

AN ABSTRACT OF THE DISSERTATION OF

Glenn K. Chen for the degree of Doctor of Philosophy in Fisheries Science presented on June 8, 1998. Title: The Relationship Between Stream Habitat Complexity and Anadromous Salmonid Diversity and Habitat Selection.

Redacted for privacy

Abstract approved:

✓ - ✓

William J. Liss

The relationship between habitat and the structure of biotic assemblages has been the subject of much interest among community ecologists. Little research has been done to determine what influence stream habitat complexity may have on species diversity of anadromous salmonid fishes. In this study, habitat and diversity relationships were examined for summer populations of coho, chinook, steelhead, and cutthroat adults/juveniles found in pool habitats within five 4th-order southwestern Oregon coastal streams. Univariate and multivariate statistical analyses demonstrated that maximum depth, mean depth, pool volume, and pool area were significantly correlated ($p < 0.10$) with measures of species diversity for 4 of the 5 study streams, but most of these relationships were statistically weak (low r^2 values). No significant correlations were obtained between dominant substrate, volume of large wood in pools, and salmonid diversity, although the relationship between diversity and wood may be influenced by the presence or absence of wood-selective species such as coho. For

stream reaches, no significant relationships were noted between habitat unit type diversity and any measure of salmonid diversity. These results suggest that habitat structure may not be the most important element determining fish diversity at the habitat unit or reach scale. Anadromous life histories and oceanic survival, and subsequent effects on juvenile seeding levels in freshwater habitats, combined with low species richness and harsh environmental conditions, may be other factors which influence salmonid diversity in southern Oregon coastal streams.

An *in-situ* factorial experiment was conducted to further investigate the habitat complexity - species diversity relationship. Test pools in an artificially-constructed channel were used to determine habitat feature selection by salmonid assemblages to treatments of maximum depth and wood. 24-h and 7-d trial periods were used in late summer and spring, respectively. Results from ANOVA demonstrated that pool depth and large wood (for 24 h trials) or depth only (7 d trials) were significant factors influencing species richness of anadromous salmonids in test pools; wood treatment effects were dependent on trial length.

Results from this study provide additional information on habitat complexity - fish diversity relationships for anadromous salmonids in the Pacific Northwest. Applications of these findings include use as a diagnostic tool to assess land management impacts on stream habitat and fish communities, and as guidance to aid habitat projects in restoring stream conditions that enhance anadromous salmonid diversity.

The Relationship Between Stream Habitat Complexity
and Anadromous Salmonid Diversity
and Habitat Selection

by

Glenn K. Chen

A DISSERTATION

submitted to

Oregon State University

in partial fulfillment of
the requirements for the
degree of

Doctor of Philosophy

Presented June 8th, 1998
Commencement June 1999

Doctor of Philosophy in Fisheries Science dissertation of Glenn K. Chen presented on June 8th, 1998

APPROVED:
Redacted for privacy

Major Professor, representing Fisheries Science

Redacted for privacy

Head of Department of Fisheries and Wildlife

Redacted for privacy

Dean of Graduate School

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

Redacted for privacy

Glenn K. Chen, Author

ACKNOWLEDGMENTS

The support and assistance from many individuals and organizations were necessary for the completion of this Ph.D. dissertation. Gordon Reeves from the U.S.F.S. Corvallis Forest Sciences Laboratory developed the original conceptual framework and provided the research foundation for this project. Gordie was also instrumental in making available the resources of his field crews to help with data collection.

I am indebted to many people for their long hours of assistance in the field. This work could not have been completed without the help of Jon Grunbaum, Bruce Hansen, Dave Anderson, and Kathy Quinn from the USFS Corvallis Forest Sciences Laboratory; and Ken Fliszar and Gary Susac from the Oregon Department of Fish and Wildlife, Elk River Research Laboratory.

The U.S. Forest Service, Powers Ranger District, and the Siskiyou National Forest are recognized for their support to this project. In particular, Cindy Enstrom and Kim Mellen are to be thanked for securing the logistics needed to complete the field data collection efforts and the *in-situ* experiments. I am especially grateful to Marshall Foster for his assistance with producing the GIS maps used in the figures.

I thank Paul Reimers and Reese Bender of the Charleston Office, Oregon Department of Fish and Wildlife, for providing much-needed electroshocking equipment, live tanks, nets, and holding pens.

Much gratitude is extended to David Turner of the U.S.F.S. Rocky Mountain Research Station, who made room in his busy schedule to accommodate my request for statistical reviews and assistance with the multivariate analyses.

Special thanks go to Stan Gregory and Gordon Reeves, who served as my two principal "advisors" over the past decade. Their support and timely advice were necessary to help me overcome many obstacles and uncertainties at critical points during my program. I am grateful to Mark Hixon, Bob Beschta, and Bruce DeYoung for their invaluable assistance and input as Graduate Committee members. I also thank Bill Liss for agreeing to serve as the major professor at the very end so that I could complete this dissertation within the Graduate School's required time line.

Charlotte Vickers is to be thanked for all of her expedient assistance in dealing with the Graduate School and University administration during those chaotic weeks in April.

Last but not least, my wife Jane deserves special recognition as my principal research assistant and companion throughout this dissertation program. The many hours we spent together snorkeling cold streams and gathering habitat data in remote areas will be cherished in our collection of memories from the south coast.

TABLE OF CONTENTS

	Page
1. INTRODUCTION.....	1
1.1 Statement of Research Objectives.....	11
1.2 Field Study Hypotheses.....	12
1.3 <i>In-situ</i> Factorial Experiment Hypotheses.....	12
2. MATERIALS AND METHODS.....	14
2.1 Streams Selected as Field Study Sites.....	14
2.2 Description of Study Sites.....	16
2.2.1 Elk River Basin.....	16
2.2.2 Sixes River Basin.....	22
2.2.3 South Fork Coquille Basin.....	24
2.3 Methods Used to Measure Complexity within Habitat Units.....	27
2.3.1 Basin Approach for Collecting Habitat Complexity Data.....	27
2.3.2 Parameters Used to Describe Physical Habitat Complexity.....	27
2.3.3 Habitat Type.....	29
2.3.4 Dominant Substrate Type.....	29
2.3.5 Large Wood.....	30
2.3.6 Habitat Unit Spatial Dimensions.....	30
2.4 Methods Used for Determining Anadromous Salmonid Community Diversity within Habitat Units.....	31
2.4.1 Salmonid Population Censuses.....	31
2.4.2 Fish Species Diversity Indices.....	33
2.5 Description of Study Design for Habitat Unit-Scale Studies.....	34
2.6 Description of Methods for Reach-Level Studies.....	36
2.6.1 Reach-level Assessments of Habitat Complexity.....	36
2.6.2 Reach-level Assessments of Fish Species Diversity.....	37
2.7 Analyses of Habitat Complexity - Community Diversity Relationships.....	38

TABLE OF CONTENTS (Continued)

	Page
3. RESULTS.....	40
3.1 Physical Habitat Complexity and Salmonid Diversity in Pools	40
3.2 Results from Analyses of Complexity - Diversity Relationships Within Pools.....	40
3.3 Multivariate Analyses of Complexity - Diversity Relationships in Pools.....	52
3.4 Complexity - Species Diversity Relationships at the Reach Scale.....	54
4. DISCUSSION OF RESULTS FROM HABITAT COMPLEXITY - SALMONID DIVERSITY STUDIES.....	57
5. <i>IN-SITU</i> EXPERIMENTS TO EVALUATE SELECTION OF HABITAT FEATURES BY ANADROMOUS SALMONID FISHES.....	67
5.1 Introduction.....	67
5.2 Materials and Methods.....	68
5.3 Experimental Design.....	72
5.4 Results.....	76
5.5 Discussion.....	76
SUMMARY.....	82
BIBLIOGRAPHY.....	86

LIST OF FIGURES

Figure		Page
1	Elk River watershed boundary and major tributaries.....	17
2	Sixes River watershed boundary and major tributaries.....	23
3	Upper South Fork Coquille River watershed boundary and major tributaries.....	25
4	Frequency distribution of anadromous salmonid species and age classes among habitat types, North Fork Elk River August 1986, 1987, and 1988.....	28
5	Diagram showing location of constructed side channel and experimental pools in Rock Creek.....	70
6	Lateral view of experimental pool.....	71

LIST OF TABLES

Table	Page
1	Mean correction factors for diver estimates by diver and fish species for pool habitat types..... 33
2	Community diversity indices..... 33
3	Summary of physical habitat data from pools, July 1990..... 41
4	Summary of physical habitat data from pools, August 1990..... 42
5	Summary of physical habitat data from pools, 1991..... 43
6	Summary of anadromous salmonid fish data, July 1990..... 44
7	Summary of anadromous salmonid fish data, August 1990..... 45
8	Summary of anadromous salmonid fish data, July 1991 (Salmon Creek) and August 1991 (Elk and Sixes River streams)..... 46
9	Results from multiple regression analysis of habitat complexity and juvenile salmonid diversity within pools..... 48
10	Significant ($p < 0.10$) complexity - diversity multiple regressions in pools for all streams..... 50
11	Correlations and standardized residual coefficients for habitat complexity variables and diversity indices (significant regression models only)..... 51
12	Results from canonical correlation multivariate analyses..... 53
13	Summary of reach data used for complexity and community diversity analyses (Elk River and Sixes River basins, July and August 1990)..... 55

LIST OF TABLES (continued)

Table	Page
14 Summary of reach data used for complexity and community diversity analyses (Elk River and Sixes River basins, August 1991).....	56
15 Species richness <i>S</i> ANOVA results for wood and depth factorial experiments, Rock Creek August-September 1991 and April-May 1992.....	77

DEDICATION

This dissertation is dedicated to my parents, Tu and Nancy Chen, whose continued encouragement throughout my education made it possible for me to realize this important milestone in my life.

The Relationship Between Stream Habitat Complexity and Anadromous Salmonid Diversity and Habitat Selection

1. INTRODUCTION

Throughout the history of community ecology, the study of ecological diversity has remained as one of its central themes (Magurran 1988). In the mid-nineteenth century, natural historians were intrigued by the patterns of diversity in the natural world (Darwin 1865). Ecologists have examined the different mechanisms that structure natural communities, including competition (Connell 1976, 1983, Schoener 1983), predation (Paine 1966, 1969, Connell 1975), and the role of disturbance (Pickett and White 1985). We now recognize that a variety of processes operating at different spatial and temporal scales function to create the patterns observed (Strong et al. 1984, Case and Diamond 1986).

Species diversity (richness, evenness, dominance, or a combination thereof) is an important attribute of assemblages and has been used as a measure of community structure (Magurran 1988). Biotic interactions (e.g., predation, competition, recruitment) and abiotic factors (e.g., disturbance, environmental gradients) have been invoked to explain patterns of diversity (Menge and Sutherland 1987). Diversity has been allied with the concepts of resource heterogeneity and niche differentiation (Hutchinson 1959). Implicit is the idea that a varied environment serves as a template for niche specialization, which results in ecological diversification and species differentiation (e.g., MacArthur 1965).

Habitat is considered to be one of the key axes used to partition resources among potentially competing species (Schoener 1974). Adaptation to habitat has influenced the morphological, physiological, and behavioral specialization in biota, and response to variability in habitat has been an important mechanism for species evolution (Begon et al. 1990). In the nineteenth century, Wallace (1890) discussed the idea that structurally complex habitats might hold more species than simple ones. The habitat diversity hypothesis was proposed by Williams (1964) to link species diversity and habitat. Karr and Roth (1971) indicated that environmental heterogeneity might satisfy a greater range of habitat needs for community members and Martin (1981) also hypothesized that resource variability might increase the number of available niches, thereby reducing the potential for competition. May (1986) suggested that a heterogeneous habitat will allow the co-occurrence of more species and thus enhance community diversity.

An abundance of empirical evidence exists to document the relationship between habitat complexity and assemblage diversity. MacArthur and MacArthur (1961) reported that, for deciduous forests, bird species diversity could be predicted by the height profile of foliage density. MacArthur (1964) and MacArthur et al. (1966) noted that vegetation density, plant height, and differential habitat selection were correlated with patterns of avian diversity they observed in tropical forests. In Australia, Recher (1969) concluded that habitat complexity, as measured by foliage profile, was a good predictor of bird species diversity. Karr and Roth (1971) found that, for temperate and tropical avian fauna, species diversity was related to foliage height diversity and percent vegetation cover.

Tomoff (1974) found a significant relationship between vegetation coverage density and the diversity of breeding birds in the Sonoran desert. Terborgh (1977), working with bird assemblages in the mountains of Peru, noted that avian diversity was highly correlated with foliage height diversity. For North American temperate forests, James and Wamer (1982) revealed through principal components analyses that canopy cover, vegetation height, and tree density (as measures of vegetation structural diversity) were correlated with bird species abundances. Reviewing bird census data collected across the North American continent, Boecklen (1986) found that habitat heterogeneity is a significant predictor of species number, even after area is factored out. Blake and Karr (1987) demonstrated that habitat structure, rather than area, accounted for bird species abundances in central Illinois.

For lizard assemblages, Pianka (1967) found that plant structural diversity, rather than type, appeared to influence patterns of species richness in southwestern North American desert ecosystems. Case (1975) determined that foliage diversity was one of three important factors correlated with the number of lizard species on islands in Baja California. Schoener and Schoener (1983) were able to document that lizard species richness on islands appeared to be related to vegetation height and its structural diversity.

Simpson (1964) suggested that habitat complexity-species diversity relationships existed among various North American mammalian assemblages. Johnson et al. (1968) found that environmental richness was one factor that appeared to contribute significantly to the regulation of terrestrial vegetation and fauna diversity on islands off

California and Baja Mexico. Poulson and Culver (1969) documented that diversity of cave organisms appeared to be linked to structural diversity within these habitats.

Murdoch et al. (1972) determined that plant structural complexity was correlated with insect diversity patterns. Complexity and diversity relationships have also been demonstrated for rodent communities (Rosenzweig and Winakaur 1969).

Examples of the complexity-species diversity relationship are also found in aquatic assemblages. Whiteside and Harnsworth (1967) noted correlations between structural complexity and species diversity for assemblages of chydorid cladocerans, as did Kohn (1967) for tropical *Conus* gastropods. Harman (1972) determined that diversity of freshwater molluscan communities was highly correlated with substrate complexity, and that habitat played a more important role than other physical and chemical factors. Neill (1975) experimented with freshwater crustaceans and documented that habitat complexity and micro-habitat selection appeared to permit co-existence of various taxa, thereby enhancing species diversity.

For benthic stream insect communities in Colorado, Allan (1975) found that increased substratum complexity led to greater species richness. Rabeni and Minshall (1977) determined that lotic insects species segregated according to substrate size, and that this may reflect the differential availability of detrital food sources among substrate types. Minshall et al. (1985), studying benthic invertebrates in the Salmon River (Idaho), noted that species richness varied with area and stream order. Abele (1974), also working with invertebrates but in the marine environment, found that substrate type was the most important factor correlated with the richness of tropical decapods. He

hypothesized that substrate diversity allows for differential microhabitat selection, co-existence, and the number of species in these assemblages.

While community ecologists generally accept that a relationship exists between habitat complexity and species diversity, it is important to note that the role of physical structure varies among different taxa, ecological groups, communities, ecosystems, and geographic locations (e.g., James and Wamer 1982, Boecklen 1986, Freemark and Merriam 1986, Blake and Karr 1987).

What role does habitat complexity play in influencing fish community structure? Wooten (1993) states that a general relationship exists between the number of fish species and the structural heterogeneity of habitat. In contrast with many other taxonomic groups and assemblages (e.g., sessile rocky intertidal invertebrates, forest birds), fish are among the most difficult subject groups for ecological study, in part due to their relative inaccessibility in the aquatic environment; much of what we have learned on the community ecology of fishes stems from the increasing amount of *in situ* field research conducted primarily within the last twenty years (Wooten 1992).

For marine and freshwater fish assemblages, the habitat complexity - species diversity relationship has been demonstrated in a number of studies. Working with tropical marine fish communities, Luckhurst and Luckhurst (1978) determined that both fish abundance and species richness were positively correlated with substrate complexity. Roberts and Ormond (1987) noted that diversity of coral substratum was highly correlated with overall fish species richness; structural complexity, as measured by the number of reef holes, accounted for much of the variance in fish abundance.

Similarly, Risk (1972), Smith and Tyler (1972), Gladfelter and Gladfelter (1978), and Carpenter et al. (1981) found relationships between reef structure, structural heterogeneity, and fish richness/diversity. However, this is in contrast to work by Sale and Douglas (1984), who determined that coral reef structural attributes (other than size) were not useful for predicting fish assemblage diversity.

An underlying premise in many habitat - diversity relationship studies is that complex habitat allows for spatial segregation of competitive species and offers increased refugia for prey. Hixon and Beets (1989) performed experimental manipulations of structural complexity in artificial reefs and noted changes in prey and predator fish densities. Large shelters appeared to enhance the abundance of piscivores, thereby indirectly reducing prey numbers, and they suggested that a heterogeneous environment composed of different size shelters may support the greatest number of reef fishes.

Experimental and observational evidence exists to document complexity-diversity relationships in freshwater stream fish communities. Habitat has been suggested as a major dimension of resource partitioning among these assemblages (Sheldon 1966, 1968, Mendelson 1975, Felley and Hill 1983, and others). Meffe and Sheldon (1990) demonstrated that fish assemblages in coastal South Carolina streams were not randomly structured, but were deterministic systems predictable from local habitat features. For their streams in Indiana and Panama, Gorman and Karr (1978) found that habitat heterogeneity influenced diversity of fish communities. Baker and Ross (1981) demonstrated correlations between cyprinid distributions and lotic aquatic

vegetation species/structure. Schlosser (1982) showed relationships between habitat size, depth, current velocity, substrate, and fish species diversity in an Indiana headwater stream. Links between habitat volume and fish richness for central America tropical rivers were demonstrated by Angermeier and Schlosser (1989). Gorman (1988) documented correlations between habitat type, depth, and guilds of cyprinids in an Ozark stream. Hickman (1975), Paragamian (1980), Angermeier and Karr (1984) have found that abundance and diversity of warm-water fish increased in stream reaches with greater amounts of wood structure. Smith and Tyler (1972), Kushlan (1976), Horwitz (1978), Moyle and Baltz (1985), Schlosser (1985), Smith and Miller (1986), Coon (1987), Finger and Stewart (1987), Bain et al. (1988), and Poff and Allen (1995) described patterns of diversity related to levels of water height and discharge. Stream width has also been suggested as a factor influencing lotic fish diversity (e.g., Matthews and Robison 1988, Gelwick 1990, Matthews and Gelwick 1990, Paller 1994, Taylor and Lienesch 1996, and others). Other habitat complexity - stream fish diversity studies include those by Fausch and Bramblett (1991), Matthews et al. (1994), and Taylor (1997).

The concepts of resource partitioning (Schoener 1974), niche differentiation (Hutchinson 1959), and community diversity can be linked by examining their relationships to habitat and habitat complexity. In his review, Schoener suggests that spatial partitioning in aquatic communities may be less important than in terrestrial assemblages. However, at least for stream fishes, this has been contradicted by a number of studies, including Sheldon (1968), Zaret and Rand (1971), Mendelson

(1975), Baker and Ross (1981), Felley and Hill (1983), Moyle and Senanayake (1984), Felley and Felley (1987), and Kinzie (1988).

A growing amount of research has been conducted on North American stream fishes primarily since 1975 (Matthews and Heins 1987). While habitat complexity and diversity relationships have been established for fish communities in a number of geographic areas (e.g., Northeast, Southeast, Midwest), as well as a variety of taxonomic groups (e.g., cyprinids, centrarchids, catostomids), such research is lacking for Pacific Northwest fluvial systems and their anadromous salmonid assemblages.

Pacific salmon (Genus *Oncorhynchus*, Order Salmoniformes, Family Salmonidae) are important members of the native fish fauna on the North American continent (Scott and Crossman 1973). This genera has representatives among all its species which exhibit anadromy, a life history pattern that incorporates spawning and early rearing in freshwater streams, ocean migration and marine residence until sexual maturation, and return by adults to natal streams where they mate and deposit eggs (Dadswell et al. 1987, Groot and Margolis 1991). Historically, Pacific Northwest (PNW) fluvial systems supported large populations of anadromous salmonids consisting of an assemblage of up to seven native species (coho salmon *Oncorhynchus kistutch*, chinook salmon *O. tshawytscha*, chum salmon *O. keta*, sockeye salmon *O. nerka*, pink salmon *O. kisutch*, cutthroat trout *O. clarki*, and steelhead rainbow trout *O. mykiss*), as well as one species of native char comprised of several sub-species including arctic, Dolly Varden, and bull "trout" char (*Salvelinus malma* and *S. confluentus* sub-species; Scott and Crossman 1973).

Habitat is a primary dimension of resource partitioning among freshwater assemblages of anadromous salmonids, which display complex behavioral patterns leading to distinct patterns of macro- and micro-habitat selection (e.g., Chapman 1962, Hartman 1965). Various researchers have suggested that these traits evolved from intra- and interspecific competition resulting from high population densities and limited food and space resources (Larkin 1956, Nilsson 1963, Hartman 1965, Chapman 1966, Everest and Chapman 1972, Bohlin 1977, Glova and Mason 1977, Hart 1983, Hearn 1987). The relationship between habitat characteristics, salmonid abundance, and fish productivity has been of considerable interest, due to its applied value in anadromous salmonid management (Stouder et al. 1997). For example, studies that have examined the role of large wood in influencing the distribution and abundance of juvenile salmon (e.g., Dolloff 1987, Sedell et al. 1988) have engendered many habitat restoration projects in the Pacific Northwest (e.g., Ward and Slaney 1980, Sedell and Luchessa 1982, Bisson et al. 1987).

Ecological studies on Pacific Northwest stream salmonids have focused on single species population biology, factors limiting production, or two-species interactions, such as predation, behavior, competition, and diet (e.g., Newman 1956, Chapman 1962, 1966, Hartman 1965, Reimers 1968, Chapman and Bjornn 1969, Mundie 1969, Hanson 1977, Nickelson and Hankin 1991). Similarly, most research on habitat-fish relationships have incorporated only one or two representative species (e.g., Chen et al. 1995). Community-level investigations are few and there is little knowledge about salmonid assemblage responses to biotic and/or abiotic influences.

Current information about the link between anadromous salmonid diversity and habitat complexity in the PNW is mostly based on research examining the effects of land management activities on stream habitat and fish populations. Many watersheds in this region have undergone significant alterations due to urbanization, forest management, hydropower development, and/or agriculture (reviewed by Everest et al. 1980, Everest and Meehan 1981, Meehan 1991). Li et al. (1987) cited cases where habitat simplification from anthropogenic activities have appeared to cause shifts in PNW salmonid assemblage structure. Sullivan et al. (1987) noted patterns of species and age class diversity related to habitat unit / hydraulic heterogeneity (impacted streams were dominated by a single age class and species). In northeastern Oregon streams, Pearsons et al. (1992) found that increased complexity, as measured by hydraulic retention, appeared to be correlated with higher fish community resilience following floods. A study by Reeves et al. (1993) examined patterns of anadromous salmonid diversity among watersheds with varying levels of timber harvest in coastal Oregon. They documented that fish diversity was negatively correlated with increasing amounts of timber harvest, and suggested that reduction of habitat complexity via logging impacts may be one of the mechanisms responsible for the patterns observed. Similarly, Chen and Ricks (1990) analyzed data from the Elk River (Oregon) and found that streams with impaired habitat condition and low species diversity had been affected by increased bedload sediment from logging/roading activities. McIntosh et al. (1993) suggested that the reduction of deep pool habitat may have contributed to the loss of anadromous species within upper Columbia River basin streams.

These results suggest that habitat complexity and anadromous salmonid diversity may be linked for PNW streams. However, they do not identify which attributes of habitat may be influencing fish diversity. In the only such study to date, Means et al. (1992) found statistically-significant relationships between several physical characteristics (e.g., abundance of pool habitat, channel gradient) and two community diversity indices. However, these analyses used reach scale data and were developed only for a single stream (Drift Creek, Oregon). There have been no studies which have examined the influence of complexity on salmonid diversity at smaller spatial scales (i.e., individual habitat units), nor has there been any research to determine if and how such relationships may differ spatially (between streams within the same basin, and/or between other basins) or temporally (between different seasons). Additionally, no controlled manipulations have been undertaken to validate the link between habitat complexity and assemblage diversity. In light of the current emphasis on maintaining aquatic diversity, restoring watershed health, and managing declining anadromous salmonid stocks, such work could provide important information for fisheries resource managers in the Pacific Northwest.

1.1 Statement of Research Objectives

The objective of this research was to determine, via analyses of field observational data and through controlled *in-situ* experiments, if relationships exist between specific attributes of habitat physical complexity and the diversity of

anadromous salmonid fishes during summer low flow periods, and how such relationships may be affected by different spatial and temporal scales.

1.2 Field Study Hypotheses

Specific hypotheses that were tested in the field study include:

H₁: Statistically significant relationships exist between one or more elements of physical habitat complexity and indices of anadromous salmonid species diversity within pool habitats (channel unit scale).

H₂: Statistically significant relationships exist between habitat complexity and indices of anadromous salmonid species diversity at the stream reach scale.

H_{0,1,2}: No statistical relationship(s) exists between these measures of habitat complexity and the diversity of anadromous salmonid fishes at one or all of these spatial scales.

1.3 In-situ Factorial Experiment Hypotheses

The hypotheses for the controlled *in-situ* factorial experiments include:

H₁: Maximum depth in pools is a habitat feature selected by assemblages of anadromous salmonid fishes (significant effect of depth on species richness).

H₂: Wood in pools is a habitat feature selected by assemblages of anadromous salmonid fishes (significant effect of wood on species richness).

H₃: The combination of depth and wood influences the species richness of anadromous salmonid fishes (interaction term of wood \times depth has a significant effect on species richness).

H_{01,2,3}: Depth, large wood, and/or depth/large wood (interaction terms) are habitat features that are not selected by assemblages of anadromous salmonid fishes.

2. MATERIALS AND METHODS

2.1 Streams Selected as Field Study Sites

The five streams used in this study were 4th-order (Strahler 1957) tributaries of three river basins located in southwest coastal Oregon. These include Red Cedar Creek, Panther Creek, and the North Fork Elk River, in the Elk River basin (T 33 S, R 14 W, section 14; T 33 S, R 13 W, sections 19 and 30; and T 33 S, R 13 W section 13 and R 12 W section 7, Willamette meridian, respectively); Dry Creek of the Sixes River basin (T 32 S, R 14 W, sections 18, 19, 20, and 29); and Salmon Creek in the upper South Fork Coquille basin (T 31 S, R 12 W, sections 13, 24, 23, 26, 27, and 34).

A principal criteria used to select sites was the amount, frequency, and timing of past anthropogenic disturbance from land uses such as timber harvest, road construction, or in-channel placer/stream side hydraulic mining. These activities have been documented to influence physical characteristics of streams and their associated biota (Meehan 1991, Salo and Cundy 1987, Everest et al. 1980). By selecting streams with no recent anthropogenic disturbance (Red Cedar Creek and Dry Creek), those in which recovery from such activities have occurred (Salmon Creek), or segments which have not been significantly affected by upstream land management (Panther Creek and the North Fork Elk River), habitat complexity-salmonid diversity relationships could be examined with reduced influence from human impacts (verified from U.S. Forest

Service watershed assessments; Siskiyou National Forest 1993, 1994, Chen and Ricks 1990, R. Bender Oregon Department of Fish and Wildlife unpublished data, U.S.F.S. Powers Ranger District unpublished data).

A large source of natural variability inherent to studies utilizing different stream basins results from geologic and/or geomorphic differences between them (Leopold et al. 1964, Knighton 1987). These landscape features have been shown to influence channel characteristics, resulting fish habitat, and distribution of salmonid species (e.g., Everest et al. 1980, Reeves et al. 1993). All study streams selected were located in a single geologic province (Klamath). Morphology in the three watersheds was similar, with topography characterized by highly incised stream channels and steep adjacent hillslopes. Basin area ranged from 440 to 3,600 ha, with summer low flow discharges varying from 0.74 to 3.7 m³/second.

Water temperature has been found to influence growth, mortality, and intra- and inter-specific interactions for salmonids (Reeves 1985, Reeves et al. 1987, Chapman and Bjornn 1969). Average maximum daily temperatures in each of the study streams ranged from 10 to 20.5 °C. Water temperature effects were partly addressed by locating study sites only where the maximum daily temperature did not exceed 18.5° C (threshold limit for growth in anadromous salmonids; Bjornn and Reiser 1991). High ambient temperatures thus resulted in the elimination of the lower 4.4 km of Salmon Creek from this study.

2.2 Description of Study Sites

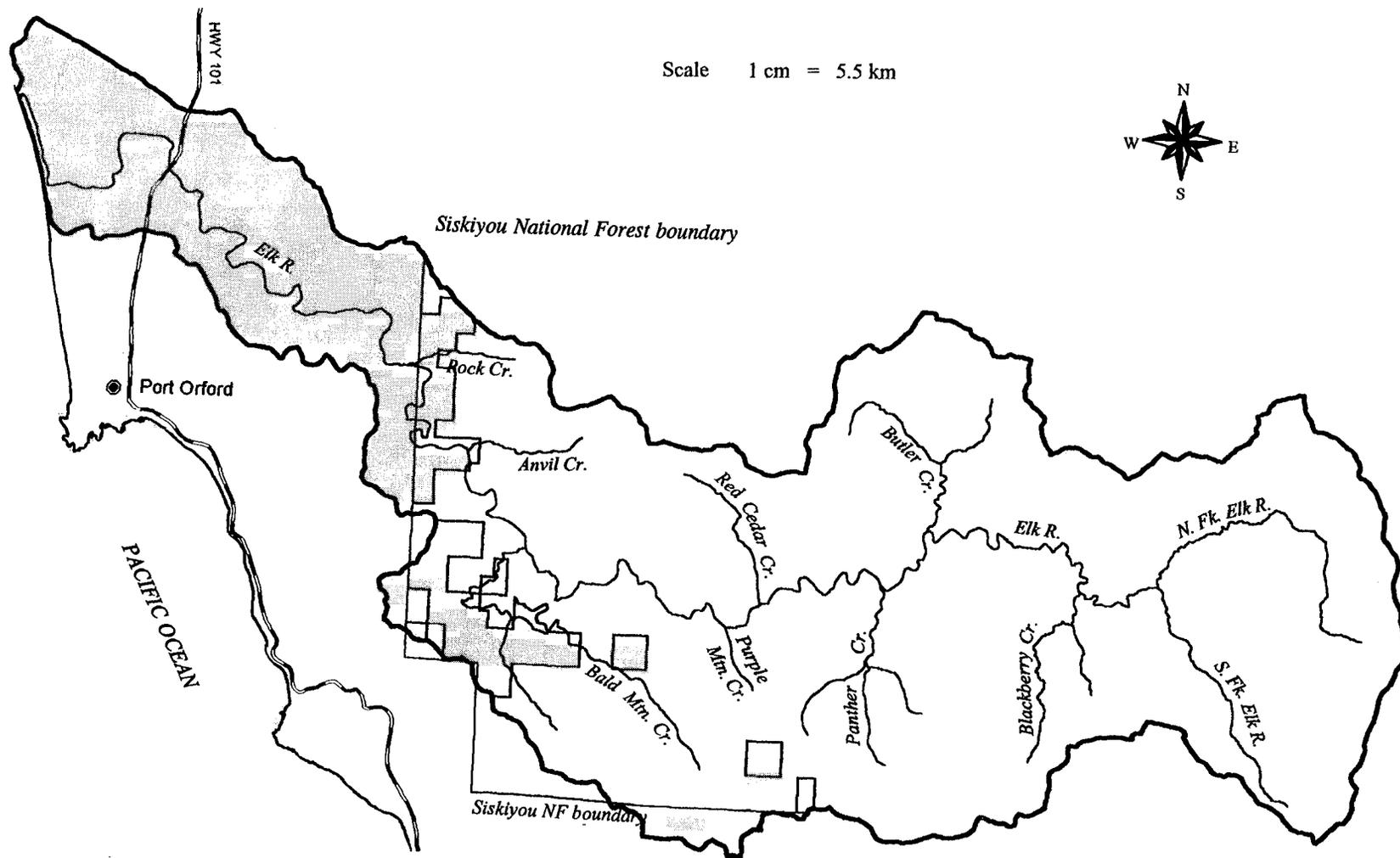
2.2.1 Elk River Basin

Red Cedar Creek, Panther Creek, and the North Fork of the Elk River are located within the Elk River basin, a watershed flowing into the Pacific Ocean near Cape Blanco and the town of Port Orford (Fig. 1). Upper Elk River is managed by the U.S. Forest Service, Siskiyou National Forest (Powers Ranger District). Terrain in Elk River is steep and rugged, with slopes that exceed 100% bordering many of the tributary streams. Parent geology includes granitic diorite, Galice shale, Rocky Point sandstone, Humbug conglomerate, serpentine, and peridotite formations uplifted by recent tectonic activity and sheared by numerous faults (Siskiyou National Forest 1993, 1994). Many of the sedimentary deposits have been hardened via igneous intrusion or other metamorphic processes.

Intense seasonal rainfall varying from 228 cm to over 330 cm per year in the Elk River combine with the unstable geology and steep morphology to produce high erosion rates. Channel roughness features such as boulders and whole trees are delivered via mass-wasting events from adjacent hillslopes, often triggered by large wildfires and storm events. Landslides are a dominant terrestrial process in this basin and are responsible for many of the observed channel features (Reeves 1988, McHugh 1986, Ryan 1989, Siskiyou National Forest 1993, 1994).

Red Cedar Creek flows southeast/south through the Grassy Knob Wilderness and enters the Elk River at river km 45 (Fig. 1). Watershed area encompasses 440 ha,

Figure 1. Elk River watershed boundary and major tributary streams.



with steep headwaters that originate at over 800 m in elevation. Average daily maximum stream temperatures varied from 10.0 to 15.5 °C during the summer months. At approximately 3,200 m upstream of the Elk River confluence, a 3 m channel-spanning log jam serves as a barrier to anadromous fish migration. No management activities have occurred in this basin, except for a ridge top road dividing the Dry Creek and Red Cedar Creek sub-basins.

Approximately 1,100 m upstream of its confluence with Elk River, Red Cedar Creek enters a broad, low-gradient valley that varies from 20 to 50 m in width. Average stream gradient was estimated at 1% in this reach. The channel is bordered by stands of mature red alder (*Alnus ruber*), broadleaf maple (*Acer macrophyllum*), Oregon myrtle (*Umbellularia californica*), middle-age to old-growth stands of Douglas-fir (60 - 100 year old+ *Pseudotsuga menziesii*), western red cedar (*Thuja plicata*), and Port-Orford cedar (*Chamaecyparis lawsonia*), mixed with western hemlock (*Tsuga heterophylla*) and occasional Pacific yew trees (*Taxus brevifolia*). The under story consists of vine maple (*Acer circinatum*), salal (*Gaultheria shallon*), Pacific rhododendron (*Rhododendrum macrophyllum*), and western azalea (*Rhododendrum occidentale*). Gravel bars are partially vegetated with stands of alder, Pacific willow (*Salix lasiandra*), common horsetail (*Equisetum arvense*) and various species of sedges, forbs, and grasses.

Red Cedar Creek flows through geology consisting primarily of Humbug conglomerate and Galice shale formations. The substrate consists of moderate to coarse-sized bedload particles comprised of the parent material. In a few areas, exposed

bedrock border the channel and create lateral scour pools. Other pool-forming elements include large boulders, wood jams, and streambank rootwads.

The low-gradient area is approximately 2,200 m in length and is surrounded by a series of old fluvial terraces above bankfull flow. These features are a result of massive natural earthflows originating from adjacent tributaries that deposited sediment and organic material into the main channel (McHugh 1986). Small streambank failures are abundant and serve to continually topple new trees into Red Cedar Creek. The entire stream from mouth up to the log jam barrier was used in this study (total distance of 3,300 m).

Panther Creek enters the main Elk River at km 49.5 (Fig.1) and has a basin area of 2,300 ha. Panther Creek flows northward into the Elk River and originates via three tributary forks that begin at over 1000 m elevation. Downstream of this confluence, the mainstem of Panther Creek becomes low gradient (estimated at 1%) and enters a broad valley which varies in width from 20 to 75 m. Anadromous salmonid fish are present to the forks and extend upstream into each branch for 100 - 300 m.

The riparian area is similar to that of Red Cedar Creek except that the stand is older (80 - 150 + years old); red and Port-Orford cedars are also less abundant, and growths of willow/alder on the stream side gravel bars are denser than in Red Cedar Creek.

Panther Creek flows through a mixed geology consisting of Galice shale, Humbug conglomerate, and peridotite rock types. A major north/south fault traverses this watershed and forms the division between the Humbug and Galice formations.

Channel substrate is comprised of small to large gravels and cobbles. Bedrock outcrops are interspersed along the channel and most of the lateral scour pools appear to be related to these features.

As with Red Cedar Creek, there are a series of fluvial terraces in Panther Creek formed by natural earthflows and subsequent deposition. At approximately 1,100 m upstream of its confluence with the Elk River, the valley narrows and Panther Creek enters a constricted gorge. The low gradient section begins at the head of the gorge and extends upstream to the tributary forks. The entire length of Panther Creek from mouth to forks was used in this study (7,700 m).

The North Fork of the Elk River joins the South Fork and mainstem at river km 66 (Fig. 1). The North Fork originates at an elevation of over 1000 m on Iron Mountain, and flows north to west, skirting the edge of Copper Mountain (which divides the North and South Fork Elk River). Basin area encompasses 2,400 ha and average maximum daily summer water temperatures range from 10.0 to 15.5° C at the mouth. A bedrock falls 4 m in height is found approximately 3500 m upstream of the Elk River confluence. These falls present an impassable barrier to anadromous fish migration.

The lower sections of the North Fork flow through a short section of constrained channel with moderate to high gradient (1.5 - 2% +). At stream distance 1300 m, the valley widens and gradient decreases to 1% or less. This reach continues upstream for another 1800 m, until the North Fork again enters a narrow canyon extending 400 m to the falls. Actually a series of three wide valleys separated by brief constrictions, the

low-gradient reach varies in width from 15 to 55 m. The entire length of stream used in this study (from mouth to fish-barrier falls) was 3,500 m.

The geology of the North Fork consists of serpentine at the headwaters, and a combination of Rocky Point sandstone, Humbug conglomerate, and Galice shale down lower in the basin; as with the other Elk River streams, substrate is composed of moderate to large gravels and cobbles. The stream exhibits some degree of meander through the wide valley section with flood plains 25 - 100 m in width. Many lateral high-flow channels are found where the stream travels around bends, and pools are associated with numerous log jams. Additional pools are located where old streambank rootwads, bedrock outcrops, single snags, and smaller accumulations of wood occur.

Riparian vegetation consists of red alder, maple, and young to moderate-age stands of Douglas-fir and western hemlock (40 - 80 years old+), with grass/forb/fern under story. A few patches of old-growth conifer (150 - 200 old+ Douglas-fir) are found adjacent to the mouths of side tributaries. Gravel bars up to 17 m in width border the channel, which are partially overgrown by common horsetail, forbs, and grasses.

The North Fork exhibits the most notable example of large-scale natural disturbances and their influence on channel morphology in the Elk River basin. As with the other low-gradient reaches in Panther and Red Cedar creeks, the valley of the North Fork bears the effects of massive upslope earthflows originating from steep head wall tributaries that transported sediment and wood to the channel, leaving deposits forming the valley floor and surrounding terraces (McHugh 1986, Ryan 1989).

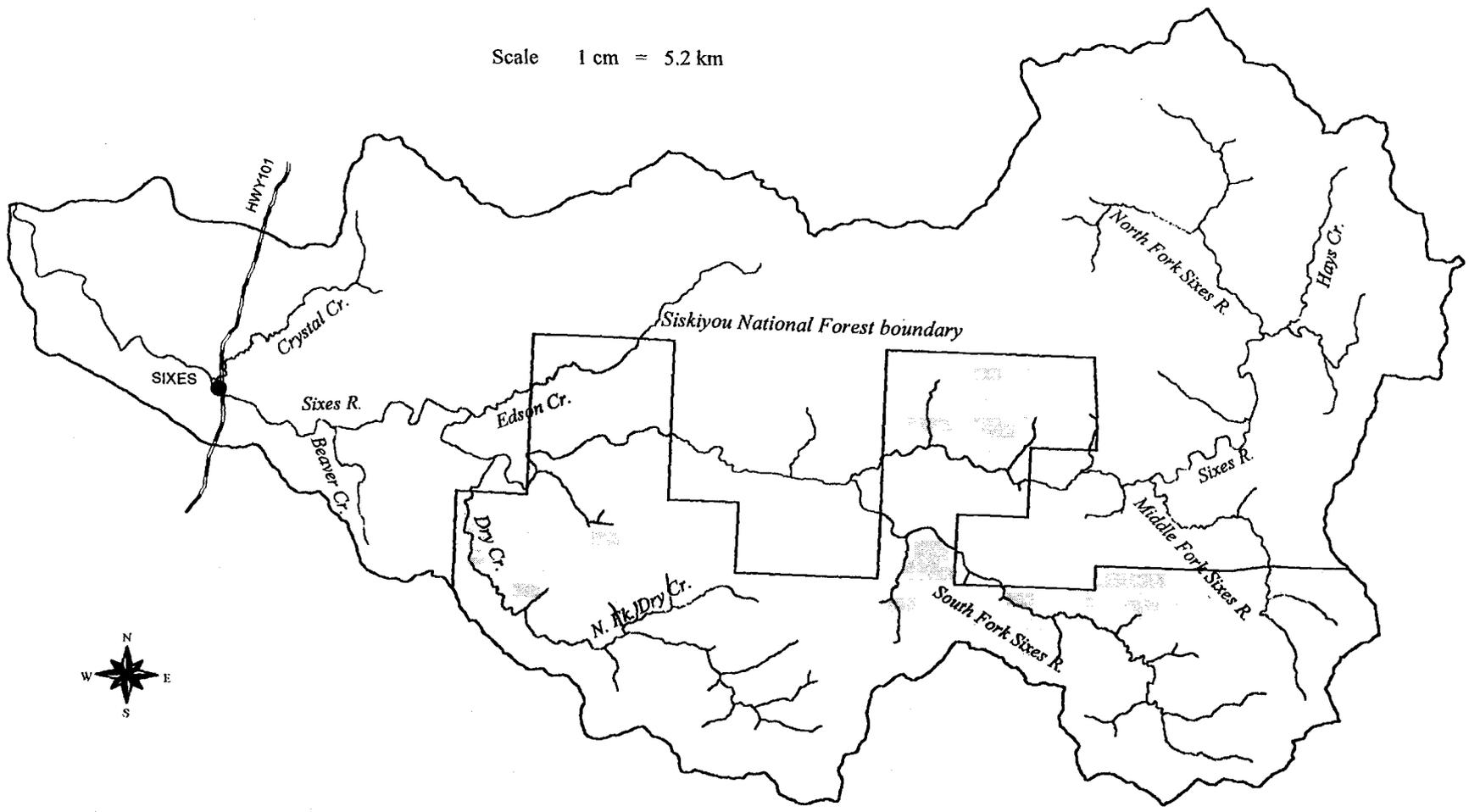
2.2.2 Sixes River Basin

The Sixes River flows west to the ocean just north of the Elk River, separated by a divide which includes the Grassy Knob Wilderness (Fig. 2). The Sixes is found at the northern edge of the Klamath geologic province and a portion of the basin is within the Tyee sandstone. Topography, rainfall, geology, and mass wasting processes have influenced stream channel characteristics in the Sixes basin. Less than 30% of the Sixes River is within the Siskiyou National Forest boundary, and it has been moderately to heavily impacted by timber harvest on private lands.

Dry Creek is a 4th-order sub-watershed that is contained within the Grassy Knob Wilderness of the Siskiyou National Forest (Fig. 2), encompassing 3,200 ha. Maximum daily summer stream temperatures 3 km upstream of the mouth have been recorded at 18.5° C. The lowest portion of Dry Creek from the Sixes River confluence upstream 2.2 km is privately owned and flows sub-surface beneath a heavily-aggraded channel.

The Siskiyou National Forest and Grassy Knob Wilderness boundary begin where perennial flow re-occurs. From this point to 2,600 m upstream, Dry Creek runs through a broad, low-gradient valley varying in width from 35 to 60 meters, with stream gradient estimated at 1.0 to 1.5 %. The geology consists of Humbug conglomerate/diorite and the channel substrate is composed of small to moderate-sized gravels, interspersed with pockets of sand. Log jams and bedrock outcrops are associated with a large proportion of pools found in Dry Creek. At a distance of

Figure 2. Sixes River watershed boundary and major tributary streams.



4900 m, Dry Creek becomes confined by a narrow, steep gorge which continues up to its headwaters.

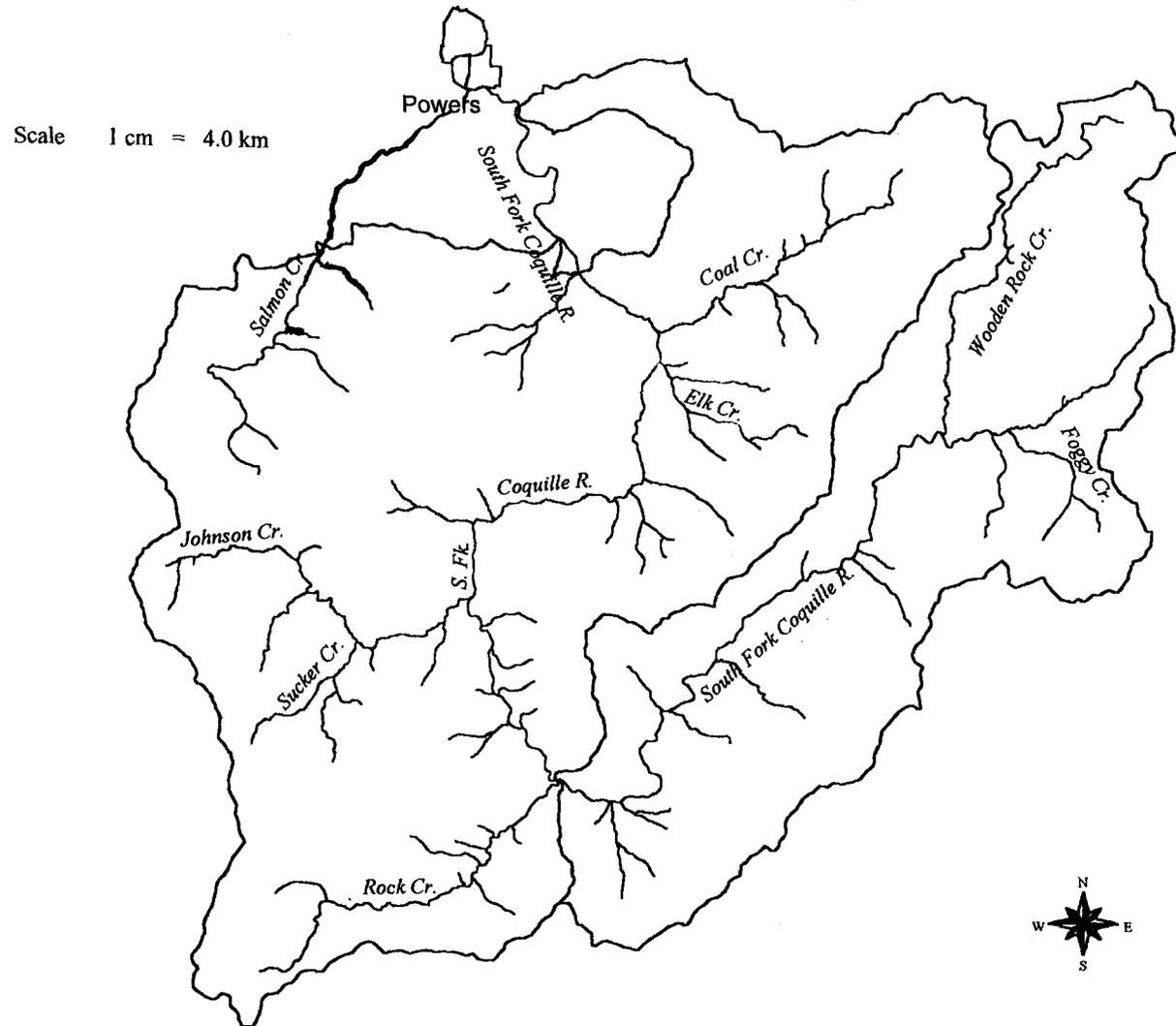
Anadromous fish traverse the entire low-gradient reach and are distributed into the constrained sections. The portion used for this study began at the abandoned Moore Mill logging bridge (2,100 m from the mouth) upstream to where Dry Creek narrows at the mouth of the gorge (5,400 m above the Sixes River confluence).

Gravel bars along Dry Creek are sparsely vegetated and contain only grasses and horsetail. The riparian area consists primarily of large, old-growth Douglas-fir (100-200 year old+), Port Orford and western red cedar, broadleaf maple, red alder, and some Pacific yew trees. A number of Port Orford cedars have been killed by an introduced fungal parasite (*Phytophthora lateralis*). Under story vegetation consists of vine maple, ferns, and forbs. Old fluvial terraces created by mass failures are found in the section of Dry Creek used in these studies.

2.2.3 South Fork Coquille Basin

The South Fork is part of the Coquille River watershed, the second largest coastal system in Oregon. It is 175 km in length and originates from the mountains dividing the Elk, Sixes, and Rogue River basins. Most of the upper South Fork is managed by the Siskiyou National Forest (Fig. 3), with much of the watershed having been affected by timber harvest; some recovery has occurred (Siskiyou National Forest 1996 draft watershed analysis). Portions of this basin are within the Tyee sandstone and Klamath geologic formations.

Figure 3. Upper South Fork Coquille River watershed boundary and major tributary streams.



Salmon Creek enters the main South Fork Coquille from the east at the town of Powers (river km 95; Fig. 3). It is a 4th-order sub-watershed 3,600 ha in size that contains a mixed geology of Rocky Point and Tyee sandstone, and Humbug conglomerate formations.

The morphology in Salmon Creek varies substantially along its length. From the mouth upstream to 1800 meters, the gradient ranges from 1% to 1.5% and the channel flows through a valley 30 - 45 m in width. It then enters a narrow gorge with gradient increasing steadily to 3%, up to a stream distance of 8,800 m. Ownership changes from private to Federal (a combination of U.S. Forest Service and Bureau of Land Management lands) within the gorge. Because stream temperatures in the lower sections were high (maximum daily greater than 20.5° C), the study site began instead at distance 4,400 m from the mouth, where sub-surface groundwater and tributaries cooled water temperatures down to levels below lethal maximums (18.5° C) for salmonids.

At stream distance 8,800 meters, the gorge ends and Salmon Creek meanders through a broad, low-gradient (1 - 1.5%) valley 50 - 150 m in width. This segment continues upstream for approximately 3,500 m. At 14,100 meters, Salmon Creek enters private ownership; this point marks the end of the study section.

Riparian area vegetation consists of red alder and salmonberry (*Rubus spectabilis*), mixed with conifer stands (mature 60- 80 year-old second-growth and remnant old-growth 150 years old+) of Douglas-fir, red cedar, and Western hemlock. Pools are found primarily in association with large wood jams adjacent to toppled trees,

or along bedrock outcrops. Stream substrate is composed of medium to fine-sized gravel, with sands deposited in pool margin areas.

2.3 Methods Used to Measure Complexity Within Habitat Units

2.3.1 Basin Approach to Collecting Habitat Complexity Data

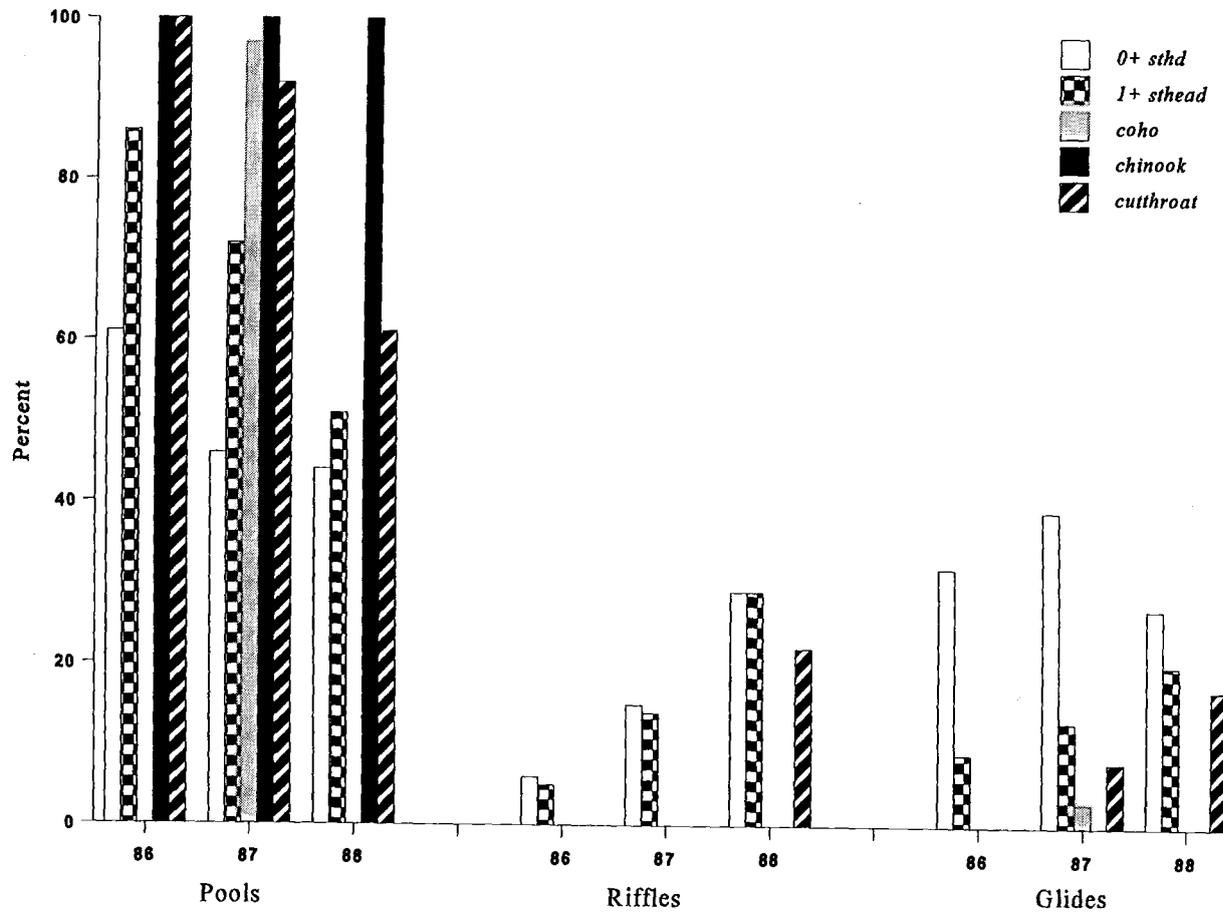
Spatial scale related to sampling effort has been documented to influence salmonid population and habitat data collected within a stream, with results from short representative reach segments varying considerably from those collected over an entire basin (Hankin and Reeves 1988). This study focused on the basin-wide approach and 85 - 100% of the entire lengths of stream inhabited by anadromous salmonids were used (exceptions discussed previously for Salmon Creek).

2.3.2. Parameters Used to Describe Physical Habitat Complexity

A review of habitat — species diversity studies indicated that a variety of parameters to measure "habitat complexity" have been employed, including spatial area, physical features within the habitat type, the diversity of habitat types, and the spatial/temporal arrangement of habitat types/features (Magurran 1988).

For their studies, Reeves et al. (1993) used habitat attributes that are typically included in stream habitat inventories (e.g., U.S.D.A. Forest Service Pacific Northwest Region Riparian Inventory, U.S.D.A. Forest Service Rocky Mountain/Intermountain Regions Stream Inventory Procedures). Parameters which were adopted for this study

Figure 4. Frequency distribution of anadromous salmonid species and age classes among habitat types (North Fork Elk River, August 1986, 1987, and 1988 [G. Reeves et al. unpublished data]).



included spatial dimensions of each habitat unit (average depth, maximum depth, surface area, volume), large wood, and dominant substrate composition.

2.3.3 Habitat Type

Bisson et al. (1982) and Hawkins et al. (1993), have developed classifications for stream habitat units according to flow and geomorphic characteristics. The habitat unit served as the basic organizational level for the other types of complexity data that were collected.

The habitat unit complexity-species diversity portion of this study (Hypotheses 1 and 2) focused on data collected only within pools. This was based upon analyses of existing information from the North Fork Elk River (1986 - 1988), which indicated that pool habitat supported the highest percentage and species richness of salmonids (Fig. 4).

2.3.4 Dominant Substrate Type

The dominant substrate within each habitat unit was recorded using a Wentworth classification system, similar to the *phi* units employed by fluvial geomorphologists (Knighton 1987). Bedrock was designated as class 1; silt/fine sand (particle diameter < 0.01 mm) = class 2; coarse sand (0.1 mm - 1.0 mm) = class 3; fine gravel (1.0 mm to 1.0 cm diameter) = class 4; gravel (1 cm - 10 cm diameter) = class 5; cobble (10 cm - 100 cm diameter) = class 6; and boulder (diameter > 100 cm) was designated as class 7.

2.3.5 Large Wood

Wood volume within each pool was measured for each piece/aggregation of wood, and summed for every habitat unit. For single pieces of wood (bare logs), volume was calculated using the following formula:

$$\text{volume} = \frac{\pi (d^2) l}{4}$$

where d = diameter 1.5 meters from the large end of the log, and l = total length of the log.

For whole trees with attached root wads and limbs, total volume was estimated by enclosing the wood within the outlines of a tapered cylinder; two diameter measurements of the cylinder (d_1 and d_2) were then taken at points 1.5 meters from each end and combined with total length in the following equation:

$$\text{volume} = \frac{\pi (d_1^2 + d_2^2) l}{8}$$

For aggregations of wood (e.g., log jams), total volume was estimated by visually enclosing it within the outlines of a square or rectangle, measuring the relevant axes, and subsequently multiplying length, width, and depth.

2.3.6 Habitat Unit Spatial Dimensions

The spatial dimensions of stream habitat units were used independently or combined as measures of habitat complexity. Corrected visual estimates of length and

width (Hankin and Reeves 1988) and measured depths were used to obtain the following data:

SURFACE AREA: From corrected ocular estimates of maximum length and mean wetted width (based on 3 measurements) of each pool

MEAN DEPTH: calculated from 5 depth measurements within the pool

VOLUME: calculated from products of mean depth and surface area for each pool

MAXIMUM DEPTH: habitat unit depth measured at location of greatest depth along the thalweg within each pool

2.4 Methods Used for Determining Anadromous Salmonid Diversity Within Habitat Units

2.4.1. Salmonid Population Censuses

Underwater visual estimates collected by snorkelers calibrated with electroshocking verifications (using a modification of Hankin and Reeves 1988) were employed to assess anadromous salmonid species diversity in pools. Each diver identified and tallied number by species and age classes of salmonids using morphological characteristics, coloration patterns, microhabitat usage, and behavioral traits of the fish. Age classes for trout juveniles were based on length criteria (0+ or fry were < 70 mm in length; 1+ or yearling parr were > 70 mm).

To minimize observer-related variability associated with unclear definition of unit boundaries, fish were sampled after the habitat measurement crew marked the

upper and lower boundaries of each pool, with intervals of 24 - 48 hours to allow fish to settle after being disturbed. To compensate for diel-related behavior and to reduce error in diver counts related to ambient light levels, all censuses were conducted between the hours of 0930 - 1500 hours Pacific Standard Time (PST).

Adjustments for observer bias in fish visual estimates were made by combining a series of electroshock verifications with dive counts on 5 pools each within 3 streams (Salmon Creek, Panther Creek, and Dry Creek). Shocking censuses were made by block netting pools and using three removal passes. The small sample size raised concerns about the validity of employing regression-based models typically used to determine total fish abundance from multiple-pass depletion data (Dolloff et al. 1993, Ricker 1975) and diver re-counts of the remaining fish were added to the shocking totals instead. This method of estimating diver accuracy is a modification of the calibration technique described in Dolloff et al. (1993) and Hankin and Reeves (1988). A correction factor ($R_{species}$) was developed for each diver by fish species and year (Table 1).

Examination of Table 1 demonstrate that diver estimates for age 0+ trout juveniles were less accurate than for other species and age classes. This was due in part to their high numbers and their use of channel margin areas which were difficult to census due to extremely shallow depth. The low R values and field observations of limited sampling efficiency led to the subsequent omission of 0+ trout from all community diversity calculations, as a means of reducing observer-related variability.

The $R_{species}$ values indicate that divers underestimated fish numbers for all species and age classes.

Table 1. Mean correction ($R_{species}$) factors for diver estimates by diver and fish species.

Observer	Year	Calculated $R_{species}$ values:				
		0+ trout	1+ steelhead	chinook	coho	cut-throat
J. Chen	1990	0.413	0.873	0.711	0.723	0.912
	1991	0.309	0.910	0.737	0.831	1.000
G. Chen	1990	0.378	0.780	0.851	0.866	0.955
	1991	0.316	0.793	0.915	0.732	1.000

2.4.2 Fish Species Diversity Indices

Multiple diversity (in particular, dominance) indices were used because they differed in their sensitivity to certain variables (Magurran 1988). Table 2 lists information on the community diversity indices selected for this study:

Table 2. Species diversity indices.

Index name	Sensitive to:	Equation:*
S (species richness)	richness	$S = \text{total number of species}$
McIntosh U Index	richness	$U = (\sum n_i^2)^{0.5}$
McIntosh D Index	dominance	$D = (N - U) / (N - N^{0.5})$
Simpson D Index	dominance	$D = \sum [n_i(n_i - 1) / N(N - 1)]$
Berger-Parker D Index	dominance	$D = N_{max} / N$

* From Magurran (1988)

where n_i = number of individuals in the i^{th} species, N = total number of individuals, and N_{max} = number of individuals in the most abundant species. (U in the McIntosh dominance equation is McIntosh U).

Although Shannon H' and E were originally included in the list of selected indices, not all fish species were present in each censused pool. H' and E rely on the assumption that all community members be represented in each sample (Magurran 1988); thus, these indices could not be calculated for all of the data sets and were subsequently dropped.

Counts of age 0 trout were not included in the species diversity calculations because of problems with sampling efficiency associated with the correction factors (Table 1). Since there were some pools in which there were no other fish present, this yielded values of zero for the diversity indices in these particular habitat units.

2.5 Description of Study Design for Habitat Unit-Scale Studies

To test Hypothesis 1, data were collected in the five streams during summer low flow periods in 1990 and 1991. Dry Creek was sampled during July 25 - August 1, 1990, and July 14 - 20, 1991. Salmon Creek was added as a study site following the 1990 field season and data were collected there from July 1 - July 15 in 1991. Elk River streams were visited from June 20 - 30, 1990, and August 3 - 18, 1991.

Sample sizes used for Elk River streams and Dry Creek were based on preliminary analyses of fish population data from 1986 - 1989 (G. Reeves et al. unpublished data, U.S.F.S. Powers Ranger District unpublished data). Using equations in Stafford (1988) and Devore and Peck (1986), calculations determined that a minimum of 21 pools needed to be sampled in order to account for 90% of the variation in fish species richness. For 1990 and 1991 efforts, pools were systematically selected by using available data on habitat frequencies (Elk River streams and Dry Creek). In Salmon Creek, a pool sampling frequency of 1:4 was used in the absence of preliminary inventories.

Differences in pools numbers between July and August 1990, and between 1990 and 1991 sessions were attributed to several factors. Declining flows caused some of the habitat units previously identified as pools to be re-classified as glides. In some cases, different observers were used, which led to discrepancies in habitat unit identification, despite the use of rigorous bed elevation/surface flow definitions established to reduce such variability. Such problems were not foreseen in 1990; thus, systematic frequencies for selecting pools were not adjusted *a priori* to ensure comparable sample sizes. However, during the single sampling session in 1991, changes were made prior to data collection to remedy this situation.

2.6 Descriptions of Methods for Reach-Level Studies

2.6.1. Reach-Level Assessments of Habitat Complexity

Hypothesis 2 states that relationships exist between habitat complexity and salmonid species diversity at the stream reach scale. To test this hypothesis, the frequency and abundance of different habitat units (habitat unit type diversity, $H'_{habitat}$) was used as a measure of physical complexity within a reach.

The definition for a "reach" in this study followed the conventions established by fluvial geomorphologists, who typically include characteristics such as gradient, valley confinement, bank features, confluence of lower-order tributaries, and geologic changes to separate reaches (e.g., Rosgen 1985). Valley morphology proved to be the most consistently identifiable feature and this was combined with secondary features to separate individual reaches.

$H'_{habitat}$ was based on the frequency of riffle, pool, and glide habitat units within each reach. These habitat types were defined according to Bisson et al. (1982). Minimum length for each habitat unit was required to be equal to or greater than the wetted width (Hankin and Reeves 1988); small sub-units found within a habitat type were included as part of the primary habitat type. Other habitat types identified by data collectors included runs, rapids, and cascades; for this study, these were lumped into the riffle category.

Counts of pools/riffles/glides in each identified reach were used in a Shannon-Wiener equation to calculate $H'_{habitat}$:

$$H'_{\text{habitat}} = - \sum p_i \ln p_i$$

where p_i is the proportion of units found in the I^{th} habitat type. The validity of using biologically-based equations to describe physical habitat diversity is discussed in Magurran (1988).

2.6.2 Reach-Level Assessments of Fish Species Diversity

Visual censuses of salmonid fish numbers by species, in systematically-selected pool, riffle, and glide habitat units, were conducted by 2 or more snorkelers. Sampling frequencies for habitat types were 1:3 for pools, 1:5 for glides, and 1:10 for riffles; these were determined from previous years' data on abundances of habitat types in the Elk River basin streams (Reeves 1988).

Crews from the USDA Forest Service Pacific Northwest Experiment Station assisted with collecting these data and correction factors were not derived for each individual. Thus the salmonid numbers obtained in this part of the study were not adjusted for observer error as described by Hankin and Reeves (1988).

Fish population data summed for each reach were used in equations for McIntosh richness U , McIntosh dominance D , Berger-Parker dominance D , Simpson dominance D , and species richness S diversity indices.

2.7 Analysis of Habitat Complexity - Species Diversity Relationships

SAS/STAT version 6 (SAS/STAT Institute Inc. 1989) were used to perform all tests and analyses. Scatter plots, non-parametric correlation analyses (Spearman Rank Correlations), Type II sums of squares analysis, multiple linear regression, and canonical correlation multivariate techniques were used to analyze the relationship between physical complexity measures and community diversity within pools and reaches (Snedecor and Cochran 1980, Devore and Peck 1986, Weisberg 1985). Data collected during all sampling periods were grouped by stream, yielding a total of 5 data sets each (representing individual streams) for pools (total pools = 296). Data from all sites were combined together for the reach analyses (total of 30 reaches). These groupings were necessary to ensure adequate sample sizes for both univariate and multivariate analyses (D. Turner, U.S.F.S. Rocky Mountain Research Station personal communication).

Pool and reach data were examined using scatter plots and Spearman Rank correlations, followed by multiple regressions in SAS/STAT to construct predictive models. For pool data, the combination of 6 habitat complexity parameters were employed as independent variables, with the 5 species diversity variables used as dependent variables for each of the 5 data sets (total number of comparisons = 25). Overall model significance ($p < 0.10$) were tested via ANOVA (Weisberg 1985). Standardized regression coefficients, and the results of significance tests (Student's t -test, $p < 0.10$) applied to the r values (correlation coefficients between independent and

dependent variables), were used to determine which habitat complexity variable(s) were statistically correlated with the species diversity measures. The same set of tests were also applied to reach data, with $H'_{habitat}$ and the five species diversity indices used as independent and dependent variables respectively.

Because age 0 trout were not used in the diversity calculations, this yielded a number of pools (1 to 5 per data set, per stream) in which the diversity value was 0. Inclusion of these pools did not yield a single significant regression model using any combination of complexity/diversity variables. These habitat units were subsequently dropped when it was demonstrated that all of the zero-fish data points were significant outliers (due to lack of fish) in the regression analyses. Gorman and Karr (1978) used similar logic to eliminate pools without fish from their community studies.

Both pool habitat and reach data were also tested using canonical correlation multivariate methods (Hotelling 1935, 1936, Cooley and Lohnes 1971). Because sample sizes were low, data were grouped by stream, and not separated by sampling period. Linear combinations of x (habitat complexity) and y (species diversity index) canonical variables maximizing their correlations were constructed and tested for significance (F value corresponding to $p < 0.10$; number of canonical variables = 5). Results from multivariate tests for pools and reaches were then compared to those derived from univariate methods.

3. RESULTS

3.1 Physical Habitat Complexity and Salmonid Diversity in Pools

Physical complexity data in pool habitats for all study streams (number of pools, and means, standard deviation, and ranges for all habitat data) collected during July 1990, August 1990, and July/August 1991, respectively are summarized in Tables 3, 4, and 5.

All fish data are summarized in Tables 6, 7, and 8, which show the mean, standard deviation, and range of juvenile coho, chinook, age 1+ steelhead, and juvenile/adult cutthroat numbers (corrected for diver bias), and derived community diversity values, recorded during July 1990, August 1990, and July/August 1991 sampling of pools.

3.2 Results from Analyses of Complexity - Diversity Relationships Within Pools

Significant regressions were produced for four out of the five streams (North Fork Elk River, Panther Creek, Dry Creek, and Salmon Creek; Table 9). Eleven out of twenty-five possible regressions (44%) between habitat complexity and species diversity produced a significant ($p < 0.10$) regression model. Richness S , diversity (McIntosh U), and dominance (McIntosh D , Berger-Parker D , Simpson D) were

Table 3. Summary of physical habitat data from pools, July 1990.

Stream		pool area (m ²)	pool volume (m ³)	maximum depth (m)	mean depth (m)	dominant substrate	wood volume (m ³)
North Fork	maximum	733	570	2.0	1.4	8.0	25
Elk River	minimum	18	12	0.7	0.4	3.0	0
	mean	141.9	127.2	1.1	0.8	6.3	2.5
	std. dev.	155.4	142.2	0.4	0.2	1.4	4.0
total pools # sampled = 21							
Panther	maximum	468	635	3.3	2.5	7.0	333
Creek	minimum	9	7	0.5	0.4	1.0	0
	mean	115.6	103.8	1.1	0.9	5.6	12.1
	std. dev.	89.5	116.1	0.5	0.4	1.3	61.8
total pools # sampled = 31							
Red Cedar	maximum	150	119	1.7	1.1	7.0	5
Creek	minimum	4	1	0.3	0.2	4.0	0
	mean	77.3	45.4	0.7	0.5	5.7	0.6
	std. dev.	43.0	35.0	0.4	0.2	0.9	1.3
total pools # sampled = 19							
Dry Creek	maximum	1338	1115	2.3	1.9	6.0	94
	minimum	32	16	0.5	0.4	2.0	0
	mean	354.5	373.8	1.3	1.0	4.8	34.8
	std. dev.	274.7	291.1	0.6	0.5	1.0	38.0
total pools # sampled = 30							

Table 4. Summary of physical habitat data from pools, August 1990.

Stream		pool area (m ²)	pool volume (m ³)	maximum depth (m)	mean depth (m)	dominant substrate	wood volume (m ³)
North Fork Elk River	maximum	557	701	1.7	1.3	7	13
	minimum	47	11	0.5	0.6	5	0
	mean	206.3	117.4	1.1	0.5	5.9	4.1
	std. dev.	115.9	165.5	0.4	0.3	0.8	4.9
total # of pools sampled = 14							
Panther Creek	maximum	208	103	1.8	0.5	8	14
	minimum	32	3	0.4	0.1	5	0
	mean	81.8	26.5	0.9	0.3	6.3	4.8
	std. dev.	55.9	28.3	0.5	0.1	0.8	4.4
total # of pools sampled = 15							
Red Cedar Creek	maximum	130	53	1.3	0.4	7	5
	minimum	17	4	0.4	0.2	6	0
	mean	72.0	21.2	0.8	0.3	6.7	0.6
	std. dev.	32.1	12.4	0.2	0.1	0.5	1.3
total # of pools sampled = 17							

Table 5. Summary of physical habitat data from pools, 1991.

Stream		pool area (m ²)	pool volume (m ³)	maximum depth (m)	mean depth (m)	dominant substrate	wood volume (m ³)
Salmon Cr July 1991	maximum	76	84	7.0	4.7	8	331
	minimum	2	1	0.5	0.3	1	0
	mean	24.6	20.3	3.1	2.2	5.0	6.9
	std. dev.	17.7	20.7	1.7	1.2	1.0	42.5
	total # of pools sampled	= 41					
North Fork August 1991	maximum	384	142	2.0	0.7	8	10
	minimum	29.7	8.7	0.5	0.3	5	0
	mean	140.4	55.3	1.0	0.4	6.0	1.4
	std. dev.	78.6	42.1	0.4	0.1	1.0	2.3
	total # of pools sampled	= 21					
Panther Creek August 1991	maximum	420	432	2.3	8.6	9	14
	minimum	13	3	0.4	0.1	5	0
	mean	112.6	59.1	0.9	0.6	6.0	2.8
	std. dev.	95.9	87.7	0.4	1.5	1.0	4.4
	total # of pools sampled	= 30					
Red Cedar Creek August 1991	maximum	186	400	1.4	5.4	9	23
	minimum	14	2	0.4	0.2	5	0
	mean	71.3	34.8	0.7	0.5	6.0	2.1
	std. dev.	38.4	74.7	0.3	1.0	1.0	4.8
	total # of pools sampled	= 27					
Dry Creek August 1991	maximum	1478	697	3.0	2.1	6	382
	minimum	45	135	0.5	0.3	2	0
	mean	410.1	390.6	1.6	1.1	5.0	46.5
	std. dev.	389.3	683.1	0.8	0.6	1.0	80.0
	total # of pools sampled	= 30					

Table 6. Summary of anadromous salmonid fish data, July 1990.

Stream	Numbers of fish by species				Total	Calculated diversity index values per pool				
	1+ steelhead	chinook	coho	cutthroat		Richness <i>S</i>	Simpson <i>D</i>	McIntosh <i>U</i>	McIntosh <i>D</i>	Berger- Parker <i>D</i>
Panther Creek										
maximum	32	25	0	1	37	3	1.88	1.00	1.71	1.00
minimum	2	1	0	1	0	0	0.00	0.00	0.00	0.00
mean	14.5	9.0	0.0	1.0	13.6	1.1	0.91	0.89	1.15	0.89
std. dev.	9.0	11.3	0.0	0.0	10.6	0.6	0.38	0.30	0.46	0.30
Red Cedar Creek										
maximum	10	12	0	1	22	3	1.00	1.00	3.41	1.00
minimum	1	10	1	0	0	0.0	0.00	0.00	0.00	0.00
mean	4.0	6.0	0.0	1.0	4.8	1.2	0.05	0.05	1.24	0.51
std. dev.	2.4	3.6	0.0	0.0	5.9	1.0	0.22	0.22	1.10	0.38
North Fork Elk River										
maximum	32	0	1	1	38	3	1.65	1.00	1.18	1.00
minimum	3	0	0	0	3	1	1.00	0.66	1.00	0.73
mean	14.6	0.0	0.3	0.2	19.9	1.5	1.23	0.80	1.11	0.90
std. dev.	7.4	0.0	0.8	0.7	12.3	0.6	0.22	0.11	0.03	0.07
Dry Creek										
maximum	44	195	47	1	258	4	3.00	1.00	1.78	1.00
minimum	2	1	1	1	0	0	0.00	0.00	0.00	0.00
mean	14.0	54.2	9.0	1.0	57.7	2.1	1.52	0.76	1.17	0.72
std. dev.	10.6	52.0	13.2	0.0	64.6	0.9	0.61	0.23	0.37	0.24

Table 7. Summary of anadromous salmonid fish data, August 1990.

Stream	Numbers of fish by species				Total	Calculated diversity index values per pool				
	1+	chinook	coho	cutthroat		Richness	Simpson	McIntosh	McIntosh	Berger-
	steelhead					<i>S</i>	<i>D</i>	<i>U</i>	<i>D</i>	Parker <i>D</i>
Panther Creek										
maximum	35	0	0	7	42	2	2.00	1.00	1.71	1.00
minimum	1	0	0	1	1	1	0.00	0.77	0.00	0.71
mean	10.3	0.0	0.0	2.9	12.0	1.6	1.26	0.90	1.30	0.89
std. dev.	9.7	0.0	0.0	2.1	11.4	0.5	0.46	0.09	0.38	0.10
Red Cedar Creek										
maximum	8	0	0	6	14	2	2.12	1.00	1.71	1.00
minimum	1	0	0	1	0	0	0.00	0.00	0.00	0.00
mean	3.3	0.0	0.0	3.5	2.9	0.9	0.58	0.74	0.74	0.73
std. var.	2.3	0.0	0.0	2.5	3.5	0.6	0.67	0.42	0.42	0.42
North Fork Elk River										
maximum	40	0	1	3	40	3	1.30	1.00	1.29	1.00
minimum	12	0	1	1	12	1	1.00	0.88	1.16	0.88
mean	20.3	0.0	1.0	1.8	21.1	1.5	1.07	0.97	1.23	0.97
std. dev.	7.4	0.0	0.0	1.0	7.8	0.6	0.01	0.04	0.04	0.04

Table 8. Summary of anadromous salmonid fish data, July 1991 (Salmon Creek) and August 1991 (Elk and Sixes River streams).

Numbers of fish by species/age class per pool					
Stream	1+ steelhead	chinook	coho	cutthroat	Total
Dry Creek					
maximum	67	111	89	4	299
minimum	1	0	0	0	0
mean	17.9	39.2	14.3	2.1	87.3
std. dev.	8.2	33.5	20.0	0.8	76.1
Panther Creek					
maximum	16	1	2	2	18
minimum	0	1	1	1	0
mean	5.3	1.0	1.5	1.7	5.4
std. dev.	4.3	0.0	0.5	0.5	4.9
Red Cedar Creek					
maximum	14	11	13	2	27
minimum	1	11	1	1	0
mean	3.8	11.0	3.7	1.2	5.6
std. dev.	3.3	0.0	3.4	0.4	5.7
North Fork Elk River					
maximum	46	5	1	5	49
minimum	0	1	1	1	0
mean	12.9	2.8	1.0	2.1	14.5
std. dev.	10.4	1.5	0.0	1.5	12.2
Salmon Creek					
maximum	19	14	286	5	319
minimum	0	0	1	0	3
mean	6.7	2.1	49.4	1.3	59.6
std. dev.	5.5	3.7	59.2	1.6	62.5

Table 8 (continued). Summary of anadromous salmonid community diversity indices, July 1991 (Salmon Creek) and August 1991 (Elk and Sixes River streams).

Stream	Calculated diversity index values per pool				Berger-Parker- <i>D</i>
	Richness <i>S</i>	Simpson <i>D</i>	McIntosh <i>U</i>	McIntosh <i>D</i>	
Dry Creek					
maximum	4	3.00	1.71	1.70	1.00
minimum	0	0.67	0.71	0.54	0.11
mean	2.11	1.14	1.09	0.95	0.73
std. dev.	0.08	0.79	0.26	0.30	0.24
Panther Creek					
maximum	3	3.00	1.00	1.78	1.00
minimum	0	0.00	0.00	0.00	0.00
mean	1.30	1.08	0.80	1.19	0.79
std. dev.	0.69	0.72	0.33	0.61	0.33
Red Cedar Creek					
maximum	3	3.00	1.00	1.78	1.00
minimum	0	0.00	0.00	0.00	0.00
mean	1.56	1.33	0.85	1.23	0.81
std. dev.	0.74	0.86	0.21	0.60	0.24
North Fork Elk River					
maximum	3	1.00	1.00	1.59	1.00
minimum	1	0.00	0.00	0.00	0.00
mean	1.71	0.83	0.33	1.33	0.88
std. dev.	0.76	0.23	0.21	0.32	0.21
Salmon Creek					
maximum	5	1.00	1.00	1.78	2.00
minimum	4	0.33	0.60	1.06	0.00
mean	4.76	0.66	0.82	1.21	0.80
std. dev.	0.43	0.20	0.11	0.14	0.28

Table 9. Results from multiple regression analysis of habitat complexity and salmonid diversity indices within pools.

Stream	Diversity indices:				
	McIntosh <i>U</i>	McIntosh <i>D</i>	Simpson <i>D</i>	Berger-Parker <i>D</i>	Richness <i>S</i>
North Fork Elk River	F = 2.15 <i>p</i> < 0.01 <i>r</i> ² = 0.204	F = 4.40 <i>p</i> < 0.01 <i>r</i> ² = 0.382	F = 9.41 <i>p</i> < 0.01 <i>r</i> ² = 0.604	F = 6.04 <i>p</i> < 0.01 <i>r</i> ² = 0.478	F = 78.56 <i>p</i> < 0.01 <i>r</i> ² = 0.934
Panther Creek	F = 2.67 <i>p</i> < 0.01 <i>r</i> ² = 0.141	n/s	n/s	F = 2.78 <i>p</i> < 0.01 <i>r</i> ² = 0.149	F = 2.49 <i>p</i> < 0.05 <i>r</i> ² = 0.127
Red Cedar Creek	n/s	n/s	n/s	n/s	n/s
Dry Creek	F = 2.15 <i>p</i> < 0.10 <i>r</i> ² = 0.204	n/s	n/s	n/s	F = 2.49 <i>p</i> < 0.10 <i>r</i> ² = 0.249
Salmon Creek	n/s	F = 3.16 <i>p</i> < 0.01 <i>r</i> ² = 0.185	n/s	n/s	n/s

predicted by 3, 3, and 5 significant regressions respectively. The North Fork Elk River accounted for 5 of 11 models, while Panther Creek, Dry Creek, Salmon Creek were used in 3, 2, and 1 model(s) respectively. Adjusted r^2 values ranged from 0.14 to 0.93. No significant regressions were found for Red Cedar Creek. Model equations are displayed in Table 10.

Table 11 lists the Spearman rank correlation coefficients between each of the independent habitat complexity variables and species diversity indices, and standardized regression equation coefficients, for the eleven significant models. Examination of these values highlight which individual habitat variable(s) were most useful for predicting species diversity. Maximum depth accounted for the highest number of significant ($p < 0.10$) values (8 or 40%), followed by mean depth (6, 30%), pool volume (4, 20%), and pool area (3, 15%). There were no significant correlation coefficients for dominant substrate and wood volume. Among the standardized equation coefficients, maximum and mean depth variables had a substantial influence on regressions (6 of 15 cases), followed by pool volume (5) and pool area (4), with wood volume and substrate again contributing little to the models (coefficient range -0.002 — 0.188).

Examination of Tables 9, 10, and 11 reveal patterns of complexity-diversity relationships among the different streams in this study. Species richness was positively correlated with pool volume, and both mean and maximum pool depth (except for the North Fork, where maximum depth was negatively correlated with richness). Diversity, a measure of richness and evenness (McIntosh U), was negatively correlated with pool area, volume, mean, and maximum depth. Patterns relating complexity and species

Table 10. Significant ($p < 0.10$) complexity-diversity multiple regressions in pools for all streams.

Stream	Multiple regression equation
Dry Creek	Richness $S = 1.77 - 6.5 \cdot 10^{-5}(\text{area}) + 2.2 \cdot 10^{-5}(\text{volume}) + 0.26(\text{maximum depth}) - 0.05(\text{mean depth}) - 0.09(\text{substrate}) + 0.002(\text{wood volume})$
	McIntosh $U = 1.38 + 5.1 \cdot 10^{-6}(\text{area}) - 1.4 \cdot 10^{-5}(\text{volume}) + 0.04(\text{maximum depth}) - 0.11(\text{mean depth}) + 0.003(\text{substrate}) + 3.2 \cdot 10^{-4}(\text{wood volume})$
North Fork Elk River	Richness $S = 5.69 + 0.01(\text{area}) + 0.03(\text{volume}) - 9.11(\text{maximum depth}) + 15.8(\text{mean depth}) - 0.53(\text{substrate}) - 0.19(\text{wood volume})$
	Simpson $D = 0.85 + 2.0 \cdot 10^{-4}(\text{area}) - 3.2 \cdot 10^{-5}(\text{volume}) - 0.25(\text{maximum depth}) + 0.17(\text{mean depth}) + 0.03(\text{substrate}) - 0.004(\text{wood volume})$
	McIntosh $U = 1.02 + 4.8 \cdot 10^{-5}(\text{area}) + 2.1 \cdot 10^{-4}(\text{volume}) - 0.13(\text{maximum depth}) - 0.05(\text{mean depth}) + 0.007(\text{substrate}) - 0.002(\text{wood volume})$
	McIntosh $D = 1.34 - 3.8 \cdot 10^{-4}(\text{area}) + 1.8 \cdot 10^{-4}(\text{volume}) - 0.06(\text{maximum depth}) - 0.11(\text{mean depth}) + 0.02(\text{substrate}) - 5.6 \cdot 10^{-5}(\text{wood vol})$
	Berger-Parker $D = 1.018 + 7.5 \cdot 10^{-5}(\text{area}) + 2.1 \cdot 10^{-4}(\text{volume}) - 0.15(\text{max depth}) - 0.06(\text{mean depth}) + 0.009(\text{substrate}) - 0.002(\text{wood volume})$
Panther Creek	Richness $S = -6.50 + 2.5 \cdot 10^{-4}(\text{area}) - 1.2 \cdot 10^{-3}(\text{volume}) + 7.9(\text{max depth}) - 0.38(\text{mean depth}) + 0.77(\text{substrate}) - 0.002(\text{wood volume})$
	McIntosh $U = 0.89 + 3.4 \cdot 10^{-5}(\text{area}) - 1.1 \cdot 10^{-6}(\text{volume}) - 0.05(\text{max depth}) - 0.02(\text{mean depth}) + 0.01(\text{substrate}) + 2.3 \cdot 10^{-5}(\text{wood volume})$
	Berger-Parker $D = 0.87 + 4.1 \cdot 10^{-5}(\text{area}) + 2.0 \cdot 10^{-6}(\text{volume}) - 0.05(\text{max depth}) - 0.02(\text{mean depth}) + 0.02(\text{substrate}) + 0.02(\text{wood volume})$
Salmon Creek	McIntosh $D = 0.74 + 0.002(\text{area}) - 0.01(\text{volume}) + 0.90(\text{max depth}) - 1.25(\text{mean depth}) - 0.02(\text{substrate}) + 3.1 \cdot 10^{-4}(\text{wood volume})$

Table 11. Correlations and standardized regression coefficients for habitat complexity variables and diversity indices (significant regression models only).

HABITAT COMPLEXITY VARIABLES:

Stream	Diversity index	Correlation coefficients:						Standardized regression coefficients:					
		pool area	pool volume	maxi- mum depth	mean depth	dominant sub- strate	wood volume	pool area	pool volume	maxi- mum depth	mean depth	dominant sub- state	wood volume
Dry Creek	richness	0.08	0.35	0.61	0.59	-0.16	0.26	-0.21	0.22	<u>0.56</u>	-0.09	-0.13	0.19
	McIntosh U	-0.33	-0.54	-0.52	-0.54	-0.06	-0.02	0.05	<u>-0.42</u>	0.25	<u>-0.57</u>	-0.01	0.12
North Fork	richness	0.54	0.57	-0.35	0.88	-0.30	0.30	0.10	<u>0.37</u>	<u>-0.39</u>	<u>0.63</u>	-0.05	-0.07
	Simpson D	0.05	0.04	-0.68	0.56	-0.21	0.26	0.12	-0.02	<u>-0.70</u>	<u>0.45</u>	0.15	-0.10
	McIntosh U	-0.08	-0.04	-0.64	-0.08	-0.09	0.04	0.07	<u>0.37</u>	<u>-0.93</u>	<u>-0.39</u>	0.10	-0.10
	McIntosh D	-0.52	-0.41	-0.17	-0.57	0.23	-0.14	<u>-0.41</u>	0.23	-0.27	<u>-0.51</u>	0.16	-0.01
	Berger-Parker D	-0.06	-0.03	-0.63	-0.07	-0.09	0.05	0.11	<u>0.34</u>	<u>-0.92</u>	<u>-0.37</u>	0.11	-0.10
Panther Creek	richness	-0.22	-0.16	0.26	-0.10	0.04	-0.01	0.03	<u>-0.43</u>	<u>0.53</u>	-0.06	0.11	-0.01
	McIntosh U	0.19	-0.04	-0.31	-0.23	0.24	0.03	<u>0.30</u>	-0.03	-0.26	-0.21	0.18	0.01
	Berger-Parker D	0.17	-0.06	-0.32	-0.24	0.24	0.04	<u>0.30</u>	-0.05	-0.27	-0.21	0.18	0.02
Red Cedar	no significant regression models												
Salmon Cr	McIntosh D	0.33	0.33	-0.22	-0.18	0.19	0.13	<u>-2.17</u>	<u>2.54</u>	<u>-1.07</u>	0.66	0.14	0.09
# significant/influential:		3	5	8	5	0	0	4	5	6	6	0	0

(**Bold** = significant r values, $p < 0.10$, t -test)

(Underline = high standardized coefficients w/ influence on regression models)

dominance (measured by Simpson's, McIntosh, and Berger-Parker D indices) were mixed. For the North Fork Elk River and Panther Creek, dominance was negatively correlated with maximum and/or mean depth (except for the correlation between mean depth and Simpson D in the North Fork), while in Salmon Creek, pool area and volume were positively correlated with dominance. Of all the habitat parameters examined, surface area, volume, and mean/maximum depths appear to be important determinants of salmonid diversity within pool habitat units, while substrate composition and wood volume were not significantly correlated with diversity in any of the study streams.

3.3 Multivariate Analyses of Complexity - Diversity Relationships in Pools

Analyses of pool data using multivariate canonical correlations show similar patterns of habitat complexity - species diversity relationships (Table 12). For Dry Creek, North Fork Elk River, Panther Creek, and Salmon Creek, the first or first and second-ranked canonical variables were significant at $p < 0.10$. The x habitat complexity variables that were emphasized (i.e., high canonical correlation coefficients) included maximum and mean depth, and pool volume (6 cases each), and pool area (4 cases). Among the y diversity index variables, McIntosh U was emphasized in 8 cases, followed by Simpson D (6), McIntosh D (3), Berger-Parker D (3), and richness S (1). No significant canonical correlations were developed for Red Cedar Creek pool data.

Table 12. Results from canonical correlation multivariate analyses.

Stream	Canonical correlation variable	x predictor variables emphasized	y predictor variables emphasized	p
Dry Creek	1	area, volume, mean depth	Simpson <i>D</i> , McIntosh <i>U</i>	0.06
North Fork Elk	1	maximum depth, mean depth	richness <i>S</i> , McIntosh <i>U</i> , Simpson <i>D</i> , Berger-Parker <i>D</i>	<<0.01
	2	volume, maximum depth, mean depth	McIntosh <i>U</i> , Berger-Parker <i>D</i>	< 0.01
Panther Creek	1	volume, maximum depth, mean depth	Simpson <i>D</i> , McIntosh <i>D</i> , McIntosh <i>U</i>	0.01
Salmon Creek	1	area, volume, maximum depth, mean depth	Simpson <i>D</i> , McIntosh <i>U</i> , McIntosh <i>D</i>	< 0.01
	2	maximum depth, mean depth	Simpson <i>D</i> , McIntosh <i>U</i> , McIntosh <i>D</i>	0.06
All streams	1	area, maximum depth, volume	McIntosh <i>U</i> , Berger-Parker <i>D</i>	<<0.01
	2	area, volume	Simpson <i>D</i> , McIntosh <i>U</i>	0.01
Tallies:		area = 4 volume = 6 maximum depth = 6 mean depth = 6	Simpson <i>D</i> = 6 McIntosh <i>U</i> = 8 McIntosh <i>D</i> = 3 Berger-Parker <i>D</i> = 3 Richness <i>S</i> = 1	

3.4 Complexity - Species Diversity Relationships at the Reach Scale

A total of 3, 4, 5, and 3 reaches were identified for Panther Creek, Red Cedar Creek, North Fork Elk River, and Dry Creek respectively (Tables 13 and 14). The number of habitat units within each reach ranged from 13 to 67, and $H'_{habitat}$ diversity values varied from 0.87 - 1.05. Tables 13 and 14 also list salmonid fish population numbers and diversity indices as well, with total fish numbers (not including age 0 trout) ranging from 4 to 1,040 per reach (1990) and 14 - 865 per reach (1991). For all streams except Dry Creek, the assemblage was dominated by age 1 steelhead juveniles (chinook salmon juveniles more abundant in Dry Creek during 1990 and 1991).

Tests of significance for non-parametric correlations (Spearman Rank), multiple regression analyses, and canonical correlations were used to examine the relationship between reach habitat complexity and salmonid diversity. Rank correlation values were -0.02, 0.13, -0.12, 0.01, and -0.35 for Berger-Parker D , McIntosh D , McIntosh U , Simpson D , and richness S respectively. None of these were significant at $p < 0.10$. Regression analysis of the relationship between reach $H'_{habitat}$ diversity and salmonid species diversity did not yield any statistically-significant ($p < 0.10$) models. Additionally, all canonical correlation variables tested for the combined set of reaches were also non-significant ($p < 0.10$).

Table 13. Summary of reach data used for complexity and community diversity analyses (July and August 1990)

Stream	Reach	Date	# of units	H' habitat	1+ sthd	coho	chinook	cutthroat	Richness S	total fish	Simpson D	McIntosh U	McIntosh D	Berger-Parker D
Panther Creek	1	8/90	56	0.98	218	0	0	23	2	241	1.21	0.91	1.06	0.90
	2	8/90	36	0.94	68	0	0	12	2	80	1.35	0.86	1.11	0.85
	3	8/90	28	0.96	32	0	0	6	2	38	1.38	0.86	1.17	0.84
Red Cedar Creek	1	8/90	32	0.97	8	18	0	2	3	28	2.08	0.71	1.20	0.64
	2	8/90	24	0.94	24	24	0	1	3	49	2.13	0.69	1.15	0.49
	3	8/90	11	0.99	3	0	0	1	2	4	2.00	0.79	1.60	0.75
	4	8/90	32	1.02	9	0	0	1	2	10	1.25	0.91	1.33	0.90
North Fork Elk River	1	8/90	64	0.98	133	0	1	1	3	135	1.03	0.99	1.09	0.99
	2	8/90	23	1.05	83	0	1	3	3	87	1.10	0.95	1.11	0.95
	3	8/90	26	0.99	444	16	16	4	4	48	1.18	0.92	1.15	0.92
	4	8/90	27	0.98	65	83	0	1	3	66	1.03	0.98	1.12	0.98
	5	8/90	32	0.90	58	44	0	1	3	59	1.04	0.98	1.13	0.98
Dry Creek	1	7/91	19	0.83	142	98	795	1	4	1040	1.62	0.79	1.03	0.77
	2	7/91	25	0.90	126	8	292	0	3	429	1.80	0.75	1.05	0.68
	3	7/91	37	0.98	109	2	159	0	3	273	1.97	0.71	1.06	0.59

Table 14. Summary of reach data used for complexity and community diversity analyses (July and August 1991)

Stream	Reach	Date	# of units	H' habitat	1+ sthd	coho	chinook	cutthroat	Richness S	total fish	Simpson D	McIntosh U	McIntosh D	Berger-Parker D
Panther Creek	1	8/91	56	0.98	40	1	0	2	3	43	1.16	0.93	1.15	0.93
	2	8/91	36	0.94	77	0	3	6	3	86	1.24	0.90	1.11	0.90
	3	8/91	28	0.96	76	1	0	8	3	85	1.24	0.90	1.11	0.89
Red Cedar Creek	1	8/91	32	0.97	26	0	15	0	2	41	1.91	0.73	1.16	0.63
	2	8/91	24	0.94	25	11	9	3	4	48	2.86	0.60	1.15	0.52
	3	8/91	11	0.99	8	0	6	1	3	15	2.44	0.67	1.29	0.53
	4	8/91	32	1.02	24	0	9	0	2	33	1.69	0.78	1.18	0.73
North Fork Elk River	1	8/91	64	0.98	167	3	0	13	3	183	0.84	0.92	1.07	0.91
	2	8/91	23	1.05	100	8	0	10	3	118	0.73	0.85	1.09	0.85
	3	8/91	26	0.99	160	13	0	16	3	189	0.73	0.85	1.07	0.85
	4	8/91	27	0.98	44	0	0	2	2	46	0.91	0.96	1.15	0.96
	5	8/91	32	0.90	2	0	1	0	2	3	0.33	0.75	1.78	0.67
Dry Creek	1	7/91	19	0.83	130	151	582	2	4	865	1.72	0.79	1.18	0.74
	2	7/91	25	0.90	105	24	219	0	3	348	1.84	0.78	1.24	0.71
	3	7/91	37	0.98	75	14	148	0	3	237	1.70	0.79	1.20	0.75

4. DISCUSSION OF RESULTS FROM HABITAT COMPLEXITY - SALMONID DIVERSITY STUDIES

This study demonstrated that statistical correlations exist between surface area, volume, mean and maximum depth, and anadromous salmonid species diversity within pools of several southwest Oregon streams. However, most of these relationships are weak, which suggests that habitat structure may not be the most important factor influencing anadromous salmonid assemblages in the selected study streams.

The majority of the multiple regression models developed between salmonid species diversity indices and habitat complexity parameters had low r^2 values (with the exception of the North Fork Elk River). Relationships also varied by diversity index type and location. Additionally, 14 out of 25 regression comparisons failed to produce a significant model, and no significant correlations (using both univariate and multivariate approaches) were obtained for Red Cedar Creek. These findings are in contrast to other studies on lotic fish assemblage - habitat complexity relationships (reviewed by Matthews 1997).

Anadromy, and its influence on recruitment, juvenile abundance, and species composition in streams, may play a role in determining the strength of complexity - salmonid diversity relationships. Assemblages comprised of migratory anadromous fish species are unique to this study, in comparison to the resident fish communities studied by Gorman and Karr (1978), Schlosser (1982, 1985), Angermeier and Schlosser (1989),

and others. Such life histories subject Pacific salmon to population control factors outside of freshwater habitats (Groot and Margolis 1991). Variability in oceanic conditions, and high rates of mortality associated with predation in estuarine and marine environments, influence survival to maturity, directly affecting the number of adult spawners (Pearcy 1997). Along the Oregon coast, coho salmon are at the southern end of the species range and are especially vulnerable to changes in ocean productivity and weak upwelling. The variability in marine conditions for the Oregon coastal zone has been correlated with large-scale fluctuations in rates of smolt-to-adult survival and juvenile recruitment to stream habitats (Nickelson 1986).

Stocks of most anadromous salmonids along the Oregon coast are in decline (Nehlsen et al. 1991, reviewed by Kostow 1997) and juvenile seeding levels in many streams are below habitat capability (Nickelson et al. 1992). Reeves and Burnett (unpublished data) have found that relationships between stream habitat features and salmonid species diversity appear to be dependent upon juvenile abundance. The lack of statistical correlations observed for Red Cedar Creek may be due to the extremely low seeding levels observed there; mean densities per pool (fish / m², excluding age 0 trout) and total number of fish were at least 50% lower in Red Cedar (0.06/m², 63 total), compared to Dry Creek (1.85/m², 557 total), Panther Creek (0.13/m², 97 total), North Fork Elk River (0.75/m², 127 total), and Salmon Creek (2.73/m², 319 total). Density-dependent intra- and interspecific interactions between stream salmonids (reviewed by Fresh 1997) may explain the relationship between juvenile abundance, habitat complexity, and salmonid diversity.

In contrast to lotic fish communities in other areas of North and Central America (Matthews 1997), the low species richness of Pacific Northwest anadromous salmonid assemblages (comprised of only 4 - 6 *Oncorhynchus* species) may also affect our ability to quantify complexity-diversity relationships. Low richness influences diversity measures sensitive to numbers of taxa, such as McIntosh U (Magurran 1988). With so few species, errors in sampling relatively rare fish such as cutthroat trout could have disproportionate effects on calculated indices that combine richness and sample size (Peet 1974). This study focused on salmonids, which comprise a large portion of the biomass found in these streams during summer low flow periods. However, a broader aquatic community approach that includes other taxonomic groups of fish (e.g., cyprinids, catostomids, gasterosteids, cottids), amphibians (ambystomids and anurans), and benthic macroinvertebrates found in these same pools could offset problems with low richness encountered in this study, so long as sampling efficiency concerns associated with these taxa (e.g., Olson et al. 1997) are adequately addressed.

Harrell (1978), Tyler (1978), and Matthews and Hill (1980) have hypothesized that specific habitat use by fishes may be moderated by the severity of local environmental factors, with "harsh" conditions resulting in less structured use of habitat by species and assemblages. Coastal streams of Oregon and other parts of the Pacific Northwest are characterized by large-scale changes resulting from floods, debris flows, and hillslope mass wasting (Swanston 1980, Swanson et al. 1987, Benda and Dunne 1987, Reeves et al. 1995). The environmental condition hypotheses suggested by these authors may also help to explain the weakness of association between specific habitat

features and salmonid community diversity patterns observed for most of the streams in this study.

The statistically-significant correlations derived between pool area, depth, and salmonid diversity are consistent with the generalized habitat area and depth-diversity relationships found among other communities of freshwater stream fishes (Matthews 1997). The importance of pools and depth to stream fish species diversity is well-supported by the literature. For lotic systems, depth can be viewed as an element of habitat heterogeneity, and this vertical dimension is unique to aquatic studies (Angermeier and Schlosser 1983). Gorman and Karr (1978), working with both temperate and tropical streams in Indiana and Panama, found that fish species diversity was significantly related to depth. Schlosser (1982) also noted that depth was correlated with fish diversity in central Illinois streams. Angermeier and Schlosser (1989) documented relationships with Shannon-Wiener H' diversity and depth used in an index of habitat complexity. Species richness was more strongly correlated with volume (which includes depth) in their Panama and Illinois sites. Angermeier and Karr (1983) noted that diversity among a variety of fish feeding guilds in Panama was also related to depth of pools. Fisher and Pearson (1987) demonstrated that two species of darters found in central Kentucky streams displayed distinct habitat selection by depth. Baker and Ross (1981) determined that vertical water column position was one of two important spatial resource gradients for cyprinids in Mississippi streams. Tramers and Rogers (1973), Mendelson (1975), Evans and Noble (1979), Smart and Gee (1979),

Harvey and Stewart (1991), Taylor et al. (1993), and Taylor (1997) have documented similar responses of fish species along habitat axes of depth in streams.

Biotic mechanisms to explain the relationship between salmonid species diversity and depth include intra- and interspecific competition and predation. The role of depth in reducing interspecific competition is suggested by the negative correlations between community dominance and maximum pool depths documented in this study. Other researchers have hypothesized that increased depth may allow for species segregation, enhance co-existence, decrease species dominance, and mediate competitive interactions. Gorman (1988) noted that fish communities segregated primarily along the vertical (depth) axis in response to interspecific competition for available food resources; greater habitat space provided by depth was related to increased species diversity. However, a more rigorous experiment that measures niche breadth and overlap (reviews by Connell 1983, Schoener 1983) may be necessary to determine the role of competition in these populations of anadromous salmonids.

This study could not determine if the relationship between depth and assemblage diversity in Oregon coastal streams was attributable to predator-related factors. Ecologists have examined the role that refugia may play in determining patterns of species diversity in terrestrial and marine systems (Crossman 1959, Paine 1969, Glass 1971, Dayton et al. 1974, Connell 1972, 1978, Menge and Sutherland 1976, Wiens 1976, Stein and Magnuson 1976, Newsome and Gee 1978, Hixon 1986, Hixon and Menge 1991) and other freshwater fish communities (Gee and Northcote 1963, Ware 1972, Fraser and Sise 1980, Dill et al. 1981, Fraser and Cerri 1982, Dill 1983, Wilzbach

1984, Fausch 1984, Angermeier 1985, Wilzbach and Hall 1985, Fraser et al. 1987).

Results from other researchers have suggested that depth may influence predator-prey interactions for stream fish communities (Stein 1979, Power 1984, Power et al. 1983, 1985, Schlosser 1987). In an *in-situ* experimental study, Lonzarich and Quinn (1995) documented that depth appeared to reduce predation risk for juvenile coho and age 1 steelhead trout in coastal Washington streams. Further work is needed to determine the role of depth as refugia for anadromous salmonids.

Although habitat complexity is a concept that is intuitive, it has been difficult to quantify in the natural environment (Buckley 1982) and other researchers studying terrestrial systems have often employed univariate analysis techniques to describe it (Power 1972, 1978, Harris 1973, Johnson and Simberloff 1974, Abbott 1978, Reed 1981, Kitchener 1982, Simberloff and Gotelli 1984). However, the univariate approach has been criticized by James and Wamer (1982), Green and Vascotto (1978), James et al. (1984), and Boecklen (1986). They argue that correlations between habitat parameters (and their coefficients which are insensitive to non linear relationships) may mask complexity-diversity patterns, providing evidence to support the use of rarefaction, principal components analysis, and contour diagrams to determine the relationships between habitat and community diversity.

For freshwater stream fish community studies, the literature is divided between univariate (Zaret and Rand 1971, Gorman and Karr 1978, Schlosser 1982, Moyle and Senanayake 1984, Ross et al. 1987, Felley and Felley 1987, Kinzie 1988, Angermeier and Schlosser 1989) and multivariate (reviewed by Matthews 1997) approaches to

analyzing habitat complexity and its relationship to diversity. In this study, comparison of results from both univariate (correlations, multiple regressions) and multivariate (canonical correlations) statistical procedures indicated that both procedures yielded similar conclusions, documenting that pool area, volume, mean, and maximum depths were correlated with richness, diversity, and dominance measures. It should be noted, however, that use of multivariate statistics was limited by the relatively low number of dependent and independent variables. Thus, additional studies which utilize a greater variety of habitat complexity factors and salmonid diversity measures would provide a better test of univariate versus multivariate analysis techniques (D. Turner pers. comm.).

The contribution of dominant substrate composition and volume of large wood to the complexity-diversity regression models was relatively insignificant compared to other habitat features, in spite of the fact that large wood and bed roughness have been demonstrated to influence many stream fish species including anadromous salmonids (Angermeier and Karr 1984, Martin et al. 1986, Mason et al. 1986, Felley and Felley 1987, Bisson et al. 1987, Sedell et al. 1988, Harmon et al. 1988). The relationship between large wood and the distribution and abundance of stream salmonid populations has been well accepted among North American stream ecologists (e.g., Forward 1984, Dolloff 1986, Elliott 1986, Quinn and Peterson 1996). However, only a few studies have focused on wood relationships at the community level (e.g., Reeves et al. 1993, Flebbe and Dolloff 1995). While no significant statistical relationships could be found between wood and anadromous salmonid diversity in this study, research by Cederholm et al. (1997) suggest that large wood - diversity

relationship may be moderated by the relative abundance of taxa, such as juvenile coho salmon, whose distributions are strongly influenced by wood (Bryant 1983, Tschaplinski and Hartman 1983, Dolloff 1987, Shirvell 1990, Spalding et al. 1995). Cederholm et al. noted that anadromous salmonid responses to large wood was species-specific; in a habitat restoration study examining the effects of instream wood structures, the number of coho juveniles increased significantly following wood additions, whereas age 1+ steelhead trout showed no significant change.

The coho and wood relationship to habitat-diversity correlations is partially supported by a re-analysis of the study data, in which only pools that contained *O. kisutch* were examined (pools that did not have coho were ignored). McIntosh *U*, Simpson *D*, and Berger-Parker *D* species diversity indices were re-calculated from this subset of data, and were compared against wood volume using Spearman Rank correlations, yielding values of -0.52, 0.81, and -0.45 for McIntosh *U*, Simpson *D*, and Berger-Parker *D* respectively (all were significant at $p < 0.10$). More detailed studies, however, need to be undertaken in order to fully support or reject this hypothesis.

The lack of relationships observed between large wood and salmonid diversity may be an artifact of the habitat unit scale used in this study. Other authors have demonstrated a correlation between wood and salmonid community diversity at different spatial scales. As an example, Reeves et al. (1993) analyzed data collected from six Oregon coastal basins and found that lower salmonid diversity was related to reduced wood in watersheds with 20% or more timber harvest. To explore this relationship, total wood volume and wood frequency (pieces per meter) values

calculated for each reach in this study were tested against fish community indices; these analyses, however, did not yield any statistically-significant ($p < 0.10$) relationships.

Benthic substrate has been shown to be a significant correlate of fish diversity in a variety of freshwater systems (e.g., Luckhurst and Luckhurst 1978, Gorman and Karr 1978, Schlosser 1982). As with large wood, however, most of the studies relating substrate composition and anadromous salmonids have focused on single species (e.g., Chapman and Bjornn 1969, Johnson and Kucera 1985) and little work has been done to determine the relationship between dominant substrate and salmonid diversity. Only weak relationships were observed in this study, which may be due to the coarse level of resolution inherent in the Wentworth classification scheme. Future investigations may need to employ more quantitative techniques to obtain continuous measures of dominant particle size (e.g., Wolman 1954, Bevenger and King 1995).

The reach-scale portion of this study did not find significant complexity and diversity correlations, although such relationships have been documented by other researchers. Means et al. (1992) used non-parametric methods (Spearman rank correlations) to demonstrate that both evenness and richness were correlated to the number of pool habitats within reaches in Drift Creek of the Alsea River watershed (Oregon). Sullivan et al. (1987) compared frequencies of pools and riffles with anadromous salmonid diversity in Thrash and Beaver Creeks (Washington) and found that increased abundance of pool habitat corresponded to greater diversity of trout/salmon species and age classes. Angermeier (1987) also examined the relationship between reach-level habitat features and fishes. He found that habitat selectivity was

greatest in structurally-simple reaches, but this varied between fish species/orders.

Other studies have found spatial scale relationships between fish diversity and stream order, longitudinal gradient, landscape-level geomorphic complexity, and river basin size (Harrell et al. 1967, Sheldon 1968, Whiteside and McNatt 1972, Lotrich 1973, Livingstone et al. 1982, Covich 1988).

Results from this research extend our current knowledge about habitat - species diversity relationships to include anadromous salmonid assemblages in the Pacific Northwest. These results have applied value as well, since there is much interest in determining the effects of land management activities on stream habitat of anadromous salmonids (reviews by Meehan 1991, Gregory and Bisson 1997). A number of these have used habitat features as diagnostics for detecting management impacts, relating such changes to shifts in salmonid abundance (e.g., McIntosh et al. 1993) or species diversity (Reeves et al. 1993). Watershed restoration efforts, with a focus on structural modification of stream channels to repair rearing environments for stream salmonids, have also increased dramatically in recent years (e.g., Beschta 1997). Thus, improved knowledge of the relationship between physical habitat and anadromous salmonid diversity should provide some of the necessary tools for managing freshwater habitat and anadromous salmonid fishes, and restoring aquatic biodiversity, in Pacific Northwest streams.

5. *IN-SITU* EXPERIMENTS TO EVALUATE SELECTION OF HABITAT FEATURES BY ANADROMOUS SALMONID FISHES

5.1 Introduction

Habitat selection is an important mechanism that influences the abundance, distribution, and diversity of biota (Southwood 1977). The relationship between habitat features and fish species diversity in lotic systems has been examined throughout North and Central America (Matthews 1997). Habitat elements that have been identified to influence stream fishes include channel width, area, volume, discharge, depth, substrate, and large wood; selection of habitat features has been shown to affect abundance, diversity, and distributions of lotic fishes (reviewed by Matthews 1997). Much research on habitat-fish relationships has been conducted on anadromous salmonids in the Pacific Northwest, in part because these fish are ecologically and economically important in this region (Meehan 1991, Stouder et al. 1997). Data obtained has been instrumental in guiding efforts to restore stream spawning/rearing habitat conditions (e.g., Beschta 1997). However, most salmonid habitat - fish relationship studies have focused only on a single species rather than the community of anadromous salmonids (Reeves et al. 1993). In addition, experimental manipulations to determine assemblage responses to particular habitat elements are few (Fausch 1993, Lonzarich and Quinn 1995).

Chen (1998) found statistically significant relationships between pool area, volume, maximum and mean depth habitat features and salmonid species dominance and diversity. However, large wood and dominant substrate were not found to be significant factors. These findings appear to be contradictory with the literature on the importance of wood or substrate to salmonids, and its influence on species abundance for anadromous representatives such as coho salmon and sea-run cutthroat trout (e.g., Everest and Chapman 1972, Tschaplinki and Hartman 1978, Glova 1978, Bisson et al. 1987, Dolloff 1987, Harmon et al. 1987, Sedell et al. 1988, and others).

To examine the role of habitat feature selection and its relationship to anadromous salmonid diversity, a series of *in-situ* factorial experiments were conducted in artificially-constructed pools in a southern Oregon coastal stream. Wood and depth were used as treatments, species richness was measured as the treatment effect, and different trial lengths were employed to determine both short and longer-term responses to varying treatment levels. Results from these habitat selection experiments were then compared to similar studies in the literature and also related to the patterns of habitat complexity - salmonid diversity relationships noted in an associated field observational study (Chen 1998).

5.2 Materials and Methods

Rock Creek is a major 4th-order tributary to the upper South Fork Coquille River (Fig. 3). A 200 m side channel was constructed in a broad flood plain section of

Rock Creek as part of a fish habitat restoration project on the Powers Ranger District (Siskiyou National Forest, Oregon). The experimental site was located approximately 400 m upstream from the Rock Creek campground and was adjacent to Forest Road 5520, just downstream of the bridge crossing the stream (Fig. 5). A hydraulic excavator was employed to build the channel and to install log drop weirs. The constructed stream diverted approximately 1/4 - 1/3 of the discharge from Rock Creek and followed the contour of an existing high flow channel. Sinuosity was moderate and gradient was less than 1%. Width varied from 2 - 3 m and the substrate was composed of the original bed materials (gravel and cobble 15 - 250 mm in diameter).

Pools were dug below each weir and these constructed pools served as the experimental units for the *in-situ* manipulations; a total of five were created in the channel (Fig. 5). Four served as experimental units and the fifth one was used as a holding area for the fish. Surface area of the four units was similar, ranging from 12.0 to 14.4 m². The holding pool was 34 m² in area with a maximum depth of 1.3 m. The substrate was modified so that all large boulders were removed, yielding consistent bed roughness in each unit. Fine nylon netting 5-mm mesh diameter was stretched in a curve at the pool tail areas, extending a minimum of 13 cm above the water surface (Fig. 6). The lower end of the netting was buried 20 cm beneath the substrate and weighted down with gravel/cobbles. The combination of an under- and above-water barrier at the tail was intended to prevent either swimming or aerial escape by fish.

At the pool tail crest location, an "escape" chamber was constructed. A 6-cm diameter black PVC drain pipe 40 cm in length was buried beneath the gravel/cobble

Figure 5. Diagram showing location of constructed side channel and experimental pools in Rock Creek.

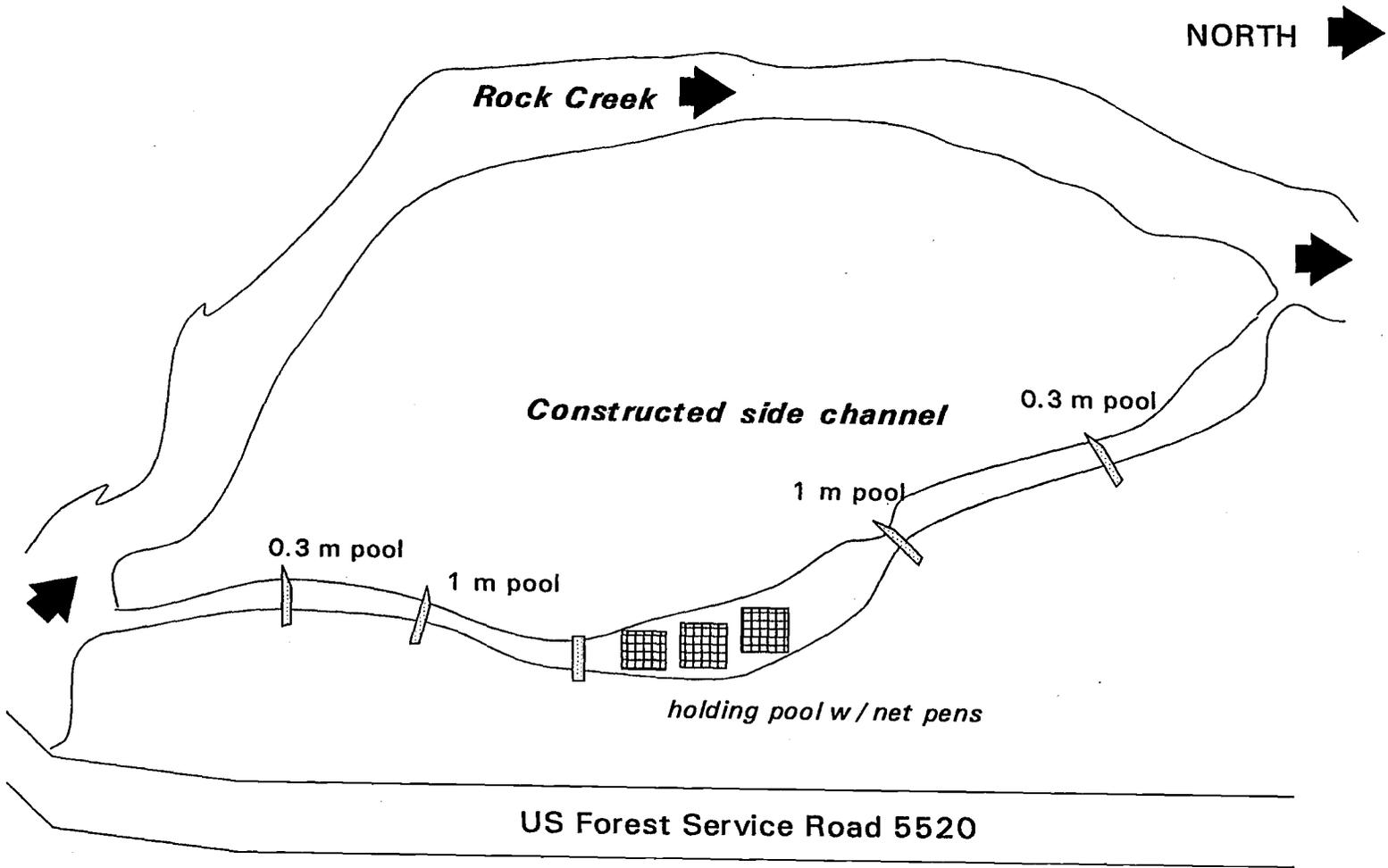
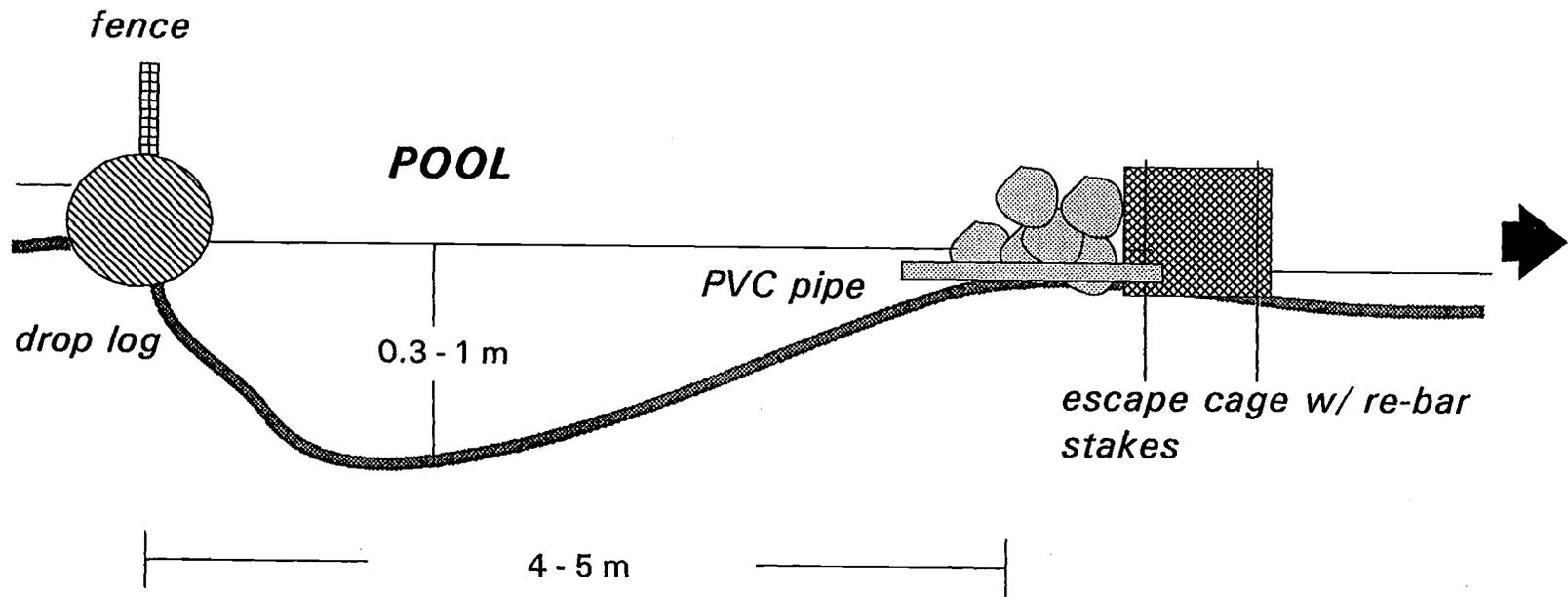


Figure 6. Lateral view of experimental pool.



substrate and escape barrier. The upstream portion protruded 9 cm into the pool and the downstream end of the pipe was attached to a cubic, completely enclosed cage made of galvanized wire cloth 7-mm mesh diameter. The cage sat directly on the stream bottom and was anchored by nylon tie wraps to four 12-mm diameter steel reinforcing bars driven 30 cm into the substrate. A 90° elbow fitting was installed approximately 5 cm from the end of the pipe above its connection with the cage. The elbow bend was designed to deter fish from re-entering the "escape" pipe and the pool. To further minimize returns, the pipe opening into the pool was narrowed with poured concrete, shaped to provide an aperture 4.4 cm in diameter (the pipe and the capture cage were the only potential outlet for any fish placed in experimental pools).

A 30-cm high fence to prevent fish from leaping over the wiers and traveling upstream was constructed of 7-mm mesh galvanized wire cloth. The fence extended across the entire length of the wier log and was stapled to its surface. To deter mammalian and reptile terrestrial predators, 12-mm diameter fine nylon netting 1 meter in height was strung along the streambank edges and attached to steel rods driven into the bank substrate. No netting was placed over the top of the pools.

5.3 Experimental Design

The 2 x 2 factorial experiment used two habitat parameters, maximum pool depth and wood. Each pool experimental unit served as the block and treatments were replicated through time to obtain multiple blocks. Since the pools depths in the

experimental units were fixed and could not be easily altered, only the wood factor was completely randomized.

Two of the experimental pools had maximum depths of 1 m (DEEP) and the other two had maximum depths of 0.3 m (SHALLOW). Two treatment levels for wood (WOOD or NO WOOD) were randomly applied. Alder trees (dbh = 30 cm), with attached branches and roots, were salvaged from the adjacent flood plain and trimmed to approximately the same size (volume 2.8 - 3.0 m³) for the wood treatments. These were hand-placed near the upper end of the pool, adjacent to the scour area, and were not anchored in any of the trials. While the wood used in these experiments did not meet typical size criteria for "large" wood as measured in PNW stream inventories (e.g., > 0.3 m in diameter and 1.5 times bankfull width in length, U.S.F.S. 1997), mobility requirements for treatment randomness necessitated the use of these relatively small pieces, which functioned more as cover rather than geomorphic scouring elements.

Juvenile coho salmon (*Oncorhynchus kistuch*), trout fry (0+ *O. mykiss* and *O. clarki clarki*), steelhead trout parr (*O. mykiss*, 1+ parr), chinook salmon juveniles (*O. tshawytscha*), and sub-adult/adult sea-run cutthroat trout (*O. clarki clarki*) were captured via electroshocking in nearby Salmon Creek (Fig. 3). Fish were sorted by species and age class, and separated into divided sections of two floating net pens staked together in the holding pool.

After a period of 24 - 72 h, fish were removed from the pens and transferred to the experimental pools. Individuals were randomly selected and the number of fish used was adjusted to correspond with mean fish densities (number/m² pool surface area)

calculated from field data collected in Salmon Creek, Dry Creek, Red Cedar Creek, Panther Creek, and the North Fork of the Elk River (July/August 1990 and 1991). The numbers of fish used were as follows: age 0+ trout = 34 to 41 individuals per pool; 1+ steelhead = 2 - 3; coho salmon = 3 - 4; chinook salmon = 4 - 5; and cutthroat trout = 1 per pool. No fish were held longer than 7 d in the pens and less than 10 fish total were lost during capture, transport, or transfer-related mortality during the experiments.

In a departure from the observational field study, age 0+ trout (young-of-the-year parr steelhead or cutthroat trout) were used as separate "species" for the experimental manipulations. 0+ fry display distinct differences in behavior and microhabitat preferences compared to older age classes of trout and other salmonids (e.g., Johnson and Kucera 1985), supporting the assumption that they function as distinct "ecological species".

Experimental trials ran for 20 - 24 h following introduction of fish into the pools. Combinations representing each factorial treatment (deep pool with no wood, deep pool with wood, shallow pool with no wood, and shallow pool with wood) were used. At the end of each trial, all fish that were found in the escape chambers were tallied. Pools were then electroshocked and a richness *S* value (Magurran 1988) was calculated based on the number/species/age class of fish remaining in the pools (wood was temporarily removed to aid in fish removal). *S* was used as the dependent variable in the analyses.

Once the trial was completed, fish were put into a separate holding pen for subsequent release back into Salmon Creek. Following a 24-h waiting period,

experiments were then repeated (using a new set of fish). A total of seven replications were performed during an 18 d period from August 25 - September 11, 1991.

A second set of experiments was run the following spring (April - May 1992). These consisted of the same factorial treatments (wood and depth) except that each trial lasted at least 168 h (7 d). No waiting period occurred between successive runs, and as with the first set of experiments, fish were not re-used. Higher water levels due to elevated flows resulted in enlargements of the experimental units (13.2 - 14.7 m² surface area). A total of four replications were conducted from April 12 - May 15, 1992. Richness *S* values were calculated based on fish remaining in the test pools. This second series of experiments were intended to determine if the patterns resulting from the 24-h runs may have been influenced by fish acclimation. Average size of post-emergent chinook and coho salmon juveniles used were smaller than in the fall and some of the cutthroat trout appeared to be spawned kelts.

Not all fish were accounted for in either the 24-h or 7-d experiments (an average of 2 - 4 fish, 96% of them 0+ trout, were not re-captured by electrofishing). Some fish may have been able to escape the experimental pools or were consumed by predators. "Missing" fish not counted in the escape traps or removal efforts were included as fish that had actually left the pool.

5.4 Results

Results obtained in both the 24-h and 7-d trials were examined via analysis of variance (ANOVA) tests (Petersen 1985; Table 15). Wood and maximum depth had statistically-significant treatment effects on salmonid species richness during the shorter 24-hour trials ($F_{(1,18)} = 5.8, p < 0.05$ for wood; for depth, $F_{(1,18)} = 207.4, p \ll 0.001$). The interaction of wood and depth, however, was not significant ($F_{(1,18)} = 3.2, p > 0.05$). No significant effects were attributed to temporal factors (blocks $F_{(6,18)} = 0.6, p > 0.05$). The coefficient of variation (CV) was calculated at 2.84% for this experiment.

In the longer 7-d trials, results were different. The wood treatment was no longer significant ($p > 0.05$), while depth remained significant ($F_{(1,9)} = 137.2, p < 0.001$). Even with the increased duration for the trials, no significant effect was associated with temporal blocks ($F_{(3,9)} = 0.8, p > 0.05$). Tests on combined wood and depth interaction did not yield significant results ($F_{(1,9)} = 0.2, p > 0.05$). The coefficient of variation (CV) was determined to be 2.16%.

5.5 Discussion

The findings in these short-term *in-situ* experiments demonstrate that pool depth is a habitat feature consistently selected by anadromous salmonid fishes. The relationship between depth and stream fish diversity has been documented in many temperate and

Table 15. Species richness *S* ANOVA results for wood and depth experiments, Rock Creek August-September 1991 and April-May 1992. (Bold face indicate significant treatment factors.)

A. Results from 24-hour trials (7 trials total, August - September 1991)

Analysis of Variance table

Source	df	SS	MS	F	<i>p</i>
Total	27	94.4			
block	6	1.4	0.3	0.6	
wood	1	2.3	2.3	5.8	< 0.05
depth	1	82.3	82.3	207.4	<< 0.01
wood*depth	1	1.3	1.3	3.2	
Error	18	7.1	0.4		

B. Results from 7-day trials (4 trials total, April - May 1992)

Analysis of Variance table

Source	df	SS	MS	F	<i>p</i>
Total	15	42.9			
block	3	0.7	0.2	0.8	
wood	1	0.6	0.6	2.0	
depth	1	39.1	39.1	137.2	<< 0.01
wood*depth	1	0.1	0.1	0.2	
Error	9	2.6	0.3		

tropical systems (Angermeier and Schlosser 1983, 1989, Gorman and Karr 1978, Schlosser 1982, Fisher and Pearson 1987, Mendelson 1975, Smart and Gee 1979). For Pacific Northwest anadromous salmonids, Bisson et al. (1988) and Lonzarich (1994) demonstrated that stream-dwelling species select deeper habitats as they increase in size. In upper Columbia River basin tributaries, a reduction in the number of deep pools has been cited as a major factor in the decline of anadromous salmonids (Sedell and Everest 1991, McIntosh et al. 1993). Reeves et al. (1993) found fewer deep pools and reduced species diversity in watersheds with timber management exceeding 20% of total basin area. Other studies have documented relationships between loss of pools, pool area/volume/depth, and changes in anadromous salmonids resulting from land management activities (e.g., Bisson and Sedell 1984, Tripp and Poulin 1986, Sullivan et al. 1987).

Lonzarich and Quinn (1995) and Fausch (1993) provide results from the few experimental manipulations examining the effects of habitat features on stream anadromous salmonid fish assemblages. Lonzarich and Quinn used four depth and structure treatments, included non-salmonid fishes (cottids and gasterosteids), and employed a 30 d trial period in their experiments. Most species and age classes selected deeper pools containing structure, and depth and structure combined appeared to strongly influence distributions. Fausch manipulated visual isolation, velocity refuge, and overhead cover as components of habitat complexity and found species-specific differences in treatment responses. Age 1+ steelhead trout showed associations with overhead cover, while coho salmon juvenile distributions were determined by large

wood (which they used as a velocity refuge) and depth of pools. Pool depth appeared to be the most important habitat feature selected by coho salmon; deep pools were preferred by coho, even in the absence of large wood.

Although this study did not examine the relationship between habitat complexity and predation for anadromous salmonid assemblages, other authors have documented that increased depth and abundance/complexity of large wood may also serve to reduce risk from predation. Lonzarich and Quinn (1995) found that depth reduced predation mortality by as much as 50% for species that utilized the water column (e.g., coho juveniles). Bugert et al. (1991) suggested that habitat elements providing cover similarly reduced predation risks for the populations they studied in southeast Alaska streams.

The *in-situ* experiments documented selection of wood habitat features by salmonids in pools, but also found that wood effects were dependent on trial duration (significant during 24-h but not for 7-d experiments). Similar patterns of temporal variability in large wood - fish relationships have been demonstrated by Angermeier (1985, 1987), Bustard and Narver (1975), Tschaplinski and Hartman (1983), and others. Hypotheses to explain the effects of time on fish relationships to wood include differences in food availability (Angermeier 1985) or temporal shifts in habitat selection (Bustard and Narver 1975). Competition for space may influence salmonid community - wood relationships, since space is an important axis of resource partitioning among salmonids (Chapman 1966). Increased habitat availability during higher flow conditions in the spring trials may have mediated interspecific interactions between the

different anadromous salmonid species (Aadland 1993), thereby masking the wood-richness relationship. Although Chen (1998) could not find any statistical correlations between large wood and salmonid species diversity measures, he suggested that the relationships may be influenced by the presence or absence of coho salmon juveniles; after data from pools that lacked coho were omitted from the analysis, statistically-significant ($p < 0.10$) values were noted between large wood volume and species diversity measures McIntosh U , Simpson dominance D , and Berger-Parker dominance D .

The wood \times depth interaction factor did not prove to be significant in the *in-situ* experiments. Previous studies of streams in the nearby Elk River basin (Chen 1991) found that wood \times depth was a better predictor of age 1+ steelhead trout abundance than either wood or depth alone. Wood plays an important role in creating salmonid habitat (e.g., Bisson et al. 1987, Bryant 1983, Murphy et al. 1986), and Chen had suggested that its influence on fish abundance might be more closely related to geomorphic function (pool scour).

Fishery management agencies have invested substantial dollars in stream habitat projects for anadromous salmonids, including many that have focused on adding large wood to the channel (e.g., Hillborn and Winton 1993, Stouder et al. 1997, Reeves et al. 1991). Although the effects of wood additions on the abundance and distribution of individual salmonid species have been well-documented (e.g., Reeves et al. 1991), its role in influencing species diversity for Pacific Northwest streams has not been well-studied. If the biological objective of these habitat restoration projects is to provide

complex habitat and increase species richness, then the results from these experiments suggest that selection of habitat features by anadromous salmonid assemblages may be temporally-dependent. Further experiments to evaluate the influences of predation, food availability, and density-dependent biotic interactions (e.g., Shirvell 1990, Fausch 1993) are needed in order to understand how habitat feature selection operates with these other complex factors to produce the patterns of salmonid diversity observed in Pacific Northwest streams.

SUMMARY

The objective of this research was to determine the influence of stream habitat complexity on diversity of anadromous salmonid fishes. Such relationships have been well-documented for a variety of terrestrial assemblages (birds, reptiles, insects), other aquatic assemblages (freshwater and marine invertebrates) and other fish communities (marine reef fishes, stream assemblages from Panama, southeast/northeast/central North America cyprinids, percids, and centrarchids).

This study had two components: *I.* Analyses of field observational data to determine *a)* if statistically significant relationships exist between specific attributes of habitat complexity (maximum and mean depth, surface area, and volume of pools, volume of large wood, and dominant streambed substrate) and indices of species diversity (McIntosh *D*, McIntosh *U*, Berger-Parker *D*, species richness *S*), in pool habitats (channel unit scale); *b)* to determine if such relationships varied between different streams; and *c)* to determine if statistically significant relationships exist between habitat unit type diversity and measures of species diversity at the reach scale. *II.* *In-situ* controlled factorial experiments to determine habitat feature selection (maximum pool depth, presence/absence of wood, the interaction term of maximum depth \times wood) by anadromous salmonids, as measured by species richness *S* of the assemblage.

Statistical analyses of 5 data sets (representing each of the study streams) from 296 pools collected during 2 - 3 sampling periods (1990 - 1991) were performed using

scatter plots, non-parametric correlation analyses (Spearman Rank), type II sums of squares analyses, multiple regressions, and canonical correlation multivariate methods (total of 25 statistical comparisons). Age 0 trout were not used in diversity calculations due to low sampling efficiency and subsequent concerns about effects on statistical relationships.

Significant but weak statistical relationships (multiple regressions with low r^2) were found between complexity and diversity in four of the five streams (none for Red Cedar Creek). Only 11 out of 25 possible regression models were significant ($p < 0.10$), with richness producing three, diversity (McIntosh U) producing three, and dominance indices (McIntosh D , Berger-Parker D , Simpson D) producing five models respectively. Among streams, the North Fork Elk River had the highest number of significant regressions (5), followed by Panther Creek (3), Dry Creek (2), and Salmon Creek (1). Twenty-two significant correlation coefficients ($p < 0.10$) were found between maximum depth (8), mean depth (5), pool volume (5), and pool area (3), and measures of species richness, diversity, and dominance. Multivariate comparisons using canonical correlations found that combinations of pool area, volume, maximum, and/or mean depth produced significant ($p < 0.10$) coefficients for all of the study streams except Red Cedar Creek. Low salmonid densities, as influenced by anadromous life histories, oceanic survival, and variable recruitment, along with poor species richness and harsh conditions encountered in Pacific Northwest coastal stream environments, are possible explanations for the weakness of these relationships,

suggesting that habitat may not be the most important factor influencing anadromous salmonid diversity in the study streams.

Large wood volume and dominant substrate were not significantly correlated with any measure of salmonid species diversity. Wood-diversity relationships may be mediated by the relative abundance of coho salmon juveniles (wood-associated taxa). Lack of relationships with dominant substrate may be an artifact of the coarse resolution inherent in the Wentworth classification used.

Reach-level habitat unit complexity (pool/riffle/glide diversity $H'_{habitat}$) and species diversity indices were examined using scatter plots and tested via Spearman Rank correlations, multiple regressions, and canonical correlations. None were significant at $p < 0.10$. Lack of correlations between reach complexity and fish diversity observed was not in concert with other studies on salmonid and non-salmonid fish communities in North America.

ANOVA was used to test results from wood (no wood versus wood) and depth (0.3 or 1.0 m depth) *in-situ* factorial habitat feature selection experiments (using time to replicate blocks). Depth and wood were significant at $p < 0.05$ in the 24 h trials (the interaction term of wood and depth, and block [temporal] effects, were not significant). In the 7 d trials, only depth was significant at $p < 0.05$ (wood, the interaction term, and block effects were not significant). Suggested hypotheses to explain the temporal nature of wood effects include food availability, and decreases in competitive interactions due to higher discharge and increased habitat space.

Results from this research extend our current knowledge about lotic habitat complexity - fish species diversity relationships to include anadromous salmonid assemblages in the Pacific Northwest. Applications to management include the use of habitat-diversity relationships as a diagnostic tools to assess land management impacts on salmonid fishes, and to provide better information on how watershed restoration efforts can be directed towards providing habitats that can support a more diverse assemblage of anadromous salmonids.

BIBLIOGRAPHY

- Aadland, L. P. 1993. Stream habitat types: their fish assemblages and relationship to flow. *N. Am. J. Fish. Mgmt.* 13:790-806.
- Abbott, I. 1978. Factors determining the number of land bird species on islands around south-western Australia. *Oecologia* 33:221-223.
- Abele, L. G. 1974. Species diversity of decapod crustaceans in marine habitats. *Ecology* 55:156-161.
- Allan, J. D. 1975. The distributional ecology and diversity of benthic insects in Cement Creek, Colorado. *Ecology* 56: 1040-1053.
- Angermeier, P. L. 1985. Spatio-temporal patterns of foraging success for fishes in an Illinois stream. *Am. Mid. Nat.* 114:342-357.
- Angermeier, P. L. 1987. Spatio-temporal variation in habitat selection by fishes in a small Illinois stream. Pages 52-60 *In: Community and evolutionary ecology of North American stream fishes.* W. J. Matthews and D. C. Heins (eds.). University of Oklahoma Press, Norman, Oklahoma.
- Angermeier, P. L., and Karr, J. R. 1983. Fish communities along environmental gradients in a system of tropical streams. *Environ. Biol. Fish.* 9:117-135.
- Angermeier, P. L., and J. R. Karr. 1984. Relationships between woody debris and fish habitat in a small warmwater stream. *Trans. Am. Fish. Soc.* 113:716-726.
- Angermeier, P. L., and I. J. Schlosser. 1989. Species-area relationships for stream fishes. *Ecology* 70:1450-1462.
- Bain, M. B., J. T. Finn, and H. E. Booke. 1988. Streamflow regulation and fish community structure. *Ecology* 69:382-392.
- Baker, J. A., and S. T. Ross. 1981. Spatial and temporal resource utilization by southeastern cyprinids. *Copeia* 1981:178-189.
- Benda, L., and T. Dunne. 1987. Sediment routing by debris flow. Pages 213-223 *In: Erosion and Sedimentation in the Pacific Rim (Proceedings of the Corvallis Symposium).* IAHS Publ. No. 165.

- Beschta, R. L. 1997. Restoration of riparian and aquatic systems for improved aquatic habitats in the upper Columbia River basin. Pages 475-491 *In: Pacific salmon and their ecosystems: status and future options.* D. J. Stouder, P. A. Bisson, and R. J. Naiman (eds). Chapman and Hall, New York, NY.
- Bevenger, G. S., and R. M. King. 1995. A pebble count procedure for assessing watershed cumulative effects. USDA Forest Service Rocky Mountain Forest and Range Experiment Station Research Paper RM-RP-319, Fort Collins, CO.
- Bisson, P. A., J. L. Nielson, R. A. Palmason, and L. E. Grove. 1982. A system of naming habitat types in small streams, with examples of habitat utilization by salmonids during low streamflow. Pages 62-73 *In: Acquisition and utilization of aquatic habitat inventory information.* N. B. Armantrout (ed.) Western Division, American Fisheries Society, Portland, OR.
- Bisson, P. A. and J. R. Sedell. 1984. Salmonid populations in streams in clearcut vs. Old-growth forests of western Washington. Pages 121-129 *In: Fish and wildlife relationships in old-growth forests.* W. R. Meehan, T. R. Merrell Jr., and T. A. Hanley (eds). American Institute of Fisheries Research Biologists, Juneau, AK.
- Bisson, P. A., R. E. Bilby, M. D. Bryant, C. A. Dolloff, G. B. Grette, R. A. House, M. K. Murphy, K. V. Koski, and J. R. Sedell. 1987. Large woody debris in forested streams in the Pacific Northwest: past, present, and future. Pages 143-190 *In: Streamside management: forestry and fisheries interactions.* E. Salo and T. Cundy (eds.) University of Washington, Institute of Forest Resources Contribution 57. University of Washington Press, Seattle, WA.
- Bisson, P. A., K. Sullivan, and J. L. Nielsen. 1988. Channel hydraulics, habitat use, and body form of juvenile coho salmon, steelhead, and cutthroat trout in streams. *Trans. Am. Fish. Soc.* 117:262-273.
- Bjornn, T. C. and D. W. Reiser. 1991. Habitat requirements of salmonids in streams. Pages 83 - 138 *In: Influences of forest and rangeland management on salmonid fishes and their habitats.* W. R. Meehan (ed.) American Fisheries Society Special Publications 19. American Fisheries Society Press, Bethesda, MD.
- Blake, J. G., and J. R. Karr. 1987. Breeding birds of isolated woodlots: area and habitat relationships. *Ecology* 68:1724-1734.

- Boecklen, W. J. 1986. Effects of habitat heterogeneity on the species-area relationships of forest birds. *J. Biogeogr.* 13:59-68.
- Bohlin, T. 1977. Habitat selection and intercohort competition of juvenile sea-trout *Salmo trutta*. *Oikos* 29:112-117.
- Bryant, M. D. 1983. The role and management of woody debris in west coast salmonid nursery streams. *N. Am. Jour. Fish. Mgmt.* 3:322-330.
- Bugert, R. M., T. C. Bjornn, and W. R. Meehan. 1991. Summer habitat use by young salmonids and their responses to cover and predators in a small southeast Alaska stream. *Trans. Am. Fish. Soc.* 120: 474-485.
- Bustard, D. R., and D. W. Narver. 1975. Preferences of juvenile coho salmon (*Oncorhynchus kisutch*) and cutthroat trout (*Salmo clarki*) relative to simulated alteration of winter habitat. *J. Fish. Res. Board Can.* 32:681-687.
- Buckley, R. 1982. The habitat-unit model of island biogeography. *J. Biogeogr.* 9:339-344.
- Carpenter, K. E., R. I. Micklat, V. D. Albalajedo, and V. T. Corpuz. 1981. The influence of substrate structure on the local abundance and diversity of Philippine reef fishes. *Proc. 4th Intl. Coral Reef Symp., Manila* 2: 497-502.
- Case, T. J. 1975. Species numbers, density compensation, and colonizing ability of lizards on islands in the Gulf of California. *Ecology* 56:3-18.
- Cederholm, C. J., R. E. Bilby, P. A. Bisson, T. W. Bumsted, B. R. Fransen, W. J. Scarlett, and J. W. Ward. 1997. Responses of juvenile coho salmon and steelhead to placement of large woody debris in a coastal Washington stream. *N. Am. J. Fish. Mgmt.* 17:947-963.
- Chapman, D. W. 1962. Aggressive behavior in juvenile coho salmon as a cause of emigration. *J. Fish. Res. Board Can.* 19:1047-1080.
- Chapman, D. W. 1966. Food and space as regulators of salmonid populations in streams. *Am. Nat.* 100:345-357.
- Chapman, D. W., and T. C. Bjornn. 1969. Distribution of salmonids in streams, with special reference to food and feeding. Pages 153-176 *In: Symposium on salmon and trout in streams.* T. G. Northcote (ed.) H. R. MacMillan Lectures in Fisheries. University of British Columbia Institute of Fisheries, Vancouver, BC.

- Chen, G. K., and C. Ricks. 1990. Progress report: analysis of cumulative watershed effects in the Elk River basin. Siskiyou National Forest, Powers Ranger District, OR.
- Chen, G. K. 1991. Use of basinwide fish habitat and fish population surveys for habitat modeling and cumulative watershed effects analyses. U.S.D.A. Forest Service Fish Habitat Relationships Bulletin FHR Currents 1:93. FHR Publications, Arcata, CA.
- Chen, G. K., J. L. Kershner, and D. Fuller (eds.) 1995. Applications of basin-wide fish habitat and population surveys. Utah State University Press, Logan, UT.
- Connell, J. H. 1975. Some mechanisms producing structure in natural communities: a model and evidence from field experiments. *In: Ecology and evolution of communities.* M. L. Cody and J. M. Diamond (eds.). Belknap Press, Cambridge, MA.
- Connell, J. H. 1976. Community interactions on marine rocky intertidal shores. *Ann. Rev. Ecol. Syst.* 3:169-192.
- Connell, J. G. 1978. Diversity in tropical rain forests and coral reefs. *Science* 199:1302-1310.
- Connell, J. H. 1983. On the prevalence and relative importance of interspecific competition: evidence from field experiments. *Am. Nat.* 122:661-696.
- Coon, T. C. 1987. Responses of benthic riffle fishes to variation in stream discharge and temperature. Pages 77-85 *In: Community and evolutionary ecology of North American stream fishes.* W. J. Matthews and D. C. Heins (eds.). University of Oklahoma Press, Norman, OK.
- Covich, A. P. 1988. Geographical and historical comparisons of neotropical streams: biotic diversity and detrital processing in highly variable habitats. *J. N. Am. Benthol. Soc.* 7:361-386.
- Crossman, E. J. 1959. A predator-prey interaction in freshwater fish. *J. Fish. Res. Board Can.* 16:269-281.
- Dadswell, M. J., R. J. Clauda, C. M. Moffitt, R. L. Sauders, R. A. Rulifson, and J. E. Cooper (eds.) 1987. Common strategies of anadromous and catadromous fishes. American Fisheries Society Symposium I, Bethesda, MD.

- Darwin, C. R. 1859. On the origin of species. London, Murray.
- Dayton, P. K., V. Currie, T. Gerrodette, B. D. Keller, R. Rosenthal, and D. Ven Tresca. 1984. Patch dynamics and stability of some California kelp communities. *Ecol. Monogr.* 54: 253-289.
- Devore, J., and R. Peck. 1986. *Statistics: the exploration and analysis of data.* West Publishing Co., San Francisco, CA.
- Dill, L. M. 1983. Adaptive flexibility in the forage behavior of fishes. *Can. J. Fish. Aq. Sci.* 40:398-408.
- Dill, L. M., R. C. Ydenburg, and A. H. G. Fraser. 1981. Food abundance and territory size in juvenile coho salmon (*Oncorhynchus kistutch*). *Can. J. Zool.* 59:1809-1816.
- Dill, L. B., and A. H. G. Fraser. 1984. Risk of predation and the feeding behaviour of juvenile coho salmon (*Oncorhynchus kisutch*). *Behav. Ecol. Sociobiol.* 16:65-71.
- Dolloff, C.A. 1986. Effects of stream cleaning on juvenile coho salmon and Dolly Varden in southeast Alaska. *Trans. Am. Fish. Soc.* 115:743-755.
- Dolloff, C. A. 1987. Seasonal population characteristics and habitat use by juvenile coho salmon in a small Southeast Alaska stream. *Trans. Am. Fish Soc.* 116:829-837.
- Dolloff, C. A., D. G. Hankin, and G. H. Reeves. 1993. Basinwide estimation of habitat and fish populations in streams. General Technical Report SE-GTR-83, U.S.D.A. Forest Service Southeastern Forest Experiment Station, Asheville, NC.
- Elliott, S. T. 1986. Reduction of a Dolly Varden population and macrobenthos after removal of logging debris. *Trans. Am. Fish. Soc.* 115:392-400.
- Evans, J. W. and R. L. Noble. 1979. The longitudinal distribution of fishes in an east Texas stream. *Am. Midl. Nat.* 101:333-334.
- Everest, F. H., and D. W. Chapman. 1972. Habitat selection and spatial interactions by juvenile chinook salmon and steelhead trout in two Idaho streams. *J. Fish. Res. Board Can.* 29:91-100.

- Everest, F. H., N. B. Armantrout, S. M. Keller, W. D. Parante, J. R. Sedell, T. E. Nickelson, J. M. Johnston, and G. N. Haugen. 1980. Salmonids. Pages 199-230 *In: Influences of Forest and Rangeland Management on Anadromous Fish Habitat in Western North America. General Technical Report PNW-GTR-104, U.S.D.A. Forest Service Pacific Northwest Range and Experiment Station, Portland, OR.*
- Everest, F. H., and W. R. Meehan. 1981. Forest management and anadromous fish habitat productivity. Pages 521-530 *In: 46th North American Wildlife and Natural Resource Conference Transactions. Wildlife Management Institute, Washington, D.C.*
- Fausch, K. D. 1984. Profitable stream positions for salmonids: Relating specific growth rate to net energy gain. *Can. J. Zool.* 62:441-51.
- Fausch, K. D. 1993. Experimental analysis of microhabitat selection by juvenile steelhead (*Oncorhynchus mykiss*) and coho salmon (*O. kisutch*) in a British Columbia stream. *Can. J. Fish. Aquat. Sci.* 50:1198-1207.
- Fausch, K. D. and R. G. Bramblett. 1991. Disturbance and fish communities in intermittent tributaries of a western Great Plains river. *Copeia* 1991:208-218.
- Felley, J. D., and L. G. Hill. 1983. Multivariate assessment of environmental preferences of cyprinid fishes of the Illinois River, Oklahoma. *Am. Midl. Nat.* 109:209-221.
- Felley, J. D., and S. M. Felley. 1987. Relationships between habitat selection by individuals of a species and patterns of habitat segregation among species: fishes of the Calcasieu drainage. Pages 61-68 *In: Community and evolutionary ecology of North American stream fishes. W. J. Matthews and D.C. Heins (eds.). University of Oklahoma Press, Norman, OK.*
- Finger, T. R., and E. M. Stewart. 1987. Responses of fishes to flooding regime in lowland hardwood wetlands. Pages 86-92 *In: Community and evolutionary ecology of North American stream fishes. W. J. Matthews and D. C. Heins (eds.). University of Oklahoma Press, Norman, OK.*
- Fisher, W. L., and W. D. Pearson. 1987. Patterns of resource utilization among four species of darters in three central Kentucky streams. Pages 69-76 *In: Community and evolutionary ecology of North American stream fishes. W. J. Matthews and D. C. Heins (eds.). University of Oklahoma Press, Norman, OK.*

- Forward, C. D. 1984. Organic debris complexity and its effect on small scale distribution and abundance of coho (*Oncorhynchus kisutch*) fry populations in Carnation Creek, British Columbia. Unpublished B.S. Thesis, University of British Columbia, Vancouver, B.C.
- Fraser, D. F., and T. E. Sise. 1980. Observations of stream minnows in a patchy environment: a test of a theory of habitat distribution. *Ecology* 61:790-97.
- Fraser, D. F., and R. D. Cerri. 1982. Experimental evaluation of predator-prey relationships in a patchy environment: consequences for habitat use patterns in minnows. *Ecology* 63:307-313.
- Fraser, D. F., D. A. DiMattia, and J. D. Duncan. 1987. Living among predators: response of a stream minnow to the hazard of predation. Pages 121-127 *In: Community and evolutionary ecology of North American stream fishes.* W. J. Matthews and D. C. Heins (eds.). University of Oklahoma Press, Norman, OK.
- Freemark, K. E. and H. G. Merriam. 1986. Importance of area and habitat heterogeneity to bird assemblages in temperate forest fragments. *Biol. Conserv.* 36:115-141.
- Fresh, K. L. 1997. The role of competition and predations in the decline of Pacific salmon and steelhead. Pages 245-275 *In: Pacific salmon and their ecosystems: status and future options.* D. J. Stouder, P. A. Bisson, and R. J. Naiman (eds.) Chapman and Hall, New York, NY.
- Game, M. and G. F. Peterken. 1984. Nature reserve selection strategies in the woodlands of central Lincolnshire, England. *Biol. Conserv.* 29:157-181.
- Gee, J. H., and T. G. Northcote. 1963. Comparative ecology of two sympatric species of dace (*Rhinichthys*) in the Fraser River system, British Columbia. *J. Fish. Res. Board Can.* 20:105-18.
- Gelwick, F. P. 1990. Longitudinal and temporal comparisons of riffle and pool fish assemblages in a northeastern Oklahoma Ozark stream. *Copeia* 1990:1072-1082.
- Gladfelter, W. B., and E. H. Gladfelter. 1978. Fish community structure as a function of habitat structure on West Indian patch reefs. *Rev. Biol. Trop.* 26 (suppl.1):65-84.

- Glass, N. R. 1971. Computer analysis of predation energetic in the largemouth bass. Pages 325-363 *In: Systems analysis and simulation in ecology*. Volume 1. C. Patten (ed.). Academic Press, New York, NY.
- Glova, G. J. 1978. Patterns and mechanisms of resource partitioning between stream populations of juvenile coho salmon (*Oncorhynchus kisutch*) and coastal cutthroat trout (*Salmo clarki*). Unpublished Ph.D dissertation, University of British Columbia, Vancouver, BC.
- Glova, G. J., and J. C. Mason. 1977. Comparisons of coastal cutthroat trout populations in allopatry and those sympatric with coho salmon and sculpins in several small coastal streams on Vancouver Island, B.C. *Fish. Mar. Serv. MS Rep.* 1434.
- Gorman, O. T. 1988. The dynamics of habitat use in a guild of Ozark minnows. *Ecol. Monogr.* 58:1-18.
- Gorman, O. T., and J. R. Karr. 1978. Habitat structure and stream fish communities. *Ecology* 59:507-515.
- Green, R. H. and G. L. Vascotto. 1978. A method for the analysis of environmental factors controlling patterns of species composition in aquatic communities. *Water Res.* 12:583-590.
- Gregory, S. V. and P. A. Bisson. 1997. Salmonid habitat degradation and loss. Pages 277-314 *In: Pacific salmon and their ecosystems: status and future options*. D. J. Stouder, P. A. Bisson, and R. J. Naiman (eds). Chapman and Hall, New York, NY.
- Groot, C. and L. Margolis [eds.]. 1991. *Pacific salmon life histories*. University of British Columbia Press, Vancouver, B.C.
- Grossman, G. D., and M. C. Freeman. Microhabitat use in a stream fish assemblage. *J. Zool.* 212:151-176.
- Grossman, G. D., P. B. Moyle, and J. O. Whitaker. 1982. Stochasticity in structural and functional characteristics of an Indiana stream fish assemblage: a test of community theory. *Am. Nat.* 120:423-454.
- Hankin, D. G., and G. R. Reeves. 1988. Estimating total fish abundance and total habitat area in small streams based on visual estimation methods. *Can. J. Fish. Aq. Res.* 45:834-844.

- Hanson, D. L. 1977. Habitat selection and spatial interaction in allopatric and sympatric populations of cutthroat and steelhead trout. Unpublished Ph.D. dissertation, University of Idaho, Moscow, ID.
- Harrell, H. L., B. J. Davis, and T. C. Dorris. 1967. Stream order and species diversity of fishes in an intermittent stream. *Am. Midl. Nat.* 78:428-436.
- Harris, M. P. 1973. The Galapagos avifauna. *Condor* 75:265-278.
- Harman, W. N. 1972. Benthic substrates: their effect on fresh-water mollusca. *Ecology* 53:271-277.
- Harmon, M. E., J. F. Franklin, F. J. Swanson, P. Sollins, S. V. Gregory, J. D. Lattin, N. H. Anderson, S. P. Cline, N. G. Aumen, J. R. Sedell, G. W. Lienkaemper, K. R. Cromack Jr., and K. W. Cummins. 1988. Ecology of coarse woody debris in temperate ecosystems. *Adv. Ecol. Res.* 15:133-302.
- Hart, D. D. 1983. The importance of competitive interactions in stream systems. Pages 99-136 *In: Stream ecology: application and testing of general ecological theory.* J. R. Barnes and G. W. Minshall (eds.) Plenum Press, New York, NY.
- Hartman, G. F. 1965. The role of behavior in the ecology and interactions of under-yearling coho salmon (*Oncorhynchus kisutch*) and steelhead trout (*Salmo gairdneri*). *J. Fish. Res. Board Can.* 22:1035-1081.
- Harvey, B. C. and A. J. Stewart. 1991. Fish size and habitat depth relationships in headwater streams. *Oecologia* 87:336-342.
- Hawkins, C. P., J. L. Kershner, P. A. Bisson, M. D. Bryant, L. M. Decker, S. V. Gregory, D. A. McCullough, C. K. Overton, G. H. Reeves, R. J. Steeman, and M. K. Young. 1993. A hierarchical approach to classifying stream habitat features. *Fisheries* 18:3-10.
- Hearn, W. E. 1987. Interspecific competition and habitat segregation among stream-dwelling trout: a review. *Fisheries* 12:24-31.
- Hickman, G. D. 1975. Value of instream cover to the fish populations of Middle Fabius River, Missouri. *Miss. Dept. Conserv. Aquat. Ser.* 14, Jefferson City, MS.

- Hill, M. O. 1972. Diversity and evenness: a unifying notation and its consequences. *Ecology* 54:427-432.
- Hillborn, R. and J. Winton. 1993. Learning to enhance salmon production: lessons from the salmonid enhancement program. *Can. J. Fish. Aqua. Sci.* 50:2043-2056.
- Hixon, M. A. 1986. Fish predation and local prey diversity. Pages 235-258 *In: Contemporary studies on fish feeding.* C. A. Simenstad & G. M. Calliet (eds.). D. W. Junk Publishers.
- Hixon, M. A., and J. P. Beets. 1989. Shelter characteristics and Caribbean fish assemblages: experiments with artificial reefs. *Bull. Mar. Sci.* 44(2):666-680.
- Hixon, M. A., and B. A. Menge. 1991. Species diversity: prey refuges modify the interactive effects of predation and competition. *Theor. Pop. Biol.* 39:178-200.
- Horwitz, R. J. 1978. Temporal variability patterns and the distributional patterns of stream fishes. *Ecol. Monogr.* 48:307-321.
- House, R. D., and P. L. Boehne. 1986. Effects of instream structures on salmonid habitat and populations in Tobe Creek, Oregon. *N. Am. J. Fish. Mgmt.* 6:38-46.
- Huston, M. 1979. A general hypothesis of species diversity. *Am. Nat.* 113:81-101.
- Hutchinson, G. E. 1959. Homage to Santa Rosalia, or "why are there so many kinds of animals?" *Am. Nat.* 93:145-59.
- James, F. C., and N. O. Wamer. 1982. Relationships between temperate forest bird communities and vegetation structure. *Ecology* 63:159-171.
- James, F. C., R. F. Johnston, H. O. Wamer, G. J. Niemi, and W. J. Boecklen. 1984. The Grinnelian niche of the wood thrush. *Am. Nat.* 124:17-30.
- Jenkins, T. M. Jr., C. R. Feldmuth, and G. V. Elliott. 1970. Feeding of rainbow trout (*Salmo gairdneri*) in relation to abundance of drifting invertebrates in a mountain stream. *J. Fish. Res. Bd. Can.* 27:2356-2361.
- Johnson, J. H. and P. A. Kucera. 1985. Summer-autumn habitat utilization of subyearling steelhead trout in tributaries of the Clearwater River, Idaho. *Can. J. Zool.* 63:2283-2290.

- Johnson, M. P. and D. S. Simberloff. 1974. Environmental determinants of island species numbers in the British Isles. *J. Biogeogr.* 1:149-154.
- Johnson, M. P., L. G. Mason, and P. H. Raven. 1968. Ecological parameters and plant species diversity. *Am. Nat.* 102:297-305.
- Karr, J. R. 1968. Habitat and avian diversity on strip-mined land in east central Illinois. *Condor* 70:348-357.
- Karr, J. R., and R. R. Roth. 1971. Vegetation structure and avian diversity in several new world areas. *Am. Nat.* 105:423-435.
- Kinzie, R. A. 1988. Habitat utilization by Hawaiian stream fishes with reference to community structure in oceanic island streams. *Environ. Biol. Fish.* 22:179-192.
- Kitchener, J. D. 1982. Predictors of vertebrate species richness in nature reserves in the Western Australian wheatbelts. *Aust. Wild. Res.* 9:1-7.
- Knighton, D. J. 1987. *Fluvial forms and processes.* University of Washington Press, Seattle, WA.
- Kohn, A. J. 1967. Environmental complexity and species diversity in the gastropod genus *Conus* on Indo-West Pacific reef platforms. *Am. Nat.* 101:251-259.
- Kostow, K. 1997. The status of salmon and steelhead in Oregon. Pages 145-178 *In: Pacific salmon and their ecosystems: status and future options.* D. J. Stouder, P. A. Bisson, and R. J. Naiman (eds.) Chapman and Hall, New York, NY.
- Kushlan, J. A. 1976. Environmental stability and fish community diversity. *Ecology* 57:821-825.
- Larkin, P. A. 1956. Interspecific competition and population control in freshwater fish. *J. Fish. Res. Board Can.* 13:327-342.
- Leopold, L. B., M. G. Wolman, and J. P. Miller. 1964. *Fluvial processes in geomorphology.* W. H. Freeman, San Francisco, CA. 324 pages.
- Li, H. W., C. B. Schreck, C. E. Bond, and E. Rexstad. 1987. Factors influencing changes in fish assemblages of Pacific northwest streams. Pages 193-202 *In: Community and evolutionary ecology of North American stream fishes.* W. J. Matthews and D. C. Heins (eds.). University of Oklahoma Press, Norman, OK.

- Livingstone, D. A., M. Rowland, and P. E. Bailey. 1982. On the size of African riverine fish faunas. *Am. Zool.* 22:361-369.
- Lonzarich, D. G. 1994. Stream fish communities in Washington: patterns and processes. Unpublished Ph.D. dissertation, School of Fisheries, University of Washington, Seattle.
- Lonzarich, D. G., and T. P. Quinn. 1995. Experimental evidence for the effect of depth and structure on the distribution, growth, and survival of stream fishes. *Can. J. Zool.* 73:2223-2230.
- Lotrich, V. A. 1973. Growth, production, and community composition of fishes inhabiting a first-, second-, and third-order stream of Eastern Kentucky. *Ecol. Monogr.* 43:377-397.
- Luckhurst, B. E. and K. Luckhurst. 1978. Analysis of the influence of substrate variables on coral reef fish communities. *Mar. Biol.* 49:317-323.
- MacArthur, R. H. 1964. Environmental factors affecting bird species diversity. *Am. Nat.* 98:387-397.
- MacArthur, R. H. 1965. Patterns of species diversity: *Biol. Rev.* 40:510-533.
- MacArthur, R. H. 1972. *Geographical ecology*. Harper & Row, New York, NY. 269 pages.
- MacArthur, R. H., and J. W. MacArthur. 1961. On bird species diversity. *Ecology* 42:594-598.
- MacArthur, R. H., R. H. Recher, and M. Cody. 1966. On the relation between habitat selection and species diversity. *Am. Nat.* 100:319-332.
- Magurran, A. E. 1988. *Ecological diversity and its measurement*. Princeton University Press, Princeton, NJ.
- Martin, D. J., L. J. Wasserman, and V. H. Dale. 1986. Influence of riparian vegetation on post-eruption survival of coho salmon fingerlings on the west-side streams of Mount Saint Helens, Washington. *N. Am. J. Fish. Manag.* 6:1-8.
- Martin, T. E. 1981. Limitation in small habitat islands: chance or competition. *The Auk* 98:715-734.

- Matthews, W. J. 1982. Small fish community structure in Ozark streams: structured assembly patterns or random abundance of species? *Am. Midl. Nat.* 107:42-54.
- Matthews, W. J. 1986. Fish faunal structure in an Ozark stream: stability, persistence and a catastrophic flood. *Copeia* 1986:388-397.
- Matthews, W. J. 1998. Patterns in freshwater fish ecology. Chapman and Hall, New York, NY.
- Matthews, W. J., and L. G. Hill. 1980. Habitat partitioning in the fish community of a southwestern river. *Southwest Nat.* 25:51-66.
- Matthews, W.J. and D.C. Heins (eds). 1987. Community and evolutionary ecology of North American stream fishes. University of Oklahoma Press, Norman, OK.
- Matthews, W. J. and H. W. Robison. 1988. The distribution of fishes in the Arkansas River: a multivariate analysis. *Copeia* 1988:358-374.
- Matthews, W. J. and F. P. Gelwick. 1990. Fishes of Crutcho Creek and the North Canadian River near Oklahoma City: urbanization and temporal variability. *Southwest. Nat.* 35:403-410.
- Matthews, W. J., B. C. Harvey, and M. E. Power. 1994. Spatial and temporal patterns in the fish assemblages of individual pools in a midwestern stream (USA). *Environ. Biol. Fish.* 39:381-397.
- May, R. M.. 1975. Patterns of species abundance and diversity. Pages 81-120 *In: Ecology and evolution of communities.* M. J. Cody and J. M. Diamond (eds.). Harvard Univ. Press, Cambridge, MA.
- May, R. M. 1986. The search for patterns in the balance of nature: advances and retreats. *Ecology* 67:1115-1126.
- McHugh, M. 1986. The effects of landslides on stream channel morphology in a southwest Oregon stream. Unpublished MS thesis, Oregon State University, Corvallis, OR.
- McIntosh, B. A., J. R. Sedell, J. E. Smith, R. C. Wissmar, G. H. Reeves, and L. A. Brown. 1993. Management history of eastside ecosystems: changes in fish habitat over 50 years, 1935-1992. Pages 291-483 *In: Eastside forest ecosystem health assessment, Volume III Assessment.* P. F. Hessburg (ed.) U.S.D.A. Forest Service, Wenatchee, WA.

- McIntosh, R. P. 1966. An index of diversity and the relation of certain concepts to diversity. *Ecology* 48:392-404.
- Means, J., S. V. Gregory, G. H. Reeves, and J. Schwartz. 1992. Reach-scale patterns of juvenile anadromous salmonid diversity in Drift Creek, Oregon. Proceedings Oregon Chapter, American Fisheries Society Meeting February 1992, Mt. Bachelor, OR.
- Meehan, W. R. 1991. Influences of forest and rangeland management on salmonid fishes and their habitat. American Fisheries Society Special Publication, Bethesda, MD.
- Meffe, G. K., and A. L. Sheldon. 1990. Post-defaunation recovery of fish assemblages in southeastern blackwater streams. *Ecology* 71: 657-667.
- Mendelson, J. 1975. Feeding relationships among species of *Notropis* (Pisces: Cyprinidae) in a Wisconsin stream. *Ecol. Monogr.* 45:199-230.
- Menge, B. A., and J. P. Sutherland. 1976. Species diversity gradients: Synthesis of the roles of predation, competition, and temporal heterogeneity. *Am. Nat.* 110:351-369.
- Menge, B. A., and J. P. Sutherland. 1987. Community regulation: variation in disturbance, competition, and predation in relation to environmental stress and recruitment. *Am. Nat.* 130:730-757.
- Minshall, G. W., R. C. Petersen, Jr., and C. F. Nimz. 1985. Species richness in streams of different size from the same drainage basin. *Am. Nat.* 125:16-38.
- Moyle, P. B., and F. R. Senanayake. 1984. Resource partitioning among the fishes of rainforest streams in Sri Lanka. *J. Zool.* 202:195-224.
- Moyle, P. B. and D. M. Baltz. 1985. Microhabitat use by an assemblage of California stream fishes: developing criteria for instream flow determinations. *Trans. Am. Fish. Soc.* 114:695-704.
- Mundie, J. H. 1969. Ecological implications of the diet of juvenile coho in streams. Pages 135-152 *In: Symposium on salmon and trout in streams.* T. G. Northcote (ed.). H. R. MacMillan Lecture Series in Fisheries, University of British Columbia Institute of Fisheries, Vancouver, BC.
- Murdoch, W. W., F. C. Evans, and C. H. Peterson. 1972. Diversity and pattern in plants and insects. *Ecology* 53:819-829.

- Murphy, M. L., J. Heifetz, S. W. Johnson, K. V. Koski, and J. F. Thedinga. 1986. Effects of clear-cut logging with and without buffer strips on juvenile salmonids in Alaskan streams. *Can. Jour. Fish. Aqua. Sci.* 43:1521-1533.
- Nehlsen, W., J. E. Williams, and J. A. Lichatowich. 1991. Pacific salmon at the crossroads: stocks at risk from California, Oregon, and Washington. *Fisheries* 16:4-21.
- Neill, W. E. 1975. Experimental studies of microcrustacean competition, community composition and efficiency of resource utilization. *Ecology* 56:809-826.
- Newman, M. A. 1956. Social behavior and interspecific competition in two trout species: *Phys. Zoo.* 29:64-81.
- Newsome, G. F., and J. H. Gee. 1978. Preference and selection of prey by creek chubs (*Semotilus atromaculatus*) inhabiting the Mink River, Manitoba. *Can. J. Zool.* 56:2486-2497.
- Nickelson, T. E. 1986. Influences of upwelling, ocean temperature, and smolt abundance on marine survival of coho salmon (*Oncorhynchus kistuch*) in the Oregon Production Area. *Can. J. Fish. Aqua. Sci.* 43:527-535.
- Nickelson, T. E., and D. G. Hankin. 1991. Limiting factors for production of chinook salmon in coastal streams. Oregon Department of Fish and Wildlife Research Report 91-2, Corvallis, OR.
- Nickelson, T. E., J. W. Nicholas, A. M. McGie, R. B. Lindsay, D. L. Bottom, R. J. Kaiser, and S. E. Jacobs. 1992. Status of anadromous salmonids in Oregon coastal basins. Oregon Department of Fish and Wildlife Report to the Governor, Corvallis, OR.
- Nilsson, N. 1963. Interaction between trout and char in Scandinavia. *Trans. Amer. Fish. Soc.* 92:276-285.
- Olson, D. H., W. P. Leonard, and R. B. Bury. 1997. Sampling amphibians in lentic habitats: methods and approaches for the Pacific Northwest. Northwest Fauna Number 4, Society for Northwestern Vertebrate Biology. Olympia, WA.
- Paller, M. C. 1994. Relationships between fish assemblage structure and stream order in South Carolina coastal plain streams. *Trans. Am. Fish. Soc.* 123:150-161.

- Paine, R. T. 1966. Food web complexity and species diversity. *Am. Nat.* 100:65-75.
- Paine, R. T. 1969. The *Pisaster-Tegula* interaction: prey patches, predator food preference and intertidal community structure. *Ecology* 50:950-961.
- Paragamian, V. L. 1980. Population dynamics of smallmouth bass in the Maquoketa River and other Iowa streams. Iowa Conserv. Comm. Fish. Sec. Study 602, Des Moines, IA.
- Pearcy, W. G. 1997. Salmon production in changing ocean domains. Pages 331-352 *In: Pacific salmon and their ecosystems: status and future options.* D. J. Stouder, P. A. Bisson, and R. J. Naiman (eds.) Chapman and Hall, New York, NY.
- Pearsons, T. N., H. W. Li, and G. A. Lamberti. 1992. Influence of habitat complexity on resistance to flooding and resilience of stream fish assemblages. *Trans. Am. Fish. Soc.* 121:427-436.
- Petersen, R. G. 1985. Design and analysis of experiments. Marcel Dekker Inc., New York, New York.
- Pianka, E. E. 1967. On lizard species diversity in North American flatland deserts. *Ecology* 48:333-351.
- Pickett, S. T., and P. S. White (eds.). 1985. The ecology of natural disturbance as patch dynamics. Academic Press, New York, NY.
- Poff, N. L. and J. D. Allen. 1995. Functional organization of stream fish assemblages in relation to hydrological variability. *Ecology* 76:606-627.
- Ponce, S. L. 1980. Statistical methods commonly used in water quality data analysis. WSDG Technical Paper WSDG-TP-00001, U.S.D.A. Forest Service Watershed Systems Technical Development Group, Fort Collins, CO.
- Poulson, T.L., and D. C. Culver. 1969. Diversity in terrestrial cave communities. *Ecology* 50:153-157.
- Power, D. M. 1972. Numbers of bird species on the California Islands. *Evolution* 26:451-463.
- Power, D. M. 1978. Avifauna richness on the California Channel Islands. *Condor* 778:394-398.

- Power, M. E. 1984. Depth distribution of armored catfish: Predator-induced resource avoidance? *Ecology* 65:523-528.
- Power, M. E., W. J. Matthews. 1983. Algae-grazing minnows (*Campostoma anomalum*), piscivorous bass (*Micropterus* spp.), and the distribution of attached algae in a small prairie-margin stream. *Oecologia* 60:328-332.
- Power, M. E., W. J. Matthews, and A. J. Stewart. 1985. Grazing minnows, piscivorous bass, and stream algae: Dynamics of a strong interaction. *Ecology* 66:1448-1456.
- Quinn, T. P. and N. P. Peterson. 1996. The influence of habitat complexity and fish size on over-winter survival and growth of individually marked juvenile coho salmon (*Oncorhynchus kisutch*) in Big Beef Creek, Washington. *Can. J. Fish. Aquat. Sci.* 53:1555-1564.
- Rabeni, C. F., and G. W. Minshall. 1977. Factors affecting microdistribution of stream benthic insects. *Oikos* 29:33-43.
- Recher, H. F. 1969. Bird species diversity and habitat diversity in Australia and North America. *Am. Nat.* 103:75-80.
- Reed, T. 1981. The number of breeding landbird species on British Isles. *J. Anim. Ecol.* 50:613-624.
- Reeves, G. H. 1985. Interaction and behavior of the redbreast shiner (*Richardsonius balteatus*) and the steelhead trout (*Salmo gairdneri*) in Western Oregon: the influence of water temperature. Unpublished P.d. dissertation, Oregon State University, Corvallis, OR.
- Reeves, G. H. 1988. Distribution patterns of fish in the Elk River basin. C.O.P.E. Report 2:4-6.
- Reeves, G. H., F. H. Everest, and J. D. Hall. 1987. Interactions between the redbreast shiner (*Richardsonius balteatus*) and the steelhead trout (*Salmo gairdneri*) in western Oregon: the influence of water temperature. *Can. J. Fish. Aquat. Sci.* 44:1603-1613.
- Reeves, G. H., J. D. Hall, T. D. Roelofs, T. L. Hickman, and C. O. Baker. 1991. Rehabilitating and modifying stream habitats. Pages 519-558 *In: Influences of forest and rangeland management on salmonid fishes and their habitats.* W. R. Meehan (ed.) American Fisheries Society Special Publications 19. American Fisheries Society Press, Bethesda, MD.

- Reeves, G. H., F. H. Everest, and J. R. Sedell. 1993. Diversity of juvenile anadromous salmonid assemblages in coastal Oregon basins with different levels of timber harvest. *Trans. Amer. Fish. Soc.* 122:309-317.
- Reeves, G. H., L. E. Benda, K. M. Burnett, P. A. Bisson, and J. R. Sedell. 1995. A disturbance-based ecosystem approach to maintaining and restoring freshwater habitats of evolutionary significant units of anadromous salmonids in the Pacific Northwest. *American Fisheries Society Symposium* 17:334-349, Bethesda, MD.
- Reimers, P. E. 1968. Social behavior among juvenile fall chinook salmon. *J. Fish. Res. Board Can.* 19:1047-1080.
- Ricker, W. E. 1975. Computation and interpretation of biological statistics of populations. *Fisheries Research Board of Canada Bulletin* 191. Ottawa, ON.
- Risk, M. J. 1972. Fish diversity on a coral reef in the Virgin Islands. *Atoll Res. Bull.* 153:1-6.
- Roberts, C. M., and R. F. G. Ormond. 1987. Habitat complexity and coral reef fish diversity and abundance on Red Sea fringing reefs. *Mar. Ecol. Progr. Ser.* 41:1-8.
- Rosenzweig, M. L., and J. Winakaur. 1969. Population ecology of desert rodent communities: habitat and environmental complexity. *Ecology* 49:558-572.
- Rosgen, D. L. 1985. A stream classification system. *Proceedings North American Riparian Conference* April 16-18, 1985, Tucson, AZ.
- Ross, S. T., J. A. Baker, and K. E. Clark. 1987. Microhabitat partitioning of southeastern stream fishes: temporal and spatial predictability. Pages 42-51 *In: Community and evolutionary ecology of North American stream fishes.* W. J. Matthews and D. C. Heins (eds.). University of Oklahoma Press, Norman, OK.
- Ryan, S. A. 1989. Riparian canopy recovery in response to channel changes, Elk River, Oregon. Unpublished MS thesis, Oregon State University, Corvallis, OR.
- Sale, P. F., and W. A. Douglas. 1984. Temporal variability in the community structure of fish on coral patch reefs and the relation of community structure to reef structure. *Ecology* 65:409-422.

- Salo, E. O., and T. W. Cundy (eds). 1987. Streamside management: forestry and fisheries interactions. University of Washington, Institute of Forest Resources Contribution 57. University of Washington Press, Seattle, WA.
- SAS Institute Inc. 1989. SAS/STAT user's guide, version 6, 4th edition, volume 1. SAS Institute Inc., Cary, N.C.
- Schlosser, I. J. 1982. Fish community structure and function along two habitat gradients in a headwater stream. *Ecol. Monogr.* 52:395-414.
- Schlosser, I. J. 1985. Flow regime, juvenile abundance, and the assemblage structure of stream fishes. *Ecology* 66:1484-1490.
- Schlosser, I. J. 1987(a). The role of predation in age- and size-related habitat use by stream fishes. *Ecology* 68:651-659.
- Schlosser, I. J. 1987(b). A conceptual framework for fish communities in small warmwater streams. Pages 17-24 *In: Community and evolutionary ecology of North American Stream Fishes.* W. J. Matthews and C. W. Heins (eds.). University of Oklahoma Press, Norman, OK.
- Schoener, T. W. 1983. Field experiments on interspecific competition. *Am Nat.* 122:240-285.
- Scott, W. B., and E. J. Crossman. 1973. Freshwater fishes of Canada. Bulletin 184 Fisheries Research Board of Canada, Ottawa, Canada. 966 pages.
- Sedell, J. R., and K. J. Luchessa. 1982. Using the historical record an aid in salmonid habitat restoration. Pages 210-223 *In: Proc. Acquisition and utilization of aquatic habitat inventory information, Western Division American Fisheries Society Symposium, October 28-30, 1981, Portland, OR.*
- Sedell, J. R., P. A. Bisson, F. J. Swanson, and S. V. Gregory. 1988. What we know about large trees that fall into streams and rivers. General Technical Report PNW-GTR-229:47-81, U.S.D.A. Forest Service Pacific Northwest Forest and Range Experiment Station, Portland, OR.
- Sedell, J. R. and F. H. Everest. 1991. Historic changes in pool habitat for Columbia River Basin salmon under study for TES listing. Draft General Technical Report PNW-GTR, U.S.D.A. Forest Service Pacific Northwest Forest and Range Experiment Station, Corvallis, OR.

- Sedell, J. R., G. H. Reeves, and P. A. Bisson. 1997. Habitat policy for salmon in the Pacific Northwest. Pages 375-387 *In: Pacific salmon and their ecosystems: status and future options*. Stouder, D. J., P. A. Bisson, and R. J. Naiman (eds) Chapman and Hall, New York, NY.
- Sheldon, A.L. 1966. Longitudinal succession and diversity of the fishes of Oswego Creek, New York. Unpublished Ph.D. thesis, Cornell University, Ithaca, NY.
- Sheldon, A. L. 1968. Species diversity and longitudinal succession in stream fishes. *Ecology* 49:193-198.
- Shirvell, C. S. 1990. Role of instream rootwads as juvenile coho salmon (*Oncorhynchus kisutch*) and steelhead trout (*O. mykiss*) cover habitat under varying streamflows. *Can. J. Fish. Aquat. Sci.* 47:852-861.
- Sih, A., P. Crowley, M. McPeck, J. Petranka, and K. Strohmeier. 1985. Predation, competition, and prey communities: a review of field experiments. *Ann. Rev. Ecol. Syst.* 16:269-311.
- Simberloff, D. S. and N. J. Gotelli. 1984. Effects of insularization on plant species richness in the prairie-forest ecotone. *Biol. Conserv.* 29:27-46.
- Simpson, G. G. 1964. Species density of North American recent mammals. *Syst. Zool.* 13:57-73.
- Siskiyou National Forest, 1993. Elk River Wild and Scenic River management plan. Siskiyou National Forest, Grants Pass, OR.
- Siskiyou National Forest, 1994. Watershed analysis for the Elk River basin, Curry County, Oregon. Grants Pass, OR.
- Smart, H. J. and J. H. Gee. 1979. Coexistence and resource partitioning in two species of darter (Percidae), *Etheostoma nigrum* and *Percina maculata*. *Can. J. Zool.* 57:2061-2071.
- Smith, C. L. and C. Tyler. 1972. Space resource sharing in a coral reef fish community. Pages 125-170 *In: Results of the Tektite program: ecology of coral reef fishes*. B. C. Collette and S. A. Earle (eds.). Nat. Hist. Museum Los Angeles County Sci. Bull. 14.
- Smith, M. L. and R. R. Miller. 1986. The evolution of the Rio Grande basin as inferred from its fish fauna. Pages 457-485 *In: The zoogeography of North American freshwater fishes*. C. H. Hocutt and E. O. Wiley (eds.). John Wiley and Sons, New York, NY.

- Snedecor, G. W., and W. G. Cochran. 1980. *Statistical methods* (7th edition). Iowa State Press, Ames, IA.
- Southwood, T. R. E. 1977. Habitat, the templet for ecological strategies? *J. Anim. Ecol.* 46:337-365.
- Spalding, S., N. P. Peterson, and T. P. Quinn. 1995. Summer distribution, survival, and growth of juvenile coho salmon under varying experimental conditions of brushy instream cover. *Trans. Am. Fish. Soc.* 124:124-130.
- Sullivan, K., T. E. Lisle, C.A. Dolloff, G. E. Grant, and L. M. Reid. 1987. Stream channels: the link between the forests and fishes. Pages 39-97 *In: Streamside management: forestry and fishery interactions*. E. O. Salo and T. W. Cundy (eds). Institute of Forest Resources Contribution #57, University of Washington, University of Washington Press, Seattle, WA.
- Stafford, S. G. 1988. How to plan a statistically sound experiment: an overview of basic statistics. PNW Technical Paper, U.S.D.A. Forest Service Pacific Northwest Forest and Range Experiment Station, Corvallis, OR.
- Stein, R.A. 1979. Behavioral response of prey to fish predators. Pages 343-53 *In: Predator-prey systems in fisheries management*. R. H. Stroud and H. Clepper (eds.). Sport Fishing Institute, Washington, D. C.
- Stein, R. A., and J. H. Magnuson. 1976. Behavioral response of crayfish to a fish predator. *Ecology* 57:751-761.
- Stouder, D. J., P. A. Bisson, and R. J. Naiman (eds). 1997. *Pacific salmon and their ecosystems: status and future options*. Chapman and Hall, New York, NY.
- Strahler, A. N. 1957. Quantitative analysis of watershed geomorphology. *Trans. Am. Geophys. Union* 38:913-920.
- Strong, D. R., J. H. Lawton, and T. R. E. Southwood. 1984. *Insects on plants: community patterns and mechanisms*. Blackwell Scientific Publications, Oxford.
- Swanston, D. N. 1980. Impacts of natural events. Chapter 2 *In: Influence of forest and rangeland management on anadromous fish habitat in Western North America: Impacts of natural events*. W. R. Meehan (ed.). General Technical Report PNW-GTR-104, U.S.D.A. Forest Service Pacific Northwest Range and Experiment Station. Portland, OR.

- Taylor, C. M. 1997. Fish species richness and incidence patterns in isolated and connected stream pools: effects of pool volume and spatial position. *Oecologia* 110:560-566.
- Taylor, C. M., M. R. Winston, and W. J. Matthews. 1993. Fish species-environment and abundance relationships in a Great Plains river system. *Ecography* 16:16-23.
- Taylor, C. M. and P. W. Lienesch. 1996. Regional parapatry of congeneric cyprinids *Lythrurus snelsoni* and *L. umbratilis*: species replacement along a complex environmental gradient. *Copeia* 1996:493-497.
- Terborgh, J. 1977. Bird species diversity on an Andean elevational gradient. *Ecology* 58:1007-1019.
- Tomoff, C. S. 1974. Avian species diversity in desert scrub. *Ecology* 55:396-403.
- Tschaplinski, P. J., and G. F. Hartman. 1983. Winter distribution of juvenile coho salmon (*Oncorhynchus kisutch*) before and after logging in Carnation Creek, British Columbia, and some implications for overwinter survival. *Can. J. Fish. Aquat. Sci.* 40:452-461.
- Tramer, E. J. and P. M. Rogers. 1973. Diversity and longitudinal zonation in fish populations of two streams entering a metropolitan area. *Am. Midl. Nat.* 90:366-374.
- Tripp, D. G. and V. A. Poulin. 1986. The effects of mass wasting on juvenile fish habitats in streams on the Queen Charlotte Islands. British Columbia Ministry of Forest and Lands Land Management Report 45, Victoria, B.C.
- Tyler, A. V. 1978. Apparent influence of fluctuations in physical factors on food resource partitioning: a speculative review. Pages 164-169 *In*: Gutshop '78. Proc. 2nd Tech. Workshop on Fish Food Habits Studies. S. J. Lipovsky and C. A. Simenstad (eds.). Washington Sea Grant, Seattle, WA.
- USDA Forest Service and USDI Bureau of Land Management. 1994. Environment assessment for the implementation of interim strategies for managing anadromous fish-producing watersheds in Oregon, Washington, Idaho, and California (PACFISH). U.S.D.A. Forest Service Pacific Northwest Region, Portland, OR.
- Wallace, A. R. 1890. *The Malay Archipelago*. 10th edition. Dover Publications, New York, New York. xvii, 515 pages.

- Ward, B. R., and P. A. Slaney. 1981. Further evaluations of structures for the improvement of salmonid rearing habitat in coastal streams of British Columbia. Pages 99-108 *In*: Proceedings, symposium of propagation, enhancement, and rehabilitation of anadromous salmonid populations and habitat in the Pacific Northwest. T. J. Hassler (ed.) California Cooperative Fishery Research Unit, Humboldt State University, Arcata, CA.
- Ware, D. M. 1972. Predation by rainbow trout (*Salmo gairdneri*): the influence of hunger, prey density, and prey size. *J. Fish. Res. Board Can.* 29:1193-1201.
- Weisberg, S. 1985. Applied linear regression. John Wiley and Sons, New York, NY. 324 pages.
- Whiteside, M. C. and R. V. Harnsworth. 1967. Species diversity in chydorid (Cladocera) communities. *Ecology* 48:664-667.
- Whiteside, B. G., and R. M. McNatt. 1972. Fish species diversity in relation to stream order and physiochemical conditions in the Plum Creek Drainage Basin. *Am. Mid. Nat.* 88:90-101.
- Whittaker, R. H. 1965. Dominance and diversity in land plant communities. *Science* 147:250-260.
- Wiens, J. A. 1976. Population responses to patchy environments. *Ann. Rev. Ecol. Syst.* 7:81-120.
- Williams, C. B. 1964. Patterns in the balance of nature. Academic Press, New York, NY.
- Williams, J. E., C. A. Wood, and M. P. Dombeck (eds.). 1997. Watershed restoration: principles and practices. American Fisheries Society, Bethesda, MD.
- Wilzbach, M. A. 1985. Relative roles of food abundance and cover in determining the habitat distribution of stream-dwelling cutthroat trout (*Salmo clarki*). *Can. J. Fish. Aquat. Sci.* 42:1668-1672.
- Wilzbach, M. A. and J. D. Hall. 1985. Prey availability and foraging behavior of cutthroat trout in an open and forested section of stream. *Verh. Int. Ver. Limnol.* 22:2516-2522.
- Wolman, M. G. 1954. A method of sampling coarse river-bed material. *Trans. Amer. Geophys. Union* 35:951-956.

- Wooten, R. J. 1992. *Fish ecology*. Chapman and Hall Inc., New York, NY.
- Wooten, R. J. 1993. *The ecology of teleost fishes*. Chapman and Hall Inc., New York, NY.
- Zaret, T. M., and A. S. Rand. 1971. Competition in tropical stream fishes: support for the competitive exclusion principle. *Ecology* 52:336-342.