considered uninhabitable by cutthroat trout.

[c] Mann-Whitney *U* test for the difference between geologic types of streams.

frequency of pools within basalt and sandstone streams was directly related to the amount of LWD in the streams, but the relationship was significant for only the basalt streams (Figure 2.5). Characteristics of individual pools, including frequency, length, area, volume, and depth, could not be distinguished between basalt and sandstone streams (Appendix Table 2.4). Combined cascade and riffle habitats accounted for more stream length and surface area in basalt streams than in sandstone streams, as did the surface area of glides.

Relative to the size of the watershed, the basalt streams that met my criteria for sampling had consistently higher stream gradients than the sandstone streams that met the criteria (Figure 2.6). Stream gradient was negatively correlated to drainage area in both basalt and sandstone basins (Pearson correlation coefficients: $r=-0.64$, $p=0.064$; $r=-0.86$, $p=0.013$). Basalt streams had a higher number of boulders, a higher percentage of boulder and cobble substrate, and a lower percentage of fines (sand and silt) than that found in sandstone streams (Table 2.6).

The population of cutthroat trout was more evenly distributed among habitat types in basalt streams than in sandstone streams. Vanderploeg and Scavia's (1979) electivity index, E*, indicated that cutthroat trout in basalt streams were more numerous in pools, pockets, and glides than could be explained by the availability of these habitat types (Figure 2.7). In sandstone streams cutthroat trout were more numerous than could be explained by the availability of a habitat type only in pools (Table 2.5).

<u>Sculpin Distribution and Association with Cutthroat Trout</u>

Nine out of the 16 streams had populations of reticulate sculpin and cutthroat trout; the cutthroat trout was the only fish species in the other seven streams. The five basalt streams without sculpin had higher biomass of age 1+ or older cutthroat trout than the four basalt streams with sculpin (Figure 2.8A). No such pattern was evident in sandstone streams.

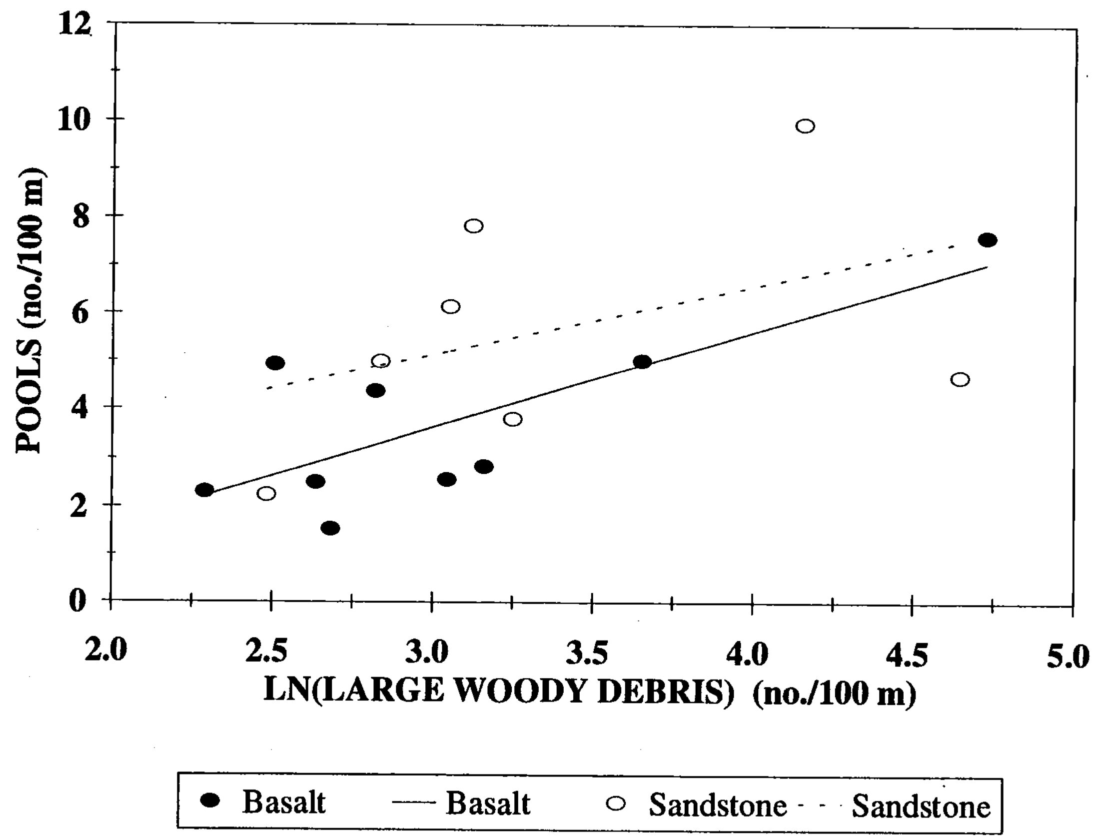


Figure 2.5. Relationship between frequency of pools and large woody debris in 16 streams of the central Coast Range of Oregon (basalt: r-squared=0.601, p=0.014; sandstone: r-squared=0.183, p=0.338).

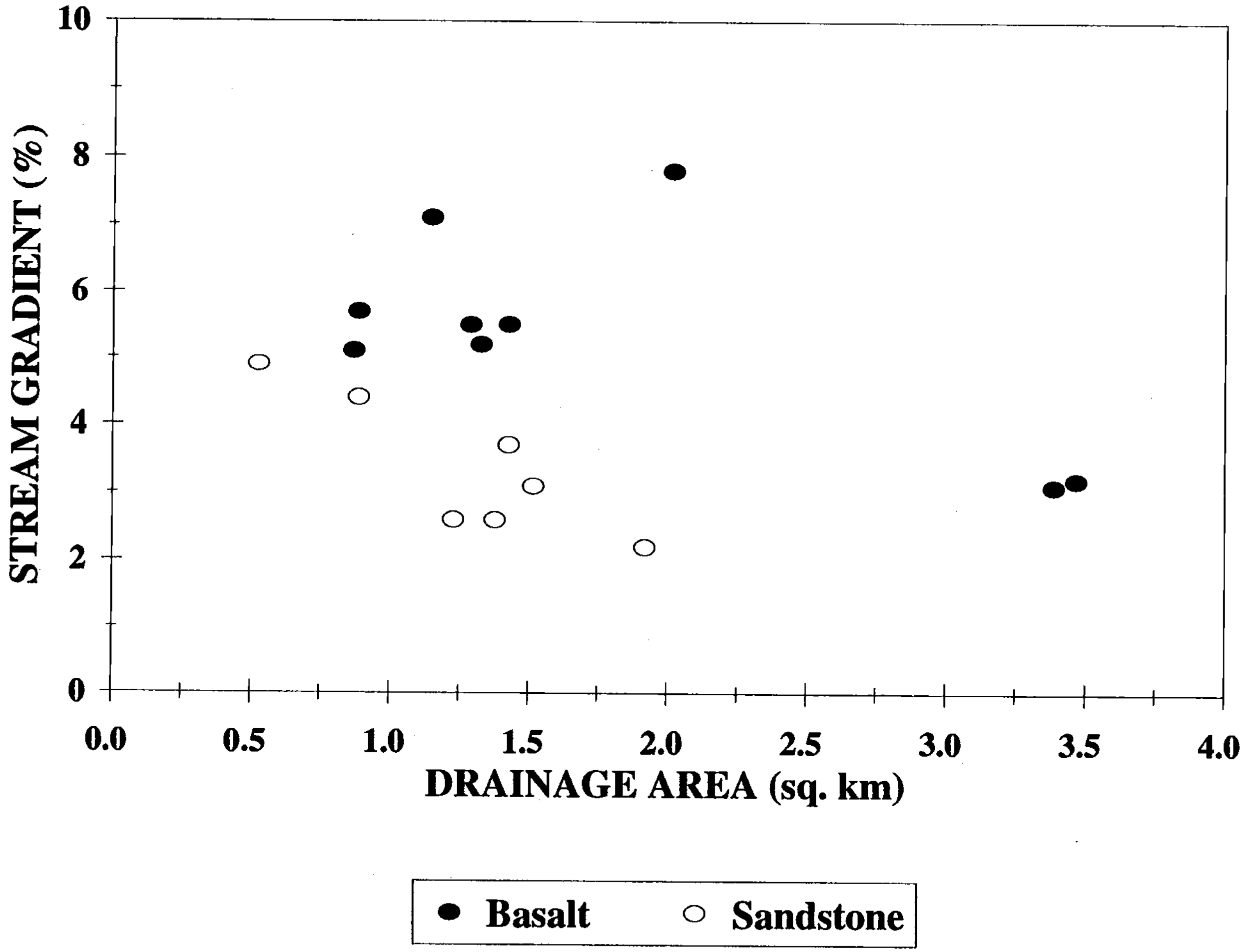


Figure 2.6. Relationship between stream gradient and drainage area in nine basalt streams and seven sandstone streams in the central Coast Range of Oregon.

Table 2.6. Physical characteristics of basalt (n=9) and sandstone (n=7) basins and streams.

Factor	Basalt				Sandstone				P-value of test[a]
	Mean	Median	Low	High	Mean	Median	Low	High	
Drainage area (km^2)	1.76	1.33	0.87	3.47	1.27	1.38	0.53	1.92	0.672
Stream gradient (%)	5.4	5.5	3.1	7.8	3.4	3.1	2.2	4.9	0.009
Mean width (m)	2.06	2.07	1.53	2.65	1.35	1.38	0.98	1.77	0.008
Boulders (no./100 m)[b]	60.4	24.5	8.7	290.2	10.2	3.0	0.2	50.1	0.008
Stream substrate (%)									
Bedrock	3.0	1.3	0.0	9.5	3.0	0.0	0.0	13.6	0.174
Boulder (>300 mm)	16.4	16.9	2.3	30.5	2.8	2.3	0.0	9.9	0.005
Cobble (101-300 mm)	26.7	26.0	13.6	38.8	7.5	7.0	0.4	18.8	0.002
Gravel (2-100 mm)	45.2	41.0	20.7	69.3	54.2	55.9	9.9	82.0	0.290
Fines (<2 mm)	8.3	7.5	1.4	16.5	29.5	20.1	8.1	73.2	0.030
Organic debris	0.3	0.1	0.0	1.3	2.9	1.6	0.0	11.2	0.033

[a] Mann-Whitney *U* test for the difference between geologic types of streams.
[b] Diameter >0.5 m.

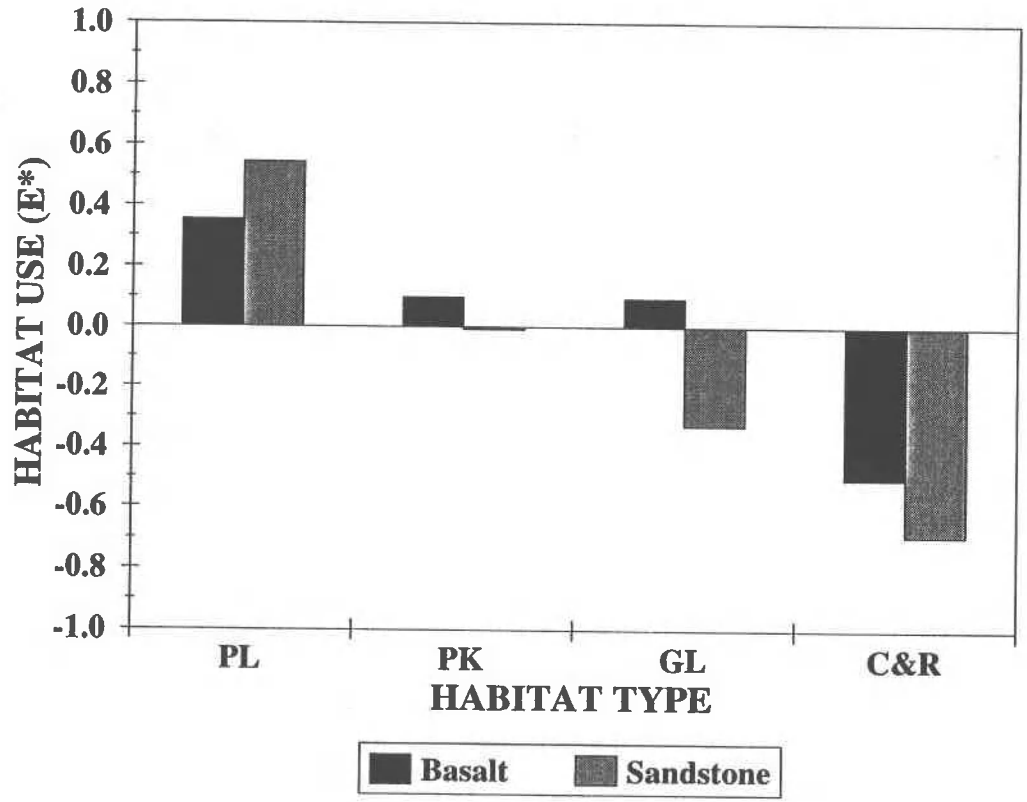
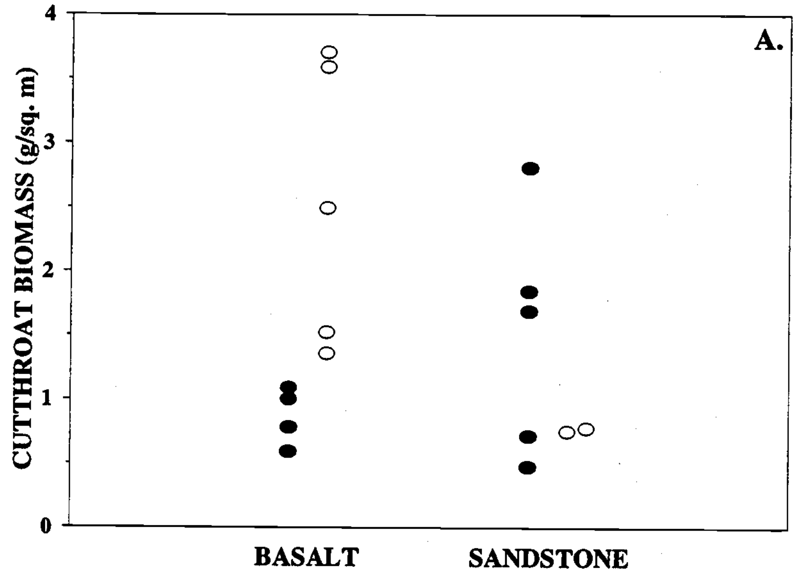


Figure 2.7. Use of habitat types by age 1+ or older cutthroat trout. Vanderploeg and Scavia's (1979) electivity index, E*, was used to calculate habitat use. Strongly positive values represent high use by cutthroat trout relative to the availability of a habitat type while strongly negative values represent low use. PL=pools, PK=pockets, GL=glides, C&R=cascades and riffles.



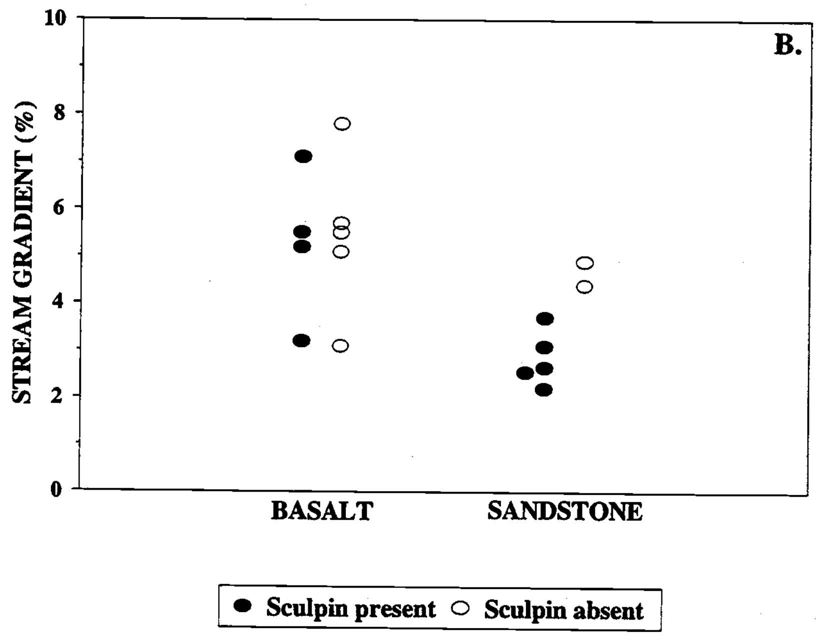


Figure 2.8. Comparison between basalt and sandstone streams for the distribution of reticulate sculpin and their relationship with A) biomass of age 1+ or older cutthroat trout, and with B) stream gradient. Sixteen coastal streams in the central Coast Range of Oregon were sampled during summer low flow, 1991-1993.

Stream gradient appears to be a factor that influences the upstream distribution of sculpins in sandstone streams. All five of the sandstone streams with gradients less than 4% had sculpin while the two sandstone streams with gradients more than 4% did not have sculpin (Figure 2.8B). Distribution of sculpin did not appear to be as affected by gradient in basalt streams as in sandstone streams. During my extensive surveys of over 30 streams to locate sites for this study, I did not find any stream that had sculpin occurring above the distribution of cutthroat trout.

Although reticulate sculpin were found above the barrier at the downstream end of my study reach in Needle Branch before logging in 1966 (Hall and Lantz 1969), I found no sculpin above this barrier during my sampling efforts in 1991-1993. This finding suggests that the sculpin mortality documented by Krohn (1968) after the Needle Branch basin was subjected to an unusually hot slash burn following logging resulted in the extirpation of this population above the barrier to upstream migration.

Discussion

Differences in the variance of biomass of cutthroat trout, LWD, number of pools, and stream shading were found among streams within three types of forest management (unlogged, logged 20-30 years ago, logged 40-60 years ago), but caution is warranted against interpreting a pattern in these differences attributable to a time sequence. For example, the moderate variance of biomass of cutthroat trout found among streams in basins logged 40-60 years ago may well not be the trajectory for recovery of basins that were logged 20-30 years ago, which exhibited high variation in biomass among streams. Logging represents an additional disturbance to the history of natural disturbances within a basin (Reeves et al. 1995). On-site management of debris and mechanical methods for cutting and removal of logs changed during the 40-year period that I investigated (Bisson et al. 1992).

Mechanisms that may explain the variation in biomass of cutthroat trout among the three types of forest management identified include the differences in potential for scour and habitat development afforded by LWD and the differences in light and organic inputs afforded by deciduous versus conifer trees in the riparian canopy. Each of these mechanisms is addressed in the discussion that follows.

The abandoned but relatively recent practice of cleaning streams of LWD at the time of logging (Bryant 1983, Sedell and Swanson 1984) may have a lingering negative effect on populations of cutthroat trout after 20-30 years post-treatment. Streams that were cleaned of LWD at the time their watersheds were logged 20-30 years ago had lower levels of biomass of cutthroat trout than streams in watersheds that were logged during the same time period but not cleaned of LWD, but the sample size was too low to confirm this pattern. Downed wood in streams provides the structure to promote scouring of pools (Bilby and Ward 1991) and the complexity to enhance salmonid habitat (Fausch and Northcote 1992).

All of the headwater streams sampled in this study were highly shaded by an overstory canopy of riparian vegetation, but annual input of light likely differed among groups of basins. A deciduous canopy allows light to reach the stream surface during late fall to early spring, but a conifer canopy restricts the amount of light reaching a stream all year long. Sedell and Swanson (1984) noted the potential for algal production in streams before the leaves come out from deciduous canopies. Several investigators have noted the higher productivity of salmonids in unshaded streams relative to shaded systems in the Pacific Northwest (Murphy and Hall 1981, Murphy et al. 1981, Hawkins et al. 1983). Moore and Gregory (1988) found that cutthroat trout fry had earlier emergence times and higher densities in a stream with a deciduous canopy compared with streams with mature conifer canopies in the Oregon Cascades, but they studied only one deciduous-shaded site and the results were confounded with site differences in elevation. Increased light has been found to increase the efficiency of foraging by coastal cutthroat trout (Wilzbach et al. 1986). The character and magnitude of the influence that the availability of light during the colder months of the year has on the life cycle of cutthroat trout warrants further attention.

When conifers colonize riparian areas after a fire, a state of high shade and low quality inputs of nutrients can persist for over 100 years (Sedell and Swanson 1984). Much of the central Oregon Coast Range area burned during the mid to late 1800s (Juday

1977). Stand-resetting wildfires have been a dominant natural disturbance within the central Oregon Coast Range and have affected the productivity of salmonids in the stream systems of the region (Reeves et al. 1995). In addition to shade, the legacy of LWD and sediment from wildfire has been identified by Minshall et al. (1989) and Reeves et al. (1995). Aquatic production within small streams can be particularly responsive to wildfire because of the extremes of open and closed canopy conditions brought about by the disturbance and recovery period (Minshall et al. 1989). As the conifer riparian forest matures and natural blowdown events occur, openings that result in increased light to the stream would be expected to gradually increase unless reset by fire or management activities (Sedell and Swanson 1984).

In Needle Branch during drought conditions in summer 1992, I found freshly dead cutthroat trout within small stagnant pools that had large accumulations of red alder leaves. Several cutthroat trout between 120-165 mm (age 2+ or older) were caught in this stream during summer 1991, but all cutthroat trout caught during summer 1993 were under 92 mm (age 1+ or younger). Hicks (1990) found that accumulation of red alder leaves in pools during late summer and fall was associated with low dissolved oxygen. He also noted direct mortality when salmonids were stressed by a diver's presence in these pools filled with alder leaves and low in oxygen. In contrast aquatic productivity can be enhanced because of the increased availability of this allochthonous material for secondary producers (Bilby and Bisson 1992). Taylor and Adams (1986) suggested that a problem with water quality associated with large accumulations of red alder leaves would likely occurs only during unusually low flow periods. The episodic character and extent of the problems associated with low flows and high loadings of red alder leaves in small streams need to be further investigated.

Prospects for natural recruitment of LWD differ widely among the basins studied, depending on prior forest disturbance and management activities. In the basins that had not been logged, input of LWD should increase in the near future as the conifer-dominated riparian vegetation matures and degenerates. Levels of LWD input from the mostly red alder riparian stands of the basins logged 20-30 years ago would be expected to increase in the near future. But the standing crop of LWD with diameters >30 cm may not increase accordingly, owing to the small girth achieved by red alder before senescence (Minore and Weatherly 1994) and their rapid decay in streams (Sedell and Swanson 1984, Veldhuisen 1990). Heimann (1988) found some remnant conifer LWD to persist for up to 140 years in coastal streams of Oregon. Andrus et al. (1988) found that it takes at least 50 years before conifers that repopulate a riparian area begin to represent sources of LWD large enough to function as those found in streams within old-growth basins. Murphy and Koski (1989) estimated that basins logged of streamside conifers in southeast Alaska will need 250 years to reach pre-logging levels of LWD in streams. How much the current levels of LWD will decline before streamside conifers are established, mature, and result in elevated levels of LWD is not known, but will be contingent upon the rate of episodic natural disturbances such as windthrow, bank cutting, and debris flows (Swanston 1991).

Some important differences in distribution and density of cutthroat trout were related to differences in the geomorphology of sandstone and basalt streams. I found that cutthroat trout were more highly associated with pools in sandstone streams than in basalt streams. I also found that sandstone streams had lower stream gradients and smaller substrate than basalt streams. These findings largely agree with those that Hicks (1990) reported for larger Coast Range streams.

The vulnerability of cutthroat trout populations to disturbance may be particularly high in small sandstone streams. Because sandstone streams tend to have lower streamflows in summer than do similar-sized basalt streams (Hicks 1990), residual pools may be the only usable habitat during low-flow periods in small sandstone streams. Pools accounted for a much larger fraction of the usable habitat in sandstone streams than in basalt streams, which may partially explain why pools in sandstone streams contained about twice the percentage of the total biomass of cutthroat trout than they did in basalt streams. In Needle Branch, a sandstone stream and the smallest stream sampled during my study, age 1+ or older cutthroat trout were found exclusively in pools during both years sampled (1991 and 1993). Osborn (1981) found that streams with small substrate have a high reliance upon LWD for pool formation. It follows that LWD could be especially important for maintaining cutthroat trout populations in small sandstone streams.

Populations of reticulate sculpin in reaches of higher gradient sandstone streams above migration barriers may be particularly vulnerable to extirpation. Reticulate sculpin were absent from isolated sandstone streams with gradients higher than 4%. Reticulate sculpin were once present above the fish barrier at the downstream end of my study reach in Needle Branch before logging in 1968, but a die-off occurred during an unusually hot slash burn just after logging of the basin (Hall and Lantz 1969). Krohn (1968) documented the failure of two age classes of this sculpin population following the disturbance. Although a disturbance that resulted in extirpation may explain the absence of reticulate sculpin in some streams, their absence may also be a consequence of the age of a barrier and timing of colonization (Maughan et al. 1980).

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CHAPTER 3

Age-Specific Use of Pools in Headwater Streams by Resident Cutthroat Trout in the Coast Range of Oregon

Patrick J. Connolly

Abstract

To investigate whether intraspecific interaction was important in determining the use of pools by young-of-year (YOY) cutthroat trout (*Oncorhynchus clarki clarki*), I used data collected from 238 pools within nine basalt and seven sandstone streams. Physical attributes of these pools and the biomass and age structure of cutthroat trout that these pools supported were compared between basalt and sandstone streams and among years. Stream gradients were higher in basalt streams than in sandstone streams. Pools in basalt streams had higher amounts of cobble and boulder substrate but lower amounts of fines than pools in sandstone streams. In pools, biomass (g/m^2) of YOY cutthroat trout was directly related to total stream gradient and inversely related to biomass (g/pool) of age 1+ or older cutthroat trout, especially in sandstone streams. In all sandstone streams and in the highest gradient basalt streams, biomass of YOY was higher in pools when age 2+ or older cutthroat trout were absent than when they were present. These findings suggest that habitat use was largely partitioned between YOY and older cutthroat trout, and that stream gradient and geology of the substrate were important stream characteristics that influenced the age structure of cutthroat trout in pools.

Three years of annual sampling indicated that age 2+ or older cutthroat trout were more affected by drought in sandstone streams than those in basalt streams. Pools abandoned by adult cutthroat trout, either by movement or death, appear to offer important rearing opportunities for YOY. The inherent suitability and increased availability of these abandoned pools to YOY may provide a mechanism for quick recovery of an isolated resident population when periodic droughts cause loss of adults.

Introduction

Pools are important habitat for adult coastal cutthroat trout (*Oncorhynchus clarki clarki*), especially during summer low-flow periods in Pacific Northwest streams (Bisson et al. 1988, House 1995). Cutthroat trout form social hierarchies in pools wherein one to a few fish are dominant (Heggenes et al. 1991a, 1991b; Mesa 1991).

During dry summers within the Pacific Northwest and British Columbia, pools in small headwater streams may become low in oxygen and become isolated because of little to no incoming or outgoing flow (Hicks et al. 1991b, Northcote 1992). Coastal cutthroat trout can withstand low oxygen levels better than most coastal stream salmonids (Northcote and Hartman 1988). They can also subsist for a substantial amount of time in the absence of drift organisms (Northcote 1992), their primary source of food (Brocksen et al. 1968, Wilzbach et al. 1986). The persistence of populations of cutthroat trout in small streams above barriers may hinge upon these adaptations to periodic low water events (Northcote 1992).

During sampling of streams above barriers for resident cutthroat trout as part of a related project (see Chapter 2), I observed that young-of-year (YOY) were unusually abundant in some pools when older fish were absent, especially in sandstone streams. One objective of this study was to determine if use of pools by YOY changed with the absence and presence of older cutthroat trout.

Another objective of this study was to determine if age-class structure differed between pools in basalt and sandstone streams. Streams in basalt basins maintain higher base flows, which allows maintenance of a diversity of habitat types, and they have larger substrates, which provides visual isolation among fish (Hicks 1990). Because of these geomorphic differences, expenditure of energy on intraspecific interactions (Li and Brocksen 1977, Metcalfe 1986) may not be as necessary, nor advantageous, for cutthroat trout in pools of basalt streams as in sandstone streams.

Study Area

The latitudinal range of streams included tributaries of the Siletz River basin to the north and Big Creek basin (Lincoln County) to the south (Figure 2.1). All of the streams were above barriers to anadromous fish and were within basins that drain the west side of the Coast Range of Oregon. Because many of the streams were unnamed, I assigned a two-letter code to them (Appendix Table 2.1). Size of the watersheds ranged from 0.5 to 3.5 km^2, and stream gradients ranged from 2 to 8% (Appendix Tables 3.1 and 3.2). Seven streams had substrates that were exclusively sandstone; the remaining eight streams had substrates that were either all basalt or basalt mixed with sandstone. No sign of angling was observed in any of these small and relatively remote streams throughout the course of the study.

Methods

Data Acquisition and Preparation

Data on habitat and biological variables were obtained as part of the sampling design used in Chapter 2 to determine the status of habitat and populations of cutthroat trout after logging 20-60 years ago. In the present analysis I used only the data collected from pools. I defined pools as slow-water channel units (Bisson et al. 1982) with maximum depths of 20 cm or greater. The data set contained a total of 126 pools from 9 basalt streams, and a total of 112 pools from 7 sandstone streams. I sampled pools in two of the basalt streams annually during 1991-1993, and I sampled pools in one of the sandstone streams in 1991 and 1993.

The habitat variables that I used for analysis included three basin variables (geology, stream gradient, and drainage area), six physical measures of pools (length, width, mean depth, maximum depth, area, and volume), percent coverage by three substrate classes (boulder-cobble, gravel, and fines), and three measures of pool cover (total, overhead, and instream). Cover included woody debris, undercut banks, substrate, surface water turbulence, and vegetation. Methods for obtaining these habitat data are described in Chapter 2.

To determine populations of age 1+ or older cutthroat trout within pools, I used a backpack electrofisher and the pass-removal method (Zippin 1956, Bohlin et al. 1989). When needed, I placed block nets at one or both ends of a pool to prevent fish from escaping or entering from the unit once sampling began. Removal passes were continued until no age 1+ or older cutthroat trout were caught on the last pass. At least two removal passes were conducted on each selected pool. Within a pool, I considered the total number of age 1+ or older cutthroat trout caught as their population size. Fork length and weight were recorded for each cutthroat trout captured. For some analyses, I segregated the total catch by age group (1+ and 2+ or older) based on length-frequency data combined with growth data obtained from marking and recapturing fish over an entire year (Appendix Figure 3.1).

Age 0+ cutthroat trout were also collected during each removal pass. As with older cutthroat trout, I considered the total number caught as the population size when the last pass yielded no YOY. But when one or more YOY were caught on the last pass, I used a Seber and LeCren (1967) or Zippin (1956) estimator to estimate the population depending on whether two, three, or more passes were conducted. The use of these estimators was required for only 20 pools out of the total of 238 pools sampled. Estimates of total biomass were calculated by adding the total weight of YOY caught to an estimate of the total weight of the YOY that were not caught (total weight caught + {mean weight caught · [population estimate – total caught]}).

To estimate the coefficient of variation (CV) for population estimates of YOY that were less than 20, I used the large-sample formula from Seber and LeCren (1967) when two passes were conducted, or from Zippin (1956) when three or more passes were conducted, following the guidelines that I present in Chapter 4. When the estimated population was 20 or more, I used the large-sample formula from Seber and LeCren

(1967) as above, but used the full multi-termed model from Zippin (1956) to calculate CV.

I eliminated a pool from any analyses that required an estimate for number or biomass of YOY if the CV exceeded 12.5%, or if the sequence of catches failed a chi-square test for equal catchability among passes (Seber 1982, p. 314). This procedure eliminated 15 pools from the total of 238 pools sampled. Seven of the eliminated pools were in basalt streams and eight of the pools were in sandstone streams.

Statistical Analysis

I used t-tests to test for the difference between characteristics of streams and pools of basalt and sandstone geology. To determine what formulation of the t-test to use, I tested for the equality of variances between the basalt and sandstone data for each characteristic with an F-test calculated by SAS (version 6.03, SAS Institute Incorporated 1988).

To ensure that the assumption of normality was appropriate for the regression analyses that I used, I inspected the residuals and normal probability plots for undesirable patterns. I used the UNIVARIATE procedure within SAS to produce residual and normal probability plots and a test, Shapiro-Wilk's W, for adherence to the assumption of normality. In all analyses that included biomass of an age class as an independent or dependent variable, these variables were log-transformed to normalize the data.

Estimates of slopes were derived by regressing the biomass of YOY cutthroat trout on the biomass of age 1+ or older cutthroat trout in pools for individual streams. I grouped the slopes by geologic type (basalt and sandstone) and tested whether the median slope within a group was significantly different from zero with a series of Wilcoxon Signed Rank Tests for one sample (Hollander and Wolfe 1973, p.27). Within a geological type (basalt and sandstone), I conducted Wilcoxon tests for all possible combinations of streams that included only a single year of data from any one stream that I sampled more than one year (NB, CM, and SF). This resulted in a total of six Wilcoxon tests for all possible combinations of slopes from basalt streams and two Wilcoxon tests for all possible combinations of slopes from sandstone streams. The consistency in the p-values among these Wilcoxon tests was used to indicate the significance of trend for the relationship between biomass of YOY cutthroat trout and biomass of age 1+ or older cutthroat trout in pools among streams.

Results

Influence of Geology on Physical Features

Geology of a watershed had an influence on some of the physical features of the streams and on the pools within the streams. Stream gradients were higher in basalt streams than in sandstone streams (Table 3.1). Seven of the nine basalt streams sampled had stream gradients of more than 5%, whereas all seven of the sandstone streams had stream gradients of less than 5% (Appendix Tables 3.1 and 3.2). These two geological types of streams had pools with similar surface areas, depths, and volumes (Table 3.1). No differences in pool cover between the two stream types were evident. Pools in basalt streams had higher amounts of cobble and boulder substrate but lower amounts of fines than pools in sandstone streams.

Influence of Drought on Surface Flow and Pools

Drought during summer 1992 differentially affected stream habitat in the three streams that were sampled in the year before, during, and after this drought. Coleman Creek (CM) retained surface flow throughout the dry summer of 1992, and the number of pools in 1992 (13) was similar to that found in 1991 (14) and 1993 (16). Although South Fork (SF) retained flow throughout 1992, the number of pools was reduced to 3 by late

Table 3.1. Means and standard errors for characteristics of streams and pools within, and results of t-tests for differences between, basalt and sandstone watersheds. Variances were equal unless footnoted[a]. A total of 125 pools from 9 basalt streams and 112 pools from 7 sandstone streams were included in the analysis.

Habitat variable	Basalt	Sandstone	T-test p-values
Stream			
Gradient (%)	5.36 (0.51)[b]	3.36 (0.38)	0.0104
Drainage area (km^2)	1.76 (0.34)	1.27 (0.17)	0.2540[c]
Pool morphology			
Length (m)	3.71 (0.42)	4.38 (0.36)	0.2660
Width (m)	2.30 (0.15)	1.87 (0.14)	0.0621
Area (m^2)	8.48 (1.18)	8.27 (1.28)	0.9066
Volume (m^3)	1.61 (0.29)	1.55 (0.32)	0.8909
Mean depth (cm)	18.0 (1.4)	18.3 (0.74)	0.9011[c]
Maximum depth (cm)	32.5 (2.5)	31.3 (1.81)	0.7104
Pool cover			
Total (%)	44 (4)	52 (5)	0.2193
Overhead (%)	12 (3)	15 (3)	0.4801
Instream (%)	33 (3)	38 (2)	0.1954
Pool substrate			
Boulder-cobble (%)	32 (5)	7 (3)	0.0016[c]
Gravel (%)	47 (7)	45 (10)	0.9106
Fines (%)	19 (6)	46 (11)	0.0441

[a] I used an F Test calculated by SAS (SAS Institute Incorporated 1988) to test for equality of variances between basalt and sandstone data for each variable.

[b] Mean of stream means (standard error of the mean).

[c] Unequal variances ($p<0.05$). When unequal variances were found, I used the t-test results from SAS Institute Incorporated's (1988) calculation of Satterthwaite's approximation.

August, compared to 8 pools found in early September 1991 and 14 pools found in mid-September 1993. In 1991 and 1993, Needle Branch (NB) had a higher number of pools per 100 m than the other 15 streams of the study (Appendix Table 3.2), but in 1992, the stream was reduced to a few isolated and shallow pools later in the summer. Because surface flow was not evident in NB by mid-August 1992, I feared harming the potentially stressed fish that persisted and did not sample NB in 1992 as originally planned.

Use of Pools by Cutthroat Trout

The percentage of pools occupied by YOY increased from 1991 to 1993 in NB and CM, where the percentage of pools occupied by age 2+ or older cutthroat trout decreased from 1991 to 1993. In SF, where percentage of pools occupied by age 2+ or older cutthroat trout increased from 1991 to 1993, the percentage of pools occupied by YOY decreased (Figure 3.1A). This pattern was especially evident in NB, where age 2+ or older cutthroat trout were present in 1991 but not in 1993. Loss of these older fish coincided with a large increase in the percentage of pools occupied by YOY from 1991 to 1993.

Age structure and distribution of biomass among age classes of cutthroat trout differed in consistent patterns before and after the 1992 drought. The lack of age 2+ or older fish in NB during 1993 was accompanied by a large increase in the number and biomass of YOY from that found in 1991 (Figure 3.1, graphs B and C; Appendix Table 3.3). Although the number of age 2+ or older cutthroat trout increased from 1991 to 1993 in one of the three streams (SF), their biomass decreased in all three streams. Coincident with this decrease in biomass of age 2+ or older cutthroat trout in the three streams from 1991 to 1993 was an increase in the number (CM, SF, and NB) and biomass (SF and NB) of YOY.

Absence of age 2+ or older cutthroat trout in the sandstone streams NB and CD in 1993 served as an indicator that effects of the 1992 drought were especially severe in sandstone streams. All five streams sampled in 1991 (four basalt and one sandstone) and

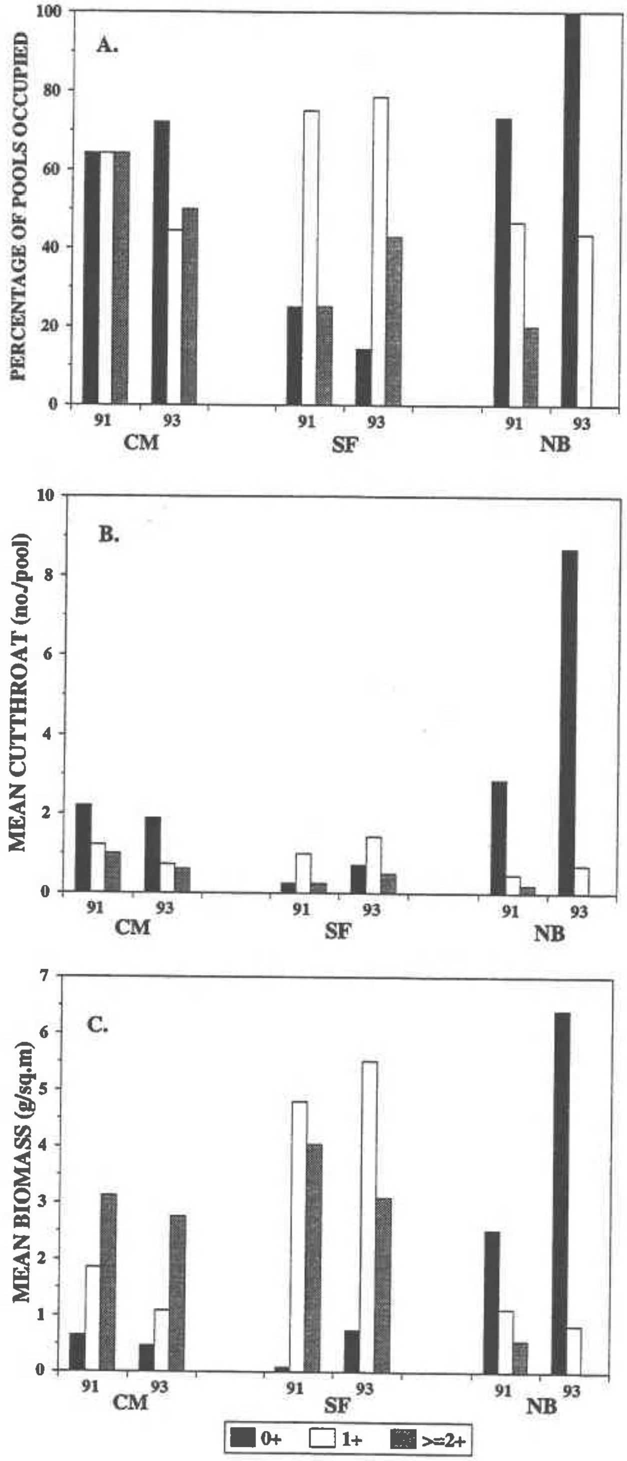

Figure 3.1. Age 0+, 1+, and 2+ or older cutthroat trout in pools of three streams during summer 1991 and 1993: A) percentage of pools occupied, B) mean number per pool, and C) mean biomass per pool. CM=Coleman Creek, SF=South Fork, and NB=Needle Branch.

all eight streams sampled in 1992 (five basalt and three sandstone) had age 2+ or older cutthroat trout present. In 1992 I sampled all streams by early September before the worst of the dry conditions occurred. In 1993 age 2+ or older cutthroat trout were present in all three of the basalt streams sampled, but were present in only one of the three sandstone streams sampled.

Biomass (g/m^2) of YOY was consistently higher in sandstone streams than in basalt streams of similar stream gradient. Biomass of YOY increased as the stream gradient increased in basalt and sandstone streams (Figure 3.2). The highest levels of biomass of YOY in pools were found in the highest gradient sandstone streams.

Age-Class Associations within Pools

Biomass of YOY cutthroat trout was inversely related to the biomass of older cutthroat trout in sandstone streams ($p<0.03$ for all possible Wilcoxon tests: $p=0.022$, $p=0.022$) but not in basalt streams ($p>0.29$ for all possible Wilcoxon tests: $p=0.294$, 0.294, 0.402, 0.402, 0.675, 0.675). The high levels of biomass of YOY in some sandstone streams were not found in any of the basalt streams sampled (Figure 3.3, Appendix Table 3.4).

The highest levels of biomass of YOY were found in 1993 within pools of CD and NB (Figure 3.2, Appendix Table 3.3). Although several pools in CD and NB had age 1+ cutthroat trout in 1993, neither of these streams had age 2+ or older cutthroat trout during that year. It is not known if CD had these older fish before the drought in 1992, but it is known than NB did. It is possible that CD lost its population of age 2+ or older cutthroat trout because of drought in 1992 in the same way that NB did.

When age 2+ or older cutthroat trout were absent from pools, mean biomass of YOY in pools was higher in all sandstone streams and was higher in most basalt streams compared to the mean biomass of YOY in pools where the older trout were present (Appendix Table 3.5). The numerical difference in mean biomass of YOY between the two types of pools (those without and those with the older fish) tended to be larger for the

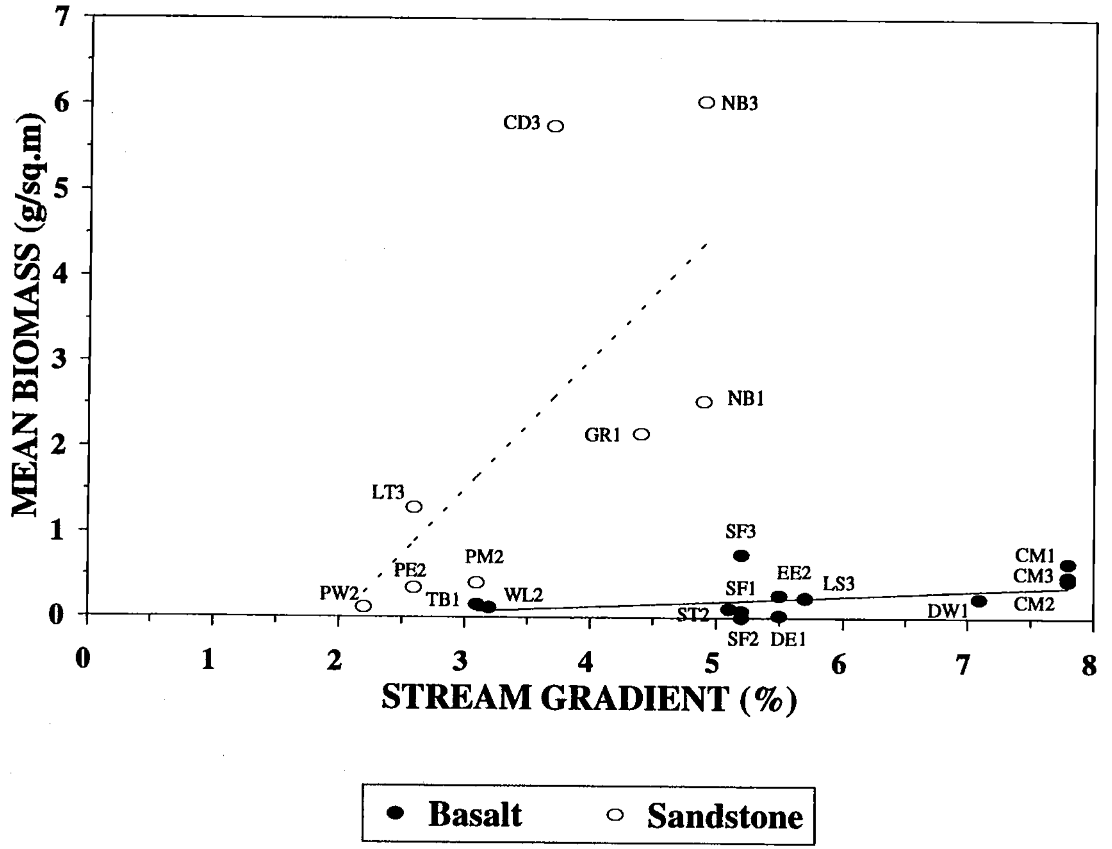

Figure 3.2. Relationship of mean biomass of age 0+ cutthroat trout in pools with gradient of basalt and sandstone streams. When a stream was sampled more than one year, the mean biomass over years was used to derive the regression lines (basalt: r-squared=0.423, p=0.058; sandstone: r-squared=0.499, p=0.076). Streams are labeled with stream code names (see Appendix Table 2.1) followed by the year sampled (1=1991, 2=1992, and 3=1993).

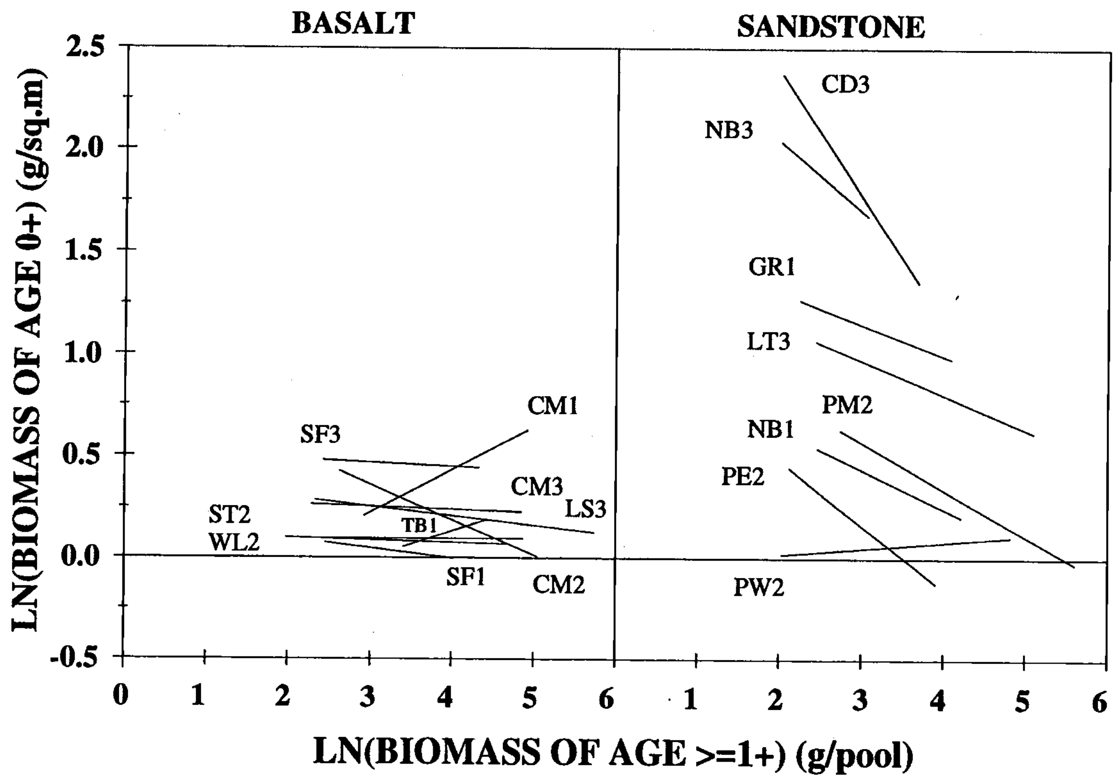

Figure 3.3. Relationships between biomass of age 0+ and age 1+ or older cutthroat trout in pools of basalt and sandstone streams. A value of 1.0 was added to a biomass datum before it was log transformed (base e). Stream code names (see Appendix Table 2.1), followed by the year sampled (1=1991, 2=1992, and 3=1993), are used as labels of the linear regression lines. Streams with less than five pools available for this analysis are not graphed. The endpoints of the regression lines represent the range of the data.

highest gradient basalt and sandstone streams than for the moderate and low gradient streams (Figure 3.4). The numerical differences were consistently higher in sandstone streams than in basalt streams for the few streams of similar gradient.

Discussion

In all sandstone streams and in the highest gradient basalt streams, biomass of YOY was higher in pools that had only YOY than in pools that included age 2+ or older cutthroat trout. Within the three streams that I sampled in both 1991 and 1993, the percentage of pools occupied by YOY increased or decreased with a corresponding opposite change in the percentage of pools occupied by age 2+ or older cutthroat trout. These findings suggest that habitat use was largely partitioned between YOY and older cutthroat trout, and that stream gradient and geology of the substrate were important stream characteristics that influenced the age structure of cutthroat trout in pools. Quinlan (1980) observed that adult Colorado River cutthroat trout (*O. c. pleuriticus*) were often present in low number, and were often the sole occupant, in pools of small mountain streams. Bozek et al. (1994) suggested that when food items in the drift become limited in headwater streams, YOY Colorado River cutthroat trout become limited by the abundance of adults. Partitioning of the available habitat among age groups and its effect on age structure and population size has been recognized in other salmonid populations (Chapman 1966, Symons and Heland 1978, Kennedy and Strange 1986).

The effects of drought on populations of cutthroat trout were more evident in sandstone streams than basalt streams, especially in streams with high gradient. Age 2+ or older cutthroat trout were absent from two of the three sandstone streams sampled in the post-drought year of 1993. But these older fish were present in all three of the basalt streams sampled that year and were present in all basalt and sandstone streams sampled in 1991 and 1992.

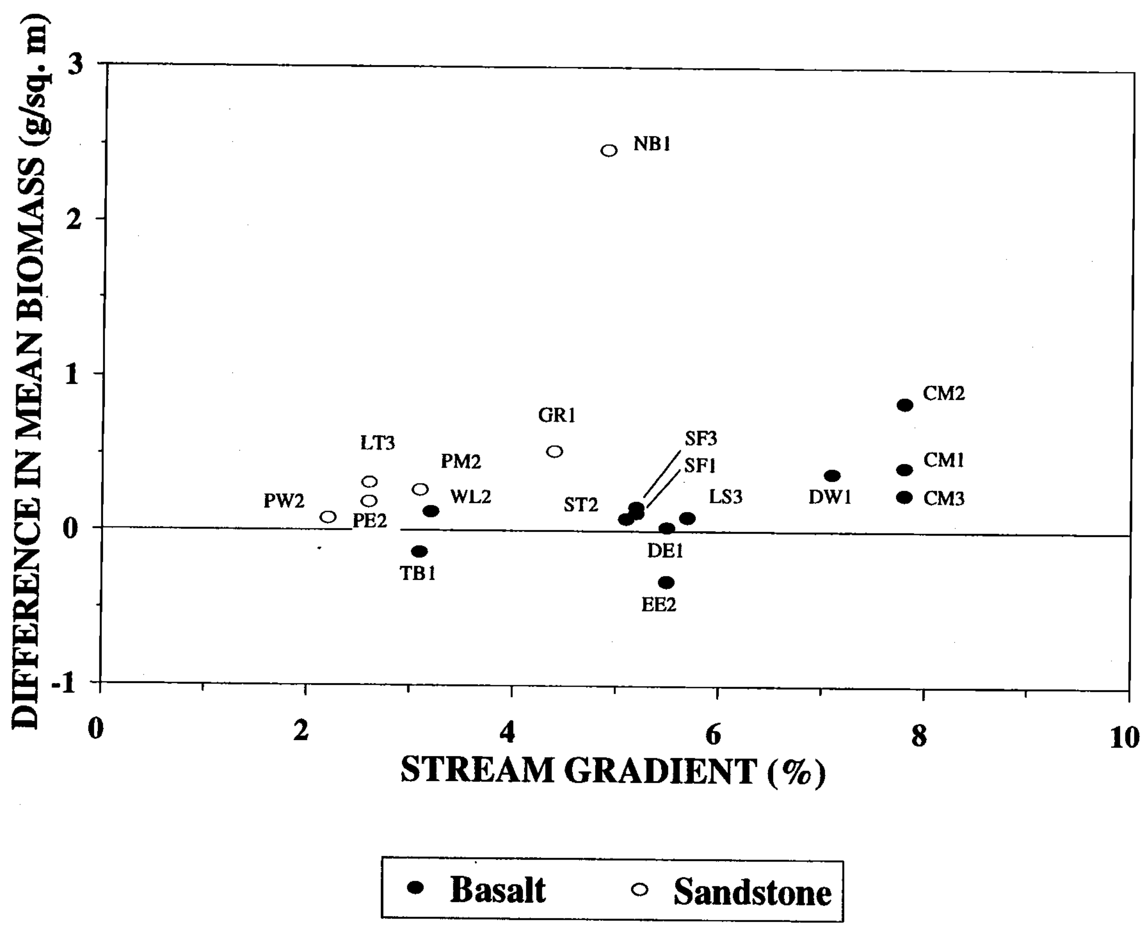

Figure 3.4. Difference in mean biomass of age 0+ cutthroat trout in pools when age 2+ or older cutthroat trout were absent compared to when they were present. Streams that had no age 0+ cutthroat trout in all pools sampled with or without the 2+ or older cutthroat trout are not included (Appendix Table 3.5). Streams are labeled with code names (see Appendix Table 2.1) followed by the year sampled (1=1991, 2=1992 and 3=1993).

The quality of non-pool habitats in streams with high gradient is largely dependent upon substrate. When stream gradients are high in boulder-rich streams such as the basalt stream CM, Grant et al. (1990) found that channel units between pools tend to be cascades. When stream gradients are high in sediment-rich streams such as the sandstone stream NB, channel units between pools tend to be braided and to lack complexity. Probably because of NB's small drainage size, channel units between pools were largely dewatered by late summer during all years of the study. In general, cascade units often held cutthroat trout of all ages, whereas shallow riffles with small gravel-sized substrate seldom held cutthroat trout of any age (unpublished data).

Life in pools of a drying stream can be perilous for cutthroat trout. Risks include lowered oxygen (Hicks 1990), lowered food input, and increased risk of predation (Northcote 1992). Adult cutthroat trout may select only those pools that have adequate flow characteristics related to food and feeding (Jenkins 1969, Fausch 1984, Heggenes et al. 1991b). If a fish chooses to seek habitat downstream in systems that have a fish migration barrier, then it may well mean the loss of the fish from the population. As also found by Northcote (1992) in other streams during dry periods, I observed fresh raccoon tracks beside many of the isolated pools in NB during 1992. When pool depths are lowered and pool surfaces shrink below habitat features that provide cover, terrestrial predators have a better chance of capturing fish.

Juvenile salmonids have been found to utilize large substrates for visual isolation from larger or more dominant salmonids (Chapman 1966, Bozek and Rahel 1991, Northcote 1992). Symons and Heland (1978) noted that large YOY Atlantic salmon (*Salmo salar*) were associated with habitats that offered boulders to provide visual isolation from yearlings. Because pools in sandstone streams had less boulder and cobble substrate than pools in basalt streams, the potential for exclusion of YOY from pools by older cutthroat trout may have been higher in the sandstone streams than in the basalt streams that I studied.

High temperature could be a factor in mortality within stagnant pools, but temperature did not appear to be a problem for the streams in my study. I never found temperatures above 15°C in any of these streams, even during the hottest days of summer.

Dense shade and close association with groundwater help keep headwater streams cool (Northcote and Hartman 1988).

The ability to exclude conspecifics from a pool may be of adaptive importance for maintaining adult cutthroat trout populations in small streams above barriers. Partial segregation of age classes may serve to broaden the niche width of a population (Polis 1984) and serve to decrease the competition between age classes (Scarnecchia and Bergersen 1987). At least two possible mechanisms are feasible: by aggressive defense of a territory (Chapman 1966, Jenkins 1969) or by cannibalism of smaller fish (McFadden 1969). While Mesa (1991) and Bozek et al. (1994) found adult cutthroat trout to be highly territorial, Aho (1977) found cannibalism to be rare in coastal cutthroat trout populations. If low-flow periods reduce all or most of the livable space to isolated pools, the chance that enough food remains to insure survival of an adult cutthroat trout may depend on its prior success at excluding conspecifics.

Pools abandoned by adult cutthroat trout, either by their movement or death, appear to offer important rearing opportunities for YOY. Highest densities of YOY in pools were found in pools that did not hold adult cutthroat trout. Increased use by YOY of pools that are abandoned by adult cutthroat trout may provide a mechanism for a quick recovery of an isolated resident population when periodic droughts cause loss of adults.

If intraspecific interactions are strong enough to negatively affect the amount of available habitat that is utilized by YOY, the predictive capability of habitat-based models will be reduced (Orth 1987, Platts and Nelson 1988). Because House (1995) observed wide annual fluctuations for YOY in a population of coastal cutthroat trout, he concluded that modeling efforts to relate density of cutthroat trout to change in habitat may fail if based on YOY. He argued that these annual fluctuations may be less related to habitat availability or change, but more related to variable timing of emergence, non-constant vulnerability to sampling, or occurrence of spawning above the sampling reach. Although one or all of House's reasons may apply at certain times and places, results of my study indicate that a disturbance to the adult population may be particularly important for explaining the variability in production of and the variability in habitat use by YOY cutthroat trout in small streams above barriers. My findings support the observations by

Orth (1987), who recognized that interpreters of the present use of available habitat need to have a knowledge of past limiting events and need to recognize the importance of temporal biotic interactions in order to adequately assess use of stream habitat by fish.

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CHAPTER 4

Sampling Protocols for Improving the Validity and Precision of the Removal Method During Census of Small Populations of Fish

Patrick J. Connolly

Abstract

I used the population estimators of Seber and LeCren (1967) and Zippin (1956) to develop tables for use in the field that list acceptable ranges of observed catch from two and three removal passes. The ranges of acceptable values were based on an estimate for coefficient of variation (CV). For data from three passes, the values were also based on results of a chi-square test for the assumption of equal catchability.

Because the full multi-termed version of Zippin's (1956) estimator of variance (i.e., with Stirling's second-order approximation) was found to be more conservative than the use of his large-sample estimator when population size was less than 200, I used the full multi-termed version to derive estimates of CV. When two passes are conducted, use of Seber and LeCren's (1967) single-termed, large-sample estimator of variance was found to be more appropriate than use of higher-termed versions of this estimator for calculating variance from data on small populations. I discuss the use of other estimators of precision that do not depend on the assumption of normality for deriving confidence intervals for estimates of population size from removal data.

I examined a "rule-of-thumb", the so-called reduction rule, that allows an investigator to decide when to stop sampling based on the percentage of reduction in catch from one removal pass to a succeeding pass. When a reduction rule is applied after two passes, I found that it resulted in an inconsistent level of estimated precision. A reduction rule applied after three passes has potential to result in invalid or imprecise population estimates, or both.

Depending on the catchability and the catch on the first pass, conducting a third pass can decrease the estimate of standard error of a population estimate from 25 to 99%. The numerical difference between the resulting estimated standard errors after two versus three passes increases when the catchability decreases and when the catch on the first pass increases. When using a two-stage design, an investigator should consider conducting more removal passes at sampling units that result in low catchability and at units with a high abundance of individuals.

Introduction

The removal method is recognized as an effective way to assess population abundance of fish in small streams (Libosvarsky 1966, Cowx 1983, Bohlin et al. 1989). Although other estimators have been developed for calculating estimates for population size and variance from removal data (e.g., Carle and Strub 1978, Bohlin 1981, Harding et al. 1984, Hirst 1994), the estimators of Seber and LeCren (1967) for two passes and Zippin (1956, 1958) for three or more passes have been widely used to estimate fish populations within the last 30 years (e.g., Johnson 1965, Keller and Burnham 1982, Reeves et al. 1993).

The purpose of this paper is to provide information to help increase the understanding of the Seber and LeCren (1967) and Zippin (1956, 1958) estimators for estimating population size and variance from data obtained from the removal method. Increased understanding should help both investigator and reader to judge the limitations and appropriate use of these estimators. Although the examples presented and literature cited refer largely to fish, the guidelines and conclusions should be applicable to work with other closed populations of animals.

The need to estimate small populations (<200) of fish accurately and precisely often arises from the way sampling units are designated. Because of potentially differential catchabilities, an aggregate catch is often separated by species (Johnson 1965) and size class (Libosvarsky 1966), which can substantially reduce the size of the population to be sampled. Because it makes good biological sense to use habitat units (i.e., pool, riffle, glide, etc.) as sampling units for populations of stream fishes (Bisson et al. 1982, Hankin 1984), the population to be sampled can be small. For example, because small habitat units were sampled, Rodgers' et al. (1992) use of Seber and LeCren's (1967) estimator after two passes were conducted resulted in estimates of populations that were fewer than 10 fish. Their application and others (Bilby and Bisson 1992, Reeves et al. 1993) have used removal-depletion estimators to assess populations much lower than the minimum population sizes recommended by Bohlin (1982): a minimum of 100 to 200 for use of the Seber and LeCren (1967) estimator with two passes and a minimum of 50 to 200 for use of the Zippin (1956) estimator with three passes, depending on catchability. Bohlin (1982) showed that underestimation of the true population size and variance can result when these estimators are used for populations smaller than those recommended.

The estimators most commonly used for calculating variance and confidence intervals for removal data from two and three passes are simplified versions referred to as large-sample approximations (Appendix Table 4.1). Seber and LeCren (1967) stated (p. 632) that the large-sample estimator was satisfactory after two passes when $Np^3>16q^2(1+q)$, where N=population size, p=catchability, and q=1-p. Solving this equation algebraically (using whole numbers for catch on the first pass but not rounding of values for catch on the second pass), catchability would need to be at least 0.375 for an estimated population size of exactly 200, and would need to be at least 0.600 for an estimated population size of exactly 20 to meet this requirement. Zippin (1956) stated (p. 170) that the large-sample estimator can be used after three passes when the population size was 200 or more and when the catchability was less than 0.536 (in his terms: $[1-q^3]\leq 0.9$, where q is defined as above). The consequences of ignoring these limitations have not been adequately investigated.

Because of the non-normality of the distributions of estimated size of populations derived from Seber and LeCren (1967) and Zippin (1956) estimators, calculation of confidence intervals that assume normality have been shown to provide poor coverage of the true population size (Rexstad and Burnham 1991, Hirst 1994). Although I do not use confidence intervals as a measure of precision in the present study, I do use the coefficient of variation (CV). Because use of CV assumes asymptotic normality, my use of CV is restricted to serve as only an index of the undetermined true precision.

An important, but often overlooked, assumption of the removal method is that catchability remains constant from one removal pass to the next (Riley and Fausch 1992). Studies with sampling data (e.g., Johnson 1965, Bohlin and Sundstrom 1977, Heggberget and Hesthagen 1979) and with simulated data (e.g., Bohlin 1982, Otis et al. 1978, Riley and Fausch 1992) have shown that the accuracy of the Zippin (1956) estimator is sensitive to violation of this assumption of equal catchability. The problem can potentially be overcome by using Otis et al.'s (1978) generalized removal estimator that incorporates unequal catchability; however, their estimator requires four or more passes (Schnute 1983).

The use of two or three passes can save time for investigators and cause less stress for fish compared to sampling protocols that demand four or more passes. A number of practical rules for determining when to stop conducting passes have been suggested. Some of these are based on catchability (e.g., Seber and LeCren 1967, Schnute 1983, Bohlin et al. 1989), but they have not been widely adopted or tested. Others (e.g., Libosvarsky 1966, Platts et al. 1983, Riley and Fausch 1992) suggest a general increasing of the number of passes, usually to an equal number of passes for all sampling units, with the assertion that the average precision and validity can be improved compared with a sampling plan that calls for fewer passes per unit. However, because of evidence that electrofishing causes injury to fish (Hollender and Carline 1994), and affects fish behavior (Mesa and Schreck 1989), physiology (Schreck et al. 1976), and growth (Gatz et al. 1986), guidelines that limit sampling to the fewest passes possible, while maintaining high precision, are justified when they limit disturbance to a population.

A guideline for determining the number of passes to conduct that has recently been used in applied studies is the so-called "reduction rule". A reduction rule declares a minimum acceptable percent reduction in catch from one pass to a succeeding pass to determine when to stop sampling. Reeves et al. (1993) stipulated at least a 75% reduction in number of fish captured on successive passes to stop sampling, while Martin et al. (1994) stipulated a 50% reduction. Rodgers et al. (1992) used a level of 50% or 66% reduction in fish caught on a succeeding pass, depending on whether the first pass caught fewer than 10 fish or more than 10 fish, respectively. Because I found that a report on the quality of estimates derived from use of a reduction rule was lacking, I investigated the validity and precision of the estimates that result from using a 50% and 75% reduction rule.

Methods

To construct tables that would be usable in the field, I created data sets of catch sequences that were limited to first-pass catches of 100 or fewer individuals. I determined acceptable ranges of catch on the last pass based on a test for the assumption of equal catchability among passes for three-pass sequences and based on a level of estimated asymptotic precision for both two- and three-pass sequences. To test for equal catchability among passes, I used a chi-square test described by Seber (1982, p. 314). To ensure adequate power of the test, I set alpha at 0.2 to detect differences in catchability, following Otis et al. (1978). It should be noted that Riley and Fausch (1992) show that power may still be low for small populations at this alpha level. The CV was used as an estimate of precision, where $CV=(SE/N)\cdot 100$. Three levels of CV (5%, 12.5%, and 25%) were used to determine limits of acceptable catch on the second and third passes. Choice of estimators for calculating SE is described later in this methods section. A catch value from the second or third pass that did not fall within the acceptable range would indicate that at least one more pass was needed to meet the desired level of estimated precision or to meet the test for equal catchability.

I assessed the effects of population size, catchability, and sampling effort on the estimated variances of population estimates derived from two-pass and three-pass removal sequences. I created spreadsheets that calculated estimates of population size from Seber and LeCren's (1967) two-pass estimator and from Junge and Libosvarsky's (1965) explicit solution to Zippin's (1956) three-pass estimator (Appendix Table 4.1). I derived estimates of variance for all possible catch sequences with first passes ranging from 1 to 100 by 1 and catchabilities ranging from 0.2 to 0.9 by 0.1. Values for catch on later passes, and other values used in intermediate steps of the calculations, were not rounded. Three versions of Seber and LeCren's estimator were used to calculate variance for all two-pass sequences, and two versions of Zippin's estimator were used to calculate variance for all three-pass sequences. One estimate of variance was derived from Seber and LeCren's equation 2.2 for two passes and from Zippin's equation 16 for three passes (Appendix Table 4.1). These are the versions of the variance estimators that are most commonly used in fisheries studies when the Seber and LeCren and the Zippin estimators of population size are used, and will be referred to as large-sample estimators in the text that follows. I derived the other two estimates of variance for the two-pass sequences by using Seber and LeCren's equation 2.1: one estimate was with and one estimate was without the correction for bias. I calculated the second estimate of variance for the three-pass sequences by using Zippin's equation 11 substituted in his equation 15. These latter three versions of the estimator of variance have more terms in the formulas than the large-sample versions, and thus these versions are referred to as "full multi-termed" in the text that follows.

To determine which version of the estimator to use for calculating variance and CV of population estimates for the field tables, I first examined the differences among estimates of variance from Seber and LeCren's (1967) and Zippin's (1956) large-sample versions and those derived from full multi-termed versions. Because differences were small among the large-sample and the two multi-termed versions when catchabilities were between 0.2 and 0.9 for two passes, I used Seber and LeCren's large-sample approximation for estimating CV and deriving values for the field table. With three passes, Zippin's full multi-termed version for estimating variance (i.e., with Stirling's second-order approximation, Appendix Table 4.1) often resulted in substantially higher estimates of variance than those from the large-sample version. Because the full multi-termed version was generally more conservative than the large-sample version (i.e., led to higher estimates of variance), I used the full multi-termed version for estimating CV and deriving values for the field tables when catch on the first pass was more than 10. When the full multi-termed version was not more conservative (e.g., most sequences of catch when catchability was 0.9), the choice of estimators had no differential effect on the acceptance of a catch sequence based on the precision levels chosen for the table (i.e., CV not more than 5%, 12.5%, and 25%). Because the behavior of the full multi-termed version was deemed unrealistic when catch on the first pass was lower than about 10, especially when catchabilities were <0.6, I used the large-sample version for calculating CV and creating a separate field table to indicate acceptable catch sequences when catch on the first pass was 10 or fewer. The differences between these estimates of variance are more fully presented in the results section below.

I evaluated two reduction rules, 50% and 75%, to determine if they were appropriate for determining when an additional pass is needed. For two-pass sequences, I determined the minimum acceptable catch on the first pass that resulted in a CV of not more than 5%, 12.5%, or 25% for all possible catch sequences that met an individual reduction rule. The values for minimum acceptable catch were obtained by solving the Seber and LeCren (1967) estimator for N and their large-sample estimator for SE for two passes (Appendix Table 4.1). For three passes, I compared the decisions that resulted from use of 50% and 75% reduction rules with the decisions that resulted from the use of my tabulated ranges of acceptable values. As more fully detailed above, these tabulated ranges were based on a test for equal catchability among passes and on levels of CV not more than 5%, 12.5%, or 25%.

To determine when it would be advantageous to conduct a third pass, I compared the estimates of SE obtained after two and three passes. Catchability was held constant and ranged from 0.2 to 0.9 by 0.1. I calculated the numerical difference and percent change in SE from estimates obtained after two passes to those obtained after three passes.

Results

Tables 4.1-4.3 can be used to decide when a third or fourth pass is needed. When two passes have been completed, Table 4.1 can be used to determine if a third pass is needed. When three passes have been completed, Table 4.2 and Table 4.3 can be used to decide if a fourth pass is needed. The use of Tables 4.1-4.3 in the field will ensure that Seber and LeCren (1967) and Zippin (1956) estimates for population size meet predetermined levels of estimated CV. When three passes have been conducted, use of Tables 4.2 and 4.3 ensures that the observed catch sequence will pass a test for the assumption of equal catchability (chi-square, $p>0.2$).

Table 4.1. Maximum acceptable catch on the second removal pass to ensure an estimate of coefficient of variation of not more than a) 5%, b) 12.5%, and c) 25% when catch on the first pass is 11-100 for a Seber and LeCren (1967) two-pass population estimate. If more are caught, at least a third pass is needed to ensure the desired level of precision.

First-pass catch	Maximum catch on second pass so that the coefficient of variation [a] is		
	≤5%	≤12.5%	≤25%
1	0	0	0
2	0	0	0
3	0	0	0
4	0	0	1
5	0	1	1
6	0	1	2
7	0	1	2
8	0	1	3
9	1	2	3
10	1	2	4
11	1	2	4
12	1	3	5
13	1	3	5
14	2	4	6
15	2	4	6
16	2	4	7
17	2	5	7
18	2	5	8
19	3	6	8
20	3	6	9
25	4	8	12
30	6	11	15
35	7	13	19
40	8	16	22
45	10	18	25
50	12	21	29
60	15	26	36
70	18	32	43
80	22	38	50
90	26	44	58
100	30	50	65

[a] Coefficient of variation = (SE/N)·100, where N = population estimate and SE = standard error estimate. N and SE were calculated with the two-pass, large-sample estimator of Seber and LeCren (1967).

Table 4.2. Range of acceptable catch on a third pass to ensure an estimate of coefficient of variation of not more than a) 5%, b) 12.5%, and c) 25% when catch on the first pass is 11-100. At least a fourth pass is needed when catch from the third pass is not within the stated range or where an "x" appears. Values are based on the maximum likelihood estimator of Zippin (1956) and a chi-square test (alpha $\geq$0.2) for equal catchability from Seber (1982, p. 314). CV was defined as (SE/N)·100, where N = population estimate using Zippin's (1956) equation 6 and SE = standard error using Zippin's (1956) full multi-termed estimator, which was derived by substituting his equation 11 in his equation 15 (see Appendix Table 4.1).

Table 4.2a. Range of acceptable catch on the third pass to ensure that the estimated coefficient of variation is not more than 5%.

Pass-one catch	Pass-two catch																			
	1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	16	17	18	19	20
11	0-1	0-1	0-1	0	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x
12	0	0-1	0-1	0	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x
13	0	0-1	0-1	0	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x
14	0	0-1	0-1	0-1	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x
15	0	0-1	0-1	0-1	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x
16	0	0-1	0-1	0-1	0	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x
17	0	0-1	0-1	0-1	0-1	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x
18	0	0-1	0-2	0-1	0-1	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x
19	0	0-1	0-2	0-1	0-1	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x
20	0	0-1	0-2	0-1	0-1	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x

Pass-one catch	Pass-two catch																			
	5	10	15	20	25	30	35	40	45	50	55	60	65	70	75	80	85	90	95	100
25	0-1	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x
30	0-3	1-2	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x
35	0-2	1-4	3	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x
40	0-2	1-6	2-5	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x
45	0-2	1-5	2-6	4-5	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x
50	0-1	1-5	2-8	4-8	6	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x
60	0-1	1-4	1-8	3-12	5-10	8-9	x	x	x	x	x	x	x	x	x	x	x	x	x	x
70	0-1	0-4	1-7	3-11	4-14	7-13	10-12	x	x	x	x	x	x	x	x	x	x	x	x	x
80	0-1	0-3	1-6	2-10	4-14	6-18	9-16	12-15	x	x	x	x	x	x	x	x	x	x	x	x
90	0-1	0-3	1-5	2-9	3-12	5-17	8-21	10-20	14-19	17	x	x	x	x	x	x	x	x	x	x
100	0-1	0-2	1-5	2-8	3-11	5-16	7-20	9-25	12-24	16-23	19-21	x	x	x	x	x	x	x	x	x

Table 4.2b. Range of acceptable catch on the third pass to ensure that the estimated coefficient of variation is not more than 12.5%.

Pass-one catch	Pass-two catch 1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	16	17	18	19	20
11	0-1	0-1	0-1	0	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x
12	0	0-1	0-1	0	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x
13	0	0-1	0-1	0	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x
14	0	0-1	0-1	0-1	1	1	1	x	x	x	x	x	x	x	x	x	x	x	x	x
15	0	0-1	0-2	0-2	1-2	1-2	1	1	x	x	x	x	x	x	x	x	x	x	x	x
16	0	0-1	0-2	0-3	0-2	1-2	1	1	2	x	x	x	x	x	x	x	x	x	x	x
17	0	0-1	0-2	0-3	0-2	1-2	1-3	1-2	2	2	x	x	x	x	x	x	x	x	x	x
18	0	0-1	0-2	0-3	0-4	1-3	1-3	1-3	2	2	x	x	x	x	x	x	x	x	x	x
19	0	0-1	0-2	0-3	0-4	1-4	1-3	1-3	1-3	2-3	2-3	x	x	x	x	x	x	x	x	x
20	0	0-1	0-2	0-3	0-4	1-4	1-4	1-4	1-4	2-3	2-3	3	3	x	x	x	x	x	x	x

Pass-one catch	Pass-two catch 5	10	15	20	25	30	35	40	45	50	55	60	65	70	75	80	85	90	95	100
25	0-3	1-6	4-5	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x
30	0-3	1-8	3-8	6-7	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x
35	0-2	1-7	3-11	6-10	9	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x
40	0-2	1-6	2-12	5-13	8-12	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x
45	0-2	1-5	2-10	4-16	7-15	11-14	x	x	x	x	x	x	x	x	x	x	x	x	x	x
50	0-1	1-5	2-9	4-15	6-18	10-17	14-16	x	x	x	x	x	x	x	x	x	x	x	x	x
60	0-1	1-4	1-8	3-13	5-19	8-23	12-23	16-22	21	x	x	x	x	x	x	x	x	x	x	x
70	0-1	0-4	1-7	3-11	4-16	7-22	10-29	14-28	18-28	23-27	x	x	x	x	x	x	x	x	x	x
80	0-1	0-3	1-6	2-10	4-14	6-19	9-25	12-32	15-34	20-34	24-33	30-32	x	x	x	x	x	x	x	x
90	0-1	0-3	1-5	2-9	3-12	5-17	8-22	10-28	14-35	17-40	22-40	26-39	32-38	37	x	x	x	x	x	x
100	0-1	0-2	1-5	2-8	3-11	5-16	7-20	9-26	12-32	16-38	19-45	24-46	28-45	33-44	39-44	x	x	x	x	x

Table 4.2c. Range of acceptable catch on the third pass to ensure that the estimated coefficient of variation is not more than 25%.

Pass-one catch	Pass-two catch																			
	1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	16	17	18	19	20
11	0-1	0-2	0-2	0-2	1-2	1-2	1	2	x	x	x	x	x	x	x	x	x	x	x	x
12	0	0-2	0-3	0-3	1-2	1-3	1-2	2	2	x	x	x	x	x	x	x	x	x	x	x
13	0	0-2	0-3	0-4	1-3	1-3	1-3	2-3	2-3	3	x	x	x	x	x	x	x	x	x	x
14	0	0-2	0-3	0-4	1-4	1-4	1-4	2-4	2-3	3	3	x	x	x	x	x	x	x	x	x
15	0	0-1	0-2	0-4	1-5	1-5	1-4	1-4	2-4	2-4	3-4	4	x	x	x	x	x	x	x	x
16	0	0-1	0-2	0-4	0-5	1-5	1-5	1-5	2-5	2-5	3-4	4	4	x	x	x	x	x	x	x
17	0	0-1	0-2	0-3	0-5	1-6	1-6	1-6	2-5	2-5	3-5	3-5	4-5	x	x	x	x	x	x	x
18	0	0-1	0-2	0-3	0-5	1-6	1-6	1-6	2-6	2-6	3-6	3-5	4-6	5-6	x	x	x	x	x	x
19	0	0-1	0-2	0-3	0-4	1-6	1-7	1-7	1-7	2-6	2-7	3-7	4-6	4-6	5-6	6	x	x	x	x
20	0	0-1	0-2	0-3	0-4	1-5	1-7	1-7	1-8	2-8	2-7	3-7	3-7	4-7	5-7	6	x	x	x	x

Pass-one catch	Pass-two catch																			
	5	10	15	20	25	30	35	40	45	50	55	60	65	70	75	80	85	90	95	100
25	0-3	1-10	4-10	8-9	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x
30	0-3	1-8	3-14	6-13	11-12	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x
35	0-2	1-7	3-13	6-17	9-16	14-15	x	x	x	x	x	x	x	x	x	x	x	x	x	x
40	0-2	1-6	2-12	5-19	8-20	13-19	18	x	x	x	x	x	x	x	x	x	x	x	x	x
45	0-2	1-5	2-10	4-17	7-23	11-23	16-22	22	x	x	x	x	x	x	x	x	x	x	x	x
50	0-1	1-5	2-9	4-15	6-22	10-27	14-26	19-26	25	x	x	x	x	x	x	x	x	x	x	x
60	0-1	1-4	1-8	3-13	5-19	8-26	12-34	16-33	21-33	27-32	x	x	x	x	x	x	x	x	x	x
70	0-1	0-4	1-7	3-11	4-16	7-22	10-29	14-36	18-41	23-40	28-40	34-39	x	x	x	x	x	x	x	x
80	0-1	0-3	1-6	2-10	4-14	6-19	9-25	12-32	15-39	20-48	24-48	30-47	36-47	42-46	x	x	x	x	x	x
90	0-1	0-3	1-5	2-9	3-12	5-17	8-22	10-28	14-35	17-42	22-50	26-56	32-55	37-55	43-54	50-54	x	x	x	x
100	0-1	0-2	1-5	2-8	3-11	5-16	7-20	9-26	12-32	16-38	19-45	24-53	28-61	33-63	39-62	45-62	51-62	58-61	x	x

Table 4.3. Range of acceptable catch on a third pass to ensure that the estimated coefficient of variation is not more than 5%, 12.5%, and 25% when catch on the first pass is 10 or fewer. Values are based on the maximum-likelihood estimator of Zippin (1956) and a chi-square test (alpha >0.2) to ensure equal catchability following Seber (1982, p. 314). At least a fourth pass is needed when catch from the third pass is not within the stated range or where an "x" appears.

Pass-one catch	Pass-two catch									
	1	2	3	4	5	6	7	8	9	10
Coefficient of variation not more than 5%.[a]										
1	x	x	x	x	x	x	x	x	x	x
2	x	x	x	x	x	x	x	x	x	x
3	x	x	x	x	x	x	x	x	x	x
4	0	x	x	x	x	x	x	x	x	x
5	0	x	x	x	x	x	x	x	x	x
6	0	0	x	x	x	x	x	x	x	x
7	0	0	0	x	x	x	x	x	x	x
8	0-1	0	0	x	x	x	x	x	x	x
9	0-1	0-1	0	x	x	x	x	x	x	x
10	0-1	0-1	0-1	x	x	x	x	x	x	x
Coefficient of variation not more than 12.5%.										
1	x	x	x	x	x	x	x	x	x	x
2	x	x	x	x	x	x	x	x	x	x
3	0	0	x	x	x	x	x	x	x	x
4	0	0	0	x	x	x	x	x	x	x
5	0-1	x	x	x	x	x	x	x	x	x
6	0-1	0	0	x	x	x	x	x	x	x
7	0-1	0	0	x	x	x	x	x	x	x
8	0-1	0-1	0-1	1	1	x	x	x	x	x
9	0-1	0-2	0-2	1	1	1	x	x	x	x
10	0-1	0-2	0-2	1-2	1	1	x	x	x	x
Coefficient of variation not more than 25%.										
1	x	x	x	x	x	x	x	x	x	x
2	x	x	x	x	x	x	x	x	x	x
3	0	0	x	x	x	x	x	x	x	x
4	0	0	0	x	x	x	x	x	x	x
5	0-1	1	1	x	x	x	x	x	x	x
6	0-2	0-1	0-1	1	1	x	x	x	x	x
7	0-1	0-2	0-2	1	1	1	x	x	x	x
8	0-1	0-2	0-2	1-2	1-2	1-2	2	x	x	x
9	0-1	0-3	0-3	1-3	1-3	1-2	2	2	x	x
10	0-1	0-2	0-4	1-3	1-3	1-3	1-3	2	x	x

[a] The coefficient of variation was defined as (SE/N)·100 where N=population estimate using Zippin's (1956) equation 6 and SE=standard error estimate calculated from Zippin's (1956) equation 16 for large-sample approximation of variance.

Use of a reduction rule with the two-pass estimator of Seber and LeCren (1967) may require the impossibility that the catch on the first pass be larger than the total population to also achieve a desired level of estimated precision (Table 4.4). If increased precision is desired, the minimum catch required on the first pass increases markedly if one wishes to be ensured that all possible two-pass catch sequences that meet the reduction rule will also meet a specified precision level. The estimated precision of a population estimate is not constant for equivalent percentages of reduction in catch over a range of first-pass catches. Therefore, use of a reduction rule becomes increasingly inefficient as the first-pass catch gets larger than the minimum required. For example, if an estimated CV of 12.5% were considered sufficient, a 75% reduction rule applied to a first-pass catch of 16 would work for all acceptable catches (range: 0-4) identified in Table 4.1. A first-pass catch of 100, however, would require a catch on the second pass to be 25 or fewer in order to stop sampling under a 75% reduction rule. From Table 4.1, we find that this rule would lead to a decision to conduct an unnecessary third pass if the catch on the second pass ranges from 26 to 50, because any catch on the second pass ranging from 0 to 50 would result in the desired CV of not more than 12.5%.

A reduction rule applied to the pattern of catch between the second and third pass may result in decisions about the need for conducting a fourth pass that conflict with decisions based on criteria of estimated CV and equal catchability. For example, a 75% reduction rule applied to a catch sequence of 100-50-10 (i.e., an 80% reduction between the second and third pass) would result in a decision not to conduct a fourth pass. In the top left graph of Figure 4.1, this catch sequence is a point that lies in the unshaded area above the 75%-rule line and to the right of the darkest shaded area. This decision would result in an invalid population estimate because it fails a chi-square test for equal catchability among passes (p=0.032). Too few passes would have been conducted no matter what precision was desired. If the catch for the third pass were 20 (i.e., a 60% reduction) instead of 10, the use of a 75% reduction rule would dictate the need for another pass when in fact the three-pass sequence of 100-50-20 would pass a chi-square test for equal catchability (p=0.548) and would result in a population estimate of 188 with

Table 4.4. Minimum acceptable catch on the first removal pass to achieve a desired level of estimated precision for all possible two-pass catch sequences that meet a 50% or 75% reduction rule. Use of a reduction rule for a first-pass catch lower than the minimum may result in a population estimate with a precision poorer than that desired for some catch sequences.

Desired level of coefficient of variation[a]	Minimum acceptable catch on pass one	
	50% rule	75% rule
≤5.0%	600	56
≤12.5%	96	9
≤25.0%	24	3

[a] Coefficient of variation = (SE/N)·100, where N = population estimate and SE = standard error estimate. N and SE were calculated with the two-pass, large-sample estimator of Seber and LeCren (1967).

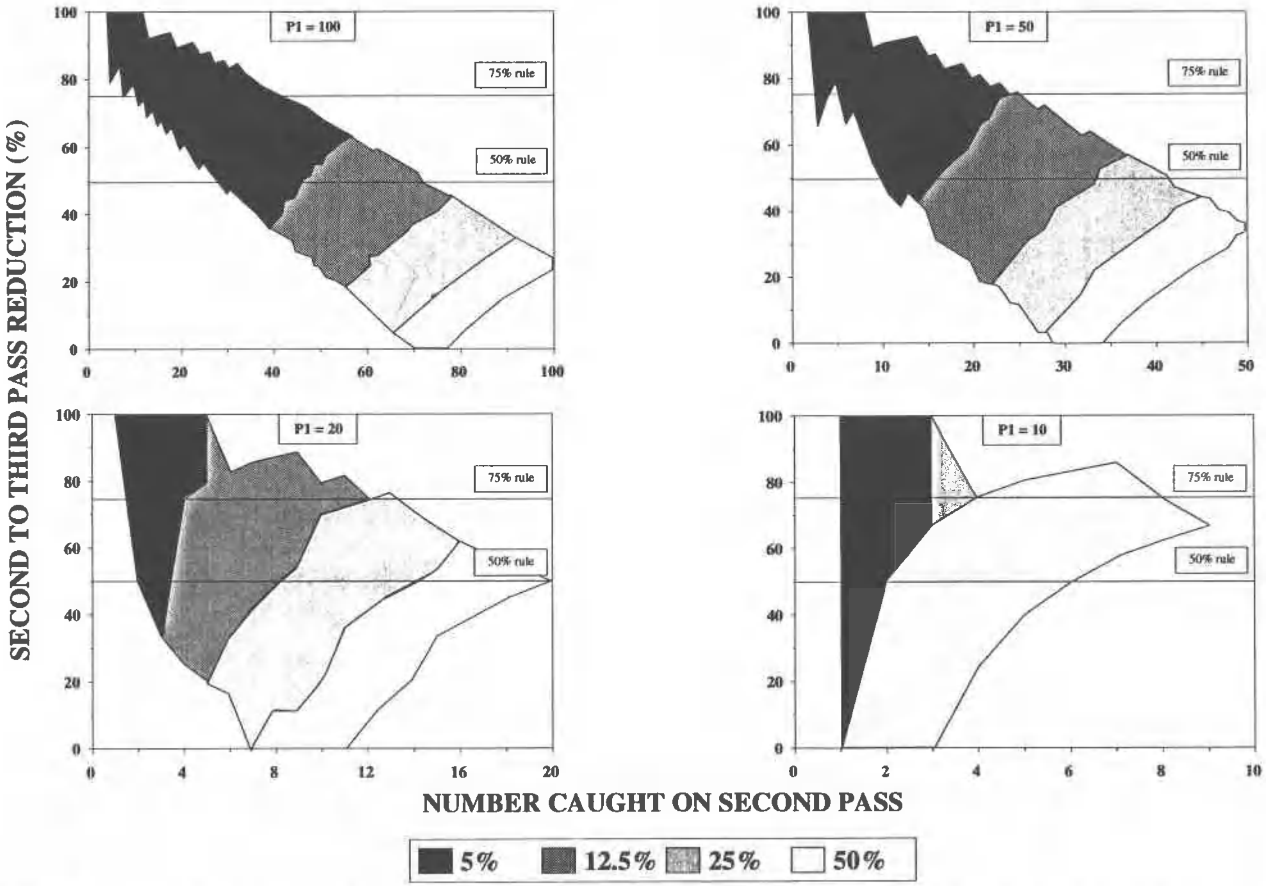

Figure 4.1. Effectiveness of two reduction rules applied to the catch on a third pass (P3) relative to catch on a second pass (P2) for catch on the first pass (P1) of 100, 50, 20, and 10. The shaded regions indicate precision levels where coefficient of variation (CV) is not more than 5%, 12.5%, 25%, and 50%. Catch sequences that fall outside the shaded regions result in a CV>50%, or fail to pass a chi-square test (alpha > 0.2) for equal catchability (Seber 1982, p. 314), or both. CV was defined as (SE/N)·100, where N=population estimate using Zippin's (1956) equation 6 and SE = standard error estimate using Zippin's (1956) equation 11 substituted in equation 15. Percentage reduction in catch from P2 to P3 was defined as [(P2-P3)/P2]·100.

a relatively low CV of 4.4%. In the top left graph of Figure 4.1, this catch sequence is a point that lies in the darkest shaded area just above the 50%-rule line.

Estimates of variance for data from two passes were directly and linearly related to the number caught on the first pass for all three versions of the Seber and LeCren (1967) estimator tested (large-sample approximation, multi-termed version without correction for bias, and multi-termed version with correction for bias) at all levels of catchability from 0.2 to 0.9 (Figure 4.2). The estimates from the large-sample version were smaller than, but similar to, those from the multi-termed version not corrected for bias. When the correction for bias was included, the magnitude of effect on the estimates of variance varied with catchability. When catchability was <0.6, negative values for estimated variance resulted with use of this latter version for some of the smaller catches on the first pass.

Estimates of variance from Zippin's (1956) large-sample estimator for three passes were sometimes substantially different than those from the full multi-termed version of this estimator. Within all tested levels of catchability (0.2-0.9), the magnitude of difference between these two estimators for variance varied with the catch on first pass and the catchability (Figure 4.3). The relationship between the estimated variance and catch on first pass was linear for the large-sample version and was non-linear for the full multi-termed version. When catch on the first pass was higher than 10 to 15, the estimates of variance from the full multi-termed version were directly related to the number caught on the first pass. When catch on the first pass was 10 or fewer, the full multi-termed version produced estimates that were subject to steep increases and decreases as catch on first pass changed, especially when catchability was 0.6 or less. As estimates for the population size decreased, the ratio between these two estimates of variance became more highly affected by catchability (Figure 4.4). Because estimates of population size were directly and linearly related to catch on first pass when catchability was held constant, the differential patterns of ratios between the two estimates of variance depicted in Figure 4.3 are similar to those depicted in Figure 4.4. The graphs of ratios in Figure 4.4 show that the large-sample version produced values that were consistently lower than the values produced from the full multi-termed version when the estimated

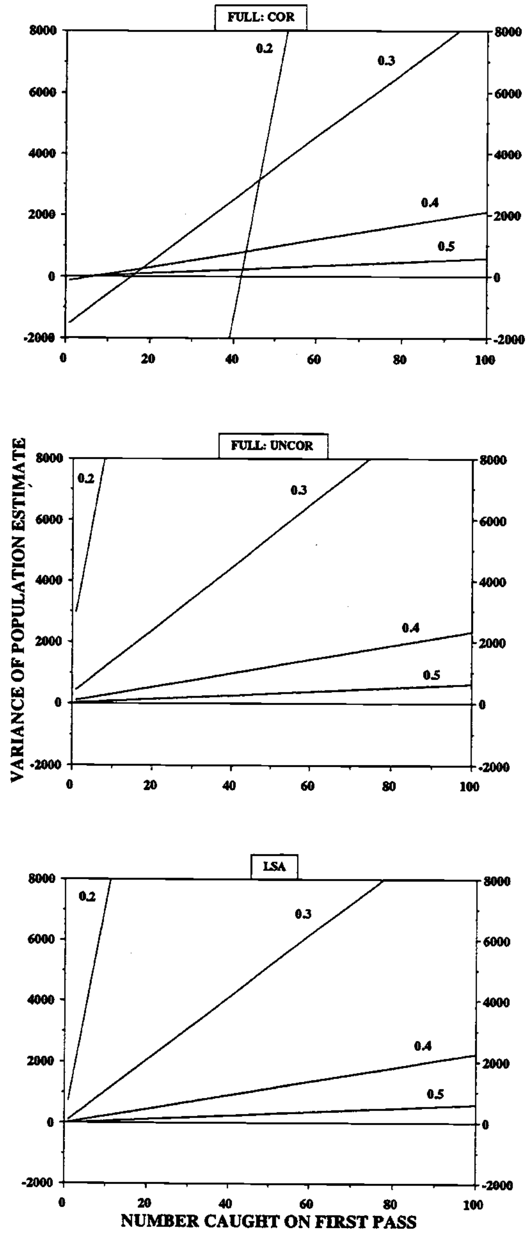

Figure 4.2. Three estimates of variance, following Seber and LeCren (1967), after two removal passes, as catch on the first pass ranges from 1 to 100. Catchabilities from 0.2 to 0.5 are depicted in the first series of three graphs, and from 0.6 to 0.9 are depicted in the second series. Note that the scale of the y-axis differs between the two series. The estimates of variance were derived from Seber and LeCren's (1967) equation 2.2 (large-sample approximation = LSA) and equation 2.1 (full multi-termed estimator): corrected (FULL-COR) and not corrected for bias (FULL-UNCOR). Catchability is the probability of capture during a pass and was held constant (see Appendix Table 4.1 for formulas).

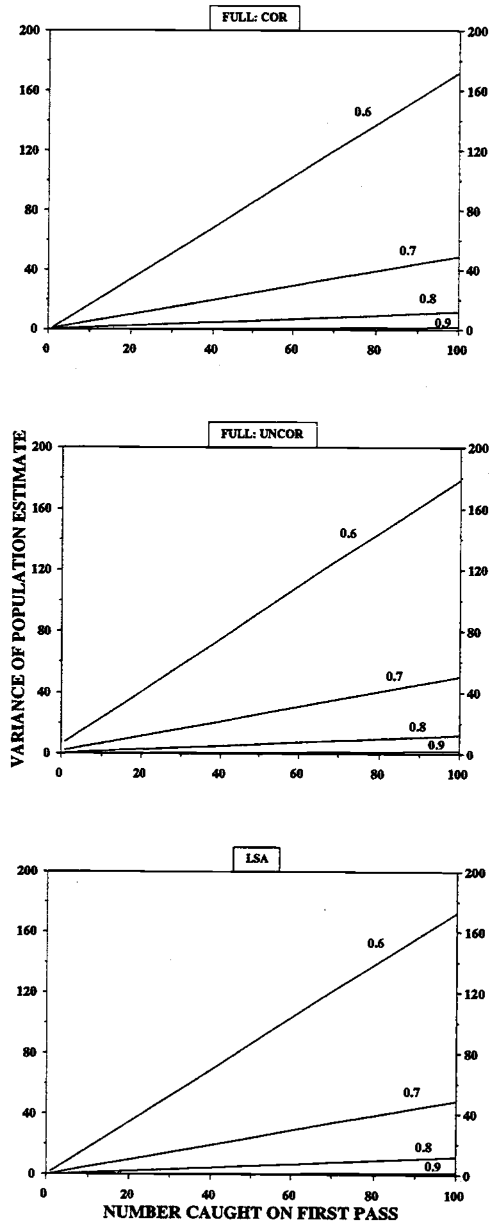

Figure 4.2. Continued.

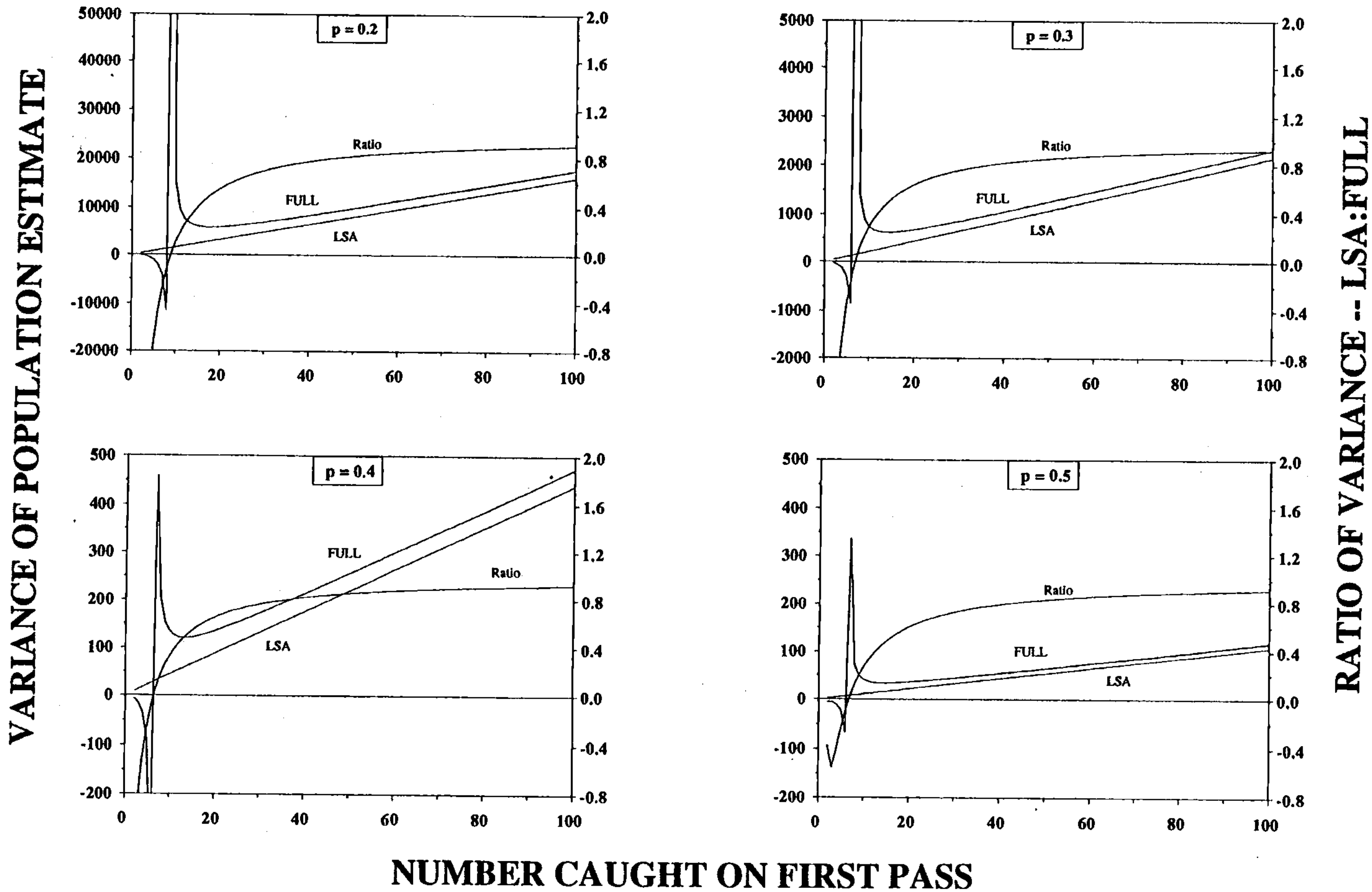

Figure 4.3. Two estimates of variance, and the ratio between them, following Zippin (1956) after three removal passes when catch on the first pass ranges from 1 to 100. Each graph depicts a different catchability (p) from 0.2 to 0.9. Note the change in scale for the y-axis among the graphs. The estimates of variance were derived by substituting Zippin's equation 11 (full multi-termed version = FULL) or equation 12 (large-sample approximation = LSA) into his equation 15. Catchability is the probability of capture during a pass and was held constant for each pass.

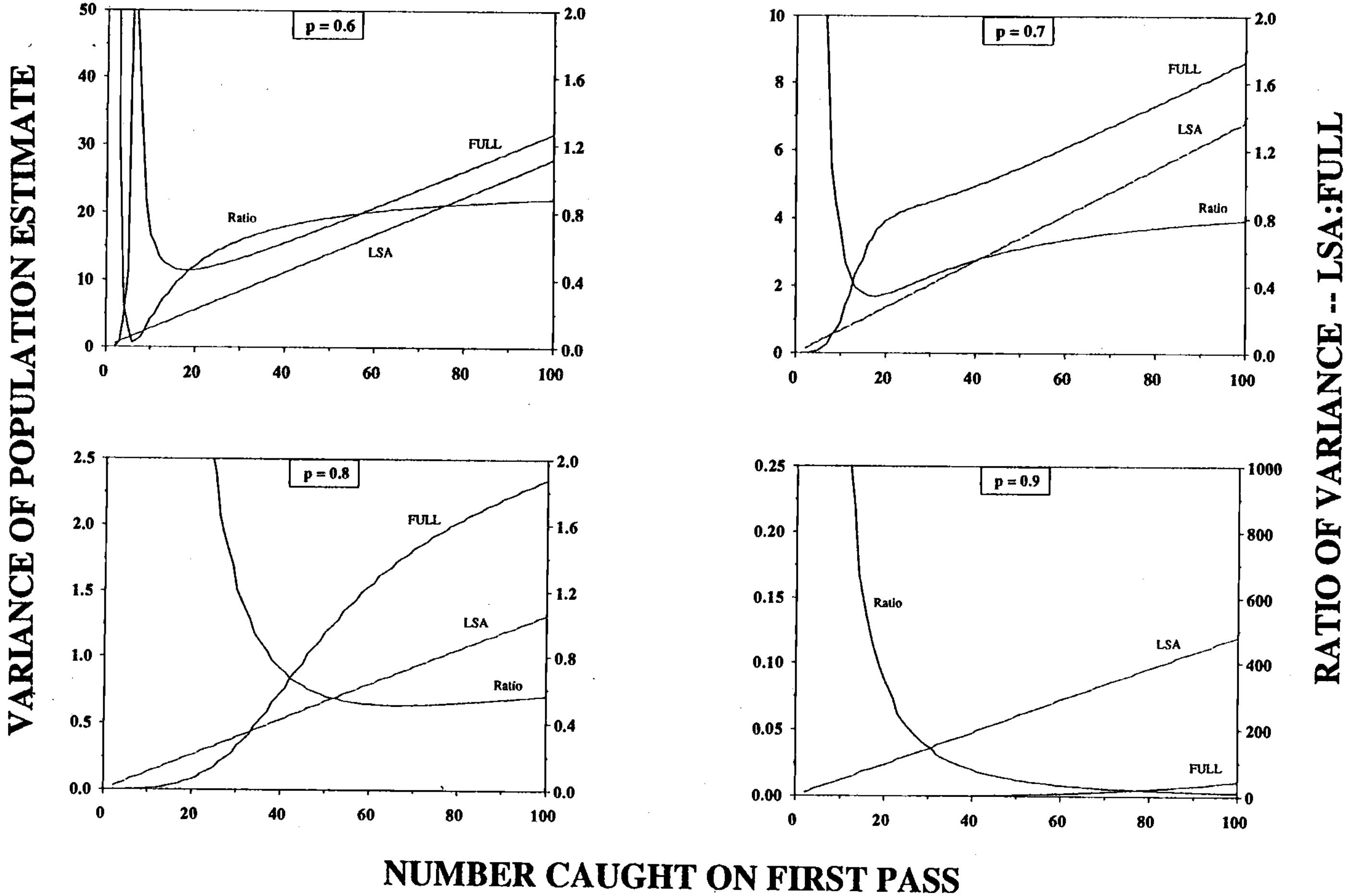

Figure 4.3. Continued.

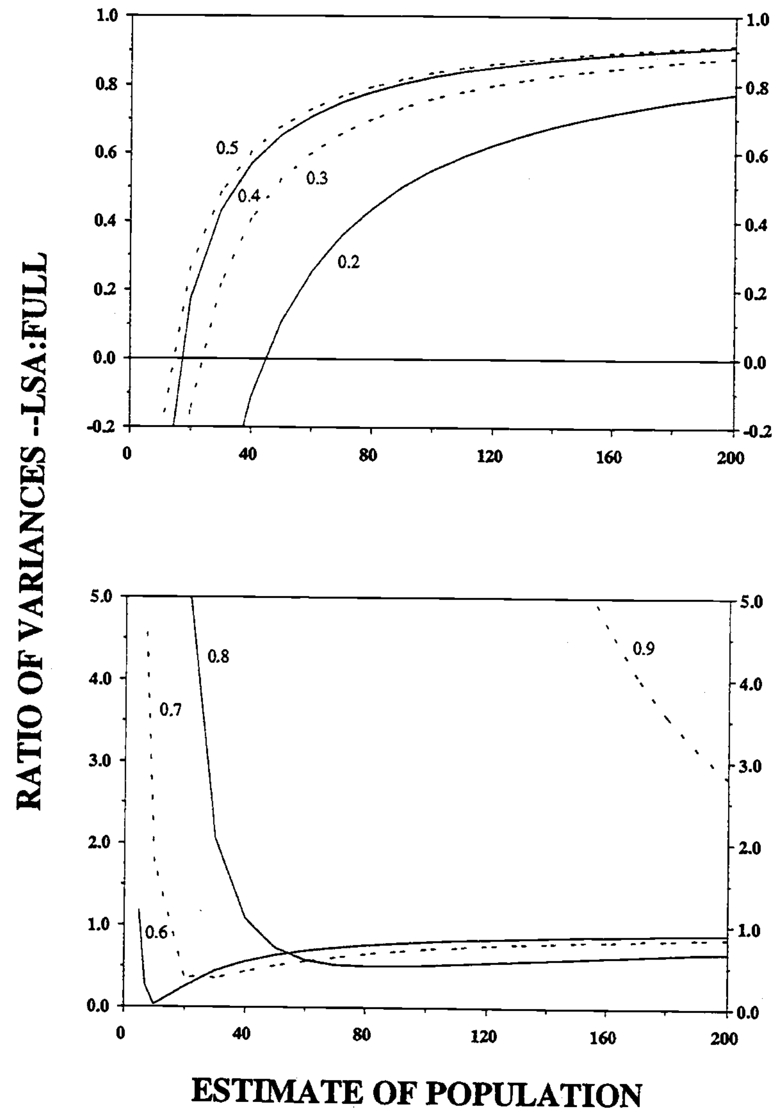

Figure 4.4. Ratios of the variances estimated from the large-sample approximation estimator (LSA) to the full multi-termed estimator (FULL) following Zippin (1956) for three removal passes. Catchability ranges from 0.2 to 0.5 in the upper graph and ranges from 0.6 to 0.9 in the lower graph. A ratio of 1.0 occurs when the two estimates of variance are equal. Note the change in scale for the y-axis between the two graphs.

population was above 100 and when catchability was between 0.3 and 0.7 (ratios: 0.71-0.92). At these catchabilities, the ratio between the large-sample and multi-termed versions progressively decreased as the estimated population decreased below 100 to at least 20. When the estimated population was below 20 and catchability was 0.6 or higher, the full multi-termed version produced some substantially higher estimates for variance than the large-sample version (ratio >2.0). At a catchability of 0.8 or 0.9, the ratio between the large-sample and full multi-termed versions deviated substantially from a ratio of 1.0 (ratio <0.7 or >1.3) at most values for estimated populations below 200.

Compared with stopping at two passes, conducting a third pass can substantially decrease the estimate of SE. It is important to note that the Seber and LeCren (1967) two-pass estimator gives the same estimate of population size that the Zippin (1956) three-pass estimator does when the catch sequence on the first two passes is the same and the catchability is constant. But, depending on the catch of the first pass and on the catchability, a 25 to 99% reduction in SE can be obtained by conducting a third pass (Table 4.5). The percentage reductions in SE for lower catchabilities are lower than those for high catchabilities at any given catch on the first pass, but the numerical differences in SE are substantially larger at the lower catchabilities than at the higher catchabilities.

Discussion

Tables in this paper (Tables 4.1, 4.2, and 4.3) provide field personnel with readily available information for making appropriate decisions about the need for a third or fourth pass during census of small populations with the removal method. The use of these tables will allow field personnel to know if an observed catch sequence after two or three passes meets the level of estimated precision that is desired and, after three passes, if the catch sequence passes a test for equal catchability. Better decisions at the sampling unit level should allow more effective distribution of effort among sampling units and will help avoid unwarranted disturbance to the aquatic community.

Table 4.5. Difference (D) and percentage reduction (PR) in the standard error of the population estimate (SE) if a third pass is conducted instead of two passes, with the condition of constant catchability. SE was calculated by taking the square root of the variance obtained from Seber and LeCren's (1967) large-sample estimator for two passes or from Zippin's (1956) fuller estimator for three passes (see Appendix 4.1).

Catch on first pass	Catchability															
	0.2		0.3		0.4		0.5		0.6		0.7		0.8		0.9	
	D	PR	D	PR	D	PR	D	PR	D	PR	D	PR	D	PR	D	PR
15	26	25	14	37	7	40	4	39	1.7	33	1.0	38	1.1	86	0.5	99
20	43	36	19	43	10	45	5	46	2.5	42	1.1	36	1.2	81	0.6	99
25	55	41	23	46	11	48	6	49	3.1	47	1.4	41	1.3	76	0.6	98
30	64	43	26	47	13	49	7	50	3.6	50	1.7	45	1.3	69	0.7	98
35	71	45	29	48	14	50	7	52	4.0	51	2.0	47	1.3	65	0.7	97
40	78	46	32	49	15	51	8	52	4.4	53	2.2	50	1.3	61	0.8	97
45	85	47	34	50	16	52	9	53	4.7	54	2.4	51	1.3	58	0.8	97
50	90	48	36	50	18	52	9	54	5.0	54	2.6	53	1.3	55	0.9	96
60	101	49	40	51	19	53	10	54	5.6	55	2.9	54	1.4	53	1.0	95
70	111	49	44	52	21	53	11	55	6.2	56	3.3	56	1.5	53	1.0	94
80	119	50	47	52	23	54	12	55	6.6	57	3.5	57	1.6	54	1.1	94
90	127	50	50	52	24	54	13	56	7.1	57	3.8	57	1.8	54	1.1	93
100	135	50	53	52	26	54	14	56	7.5	57	4.0	58	1.9	55	1.2	92

Use of reduction rules to determine the need for an additional pass can result in potentially poor decisions for many catch sequences. A reduction rule applied after two passes can result in poor estimates of precision for small populations and can result in unnecessarily high precision for large populations. A reduction rule applied after three passes can result in too little effort or too much effort to meet a desired level of estimated precision, and it may lead to catch sequences with unequal catchabilities. Because true precision was not determined, my comparison of the results from use of a reduction rule to those from use of the field tables was not a definitive comparison, but the potential for violating the assumption for equal catchability with use of a reduction rule is clearly a problem that needs to be addressed.

Comparisons between removal and mark-recapture methods deserve further attention. When electrofishing lowers subsequent catchability of fish, it has been reported that the removal method provides less accurate and less precise estimates for populations of stream fishes than those from mark-recapture methods (Bohlin et al. 1989). However, some investigators who have compared mark-recapture with removal methods used catch sequences that were not tested for the assumption of equal catchability and either were obtained from a set number of passes per unit (e.g., Heggberget and Hesthagen 1979, Peterson and Cederholm 1984) or were obtained after the use of a reduction rule to determine when to stop conducting passes (e.g., Rodgers et al. 1992). Stopping removal efforts before a desired level of precision is met, or when the assumption of equal catchability is not met, may not allow an adequate comparison of the methods; it may simply limit the chance that the removal method will perform adequately.

The large-sample version of the Seber and LeCren (1967) estimator was generally preferable to the two multi-termed versions of the estimator for variance of a population estimate derived from two passes for the ranges of catch sequences that I considered (catch on first pass $\leq$100). Many of the values obtained from the full multi-termed version that included a correction for bias did not appear reasonable because negative values resulted when the catch on first pass and the catchability were low. However, it was not determined which of the three versions of the estimator would result in estimates closer to the true variances.

Use of Stirling's second-order approximation within Zippin's (1956) estimator for variance is generally more conservative than use of his simplified large-sample version when the estimated population size is less than 200, especially when catchability is low (<0.6). When population size is about 40 or lower and catchability is high (>0.7), estimates of variance from the large-sample version may appear more reasonable than those derived from the full multi-termed version, but neither estimator may provide adequate estimates of the true variances. Additional theoretical work is needed in this area.

Confidence intervals constructed from estimators that assume an asymptotic normal distribution of the estimate of population size tend to be too narrow for small populations (Aitkin et al. 1989, p. 83). For this reason the preferred option may be to use other estimators to derive confidence intervals that do not depend on the assumption of normality, such as those based on the log-normal distribution or a profile likelihood ratio (Rexstad and Burnham 1991). Hirst (1994) showed that the assumption of asymptotic normality for constructing confidence intervals based on maximum likelihood estimates can fail for some commonly observed catch sequences, and he suggests the use of the asymmetric profile likelihood to construct confidence intervals (Figure 4.5). Recently Fausch and Northcote (1992) and Riley and Fausch (1995) used log-based intervals for estimating precision of population estimates for stream salmonids obtained by the removal method.

When reduction of variance, or increase in precision, is desired, substantial gains may be made by increasing the number of passes from two to three. At least three passes are needed to test for the assumption of equal catchability, and at least four passes are needed to use estimators that account for unequal catchability among passes (White et al. 1982, Schnute 1983). A number of investigators have recognized that more than three passes are needed to achieve adequate precision in some situations (Libosvarsky 1966, Raleigh and Short 1981, Van Deventer and Platts 1983). Some degree of unequal catchability was allowed in the field tables (Tables 4.2 and 4.3), but large deviations were

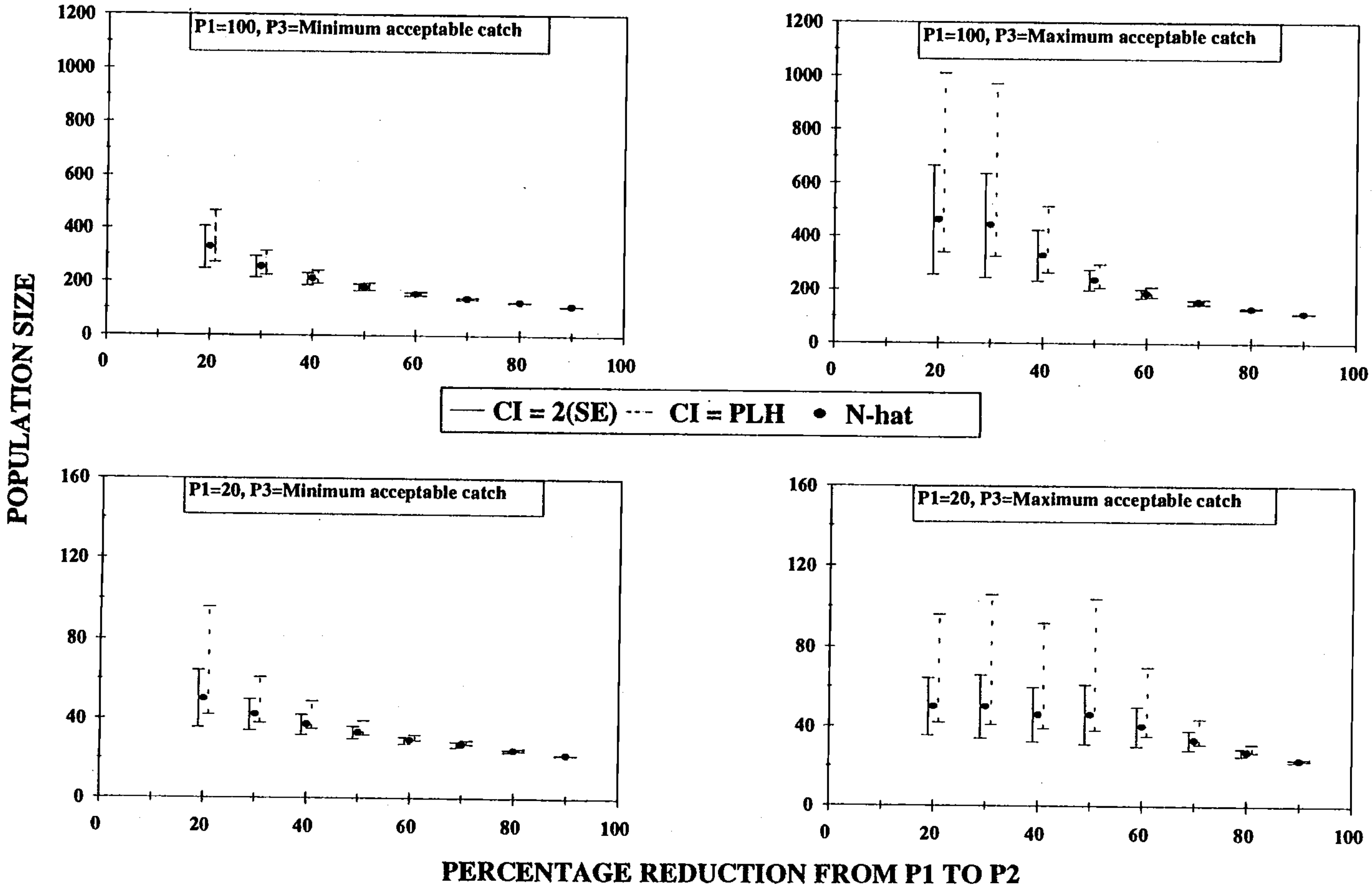

Figure 4.5. Comparison of two confidence intervals (CI) that could result when sequences of catch for three removal passes are within the acceptable limits obtained from Table 4.2c (CV not more than 25%). The x-axis is the percentage reduction from catch on the first pass (P1) to catch on the second pass (P2) when P1 is either 100 or 20. The confidence intervals shown include the interval calculated as 2·SE and the interval derived from profile likelihood (PLH) as calculated by CAPTURE (White et al. 1982). The intervals are shown relative to the estimate of the population (N-hat).

controlled by using a chi-square test to serve as a signal when catchability became too erratic among passes. The use of Tables 4.2 and 4.3 allow limiting the use of three passes to times when it is most likely to be effective and appropriate.

Without flexibility in the number of passes to be conducted, sampling protocols can be insensitive to units that have exceptionally high or low populations, exceptionally high or low catchabilities, or a combination of both. For example, the combination of a high fish population with a low catchability within one pool can be a heavy contributor to total variance of the population estimate for a small stream reach. A riffle with a small population of fish that has high catchability would contribute very little to total variance. A sampling protocol that allows more passes to be conducted at the pool, and fewer passes at the riffle, should result in a more precise population estimate compared to conducting the same total number of passes divided equally between the habitat units. If only a few units required more effort, but most units required less effort, then more time could be available for sampling additional units.

Within a two-stage sampling design, precision of a population estimate for an entire stream, or basin, can often be gained if the number of units sampled is increased (Bohlin et al. 1982, Hankin and Reeves 1988). If a large number of sampling units are to be sampled by a rapid method, such as snorkeling, and the results are to be calibrated with the removal method, as in Dolloff et al. (1993), then a premium will be placed on the time available for removal efforts. To save time, the slower method needs to be restricted to a minimum number of units. If a minimum number of units were to be sampled, returning from the field with invalid data from one or more units could not be tolerated. Use of the tables presented here should minimize such an occurrence.

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CHAPTER 5

Conclusions and Management Implications

Conclusions

The most significant conclusions that I reached from the studies I report on in Chapters 2-4 are as follows:

- Relative to basins that had not been logged and to basins logged 40-60 years ago, basins logged 20-30 years ago supported the widest range of mean biomass of age 1+ or older cutthroat trout (g/m^2) and the widest range in frequency of LWD (number of pieces/100 m) and pools (number/100 m), including the lowest and highest levels of these variables encountered in the study. However, mean values for these variables were not significantly different across the three classes of forest management.
- Although sample size was too low to conduct statistical tests, the level of biomass of age 1+ or older cutthroat trout in basins logged 20-30 years ago was consistently higher in basalt and sandstone streams that had not been cleaned of LWD than in streams that were cleaned of LWD. These cleaned streams had lower levels of LWD and lower number of pools than the other streams within a geologic type.
- The variable that explained the most variation in biomass of age 1+ or older cutthroat trout among all streams was LWD.
- Although all streams were highly shaded by mostly closed canopies of overstory trees during the summer, streams with >35% shading by conifers always had low levels of biomass of age 1+ or older cutthroat trout (<1.2 g/m^2).
- Biomass (g/m^2) of young-of-year cutthroat trout in pools was directly related to stream gradient and inversely related to the biomass (g) of age 1+ or older cutthroat trout, especially in sandstone streams.

- Use of the tables provided in Chapter 4 will decrease the chance of returning from the field with invalid or imprecise data when using the removal method and the estimators of Seber and LeCren (1967) and Zippin (1956) to assess fish populations. In addition, use of these tables has promise to increase the efficiency of sampling in the field.
- Use of a reduction rule with pass-removal sampling does not provide adequate assurance of precision or validity of the resulting population estimate.
- Depending on the catchability and the catch on the first pass, conducting a third pass can decrease the estimate of standard error of a population estimate from 25 to 99% when catchability is equal among passes.

Management Implications

The translation of the findings presented in Chapter 2 to management of larger, more complex systems may be inappropriate. Relative to other isolated populations of cutthroat trout in streams of the Coast Range and Cascade Mountains in Oregon, the populations of cutthroat trout in the streams that I studied were low to moderate (Table 5.1). But the multitude of small watersheds that exist should be recognized as an important part of the landscape of the central Coast Range of Oregon. These systems cannot be ignored if the overall productivity of the forests and streams of the central Coast Range is to be maintained or enhanced.

It must be emphasized that my conclusions about relationships of cutthroat trout and their habitat with forest management are based on studies of small stream systems that have high potential for completely closed canopies. Logged watersheds that I studied had been intensively logged. Buffer strips were not provided. How different the responses would be in partially cut or staggered-cut basins is not known, but the effect would likely be related to the proportion of the basin that was logged (Hicks 1990, Reeves et al. 1993) and to the types of logging practices used Where cautious logging practices have been used, such as leaving buffer strips along stream margins, the types of

Table 5.1. Biomass (g/m2) and population (no./100 m) of age 1+ or older cutthroat trout in streams of the Coast Range and Cascade Mountains of Oregon. The cutthroat trout was the only salmonid in all streams listed; each population was above a barrier to anadromous fish.

Location / Study	Forest management	Number of streams	Range of values for age 1+ or older cutthroat trout: g/m2	Range of values for age 1+ or older cutthroat trout: no./100 m
Coast Range				
Present study	Unlogged	4	0.8--1.4	7.2--17.1
	Logged (20-30 years prior)	7	0.6--3.7	5.8--51.5
	Logged (40-60 years prior)	5	0.7--1.8	5.6--21.3
Schwartz (1991)	Unlogged	2	----	18.8--67.4[a]
	Partially logged	2	----	6.8--9.2
Cascades				
Murphy and Hall (1981)	Unlogged	6	2.4--5.7	----
	Logged (5-17 years prior)	7	0.4--7.7	----
	Logged (12-35 years prior)	4	1.8--3.0[b]	----
Lamberti et al. (1991)	Partially logged	1	----	55--60[b,c]
House (1995)	<50% logged	1	----	80.4--185.8[d]

[a] Values are from a total of three separate reaches from two streams.
[b] Values approximated from graph.
[c] Range of values for 1986-1988 (mean = 58 cutthroat trout/100 m). Data are from a section of stream above a debris flow.
[d] Range of values for 1981-1991 (mean = 135.1 cutthroat trout/100 m).

change and trends that I observed may not occur or occur with less intensity. Research and monitoring will be needed to understand the differences in long-term productivity for cutthroat trout in systems that were logged under past and current forest practices.

I compared the populations in basins that were logged with those in basins that were not logged. While not logged, the basins that I used for comparison had undergone disturbance by wildfire within the past 150 years. Currently, these basins support forests of large second growth according to Ripple's (1994) classification.

The post-logging period of 20-60 years does not provide the long-term perspective needed to assess the probability of persistence of populations of cutthroat trout above barriers. The potential for serious decline of remnant LWD and, possibly, in populations of cutthroat trout appears to be sometime after 60 years post-logging in these systems. Sedell and Swanson (1984) predicted that the long-term abundance of fish populations depends on the timing of the coincident decline of remnant LWD and the recovery of sources for recruitment of LWD. This may be especially applicable to small high-gradient sandstone streams of Oregon's Coast Range because these streams lack large substrates that provide an alternative source for creating and maintaining pool habitat by scouring.

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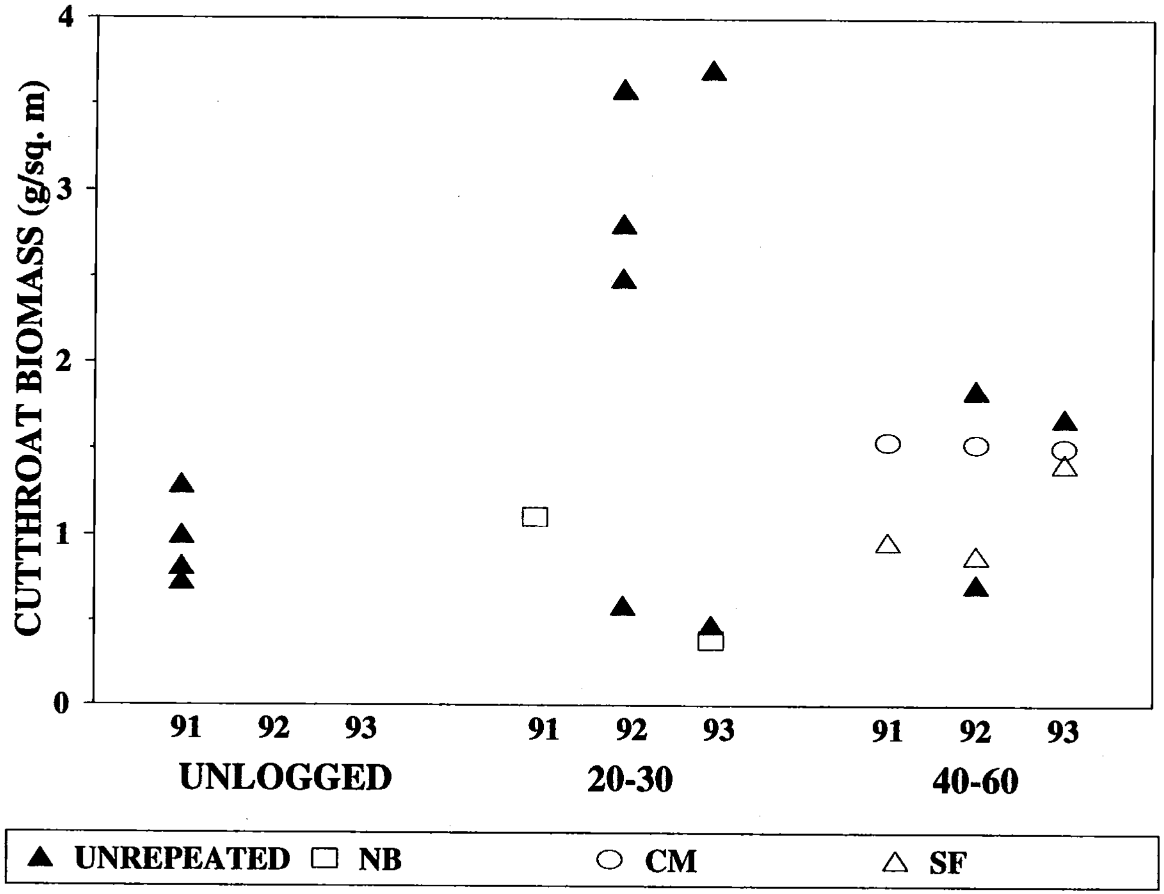
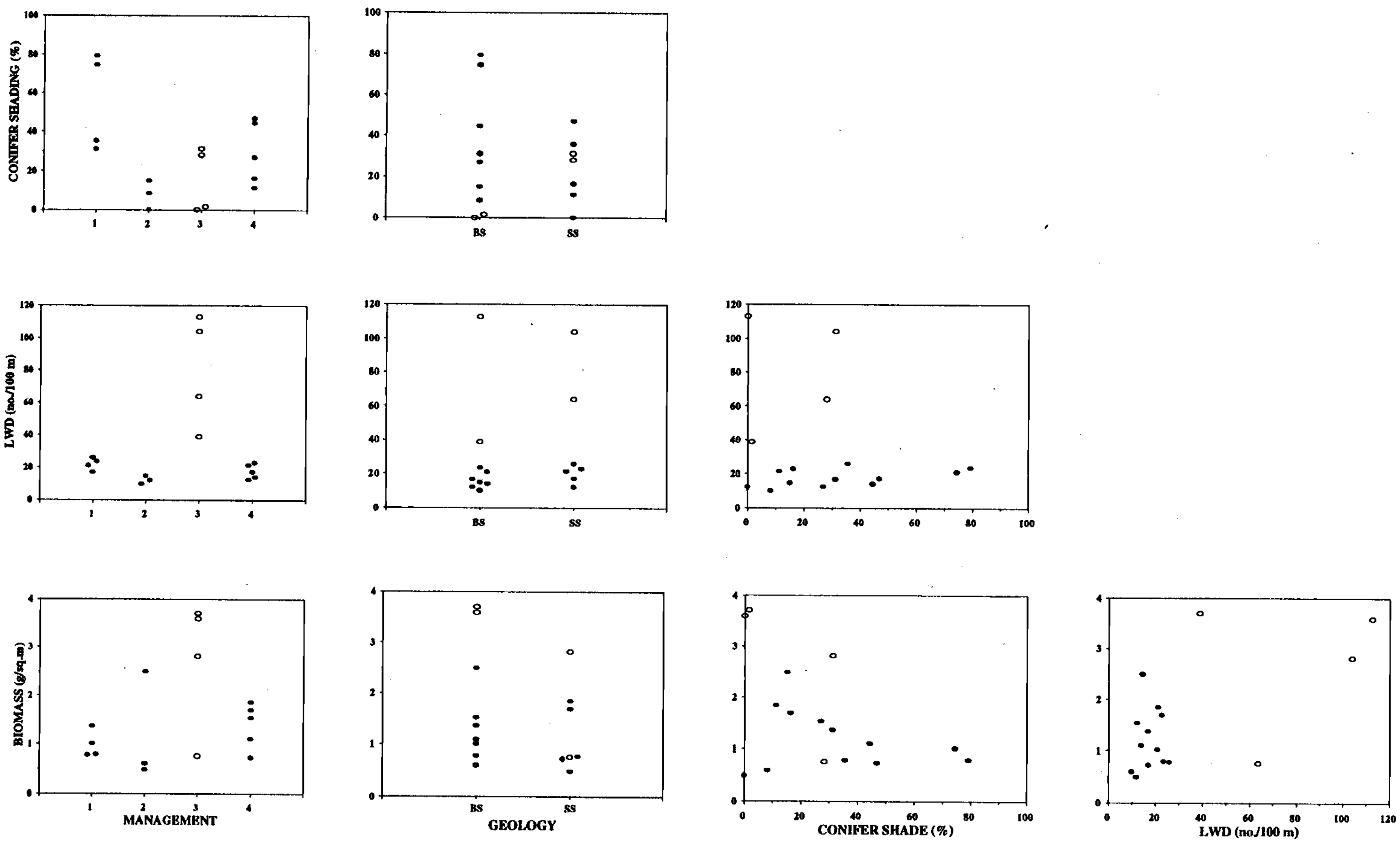
APPENDICES

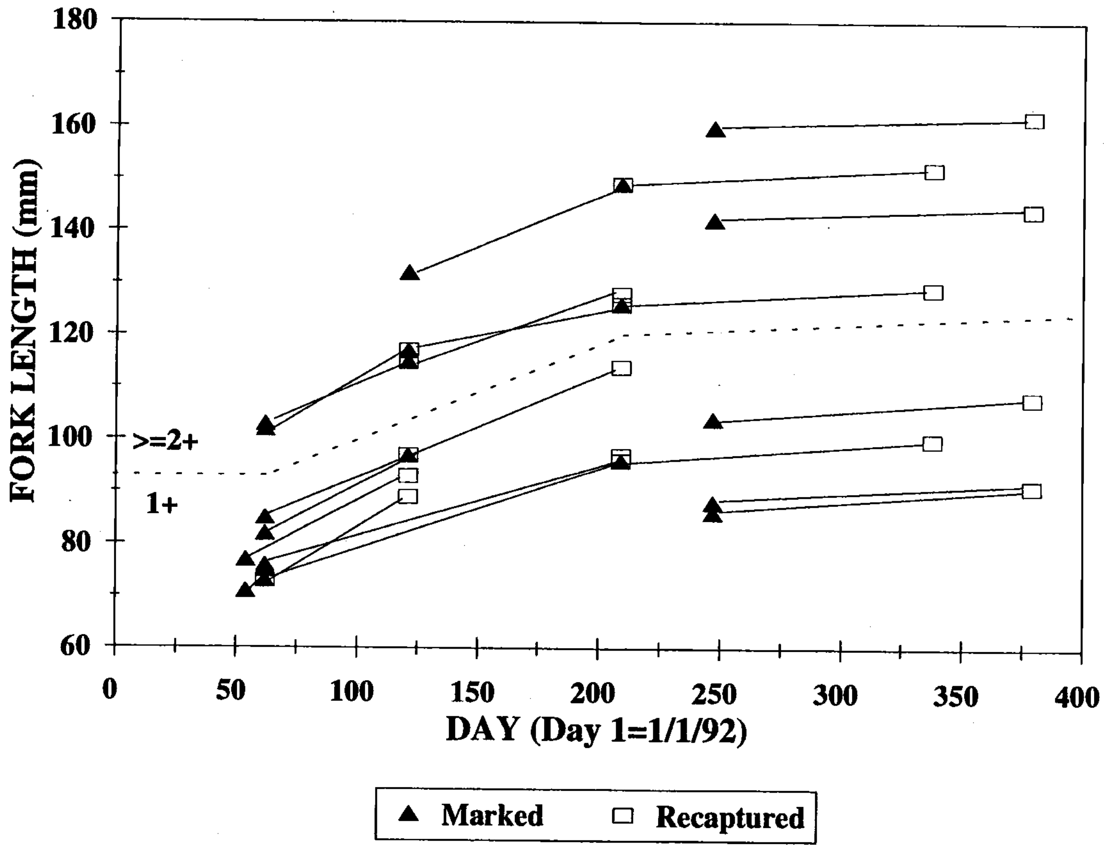
Appendix Figures



Appendix Figure 2.1. Biomass of age 1+ and older cutthroat trout among 16 streams of the central Coast Range of Oregon sampled during 1991-1993. The streams have been classified into three groups based on forest management activities within their basins: unlogged, logged 20-30 years ago, and logged 40-60 years ago. UNREPEATED=streams sampled only one year, NB=Needle Branch, CM=Coleman Creek, and SF=South Fork.



Appendix Figure 2.2. Scatter plots of selected variables for data collected from 16 streams. LWD=large woody debris (length >1 m, diameter >0.3 m); management classes: 1=unlogged, 2=logged 20-30 years ago and cleaned of LWD, 3=logged 20-30 years ago (open circles), 4=logged 40-60 years ago; biomass is for age 1+ or older cutthroat trout.



Appendix Figure 3.1. Fork length of 14 age 1+ or older cutthroat trout at time of capture and recapture. Data are from four tributaries of the South Fork Alsea River, Oregon, 1992-1993. The dotted line represents my best interpretation of the separation of age groups based on length-frequency data from over 200 age 1+ or older cutthroat trout.

Appendix Tables

Appendix Table 2.1. Names of streams studied, their downstream outlets, and map location.

Forest management and stream code	Stream name	Next named stream downstream	Last stream downstream before ocean entry	Township, range	Section
Unlogged					
GR	Gopher Creek	Drift Creek	Alsea River	12S, 9W	16SW
DE	(unnamed)	Dicks Fork	Big Creek	14S, 11W	8SE
DW	(unnamed)	Dicks Fork	Big Creek	14S, 11W	8SW
TB	Tobe Creek	South Fork Alsea River	Alsea River	14S, 7W	32SW
Logged					
20-30 years ago					
CD[a]	Cedar Creek	Little Yaquina River	Yaquina River	10S, 8W	23SE
WL[a]	Williams Creek	South Fork Alsea River	Alsea River	15S, 7W	1NE
EE[a]	(unnamed)	Euchre Creek	Siletz River	8S, 9W	29NE
NB	Needle Branch	Drift Creek	Alsea River	12S, 10W	24NW
PM	Peak Creek	South Fork Alsea River	Alsea River	13S, 7W	25SW
ST	(unnamed)	Euchre Creek	Siletz River	8S, 9W	31NW
LS	(unnamed)	Euchre Creek	Siletz River	9S, 10W	1NE
40-60 years ago					
PE	(unnamed)	Peak Creek	Alsea River	14S, 6W	17SW
SF	(unnamed)	South Fork	Big Creek	14S, 11W	18SW
CM	(unnamed)	Coleman Creek	Alsea River	15S, 7W	2NW
LT	Long Tom Creek	Siletz River	Siletz River	10S, 10W	13NE
PW	(unnamed)	Peak Creek	Alsea River	14S, 7W	11SE

[a] Stream was cleaned of large woody debris at time of logging.

Appendix Table 2.2. The best one-, two-, and three-variable model resulting from unweighted linear regression analysis for biomass of age 1+ or older cutthroat trout (g/m^2) in 16 streams of the central Coast Range.

Independent variables	P-value of independent variable within best model with number of variables equaling		
	One	Two	Three
LWD (no./100 m)[a]	0.015	0.013	0.002
Conifer shade (%)[b]		0.058	0.013
Geology[c]			0.017
p-value of model	0.015	0.009	0.002
R^2	0.356	0.517	0.705
df (model, error)	(1,14)	(2,13)	(3,12)

[a] LWD=large woody debris with length >1 m, diameter >30 cm. The LWD data were log transformed.
[b] Percent of stream shaded by conifers.
[c] Two classes: basalt and sandstone. Basalt includes streams with mixed geology of basalt and sandstone.

The equations for these models are given below.

a) The best one-variable model was:

$$B = -1.1100 + 0.8420 \ln(LWD).$$

b) The best two-variable model was:

$$B = -0.4313 + 0.7838 \ln(LWD) - 0.0175 (CS).$$

c) The best three-variable model was:

$$B = -0.3601 + 0.9093 \ln(LWD) - 0.0200 (CS) - 0.9173 (G).$$

Where: B=biomass (g/m^2), LWD=large woody debris (no./100 m), CS=conifer shading (%), G=geology (=0 if basalt, =1 if sandstone).

Appendix Table 2.3. The best one-, and two-variable model resulting from unweighted linear regression analysis for biomass of age 1+ or older cutthroat trout (g/m^2) in nine basalt and seven sandstone streams of the central Coast Range.

Independent variables	P-value of independent variable within best one-and two-variable model			
	Basalt		Sandstone	
	One	Two	One	Two
LWD (no./100 m)[a]	0.021	0.024	0.155	0.033
Sculpin[b]		0.025		0.056
p-value of model	0.021	0.006	0.155	0.053
R^2	0.556	0.820	0.359	0.770
df (model, error)	(1,7)	(2,6)	(1,5)	(2,4)

[a] LWD=large woody debris with length >1 m, diameter >30 cm. The LWD data were log transformed.
[b] Sculpin=presence or absence of reticulate sculpin.

The equations for these models are given below.

a) The best one-variable models were:

Basalt: $B = -1.8327 + 1.1865 \ln(LWD)$.

Sandstone: $B = -0.9466 + 0.6669 \ln(LWD)$.

b) The best two-variable models were:

Basalt: $B = -0.3487 + 0.8800 \ln(LWD) - 1.2300 (S)$.

Sandstone: $B = -2.5452 + 0.8939 \ln(LWD) + 1.1691 (S)$.

Where: B=biomass (g/m^2), LWD= large woody debris (no./100 m), S=sculpin (=0 if absent, =1 if present).

Appendix Table 2.4. Physical characteristics of habitat units within basalt (n=9) and sandstone (n=7) basins and streams.

Factor	Basalt				Sandstone				P value for test of difference[a]
	Mean	Median	Low	High	Mean	Median	Low	High	
Pools									
Number/100 m	3.8	2.8	1.5	7.6	5.7	5.0	2.2	10.0	0.169
Mean length (m)	3.6	3.6	2.0	6.0	4.4	4.1	3.5	6.1	0.244
Mean area (m^2)	8.1	9.2	3.2	13.3	8.2	6.7	5.2	13.8	0.999
Mean depth									
Maximum (cm)	31.5	30.0	24.6	49.2	30.0	27.8	26.8	36.2	0.832
Mean (cm)	17.5	16.8	14.2	28.2	17.6	17.8	15.3	21.0	0.397
Glides									
Number/100 m	3.0	2.8	0.8	5.3	3.2	2.8	1.2	5.2	0.999
Mean length (m)	3.9	3.9	3.2	4.8	4.3	4.2	2.9	5.5	0.397
Mean area (m^2)	9.7	7.8	5.1	24.2	5.1	5.1	1.8	7.8	0.034
Cascades and riffles									
Number/100 m	7.8	7.6	6.2	10.7	7.6	7.0	5.9	9.6	0.751
Mean length (m)	9.2	9.4	6.2	11.9	6.1	5.8	2.4	8.8	0.020
Mean area (m^2)	18.8	18.0	8.9	26.5	8.0	6.0	1.6	16.3	0.004
Pockets									
Number/100 m	0.5	0.1	0.0	2.1	3.1	1.2	0.0	10.5	0.132
Mean length (m)	1.3	0.9	0.0	3.9	1.9	2.2	0.0	2.9	0.452
Mean area (m^2)	2.9	1.4	0.0	10.5	2.6	3.1	0.0	3.3	0.999

[a] Mann-Whitney *U* test for the difference between geologic types of streams.

Appendix Table 3.1. Means and standard deviations of reach and pool habitat characteristics for streams sampled once during the study.

Habitat variable	Basalt						
	DE(91)[a]	DW(91)	EE(92)	LS(93)	ST(92)	TB(91)	WL(92)
Reach							
Gradient (%)	5.5	7.1	5.5	5.7	5.1	3.1	3.2
Drainage area (km^2)	1.43	1.15	1.29	0.89	0.87	3.39	3.47
Pools per 100 m	2.8	2.6	1.5	5.0	6.9	4.4	2.3
Total pools in reach	7	6	3	13	10	19	11
Total pools sampled	6	5	3	13	8	7	11
Pool morphology							
Length (m)	3.0(1.3)[b]	2.0(0.5)	6.0(2.9)	4.1(1.3)	4.5(2.3)	4.0(1.4)	4.4(2.3)
Width (m)	2.0(0.6)	2.0(0.3)	2.5(1.0)	2.8(0.8)	1.8(0.6)	3.0(1.0)	2.3(0.6)
Area (m^2)	5.5(1.6)	3.8(0.8)	13.3(2.4)	11.1(4.2)	8.8(5.4)	11.6(3.7)	9.6(4.7)
Volume (m^3)	0.9(0.4)	0.6(0.1)	2.0(0.7)	3.1(1.7)	1.7(1.3)	2.5(1.2)	1.4(0.8)
Mean depth (cm)	17.5(7.4)	16.4(2.5)	14.7(3.2)	27.5(7.1)	17.8(7.8)	21.3(5.5)	14.2(3.8)
Maximum depth (cm)	29.8(8.5)	25.2(5.1)	32.3(11.0)	49.2(13.7)	36.1(14.4)	35.3(6.4)	28.5(8.9)
Pool cover							
Total (%)	45(22)	55(15)	25(13)	40(17)	65(21)	57(25)	31(11)
Overhead (%)	8(12)	28(18)	7(12)	8(10)	20(18)	17(15)	6(8)
Instream (%)	37(17)	27(10)	18(3)	32(11)	45(15)	40(19)	25(9)
Pool substrate							
Boulder-cobble (%)	45(16)	60(20)	22(3)	24(10)	8(7)	22(11)	42(13)
Gravel (%)	40(14)	25(16)	73(12)	67(8)	69(27)	12(10)	40(14)
Fines (%)	13(14)	15(15)	0(0)	5(7)	23(28)	63(15)	11(7)

Continued.

Appendix Table 3.1. Continued.

Habitat variable	Sandstone					
	CD(93)	GR(91)	LT(93)	PE(92)	PM(92)	PW(92)
Reach						
Gradient (%)	3.7	4.4	2.6	2.6	3.1	2.2
Drainage area (km^2)	1.43	0.89	1.38	1.23	1.52	1.92
Pools per 100 m	2.2	3.8	7.8	5.0	4.7	6.1
Total pools in reach	11	8	20	29	10	29
Total pools sampled	11	8	15	17	9	14
Pool morphology						
Length (m)	4.1(2.4)	3.9(1.7)	4.3(2.3)	3.4(1.7)	5.5(2.4)	5.9(2.1)
Width (m)	1.6(0.6)	1.6(0.5)	1.8(0.6)	1.5(0.7)	2.6(0.6)	2.1(0.9)
Area (m^2)	6.6(3.8)	6.0(3.3)	7.8(4.9)	5.0(2.9)	14.5(7.4)	11.2(3.2)
Volume (m^3)	1.1(0.7)	1.1(0.7)	1.3(0.8)	1.0(0.5)	3.3(1.5)	1.9(1.3)
Mean depth (cm)	16.3(3.0)	17.8(5.6)	17.2(6.3)	20.9(7.6)	21.1(4.5)	16.7(7.3)
Maximum depth (cm)	27.5(4.8)	26.8(7.5)	29.7(10.1)	33.6(9.9)	35.4(11.1)	39.0(14.4)
Pool cover						
Total (%)	42(22)	38(12)	46(22)	61(19)	73(22)	51(20)
Overhead (%)	8(7)	6(9)	12(11)	12(16)	33(16)	11(12)
Instream (%)	34(17)	32(17)	34(16)	49(23)	41(12)	40(15)
Pools substrate						
Boulder-cobble (%)	4(9)	21(14)	8(14)	0(0)	4(7)	5(7)
Gravel (%)	68(21)	39(21)	67(16)	13(11)	7(12)	76(15)
Fines (%)	29(19)	34(18)	21(16)	87(11)	89(16)	19(16)

[a] Stream code (year sampled). See Appendix Table 2.1 for stream codes.
[b] Mean (standard deviation).

Appendix Table 3.2. Means and standard deviations of reach and pool characteristics for streams sampled two or more years.

Habitat variable	Basalt						Sandstone	
	CM(91)[a]	CM(92)	CM(93)	SF(91)	SF(92)	SF(93)	NB(91)	NB(93)
Reach								
Gradient (%)	7.8	7.8	7.8	5.2	5.2	5.2	4.9	4.9
Drainage area (km^2)	2.02	2.02	2.02	1.33	1.33	1.33	0.53	0.53
Pools per 100 m	4.8	4.4	5.6	2.5	0.9	4.2	8.1	11.8
Total pools in reach	14	13	16	8	3	14	16	23
Total pools sampled	14	15[c]	18[c]	8	3	14	16	23
Pool morphology								
Length (m)	3.4(1.0)[b]	3.5(1.1)	3.6(1.4)	2.2(1.0)	1.8(1.2)	1.9(0.7)	3.3(1.5)	3.7(1.9)
Width (m)	2.6(0.5)	2.7(0.8)	2.6(0.6)	2.0(0.8)	1.6(1.0)	1.8(0.9)	2.0(0.7)	1.8(0.7)
Area (m^2)	8.9(3.6)	9.6(4.9)	9.5(4.9)	4.1(1.9)	2.3(0.8)	3.3(1.5)	6.8(4.2)	6.7(3.9)
Volume (m^3)	1.9(1.1)	1.5(0.8)	2.0(1.5)	0.6(0.3)	0.2(0.1)	0.5(0.2)	1.3(1.1)	1.1(0.6)
Mean depth (cm)	20.8(4.2)	16.0(4.1)	20.2(5.0)	15.1(2.6)	11.3(1.5)	16.0(3.7)	17.8(4.4)	18.0(4.7)
Maximum depth (cm)	31.6(6.3)	30.6(7.8)	32.8(8.0)	26.2(4.3)	22.3(2.1)	25.4(4.5)	26.2(5.1)	28.1(7.3)
Pool cover								
Total (%)	28(10)	39(16)	36(13)	41(12)	50(0)	41(15)	51(16)	58(19)
Overhead (%)	3(4)	4(13)	3(5)	7(8)	6(6)	4(4)	21(7)	18(12)
Instream (%)	25(8)	35(11)	33(9)	34(16)	43(6)	37(15)	30(12)	40(15)
Pool substrate								
Boulder-cobble (%)	43(6)	39(7)	44(13)	29(11)	22(18)	18(16)	13(17)	3(6)
Gravel (%)	41(7)	38(7)	44(12)	49(15)	52(3)	58(19)	44(16)	50(25)
Fines (%)	16(8)	23(8)	12(7)	21(6)	27(20)	24(23)	37(15)	45(27)

[a] Stream code (year sampled). See Appendix Table 2.1 for stream codes.
[b] Mean (standard deviation).
[c] An additional two pools that were above the established reach were sampled in 1992 and 1993.

Appendix Table 3.3. Means and standard errors of biomass of age 0+ and age 1+ or older cutthroat trout in pools of nine basalt and seven sandstone streams. Note that three streams were sampled during two or more years.

		Mean (SE[a]) per pool									
		Age 0+					Age 1+ or older				
Stream	Year sampled	n[b]	(g)	(g/m)	(g/m^2)	(g/m^3)	n	(g)	(g/m)	(g/m^2)	(g/m^3)
Basalt											
CM	91	14	5.46(1.53)	1.69(0.44)	0.65(0.17)	3.20(0.84)	14	46.91(10.31)	13.54(2.39)	4.99(0.74)	23.44(3.10)
CM	92	14	2.82(0.96)	0.95(0.34)	0.47(0.19)	3.40(1.44)	15	53.86(11.39)	14.38(2.46)	5.25(0.79)	33.98(5.61)
CM	93	18	4.02(0.79)	1.28(0.28)	0.47(0.10)	2.54(0.57)	18	34.22(8.20)	9.08(1.88)	3.86(0.83)	20.33(4.80)
DE	91	6	0.12(0.12)	0.02(0.02)	0.02(0.02)	0.10(0.10)	6	19.87(7.88)	7.65(3.91)	3.65(1.54)	17.30(5.71)
DW	91	5	1.03(0.63)	0.48(0.30)	0.23(0.14)	1.58(0.97)	5	16.29(6.71)	7.55(3.10)	4.11(1.74)	24.56(10.10)
EE	92	2	4.00(2.55)	0.81(0.65)	0.27(0.16)	1.64(1.03)	3	95.97(19.08)	18.61(5.97)	7.12(0.81)	49.98(7.37)
LS	93	11	2.53(0.79)	0.60(0.16)	0.24(0.07)	0.98(0.26)	13	125.12(29.61)	30.46(7.64)	10.55(2.36)	36.66(7.31)
SF	91	8	0.38(0.28)	0.15(0.11)	0.08(0.05)	0.65(0.44)	8	20.87(7.05)	13.32(6.94)	8.85(4.97)	55.15(29.12)
SF	92	3	0.00(0.00)	0.00(0.00)	0.00(0.00)	0.00(0.00)	3	20.32(11.12)	13.07(9.65)	12.38(8.64)	101.46(65.22)
SF	93	14	1.92(0.45)	1.01(0.28)	0.75(0.20)	4.50(1.16)	14	28.86(6.85)	14.14(2.83)	8.62(2.00)	56.30(12.41)
ST	92	6	0.95(0.33)	0.21(0.07)	0.11(0.04)	0.75(0.37)	8	52.41(16.62)	10.38(1.78)	6.16(1.10)	41.59(8.46)
TB	91	6	2.13(1.40)	0.37(0.20)	0.15(0.09)	0.81(0.50)	7	45.79(12.63)	11.81(3.58)	4.03(0.90)	19.12(4.38)
WL	92	11	0.56(0.37)	0.18(0.16)	0.11(0.10)	0.92(0.82)	11	27.14(8.47)	5.68(0.91)	2.68(0.47)	20.08(3.68)

Continued.

Appendix Table 3.3. Continued.

		Mean (SE[a]) per pool									
		Age 0+					Age 1+ or older				
Stream	Year sampled	n[b]	(g)	(g/m)	(g/m²)	(g/m³)	n	(g)	(g/m)	(g/m²)	(g/m³)
Sandstone											
CD	93	10	28.78(6.21)	7.97(1.67)	5.75(1.79)	37.89(14.29)	11	15.55(4.24)	4.51(1.64)	2.45(0.69)	15.57(4.19)
GR	91	7	12.39(2.42)	3.38(0.65)	2.16(0.30)	13.23(2.03)	8	15.92(6.77)	3.38(0.94)	2.29(0.65)	13.70(4.13)
LT	93	14	10.64(2.97)	2.24(0.45)	1.29(0.25)	8.87(1.94)	15	46.89(11.85)	13.36(4.59)	7.69(2.82)	35.70(9.00)
NB	91	15	11.28(2.50)	3.95(0.89)	2.54(0.73)	15.54(4.42)	16	13.75(5.08)	3.43(1.20)	1.59(0.55)	8.01(3.08)
NB	93	23	30.97(3.16)	9.42(0.93)	6.40(1.10)	34.57(5.10)	23	4.68(1.36)	1.39(0.42)	0.84(0.28)	4.61(1.48)
PE	92	17	1.03(0.38)	0.34(0.12)	0.34(0.15)	1.42(0.70)[c]	17	12.41(3.57)	3.79(1.19)	2.72(0.79)	14.58(4.44)[c]
PM	92	8	4.11(1.82)	0.85(0.38)	0.41(0.19)	1.84(1.11)[c]	9	85.42(28.22)	15.74(4.59)	5.55(1.32)	22.73(6.33)[d]
PW	92	11	1.26(0.49)	0.20(0.08)	0.12(0.05)	1.08(0.64)[d]	14	45.37(9.88)	9.75(2.44)	3.95(0.88)	23.96(5.57)[e]

[a] SE = standard error of the mean with an individual pool as the sampling unit. The error associated with estimating the number or biomass of cutthroat trout per pool is not included.
[b] n = number of pools for which valid estimates of population size could be made.
[c] Because mean depth was not determined on one pool, number of pools=n-1 for the estimate per m³.
[d] Because mean depth was not determined on two pools, number of pools=n-2 for the estimate per m³.
[e] Because mean depth was not determined on three pools, number of pools=n-3 for the estimate per m³.

Appendix Table 3.4. Results of simple linear regression with the dependent variable of biomass (g/m^2) of age 0+ and the independent variable of biomass (g) of age 1+ or older cutthroat trout. The experimental unit was individual pools within basalt and sandstone streams. Number of pools indicate pools that had the older aged cutthroat trout present. The independent and dependent variables were log (base e) transformed.

Geology	Stream[a]	Year sampled	Number of pools	Y-intercept	Slope	P-value of test: slope=0	r^2
Basalt	CM	1991	13	-0.4063	0.2101	0.1744	0.161
	CM	1992	13	0.8836	-0.1739	0.1010	0.226
	CM	1993	13	0.3025	-0.0152	0.8837	0.002
	DE	1991	4	0.0088	0.0071	0.9517	0.002
	DW	1991	3	8.9379	-2.6320	0.2460	0.858
	EE	1992	2	---	---	---	---
	LS	1993	11	0.3981	-0.0472	0.3425	0.100
	SF	1991	6	0.1984	-0.0499	0.5245	0.108
	SF	1992	2	---	---	---	---
	SF	1993	11	0.5252	-0.0191	0.9285	0.001
	ST	1992	6	0.0960	0.0001	0.9845	<0.001
	TB	1991	5	-0.3986	0.1332	0.5645	0.122
	WL	1992	10	0.1244	-0.0116	0.9218	0.001

Continued.

Appendix Table 3.4. Continued.

Geology	Stream[a]	Year sampled	Number of pools	Y-intercept	Slope	P-value of test: slope=0	r^2
Sandstone	CD	1993	7	3.6196	-0.6138	0.1287	0.398
	GR	1991	5	1.6288	-0.1581	0.3216	0.319
	LT	1993	11	1.4899	-0.1713	0.2659	0.135
	NB	1991	7	1.0163	-0.1918	0.6117	0.055
	NB	1993	10	2.7216	-0.3383	0.4154	0.084
	PE	1992	9	1.1216	-0.3175	0.1102	0.323
	PM	1992	7	1.2619	-0.2297	0.1040	0.440
	PW	1992	10	-0.0431	0.0313	0.4280	0.080

[a] See Appendix Table 2.1 for stream codes.

Appendix Table 3.5. Biomass of age 0+ cutthroat trout when age 2+ or older cutthroat trout were absent and when age 2+ or older cutthroat trout were present in pools of basalt and sandstone streams. The streams listed had at least one pool without the older cutthroat trout and at least one pool with the older cutthroat trout. See Appendix Table 2.1 for a legend of stream codes.

			Number of pools		Mean biomass of age 0+ (g/m^2)		
Geology	Stream[a]	Year sampled	Age ≥2+ absent	Age ≥2+ present	Age ≥2+ absent	Age ≥2+ present	Difference
Basalt	CM	91	5	9	0.806	0.562	0.244
	CM	92	4	10	1.069	0.224	0.844
	CM	93	9	9	0.684	0.259	0.426
	DE	91	5	1	0.028	0.000	0.028
	DW	91	3	2	0.382	0.000	0.382
	EE	92	1	1	0.104	0.428	-0.324
	LS	93	3	8	0.306	0.211	0.095
	SF	91	6	2	0.107	0.000	0.107
	SF	92	2	1	0.000	0.000	----
	SF	93	8	6	0.814	0.670	0.144
	ST	92	5	2	0.117	0.032	0.085
	TB	91	3	3	0.081	0.220	-0.139
	WL	92	8	3	0.147	0.019	0.128
Sandstone	GR	91	6	1	2.239	1.712	0.526
	LT	93	8	6	1.431	1.113	0.318
	NB	91	12	3	3.030	0.557	2.474
	PE	92	12	5	0.399	0.209	0.191
	PM	92	3	5	0.575	0.306	0.269
	PW	92	5	6	0.163	0.083	0.080

[a] See Appendix Table 2.1 for stream codes.

Appendix Table 3.6. Results of covariate analysis for effect of stream gradient, year of sample, and geology of stream on the difference of mean biomass of age 0+ cutthroat trout in pools without older-aged cutthroat trout compared to pools with age 2+ or older cutthroat trout. A stream was included in the analysis if at least two pools were sampled including at least one without older-aged cutthroat trout and at least one with age 2+ or older cutthroat trout. An interaction term (gradient x geology) was included in a preliminary model, but it was dropped from the final model when found to be non-significant (p>0.10).

Independent variables in model	P-value of independent variables	Coefficient of covariate	R^2	Degrees of freedom (model, error)	P-value of model
Dependent variable = difference in mean biomass (g/m²) of age 0+ cutthroat trout [a]					
Stream gradient (%)	0.0041	0.2093	0.567	5, 11	0.0163
Year[b]	0.3479				
Geology[b,c]	0.0724				
Intercept	0.0203				

[a] Biomass (B) data were log (base e) transformed: ln(B+1).
[b] Class variable.
[c] Geology includes two types of streams: basalt or sandstone.

Appendix Table 4.1. Formulas for the population and variance estimators of Zippin (1956), Junge and Libosvarsky (1965), and Seber and LeCren (1967), as well as the chi-square goodness-of-fit test from Seber (1982). Pages where the formulas can be found in these papers, as well as equation numbers used by the authors, are provided. In some cases, original notation has been changed to provide consistency across estimators.

The notation is as follows:

$\hat{N}$ = estimated population size.

$\hat{V}(\hat{N})$ = estimated variance of population estimate

$\hat{p}$ = estimated catchability.

$\hat{q}$ = $1-\hat{p}$.

c_i = number caught on *i*th removal pass.

T = total number caught.

x_i = total number captured prior to *i*th removal pass.

k = number of removal passes.

When needed, additional notation is defined below individual formulas.

I. Zippin (1956) estimator when $k \geq 3$.

A. Estimate of Population

1. By iterative solution, the value of N that best satisfies the equation:

$$(\hat{N}-T)/\hat{N} = [(k\hat{N} - Q)/(k\hat{N} - \sum_{i=1}^{k} x_i)]^k \qquad \text{(p. 166, eq. 6)}$$

Where: $$Q = \sum_{i=1}^{k} x_i + T \qquad \text{(p. 164)}$$

2. When the catchability (p) is known:

$$\hat{N} = T/(1-\hat{q}^k) \qquad \text{(p. 166, eq. 8)}$$

B. Estimate of Catchability

$$\hat{p} = T/(k\hat{N} - \sum_{i=1}^{k} x_i) \qquad \text{(p. 165, eq. 4)}$$

Continued.

Appendix Table 4.1. Continued.

C. Estimate of Variance

$$\hat{V}(\hat{N}) = \frac{\hat{N}(1-\hat{q}^k)}{\hat{N}(-F')(1-\hat{q}^k) - [(k\hat{p})^2/\hat{q})]} \qquad \text{(p. 171, eq. 15)}$$

Where: value of F' depends on choice of estimator as below.

1. Full Multi-Termed Estimator (Stirling's second-order approximation)

$$F'=-1/\hat{N}\ \{[(1-\hat{q}^k)/\hat{q}^k]-[(1-\hat{q}^{2k})/2\hat{N}\hat{q}^{2k}]+[(1-\hat{q}^{3k})/6\hat{N}^2\hat{q}^{3k}]\} \qquad \text{(p. 170, eq. 11)}$$

2. Large-Sample Approximation Estimator

$$F' = -1/\hat{N}\ [(1-\hat{q}^k)/\hat{q}^k] \qquad \text{(p. 170, eq. 12)}$$

or, with substitution and rearrangement,

$$\hat{V}(\hat{N}) = \frac{\hat{N}(1-\hat{q}^k)\hat{q}^k}{(1-\hat{q}^k)^2 - (\hat{p}k)^2\hat{q}^{k-1}} \qquad \text{(p. 171, eq. 16)}$$

II. Junge and Libosvarsky's (1965) explicit solution to the maximum likelihood estimate of Zippin (1956) when k=3.

A. Estimate of Population

$$\hat{N} = \frac{6X^2 - 3XY - Y^2 + Y(Y^2 + 6XY - 3X^2)^{0.5}}{18(X - Y)} \qquad \text{(p. 175, eq. 1)}$$

Where: $X = 2c_1 + c_2$
$Y = c_1 + c_2 + c_3 = T$

Continued.

Appendix Table 4.1. Continued.

B. Estimate of Catchability

$$\hat{p} = \frac{3X - Y - (Y^2 + 6XY - 3X^2)^{0.5}}{2X} \qquad \text{(p. 175, eq. 2)}$$

Where: X and Y as above.

III. Seber and LeCren (1967) estimator when k=2, a special case of the Zippin estimator given above.

A. Estimate of Population

$$\hat{N} = (c_1)^2/(c_1 - c_2) \qquad \text{(p. 632)}$$

B. Estimate of Catchability

$$\hat{p} = (c_1 - c_2)/\, c_1 \qquad \text{(p. 632)}$$

C. Estimate of Variance

1. Full Multi-Termed Estimator

$$\hat{V}(\hat{N}) = \frac{\hat{N}\hat{q}^2(1+\hat{q})}{\hat{p}^3} + \frac{2\hat{q}(1-\hat{p}^2-\hat{q}^3)}{\hat{p}^5} - b^2 \qquad \text{(p. 632, eq. 2.1)}$$

Where: $b = \text{bias} = [\hat{q}(1+\hat{q})]/\hat{p}^3$

2. Large-Sample Approximation Estimator

$$\hat{V}(\hat{N}) = \frac{\hat{N}\hat{q}^2\,(1+\hat{q})}{\hat{p}^3} = \frac{(c_1)^2\,(c_2)^2\,(c_1+c_2)}{(c_1-c_2)^4} \qquad \text{(p. 632, eq. 2.2)}$$

Continued.

Appendix Table 4.1. Continued.

IV. Goodness-of-Fit Test Statistic from Seber (1982).

$$S = \sum_{i=1}^{k} (c_i - E_i)^2 / E_i \qquad \text{(p. 314)}$$

Where: S = test statistic with a chi-square distribution and k-2 degrees of freedom.

E_i = $\hat{N}\hat{p}\hat{q}^{i-1}$.
