

# THE EFFECT OF FOREST PRACTICES ON FISH POPULATIONS

FINAL REPORT

By

Dr. Thomas P. Quinn  
N. Phil Peterson



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**The Effects of Forest Practices on Fish Populations  
(Project 19)**

**Final Report for the Washington Department of Natural Resources  
and  
Cooperative Monitoring, Evaluation and Research Committee  
Timber - Fish - Wildlife Program**

**Dr. Thomas P. Quinn, Principal Investigator  
N. Phil Peterson, Project Manager  
School of Fisheries and Center for Streamside Studies  
University of Washington  
Seattle, WA 98195**

**Fish Steering Committee**

**Mark Mobbs, Chairman, Quinault Indian Nation  
Dr. Peter Bisson, Weyerhaeuser Co.  
C. Jeff Cederholm, Washington Department of Natural Resources  
Gino Lucchetti, King County Surface Water Management  
Kurt Nelson, Tulalip Indian Nation  
Art Noble, Washington Environmental Council  
Sam Wright, Washington Department of Fish and Wildlife**

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# The Effects of Forest Practices on Fish Populations

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## Executive Summary

Studies were conducted in field and laboratory settings to investigate aspects of the physical and biological effects of forest practices on fish populations in Washington streams. The incubation environment of chum salmon was studied in Kennedy Creek, where we examined the architecture of the egg pocket as created by the female salmon, and the patterns of gravel scour and fill, sediment deposition and dissolved oxygen during the period of embryonic development. Background levels of fine sediment were greatly altered by the female salmon but fine material infiltrated into the egg pocket during incubation. Dissolved oxygen levels varied greatly among egg pockets and over time but were not correlated with fine sediment concentration in the egg pockets. Scour of egg pockets is likely to be a major source of mortality for chum salmon fry in this and similar streams, though the modifications in the stream channel morphology and surface bed composition by the salmon themselves may reduce the likelihood of scour.

Examination of the stream ecology of juvenile coho salmon in Big Beef Creek revealed that the complexity of the stream environment and the size of the fish at the end of the summer have strong, interacting influences on survival to the smolt stage. Variation in survival between years, among reaches of the stream, and among size classes was evident. Experiments in an artificial rearing channel indicated that the brushy material was not attractive to juvenile coho salmon in early summer and its presence (in pools 0.5 m deep) did not influence survival or growth. However, experiments conducted later in the summer with more complex fish communities revealed a clear interaction between depth and brushy cover in the distribution and survival of juvenile salmonids. Shallow pools without cover were underutilized and fish confined to them suffered higher mortality than those in deeper pools without cover or shallow pools with cover, and deep pools with cover were most attractive and beneficial.

Analysis of long-term data sets from Big Beef Creek revealed a freshwater carrying capacity for juvenile coho salmon that was affected by the summer low flow period (lower flows, fewer smolts) but density did not seem to affect smolt size. Interannual variation in marine survival was poorly explained by smolt size or physical oceanographic variables examined (sea surface temperature, salinity and upwelling), though marine growth was positively correlated with salinity. While these data revealed complex interactions between density-dependent and climate-dependent factors affecting coho salmon, our ability to integrate this information with land use practices was hampered by the absence of habitat data at this site.

Examination of stream fish communities in a series of Washington streams over several years revealed changes in composition associated with season but considerable resilience in the face of high flow events. The species are apparently well adapted to persist in or recolonize streams after flood events but the timing of floods may be more important than their magnitude. Species richness was positively correlated with indices of habitat complexity and the abundance of coho salmon and speckled dace was positively correlated with the amount of pool habitat in the study sections.

## Introduction to Project 19

A single research endeavor, designated Project 19, attempted to provide fill the fisheries research needs of the TFW Program by working collaboratively with other TFW projects and addressing several important questions. Quantified relationships between fish production and habitat characteristics that could be affected by forest practices were produced through a combination of interrelated monitoring and process-oriented field and laboratory sub-projects. Long term data were integrated with on-going population-level studies conducted by state agencies. Broad relationships between fish populations and environmental variables were developed from these data bases and used to formulate hypotheses for investigation in field or experimental studies. These studies were designed around fluvial geomorphic processes and a hierarchical habitat classification system to facilitate transfer of information to other projects.

### Background

During the initial (1986) Timber Fish and Wildlife (TFW) negotiations, participants agreed to use various measures of fish production as one of the indicators for the effectiveness of new forest practice regulations. Scientists had previously tried this approach but their efforts were frequently frustrated by natural environmental variability, simultaneous positive and negative impacts of forest practices on fish production, inadequate spawning escapement, inconsistent or unknown fishing mortality or other marine survival patterns and an insufficient study duration. As a result, scientists have often been unable to draw strong conclusions about the impacts of forest practices on fish populations. Some participants in the negotiations believed that the commitment to quantitatively link forest management to salmonid population abundance was not a realistic goal. Nevertheless, the consensus among TFW participants was that fish response was the most meaningful test of new protective measures. Rather than independently pursue the myriad facets of the fish research, the Coordinated Monitoring Evaluation and Research Committee (CMER), elected to subsume most of the fishery questions on it's agenda into "Project 19". Project 19 was developed to integrate a complex of short term and long term sub-projects.

The goal of Project 19 was to develop quantified relationships between habitat changes often caused by forest practices and fish populations. There were four purposes for developing these relationships: 1) to identify the factors regulating fish populations and limiting their freshwater production, 2) to describe how changes in those factors caused by forest practices affect fish populations, 3) to establish conventions for assessing potential risks to fish populations from carrying out particular forest practices in different basins, and 4) to facilitate protection and rehabilitation of fish populations in forested streams.

### Study Design Consideration

The benchmark case studies on the effects of forest practices on anadromous fish populations, the Alsea Watershed Studies in Oregon and the Carnation Creek Watershed Project in British Columbia, both involved assessment of fish populations before and after logging. These studies provided insights attainable only through this design and placed the effects of forest practices into context with the natural physical and biological variability of streams. However, these costly projects required lengthy time periods (15-20 years) to develop specific impact information. Given the current state of flux in Washington forest practice regulation, by the time

such information could be generated, management prescriptions might have already changed, requiring the evaluation of yet another set of treatment conditions. Long term case studies are also beset with the same kinds of interpretive problems that plague other environmental study designs such as natural interannual variability of physical and biological criteria and geographical context. Because TFW information needs are both immediate and geographically broad, it did not seem wise to propose another case study with scheduled pre- and post-treatment assessment of specific forest practices.

Other general approaches to studying the effects of forest practices on salmonid populations involve the comparison of paired control and treatment streams or streams with upstream control and downstream treatment sections. Even though this design can be a powerful way to look at impacts through time (Hall et al. 1978), it too was rejected as the sole research approach for Project 19. The problems associated with such studies are that control sites are frequently absent, the treatment usually integrates impacts from a variety of sources, and today's management prescriptions differ substantially from those imposed on most streams when they were first logged. This latter problem negates the advantage of a long term perspective on forest management, at least as it is practiced today. In addition, the key assumption of this design, that the observed responses are a result of the treatment only and not basic differences in habitat that existed prior to treatment, is difficult to meet and can be satisfied only through very careful selection of sites and biological response (Grant et al. 1986).

Notable arguments have been made over the last decade that the impacts of many natural resource management decisions and environmental alterations are not efficiently or effectively studied through either baseline or process studies (Hilborn and Walters 1981; Walters and Collie 1988). These authors argue that traditional approaches to environmental and fish distribution and abundance studies are inadequate to deal with the space and time elements of both management and natural landscape processes. In lieu of traditional approaches, they propose a combination of retrospective studies, experimental management and direct monitoring to achieve the temporal, spatial, and stock abundance perspectives necessary to evaluate management options.

### Project 19

The series of studies collectively referred to as Project 19 investigated the response of fishes to several key habitat features that could be affected by forest practices. The project did not explicitly link forest practices to these features. The cause and effect linkages between forest practices and habitat conditions were to be made through other TFW sponsored research. Project 19 employed a combination of research techniques: analysis of existing long term data bases, observational and manipulative experiments in natural streams, laboratory and artificial stream channel experiments and modeling. We approached our research in this manner to efficiently address the questions being posed, avail ourselves of existing information and produce both short and long term results. Each of these approaches has an inherent level of control that the investigator may exert over the topic under study (Eberhardt and Thomas 1991). Utilization of several research techniques should improve our ability to test specific hypotheses and extend our information to areas and populations not directly sampled.

When a basin is logged, two general categories of actions occur; roads are constructed and vegetation is removed. These actions result in alterations to the normal delivery pattern of the basic channel inputs. Sediment and flow regimes, and large woody debris and thermal loading are frequently altered in streams draining managed forests. These alterations may change stream channels and have considerable consequences for fish. Project 19 investigated the responses of fishes to a range of conditions in these four channel inputs. Wherever possible we described our work in the context of the fluvial geomorphic processes that have defined specific habitat conditions. Because our work was based on physical processes, it should be readily integrated into other work sponsored by CMER.

### Response Levels

The primary focus of Project 19 was on the response of salmonid fishes to forest practices. However, we recognized that non-salmonid species are important both as aquatic resources in their own right and as part of the conservation of natural biodiversity. We therefore examined the habitat use patterns of non-salmonids, particularly with regard to the changes in fish community structure and function.

Responses by individual fish to forest practices may find expression in behavior, growth or survival. Such responses form the basis for changes in population abundance. Individual responses can be monitored through experiments specifically designed to test hypotheses. They can also be studied in the course of population estimation or complete counts at particular life history stages.

There are significant implications of natural variation in abundance of salmonids for the design of impact studies. Fluctuations due to naturally occurring environmental events such as floods and droughts are often sufficient to mask any affect from the cumulative effects of forest practices. After analyzing variation in several important population attributes of anadromous salmonids, Lichatowich and Cramer (1979), concluded that studies of survival and abundance could require 20-30 years to produce an 80% chance of detecting a 50% change. While seeding levels may contribute to the high variability, these results send a cautionary note to those planning long-term studies. However, their results suggested that only 8-10 years might be required to provide an 80% chance of detecting a 5-15% change in time and size of important life history stages. These responses can in turn be linked to freshwater and marine survival. Measurement of responses at several life history stages will broaden our interpretive ability in Project 19.

Measurement of population level responses requires smolt and adult counting and smolt tagging. Without tagging it is impossible to accurately determine marine survival. Even salmon from streams that enter the marine environment relatively near each other may have quite different marine survival rates and fishing patterns (Dave Seiler, WDF pers. comm.). Population abundance and survival studies must extend over a long period to measure compensatory population characteristics and habitat carrying capacity. Fifteen or more years may be required to gain sufficient perspective to provide even relatively simple management information such as an appropriate escapement goal. Population level response, as measured by abundance, is the most expensive to measure, takes the longest time to develop and (without added interpretive information), is the most difficult to use in demonstrating impacts from forest practices. Fish community responses to habitat alteration have received little attention in the Pacific Northwest in comparison to other regions. In part, this may be due to the comparatively simple community structure in mid- to small order forested watersheds in our region. However, a preoccupation with determining the relationships between salmonid biomass or density with habitat quantity and quality, may have caused us to overlook important ecological relationships. The magnitude of these interactions may be controlled by habitat characteristics that are subtly affected by land management (Reeves et al. 1987). Therefore, a portion of our work investigated community structure and interactions of non-salmonid fishes and salmonids in disturbed and undisturbed forest settings.

### **Quantification of Fish and Habitat Relationships**

Project 19's overall goal, to develop quantified relationships between habitat changes caused by forest practices and salmonid populations, must be qualified by the experience available in the scientific literature. The goal of linking habitat variables to fish production is one that has captured the interest of fisheries biologists for at least the last 35 years (Fausch et al. 1988). Linear regression with one or more independent habitat variables has been the most common mathematical technique for quantifying relationships between fish production and habitat. Fausch et al. (1988) reviewed this body of scientific information and concluded that: 1) relatively precise models lacked generality, 2) sound statistical procedures were often overlooked or minimized during model development, 3) major biological assumptions were not addressed, and 4) for models to be useful in analyzing land management alternatives, models must include variables affected by management and be specific for a homogeneous area of land. Another common problem is the lack of attention to describing stock abundance as it may be affected by fisheries management (Rinne 1988). Without this information it is difficult to assign variability in observed biomass or density, to habitat conditions, especially for single species models.

Transferability of habitat models is a common problem. Shirvell (1989), concluded that six of the more widely recognized models of the relationships between fish populations and their habitat explained on average 76% (range = 50-96%) of the variability in fish numbers or biomass for data sets from which they were derived. However, for data sets from which they were not derived, they explained on average only 24% (range = 7-30%). Models were valid only for the geographical areas for which they were developed and could not be extrapolated to new situations without calibration.

### Acknowledgments

Many individuals participated in aspects of this project, providing assistance with field and laboratory work, and providing constructive criticism on one or more of the chapters. We thank these individuals in the appropriate chapters but we wish to especially thank the past and present members of the Fisheries Steering Committee who gave so freely of their time and ideas: Mark Mobbs (chairman), Quinault Indian Nation; Dr. Peter Bisson, Weyerhaeuser Co.; C. Jeff Cederholm, Washington Department of Natural Resources; Mark Hunter, Washington Department of Fish and Wildlife; Gino Lucchetti, King County Surface Water Management; Kurt Nelson, Tulalip Indian Nation; Art Noble, Washington Environmental Council; Dr. Gordon Reeves, U.S. Forest Service; Sam Wright, Washington Department of Fish and Wildlife. In addition to their duties on the committee, Gino Lucchetti, Jeff Cederholm, Sam Wright and Mark Hunter reviewed the entire draft report, for which we are very grateful. **Some of the chapters that follow have been submitted for publication or comprise work in partial fulfillment of requirements for graduate students. This report should not be cited as a primary publication; rather, the authors should be contacted for the status of the chapters.** The research was funded initially by the Washington Department of Natural Resources but additional support was provided for one or more elements of the study by the U.S. Forest Service, the National Oceanic and Atmospheric Administration through the Washington Sea Grant Program, the Bonneville Power Administration, the Washington Forest Protection Association and the H. Mason Keeler Endowment to Thomas Quinn. In addition, the Washington Department of Natural Resources provided office and laboratory space which was greatly appreciated, and David Seiler of the Washington Department of Fish and Wildlife generously shared his data and insights on Big Beef Creek coho salmon. We are very grateful to these agencies and individuals for their support.

## Chapter 1.

### Incubation Environment of Chum Salmon (Oncorhynchus keta) in Kennedy Creek

#### Part A. Persistence of Egg Pocket Architecture in Chum Salmon Redds

N. Phil Peterson and Thomas P. Quinn

#### Abstract

Analysis of frozen cores of chum salmon egg pockets collected in the fall revealed that spawning activity purged about 75% of the fine sediments from the stream bed. The egg pocket was one of four distinct vertical strata detected in the cores. There was an undisturbed layer below the egg pocket and cover and bridge strata above the egg pocket, defined by their particle size distributions. However, by spring most of the egg pockets had been infiltrated with fines approaching background levels. The most likely physical factors responsible for these results were: 1) intrusion of fine sediments through the cleaned surface gravel, 2) lateral sub-surface migration of fine sediment into interstitial voids, 3) scour of the cleaned surface gravel and subsequent deposition of a sand rich bedload, and 4) superimposed spawning activity of other fish, causing disturbance of the cleaned surface gravel and exposing the egg pocket to intrusion of fines. Our results indicate that sediment transport processes and fine bedload flux are more important to the assessment of the salmonid incubation environment than is background stream bed composition.

### Introduction

Among salmonid fishes the majority of life-time mortality usually takes place between the time fertilized eggs are deposited in the gravel and when they emerge as full-formed fry (survival to emergence, abbreviated STE) several months later. Under conditions of high spawner density, redd superimposition by other females can be a significant cause of mortality (McNeil 1964). Otherwise, the major factors affecting survival during this period are physical: 1) displacement by high stream flows that scour the streambed (McNeil 1964; Holtby and Healey 1986; Tripp and Poulin 1986; Thorne and Ames 1987), 2) suffocation of the developing embryos due to inadequate circulation of inter-gravel water (Everest et al. 1987), and 3) entombment of hatched and fully formed fry in the gravel bed (Bjornn 1969). The latter two mortality agents are considered to be closely associated with high concentrations of fine sediment in streambed gravel.

Fine sediment is a natural component of stream substrates but land practices that disturb vegetative cover often cause erosion that delivers significant quantities of fine sediment (sand and silt) to stream courses. Although natural background rates and dominant sediment delivery processes vary considerably over the forested landscape of the Pacific Northwest, industrial scale logging operations frequently result in elevated rates of sediment delivery to stream channels. Some of the most compelling evidence that forest practices harm salmonid fishes comes from studies of fine sediment and STE (Scrivener and Brownlee 1989). Given the widespread concern over the loss of salmon populations and the economic ramifications of listing salmon populations under the Endangered Species Act (Nehlsen et al. 1991), it is imperative to define the relationships between land use practices and salmon survival as precisely as possible.

The relationship between fine sediment and STE is characterized by high levels of variation (Chapman 1988). Moreover, the relationship is apparently extraordinarily steep (e.g., Tagart 1984). That is, slight changes in fine sediment concentration seem to produce large changes in embryo mortality. The variation and steepness of the STE relationship, as well as the uncertainty of how bedrock and surficial geology, large storm events, and historical forest practices have affected the fines fraction in streambed gravel (Adams and Beschta 1980), have made it difficult to choose a standard that constitutes an excessive amount of fine sediment for purposes of forest practice regulation. In spite of methodological and sample design problems associated with bulk sediment sampling in flowing water (Gomez 1983; Mosley and Tindale 1985; Grost et al. 1991a; Young et al. 1991a), and the analytical vagaries of particle size determination as typically applied in the fisheries field (Lotspeich and Everest 1981; Young et al. 1991b), government regulators have used fine sediment levels to guide the application of forest practice prescriptions.

In his review of the STE literature, Chapman (1988) concluded that the application of much of the existing information to natural streams was plagued with essentially two problems, both of which related to the lack of understanding of salmonid egg pockets. First, field studies had not accurately located and studied conditions in egg pockets but only in the redd proper. Second, controlled studies in the lab or artificial channels had not accurately mimicked natural egg pockets. Chapman (1988) and later workers (Young et al. 1990) concluded that more precise measurements of the characteristics of natural egg pockets would provide important information that could be used to design laboratory studies for understanding survival variation in the field.

We decided to make a detailed study of the egg pocket itself and assemble information on the incubation environment of large salmonids that would be of value in studying natural variation in STE. Accordingly the objectives of our work were to determine how spawning salmon

changed the surface and subsurface texture of the streambed and if those changes persisted through the incubation period. We selected chum salmon for our work because they are abundant in many small forested streams in Washington and because their freshwater production is typically limited by the quantity and character of streambed gravel (Salo 1991).

## Materials and Methods

### Study Site

Kennedy Creek is a third-order drainage originating on the north slope of the Black Hills and flows about 16 km in a northerly direction into Totten Inlet in southern Puget Sound (Figure I-A-1). Elevation in the 5300 ha watershed ranges from sea level to 721 m. The uplands consist of moderately steep hillslopes underlain by marine volcanics of the Crescent formation. The main valley and some lower valley walls are mantled with undifferentiated glacial till and variable recessional outwash materials deposited during episodic continental glaciation.

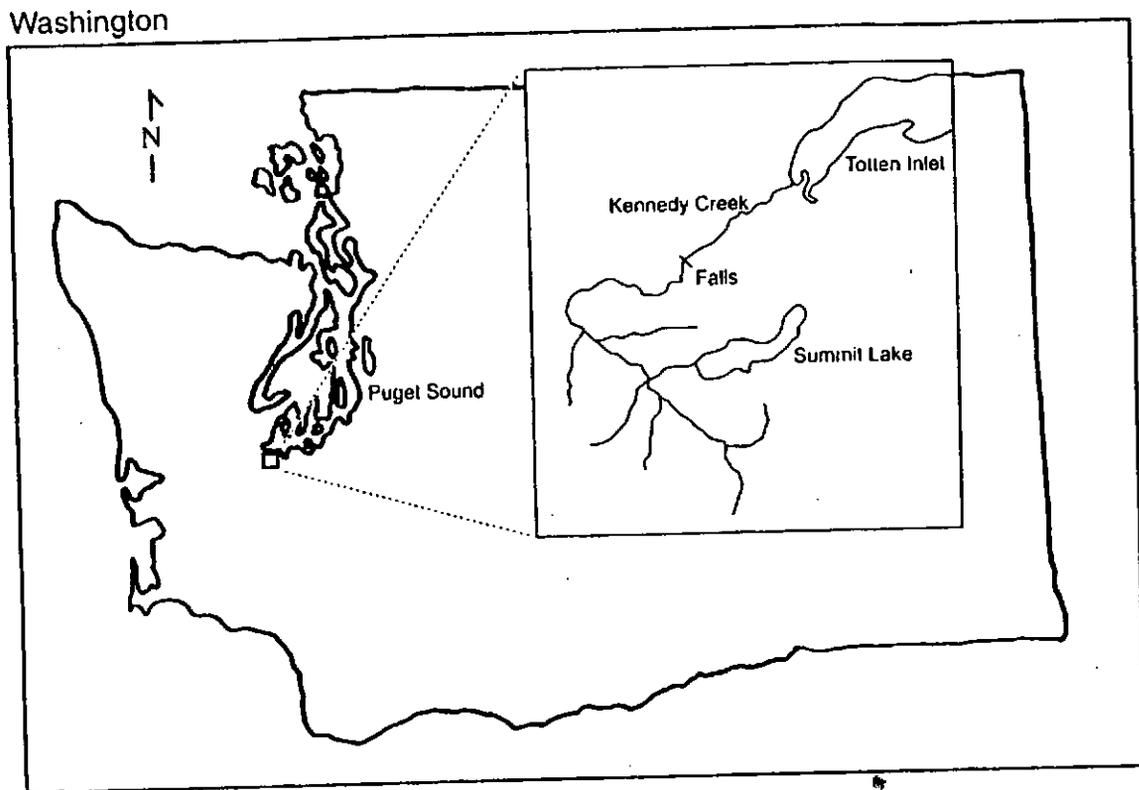
The headwaters of Kennedy Creek consist of numerous high-gradient first and second order channels draining steep hillslopes flowing immediately into a large, flat valley created by glacio-fluvial erosion and deposition. The valley gradually narrows into a bedrock canyon near river km 4.4, where the stream flows over a large falls and through a narrow canyon that blocks upstream migration of anadromous salmonids. Below the gorge, the stream flows through a narrow V-shaped valley for about a mile where the channel is occasionally restricted by bedrock outcrops. Gradually the channel becomes more sinuous and less constricted. The reach where the study sites are located (river km 1-2), is moderately confined by valley walls and is slightly incised into non-cohesive highly erodible glacio-fluvial deposits.

The climate is maritime with relatively wet, mild winters and cool dry summers. Annual precipitation averages 147 cm and occurs mostly as rain from October through April. Discharge responds to precipitation and ranges from a mean low flow of 0.1 m<sup>3</sup>/s in August to a mean high flow of 4.8 m<sup>3</sup>/s in January, with a mean annual discharge of 1.7 m<sup>3</sup>/s. The highest peak flow recorded between 1960 and 1979 (the period of record for the USGS gaging station) was 39.1 m<sup>3</sup>/s and the mean annual peak flow (recurrence interval 2.33 years) is approximately 22.9 m<sup>3</sup>/s (Williams et al. 1985). Most forests in the watershed were harvested earlier in the century and now consist of second-growth stands of harvestable age Douglas fir (*Pseudotsuga menziesii*) in well-drained sites and red alder (*Alnus rubra*) in wetter sites. Harvest of second-growth timber in the basin is underway and a dense system of roads is in place.

### Sample Collection and Analysis

One-hundred fifty-six bulk sediment samples were taken with a 6 inch diameter McNeil core sampler (McNeil and Ahnell 1960) to characterize the background sediment composition to a depth of 25 cm in four reaches of Kennedy Creek. Each reach was approximately 100 m long but varied in other important characteristics such as the woody debris loading, bankfull width, bar relief, and frequency and magnitude of relief in the long profile. The samples were taken on 2 m grids in habitat where we expected chum salmon to spawn based on observations in previous years. Samples were generally taken only within the wetted perimeter of the channel but some lateral bar samples also were collected. In addition to the samples from the stream, we also collected 25 sediment samples from the exposed streambanks at several locations.

Figure I-A-1. Location map of Kennedy Creek.



The McNeil cylinder samples the surface and subsurface gravels but does not preserve the vertical strata intact. To characterize the detailed structure of chum salmon redds and the persistence of this structure over time, we used liquid nitrogen to freeze cores of gravel for removal from the stream and careful analysis after thawing. Nine samples of egg pockets were obtained in the fall by observing pairs of chum salmon until they spawned, momentarily interrupting them and inserting tri-tube freeze core probes into the egg pocket. As soon as the probes were positioned (about 10 minutes), we left the immediate area. The female invariably returned and began normal redd covering activity within 10-30 minutes. Additional egg pockets were constructed in succession and fully completed redds were constructed within the normal time span of about one day. After the female completed spawning at these sites the egg pockets were frozen by introduction of liquid nitrogen into the hollow tubes and withdrawn from the streambed (Everest et al. 1980) within two days of redd completion.

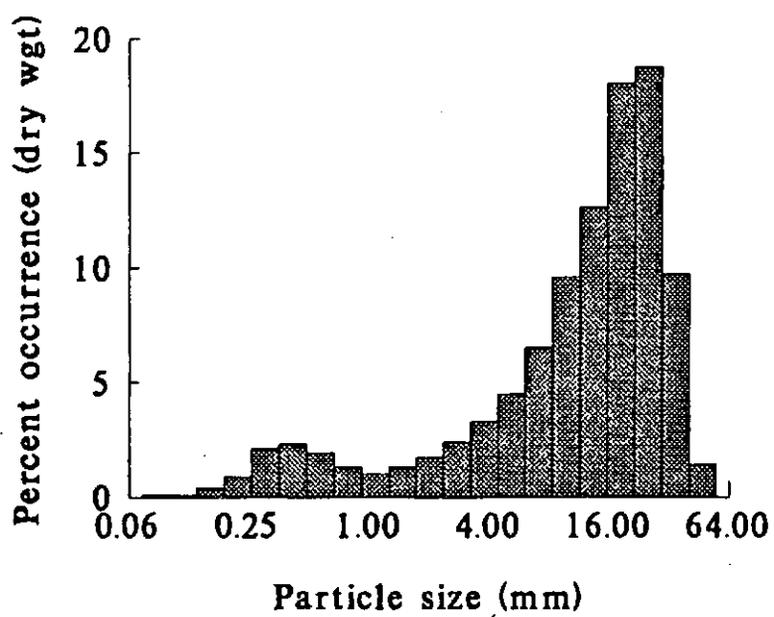
The positions of 29 other egg pockets were marked in the fall with survey measurements from rebars located on shore away from the active channel. The surveying procedure took about 7 minutes and the female salmon always returned (usually within 10 minutes), and resumed normal covering activity. In late March these egg pockets were frozen and withdrawn from the streambed and processed in a similar manner to the fall samples. The only exception to the fall procedure is that in the spring the tri-tube probes were driven into the egg pocket through the surface gravel which in the fall were deposited around the probes by the spawning fish after probe insertion.

After the frozen cores were withdrawn, they were laid across sampling boxes and melted off the probes. The boxes were of varying widths, arranged to collect sediment from each of four strata: the undisturbed sediments underlying the egg pocket, the egg pocket itself, the bridging layer (the layer of particles deposited by initial covering actions of the female), and the rest of the cover material up to and including the surface layers of gravel. These four layers will be referred to as the undisturbed, pocket, bridge, and cover respectively. Sediments from all strata were individually packaged for laboratory processing.

In the lab, sediment samples were dried to a constant weight and mechanically shaken through 21 standard sieves representing a  $1/2$  phi ( $-\log_2$  x particle size diameter) gradation starting at -6 phi (64 mm) and ending with 4 phi (0.063 mm). In all, 24 size fractions including the pan silts, were weighed to the nearest 0.1 g. This sieve series was selected to conform to standard particle size determination methods used in sedimentology and so that comparisons could be made directly to the Wentworth particle size scale (Wentworth 1922).

Fluvial gravel size distributions can be polymodal (Carling and Reader 1982), and typically have a long tail (Lisle and Thomas 1992), making the statistical distribution difficult to describe (Figure I-A-2). Consequently it is difficult to determine an appropriate summary statistic to use in testing for differences (e. g. the mean and variance are used for a t-test). To avoid questionable assumptions we used a k-sample Smirnov test (Conover 1980), to compare entire gravel dry weight distributions. Kolmogorov-Smirnov type statistics use the maximum vertical distance between the empirical distribution functions to measure how much the underlying distributions resemble each other. The null hypothesis can be stated as: the population distribution functions are identical. The alternative hypothesis states that at least two of the population distribution functions are not identical. A second comparison was made with a Kruskal-Wallis test (Conover

Figure I-A-2. Distribution of size class occurrence in Kennedy Creek gravels (proportion by gravel dry weight) prior to salmon spawning.



1980), the non-parametric analog of a one-way ANOVA to examine differences in the proportion of fines (<1.0 and 4.0 mm) between study reaches and by lateral channel location. The Kruskal-Wallis test was not used to compare differences between egg pocket strata due to smaller sample sizes.

### Results

Analysis of the McNeil samples from the four study reaches using the k-sample Smirnov test indicated that there was no difference in the distributions of gravel dry weight among the four reaches ( $T=0.09$ ) or by lateral channel location when data from all four study reaches were pooled ( $T=0.11$ ). The Kruskal-Wallis tests, which looked only at a single attribute of the dry weight distribution (percent fines), suggested that for both size classes (1.0, and 4.0 mm) there were differences between reaches ( $P < 0.01$ ) and for one size class (1.0 mm) lateral channel locations differed ( $P < 0.05$ ). The background level of fines for the study reaches and channel locations are given in Table I-A-1. Samples from the banks indicated a high availability of fine material, similar in size distribution to that found in streambed gravels (Figure I-A-3)

In 1991-92 approximately 5,000 chum salmon spawned per km throughout the accessible length of Kennedy Creek (Washington Department of Fisheries, unpublished data). Numerous changes in channel bedforms (Chapter I-C), bed surface texture (Montgomery et al. in prep.), and subsurface gravel composition and structure were associated with this activity. The entire active channel (except the bottoms of pools) and up to 2 m laterally into the bars were disturbed down to a depth of approximately 30 cm by the spawning salmon.

During egg pocket excavation, the female turns on her side and vigorously flexes her body 7-10 times in rapid succession approximately every 2 minutes, frequently causing her caudal fin to contact the bed surface. This action causes turbulence that raises the smaller particles which are entrained by the current. The sand bed fraction, as well as the finer gravels (granules and small pebbles) are thus sorted from the framework gravels and deposited in low velocity areas of the channel downstream. Each female constructs several egg pockets (a completed redd may have 3-5) which consist of a depression in the streambed about 20 cm deep with larger particles concentrated in the bottom. The larger particles frequently come from the armor layer, gradually assuming a deeper position in the streambed as the smaller framework gravels and matrix material is removed by digging. The 10-12 cm zone below this depression is purged of the finer particle sizes by the digging action of the female and it is in this "labyrinth" of interstitial voids that the eggs are deposited (Figure I-A-4). After spawning, the female covers each successive egg pocket with gravels derived immediately upstream. Covering begins with gentle flexations of her body (2 in number every 10-15 seconds). This initial covering behavior brings a layer of finer material (granules and pebbles) over the egg pocket ceiling, forming a layer we refer to as the "bridge" (Figure I-A-4).

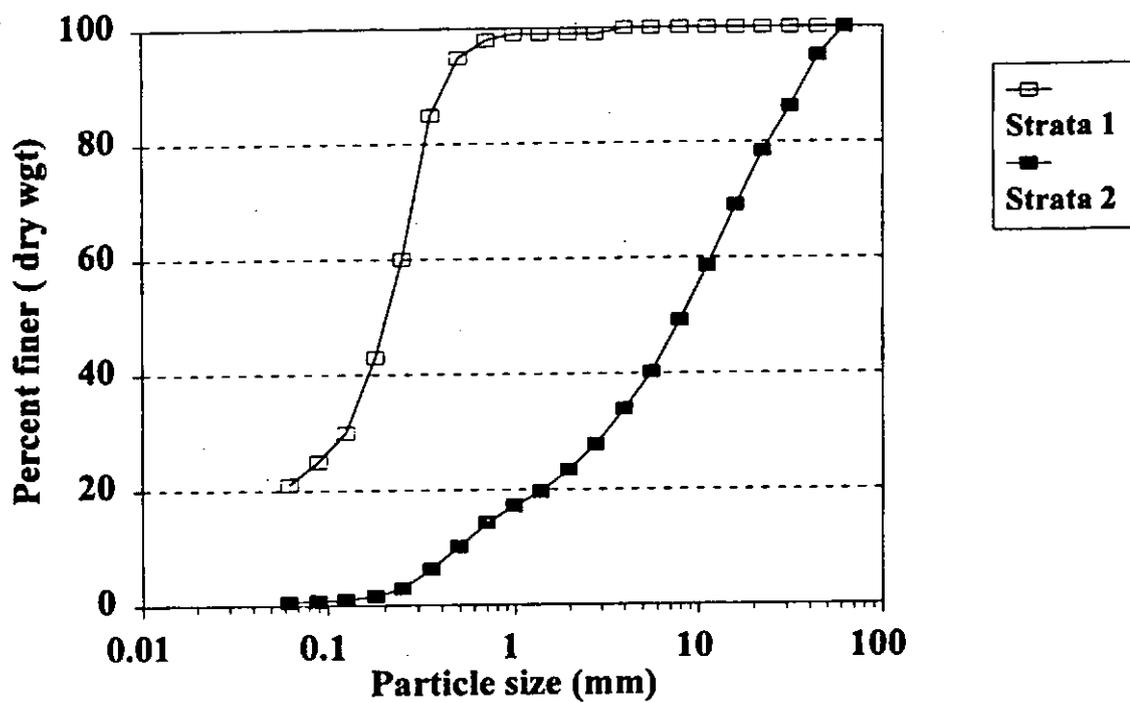
**Table I-A-1.** Bulk sediment sample composition for study reaches in Kennedy Creek. Samples were taken with a McNeil core sampler and analyzed by dry gravimetric methods.

Reach or Channel Location	Percent < 1 mm (SD)	Percent < 4 mm (SD)
A	10.4 (4.22)	21.2 (8.88)
B	9.3 (9.90)	18.7 (16.44)
C	10.8 (3.46)	25.6 (6.12)
D	9.7 (3.39)	20.5 (5.29)
Mid active channel	8.5 (3.72)	18.7 (8.23)
Lateral active channel	10.3 (4.98)	22.0 (13.07)
Lateral bar	12.7 (8.83)	23.9 (16.80)

**Table I-A-2.** Gravel composition in fall and spring tri-tube freeze core samples of chum salmon egg pockets.

Strata	$d_{50}$		Percent < 1 mm		Percent < 4 mm	
	Fall	Spring	Fall	Spring	Fall	Spring
Cover	19.7	15.2	2.4	6.2	5.0	14.1
Bridge	17.6	11.9	3.0	8.2	7.3	18.3
Pocket	28.3	16.9	2.4	7.2	4.5	15.1
Undisturbed	13.2	14.4	9.3	8.5	15.8	16.8

Figure I-A-3. Cumulative sediment dry weight distributions for representative embankment material in Kennedy Creek.



The texture and the percent fines of all four strata of the fall egg pockets differed (Figure I-A-4). The three strata that the fish had modified, were all substantially purged of their sand fraction. The percent fines, < 1.0 mm were reduced by approximately 75% in the egg pocket (Table I-A-2). Results of the k-sample Smirnov test, which tested for differences between the cumulative gravel dry weight distributions for the four strata (combined samples; Figure I-A-5), were significant ( $P < 0.05$ ). The egg pockets sampled in the spring showed few differences between strata texture or fines content (Table I-A-2). The k-sample Smirnov test did not detect differences between the cumulative gravel dry weight distributions,  $T = 0.17, 0.27, 0.22, \text{ and } 0.13$ , ( $P > 0.10$ ), for reaches A, B, C, and D respectively. All strata in the spring samples, with the exception of the underlying undisturbed, (which was essentially constant), were finer than they were in the fall and their cumulative dry weight distributions appeared similar (Figure I-A-6).

### Discussion

Considerable spatial and temporal variability in gravel composition has been documented even in unmanaged streams (Adams and Beschta 1980; Edington 1984; Sheridan et al. 1984; Cederholm and Reid 1987; Scrivener and Brownlee 1989). The principal factors contributing to the fines fraction in the streambed, other than management impacts such as gravel roads (Reid and Dunne 1984), appear to be related to surficial and bedrock geology of the basin and the natural characteristics of the geomorphic setting, all of which are linked to the geological history of the region. The relatively high levels of fine sediment in Kennedy Creek are directly related to the availability of these size fractions in the embankments (Figure I-A-3). Bank material is composed of highly erodible recessional outwash sand and gravel and glacial till deposited after episodic continental glaciation.

In our examination of background gravel conditions, the differences between results of the k-sample Kolmogorov test and the Kruskal-Wallis test were surprising. The discrepancy may lie in the fact that composite cumulative distribution curves are used in the k-sample Kolmogorov-Smirnov test whereas the Kruskal-Wallis test compares all ranks based on actual values. Reach B had many small scores and a few high ones (when averaged they are approximately equal to the other three reaches), and so they may not have affected the cumulative distribution function whereas the Kruskal-Wallis retained information on these extreme data values in the form of ranks. It is the retention of this information that apparently caused it to support the alternative hypothesis: that at least one of the reaches or lateral channel locations differed from at least one other. We concluded that the Kruskal-Wallis test may be too sensitive for this kind of analysis.

**Figure I-A-4.** Stratigraphic architecture of typical chum salmon egg pocket and indices of gravel texture immediately after spawning (n=9).

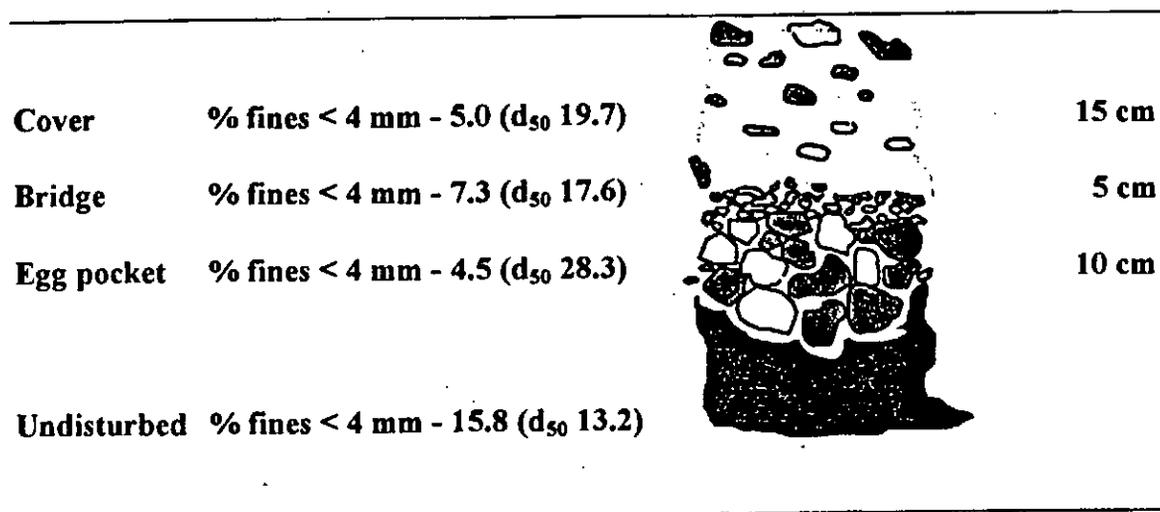


Figure I-A-5. Cumulative distribution (combined sample dry weights) for nine egg pockets in the fall.

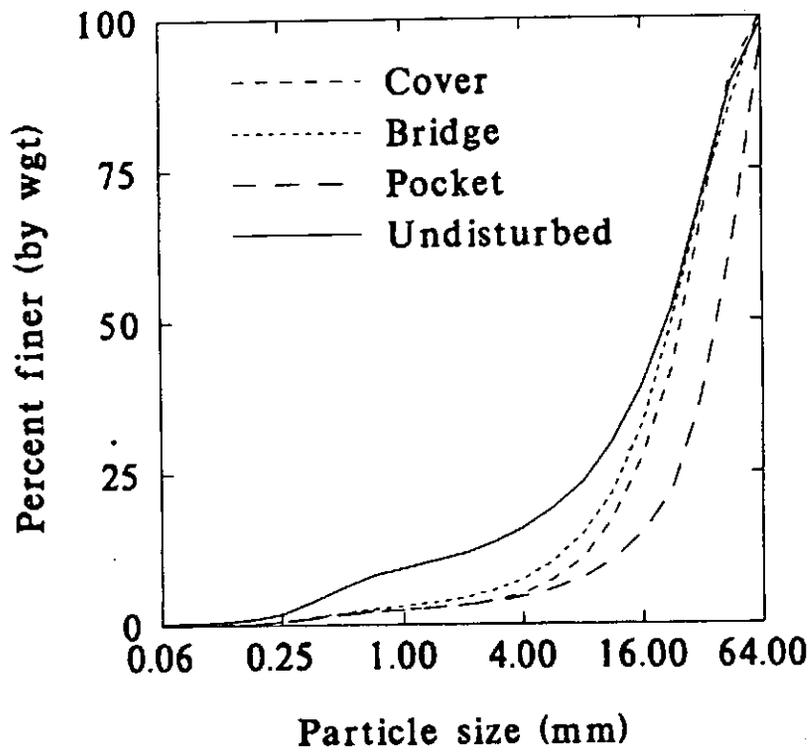
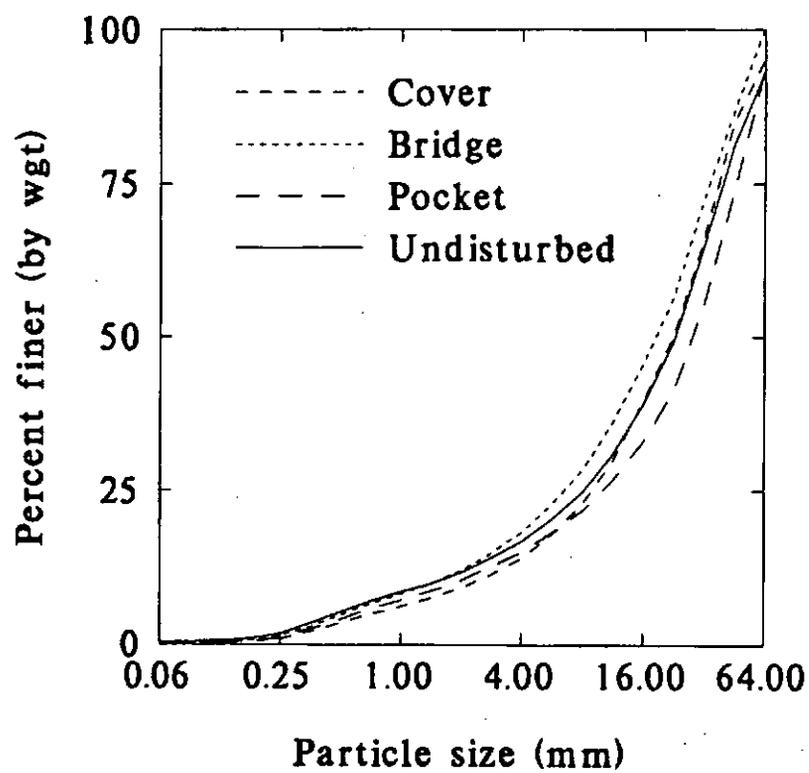


Figure I-A-6. Cumulative distribution (combined sample dry weights) for 29 egg pockets in the spring.



The physical modifications of the streambed produced by high densities of spawning chum salmon resulted in a wider active channel with greater suitable spawning habitat. Aside from the primary role of developing interstitial space for the eggs and burying them at a depth of 20-30 cm, the digging action of the female coincidentally coarsens the surface of the bed. It may be that the general coarsening of the bed surface and the micro-topography of the redds, adds enough roughness to cause a measurable increase in the discharge required to mobilize the bed and initiate scour, at least initially (Montgomery et al. in prep.). There may, however, be a negative feedback due to salmon spawning as the consolidated stream bed is loosened, making it easier for peak flows to entrain. Reid and others (1985) for example, have shown that when floods follow each other closely, bed material is more readily entrained, than when long periods of inactivity allow the channel bed to consolidate. The bed coarsening and loosening effects may be off-setting and of particular importance in the adaptation of salmonids spawning in streams. Regardless of the direction of these particular effects, the fish, in concert with small peak flows (return interval < 1.5 year) leveled the channel laterally and longitudinally (Chapter I-C). Although the dune like bed surface produced by spawning salmon was flattened by winter peak flows, the general channel widening and longitudinal leveling they produced, was not affected.

On a fine scale, the spawning activity of the salmon largely removed the fine sediment in the egg pocket and covering gravel layers. Other studies have shown similar effects by spawning salmonids, although none have used cryogenic sampling in the same manner to document these changes (Everest et al. 1987; Young et al. 1989; Young et al. 1990; Grost et al. 1991b). Removal of the matrix material from the stream bed makes space for the eggs and although it is a secondary and coincidental effect, increases the porosity of the gravel. It is this increase in porosity that many studies suggest is instrumental in increasing the rate of delivery of subsurface flows to the incubating embryos and increasing the exchange between surface and sub-surface water; factors thought to be critical to STE (Chapman 1988). After the initial modification of the stream bed during spawning, the survival of incubating embryos is largely determined by the sediment input and transport processes controlling stream bed conditions. These processes are extremely variable in time and space, being influenced by both climatic events and complexity of natural channels (Lisle and Thomas 1992).

The lack of persistence in egg pocket architecture that we observed was probably due to a combination of one or more of the following factors: 1) intrusion of fine sediments through the cleaned surface gravel, 2) sub-surface migration of fine sediment into interstitial voids, 3) scour of the cleaned surface gravel and subsequent deposition of a sand rich bedload, 4) superimposed spawning activity of other fish, causing disturbance of the cleaned surface gravel and exposing the egg pocket to intrusion of fines. In addition to these fundamental processes, two methodological processes may have affected the comparison of sample strata: 1) imprecise location of egg pocket sampling during the spring period, and 2) destruction of the gravel structure by driving the freeze core probes through the gravel layers.

Intrusion of fine sediment into gravel surfaces has been studied in flume and field studies (Einstein 1968; Beschta and Jackson 1979; Reckendorff and Van Liew 1989; Lisle 1989; Lisle and Thomas 1992). Deposition of fines by this process is significant, especially in the upper 10 cm of the bed, (Beschta and Jackson 1979), and may operate over a wide range of stream discharges. The degree of intrusion is controlled by flow conditions, size of gravel framework, particle size of intruding sediment, and the flux of fine bedload.

Beschta and Jackson's (1979) experiments used gravels and sand similar in size to the natural gravels in Kennedy Creek for their flume studies. Their observation, that the fine sediments did not intrude deeper than about 10 cm into the bed and formed a seal there, suggests that intrusion was only one process operating in our study, since our samples showed increases of sand to egg pocket depths (20-30 cm). We originally hypothesized that the bridge layer (Figure I-A-4) would seal the voids between the larger egg pocket stones preventing intrusion of finer sediments into the egg pocket. Our spring sampling suggested that this was not the case and that additional factors were involved.

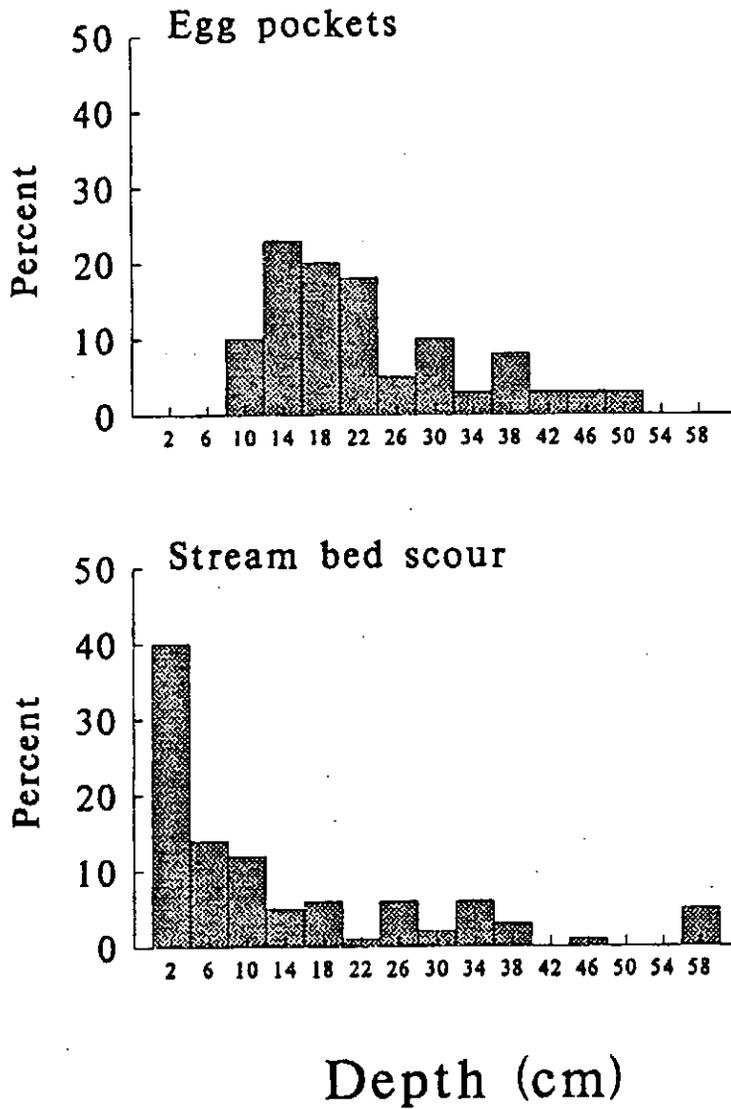
To our knowledge, the sub-surface migration of fine sediment has not been studied and its influence on filling void spaces is probably minor and local in nature. We did note, however, that the whiffle golf balls our scour monitors were constructed from, often completely filled with sand at depths greater than 10 cm. Thus sub-surface migration of fines may play some role in the infiltration of egg pockets in a sand rich gravel bed.

Scour of the cover layers of gravel after spawning and subsequent deposition of a sand rich bedload is a likely process contributing to the infiltration of the gravel bed to egg pocket depths in our study. Removal of the cover layers, exposes the egg pocket itself to intrusion of fine sediments, particularly in streams that have large quantities of sand in transport such as Kennedy Creek. During deposition of a gravel mixture rich in sand, the interstices in the gravel are more thoroughly filled with sand than is possible through infiltration alone, creating a formidable obstacle to emergence (Lisle 1989). We recorded scour to egg pocket depths in nearly 20% of the monitor locations (Chapter 1-C; Figure I-A-7), and believe this process could have been a major factor affecting the composition of the upper layers of the streambed.

Superimposition of spawning on previously completed redds was observed. Although our observation did not permit a detailed or systematic evaluation of this process on the texture of our referenced samples, it is likely that some, but not all were affected. Our observations indicate the effect is more to uncover the egg pocket, thus exposing it to infiltration of fines from nearby digging, than to actually disturb the structure of the pocket itself. This seems to be true since at any given flow, the majority of fish appear to dig to similar depths. The exception to this would be if superimposition were to take place on higher flows when the stream had a greater competence. In these circumstances, it would be possible for later spawners to actually dig up previous egg pockets. In our experience, this latter situation was the exception rather than the rule.

We must also consider the effects of freeze core sampling on our perception of the conditions in gravel strata. Although freeze coring is the principal means by which scientists can study the structure of gravel beds and the stratification of fines within salmonid redds, the procedure is itself somewhat disruptive. Fine sediment could be carried from surface layers into deeper strata as the probes are driven into the bed (Beschta and Jackson 1979; Lisle and Eads 1991). We are unable to document to what degree the procedure itself affected our results and we do not discount the possibility that we recorded higher levels of fines at depth in the spring

Figure I-A-7. Frequency distributions for egg pocket depth (n=41), and depth of scour for individual scour monitors (n=101).



than we might have, had we been able to freeze the samples in place without inserting the probes. However, some of our samples showed "clean" egg pockets with comparatively high levels of fines in the overlying layers of cover, patterns inconsistent with the biasing effect of the freeze core procedure (e. g. sample C9 had 16.4, 7.4, 3.9, and 7.6, percent fines <1.0 mm in the cover, bridge, egg pocket, and undisturbed strata respectively).

The other methodological factor that could have affected our results is the precise determination of egg pocket location. Even though, we surveyed the locations of the egg pockets immediately after spawning, there is always some slight difficulty (perhaps up to 10 cm) in finding a point and centering the probes over it to a depth sometimes in excess of 50 cm. Our observations of the lateral variation of particle size in egg pocket structure, suggests that slight variation in location could affect the textural composition of the samples.

### **Implications for Forest and Fish Management**

Our findings show that large salmon are capable of purging stream bed gravels of fine sediment during redd preparation but that the egg pocket is returned to essentially pre-spawning conditions by subsequent sediment transport processes. A high availability of fine sediment (particle sizes <4 mm) to a stream channel creates a high risk for incubating salmonid embryos. In watersheds where these kinds of sediment sources exist naturally, managers should determine what kinds of practices may exacerbate their delivery to the channel network and prevent it. In Kennedy Creek for example, the road system appears to play a minor role in the delivery of these kinds of sediment to the channel, but massive quantities are immediately available from the stream embankments (Figure I-A-7). These kinds of observations lead to quite different conclusions in risk assessment and application of best management practices. Fisheries managers should also consider the role large populations of spawning salmon have on the maintenance of the incubation environment. It may be that the physical effects large populations have on the channel, are one more factor necessary to the long term maintenance of healthy salmon populations.

### **Acknowledgments**

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## Chapter I.

### Incubation Environment of Chum Salmon (Oncorhynchus keta) in Kennedy Creek

#### Part B. Variability of Dissolved Oxygen in Natural Egg Pockets of Chum Salmon

N. Phil Peterson and Thomas P. Quinn

#### Abstract

Even though the effects of dissolved oxygen on incubating salmonid embryos have been studied extensively in the laboratory, there is limited information that can be used to link those effects to conditions wild salmon embryos are exposed to in complex natural channels. Our study of 33 natural chum salmon egg pockets, from shortly after spawning until emergence found levels of DO were variable between and among stream reaches and within egg pockets over time. Much of this variability may be attributed to local channel topography. We did not detect differences in DO based on sediment composition (percent sample  $< 4.0$  mm).

### Introduction

Among salmonid fishes the majority of life-time mortality usually takes place between the time fertilized eggs are deposited in the gravel and when they emerge as fry (survival to emergence STE) several months later. Under conditions of high spawner density, redd superimposition by other females can be a significant cause of mortality (McNeil 1964). Otherwise, the major factors affecting survival during this period are physical: 1) displacement by high stream flows that scour the streambed (McNeil 1964; Tripp and Poulin 1986; Thorne and Ames 1987), 2) suffocation of the developing embryos due to inadequate circulation of intergravel water (Everest et al. 1987), and 3) entombment of hatched and fully formed fry in the gravel bed (Bjornn 1969). The latter two mortality agents are considered to be closely associated with high concentrations of fine sediment in streambed gravels.

Fine sediment is a natural component of stream substrates but land practices that disturb vegetative cover often cause erosion that delivers significant quantities of fine sediment (sand and silt) to stream courses. Although natural background rates and dominant sediment delivery processes vary considerably over the forested landscape of the Pacific Northwest, industrial scale logging operations frequently result in elevated rates of sediment delivery to stream channels. Some of the most compelling evidence that forest practices harm salmonid fishes comes from studies of fine sediment and STE (Scrivener and Brownlee 1989). Given the widespread concern over the loss of salmon populations and the economic ramifications of listing salmon populations under the Endangered Species Act (Nehlsen et al. 1991), it is imperative to define the relationships between land use practices and salmon survival as precisely as possible.

The relationship between fine sediment concentration and STE is characterized by high levels of variation (Chapman 1988). Moreover, the relationship is apparently extraordinarily steep (e.g., Tagart 1984). That is, slight changes in fine sediment concentration seem to produce large changes in embryo mortality. In most of the STE studies, the precise mechanism of mortality is never identified. Often, however, dissolved oxygen (DO) is implicated because it has been shown to vary with stream bed porosity, and apparent velocity, both of which are inversely related to fine sediment concentrations (Coble 1961; Tagart 1984).

Even though the DO requirements and effects of hypoxial stress on salmonid embryos and larvae have been extensively studied (Wickett 1954; Alderdice et al. 1958; Silver et al. 1963; Shumway et al. 1964; Koski 1975), the information comes largely from the laboratory or artificial channels. These controlled studies may indicate the effects of DO concentrations at different developmental stages, but only information from natural field settings can indicate the range and temporal patterns of DO concentrations experienced by wild salmon embryos. Because this information is largely lacking, especially from undisturbed natural egg pockets, we decided to make a study of the variability of DO in undisturbed chum salmon (*Oncorhynchus keta*) egg pockets in a complex natural channel. This information is needed to provide a link between the controlled studies and studies of physical conditions in streams draining intensively managed forest lands.

## Materials and Methods

### Study Site

Kennedy Creek is a third-order drainage originating on the north slope of the Black Hills and flows about 16 km in a northerly direction into Totten Inlet in southern Puget Sound (Figure 1-B-1). Elevation in the 5300 ha watershed ranges from sea level to 721 m. The uplands consist of moderately steep hillslopes underlain by marine volcanics of the Crescent formation. The main valley and some lower valley walls are mantled with undifferentiated glacial till and variable recessional outwash materials deposited during episodic continental glaciation.

The headwaters of Kennedy Creek consist of numerous high-gradient first and second order channels draining steep hillslopes flowing immediately into a large, flat valley created by glacio-fluvial erosion and deposition. The valley gradually narrows into a bedrock canyon near river km 4.4, where the stream flows over a large falls and through a narrow canyon that blocks upstream migration of anadromous salmonids. Below the gorge, the stream flows through a narrow V-shaped valley for about 1.5 km where the channel is occasionally restricted by bedrock outcrops. Gradually the channel becomes more sinuous and is less constricted. The reach where the study sites are located (river km 1-2), is moderately confined by valley walls and is slightly incised into non-cohesive highly erodible glacio-fluvial deposits.

The climate is maritime with relatively wet, mild winters and cool dry summers. Annual precipitation averages 147 cm and occurs mostly as rain from October through April. Discharge responds to precipitation and ranges from a mean low flow of 0.1 m<sup>3</sup>/s in August to a mean high flow of 4.8 m<sup>3</sup>/s in January, with a mean annual discharge of 1.7 m<sup>3</sup>/s. The highest peak flow recorded between 1960 and 1979 (the period of record for the USGS gaging station) was 39.1 m<sup>3</sup>/s and the mean annual peak flow (recurrence interval 2.33 years) is approximately 22.9 m<sup>3</sup>/s (Williams et al. 1985).

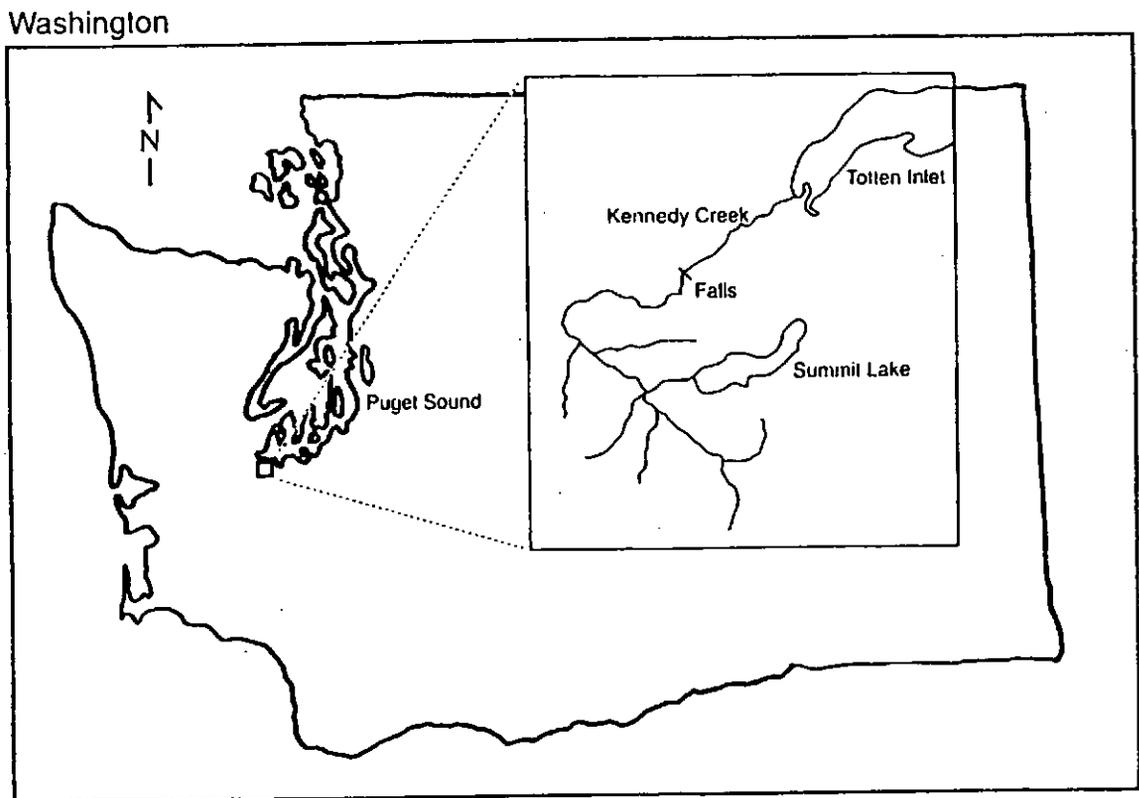
Most forests in the watershed were harvested earlier in the century and now consist of second-growth stands of harvestable age Douglas fir (*Pseudotsuga menziesii*) in well-drained sites and red alder (*Alnus rubra*) in wetter sites. Harvest of second-growth timber in the basin is underway and a dense system of roads is in place. Residential development is largely confined to the shores of Summit Lake, a 211 ha natural lake located on a tributary in the upper watershed.

Four separate study reaches (A, B, C, and D) were selected based on differences in general physical criteria. A and C were "simple" reaches, having relatively smooth, gradually changing long profiles, relatively narrow bankfull channel widths, low lateral bar relief, and little coarse woody debris. B and D were "complex" reaches, having abruptly changing long profiles, relatively wide bankfull channel widths, high lateral bar relief, and large quantities of large woody debris. Reach D had a large channel-spanning log jam (126 pieces) which locally moderated sediment storage in the channel upstream and downstream.

### Sample Collection and Analysis

Egg pockets were identified by observing pairs of chum salmon until they spawned, and inserting a sampling tube attached to a 15 cm plastic tent peg into the center of the egg pocket before the female began to cover the egg pocket. The last 6-8 cm of this tube was perforated and covered by a fine mesh stainless steel screen. As soon as the sampling tube was set, the location of the pocket was surveyed and referenced to at least two and often three rebar benchmarks away from the active channel. These procedures took an average of 7-10 minutes after which the female invariably returned (within 5-10 minutes) and began normal redd covering. The sampling

Figure I-B-1. Location map of Kennedy Creek.



tube trailed back over the tailspill of the redd and allowed us to withdraw water samples from the egg pocket without further disturbance. The female later constructed additional egg pockets in succession and redds were completed within the normal time span of about one day. . At this time we also designated what kind of habitat the egg pocket was in using four channel location designations; 1) pool tailout, 2) glide, 3) riffle, or 4) lateral bar. When egg pockets were located, no attempt was made to establish a particular number in specific habitat types as this was usually controlled by field circumstances that limited our abilities to view spawning pairs and the predominant habitat type within the study reaches.

Sampling tubes were inserted into 41 egg pockets and water samples were withdrawn every 7-14 days. We first evacuated a volume sufficient to empty the tube to the egg pocket, then pulled in 60 ml for a temperature sample, and finally a 125 ml sample was pulled into the sample bottle, fixed chemically, and taken to the lab for oxygen analysis by idiometric titration. Temperatures were taken so that we could compute DO saturation and estimate the embryos' developmental stage, using data obtained from Kennedy Creek chum salmon by the Washington Department of Fisheries (Tom Burns, pers. comm.).

In late March we sampled the particle size distribution in the egg pockets we had been sampling for DO by placing tri-tube freeze core probes into the egg pocket and withdrawing the frozen samples from the streambed. The cores were then laid across sampling boxes and melted off the probes. The boxes were of varying widths arranged to collect sediment from each of four strata: the undisturbed sediments underlying the egg pocket, the egg pocket itself, the bridging layer (the layer of particles deposited by initial covering actions of the female), and the rest of the cover material up to and including the surface layers of gravel. These four layers will be referred to as the undisturbed, pocket, bridge, and cover respectively. Sediments from all strata were individually packaged for processing. In the lab, sediment samples were dried to a constant weight and mechanically shaken through 21 standard sieves representing a  $1/2$  phi ( $-\log_2$  x particle size diameter) gradation starting at -6 phi (64 mm) and ending with 4 phi (0.063 mm). This sieve series was selected to conform to standard particle size determination methods used in sedimentology studies and to facilitate comparisons with the Wentworth particle size scale (Wentworth 1922). All 22 size fractions, including the pan silts, were weighed to the nearest 0.1 g.

### Results

Forty-one egg pockets were located and outfitted with sampling tubes. Of those 41, we obtained complete records (samples collected from 1-5 days after they were constructed to the final sample during emergence in the last two weeks of March) for only 33. The other eight sampling tubes were displaced by streambed scour or dug out by other females constructing redds later in the spawning period. The distribution of egg pockets by study reach and habitat unit is given in Table I-B-1. We standardized our analysis of DO on "days since fertilization" rather than calendar date because the DO requirements change with the stage of embryonic development and our egg pockets were constructed over a period of several weeks (October 31 to December 5).

**Table I-B-1.** Distribution and number of sampled egg pockets by study reach and habitat units for which complete records are available.

Habitat type	Reach A	Reach B	Reach C	Reach D
Pool tailout	1	5	3	2
Glide	2	0	3	5
Riffle	3	2	2	1
Lateral bars	1	0	0	3

**Table I-B-2.** Mean dissolved oxygen levels and (SD) by study reach and developmental stage.

Developmental stage	Reach A	Reach B	Reach C	Reach D
Spawning	8.7 (1.90)	8.8 (1.14)	6.6 (2.74)	8.2 (1.98)
Hatching	7.4 (1.87)	9.3 (2.47)	7.7 (2.91)	10.0 (1.31)
Emergence	3.9 (2.24)	8.1 (3.24)	5.5 (3.24)	6.9 (2.99)

There was a general deterioration of DO with time (Table I-B-2; Figure I-B-2) but it was not particularly pronounced, especially in some study reaches. Wilcoxon signed rank tests detected differences between spawning and hatching ( $P < 0.05$ ), and between hatching and emergence ( $P < 0.01$ ). We also observed reach level differences in DO levels. A Kruskal-Wallis test (non-parametric one-way ANOVA) indicated differences among study reaches in DO at hatching and emergence ( $P < 0.05$ , for both cases), but not among reaches at the time of spawning ( $P = 0.27$ ). Plots of individual egg pocket DO values suggested a number of temporal patterns (Figure I-B-3). There was considerable variation in DO levels over time within reaches, making it difficult to define reach-specific patterns. However, the patterns of DO depicted in Figure I-B-3 were generally characteristic of the reaches. DO levels at emergence were generally lower than those at fertilization but some egg pockets experienced little change while others fluctuated but did not decline overall. In all the reaches there appeared to be a time early in the incubation period, during which DO fluctuated more than it did later in the incubation period (Figure I-B-3).

In some cases the maximum range of DO measured for egg pockets was extreme (Figure I-B-4). The distribution of these ranges in DO tended to exhibit different patterns by habitat type (Figure I-B-5). Pool tailouts tended to be the least variable while the glides seemed to be bimodal in the range of DO measured. Riffles tended to have a fairly even distribution, and the lateral bar egg pockets (small sample size,  $N=4$ ) showed high variability with 3 of the 4 pockets experiencing levels of DO that changed between 7-9 mg/l. Figure I-B-6 displays the spread of the data by habitat unit at the time of hatching. Pool tailouts were uniformly high, while the glides had a similar median value, they were much more variable. By the time of emergence these same trends had persisted and become more pronounced but the variability of the data had become more widespread (Figure I-B-7). We did not detect any correlation between DO levels and substrate composition as measured by any index of "percent fines" (Figure I-B-8). The average percent fines  $< 4.0$  mm for all 33 egg pockets was 15.4%, SD 4.76. Small sample sizes preclude a statistically rigorous evaluation of sediment composition by habitat type, but the trend was for increasing fines from pool tailout, to riffles, to glides, and lateral bars. Pool tailouts had the least variable and the highest level of DO, whereas lateral bars were variable and in general, had the lowest DO.

Figure I-B-2. Distribution of DO for all egg pockets (N=33), at three developmental stages.

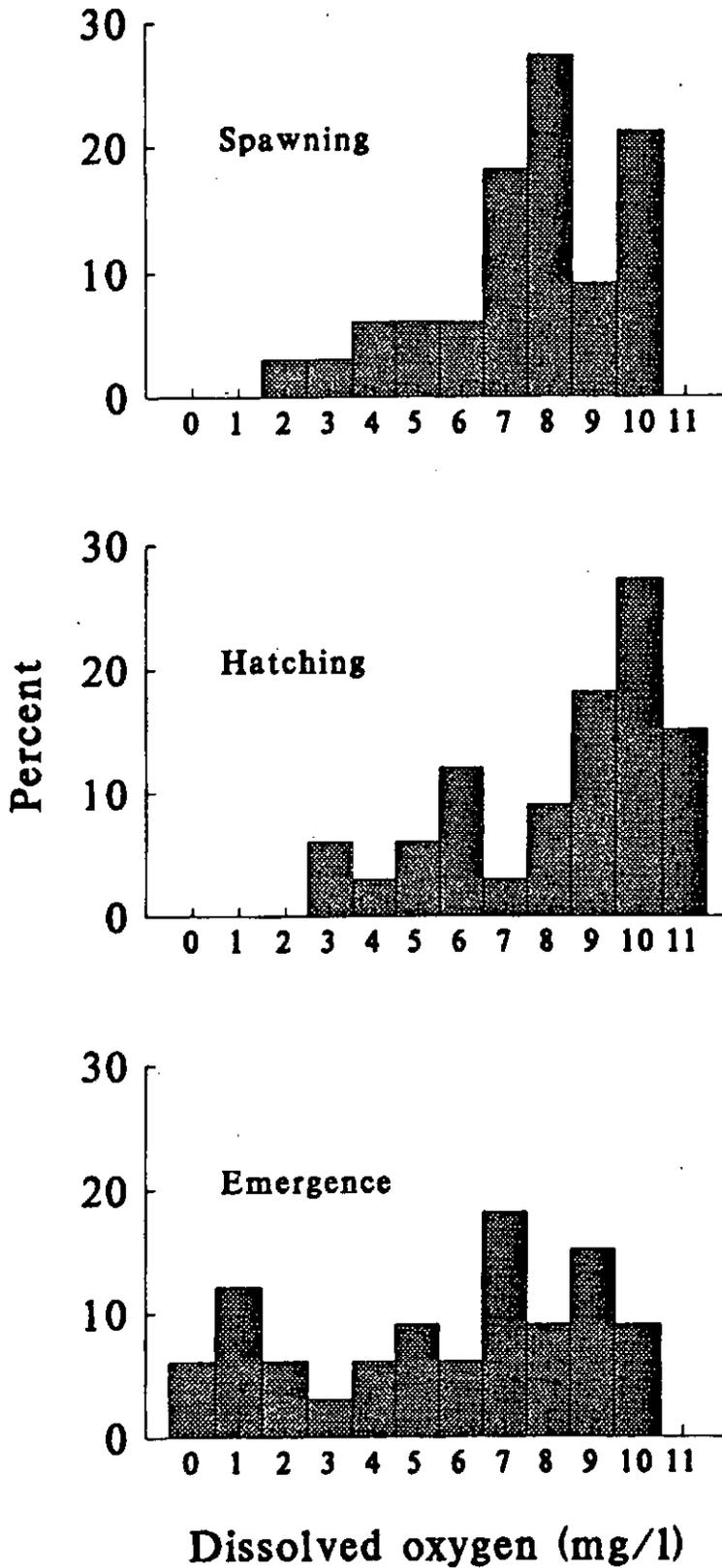
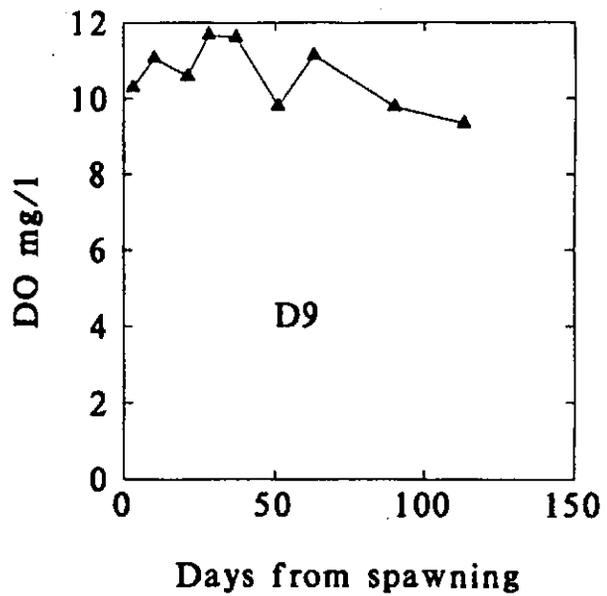
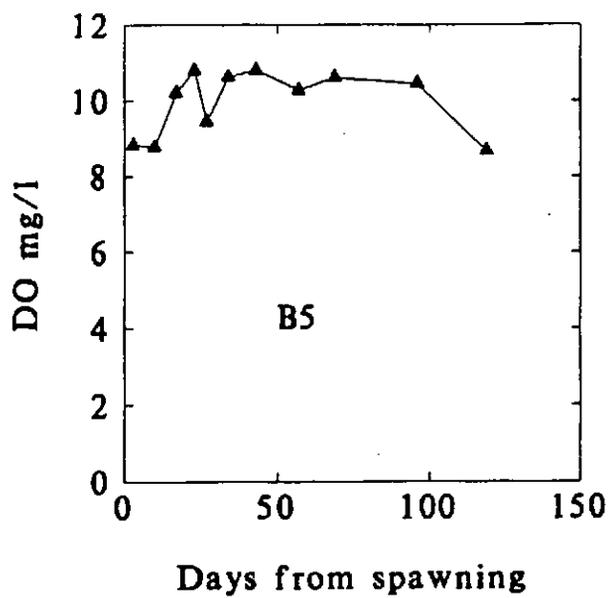
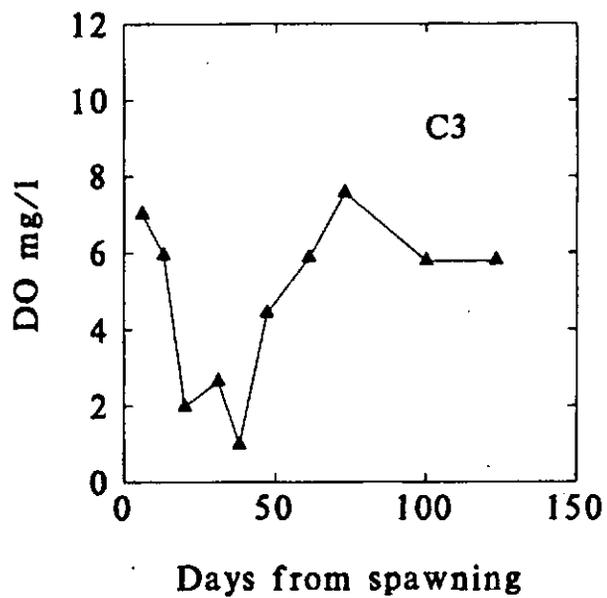
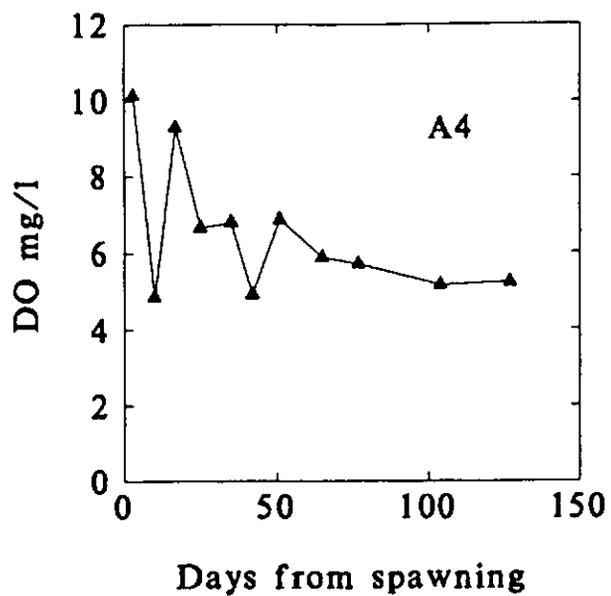


Figure I-B-3. Temporal trends in DO for four egg pockets from different study reaches.



**Figure I-B-4.** Distribution of the maximum range of DO in individual egg pockets (N=33). Two modes are apparent, one group had little fluctuation in DO, while the other group varied considerably.

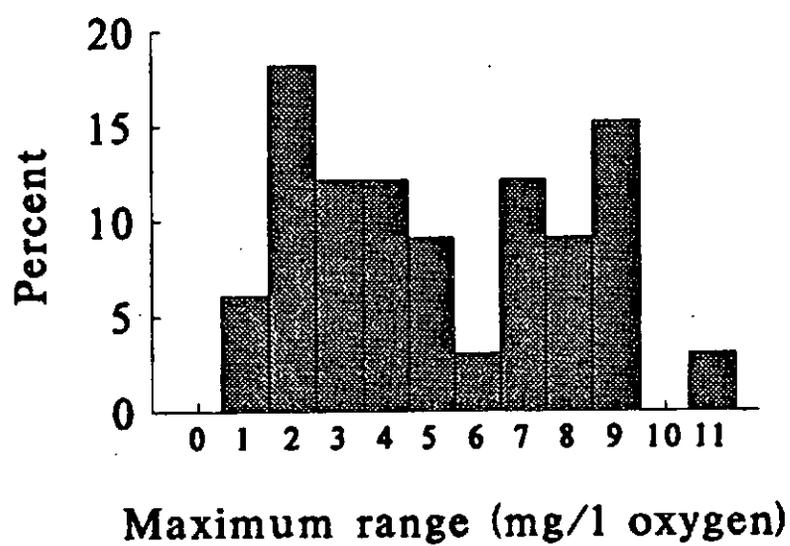


Figure I-B-5. Distribution of maximum range of DO in individual egg pockets by habitat type.

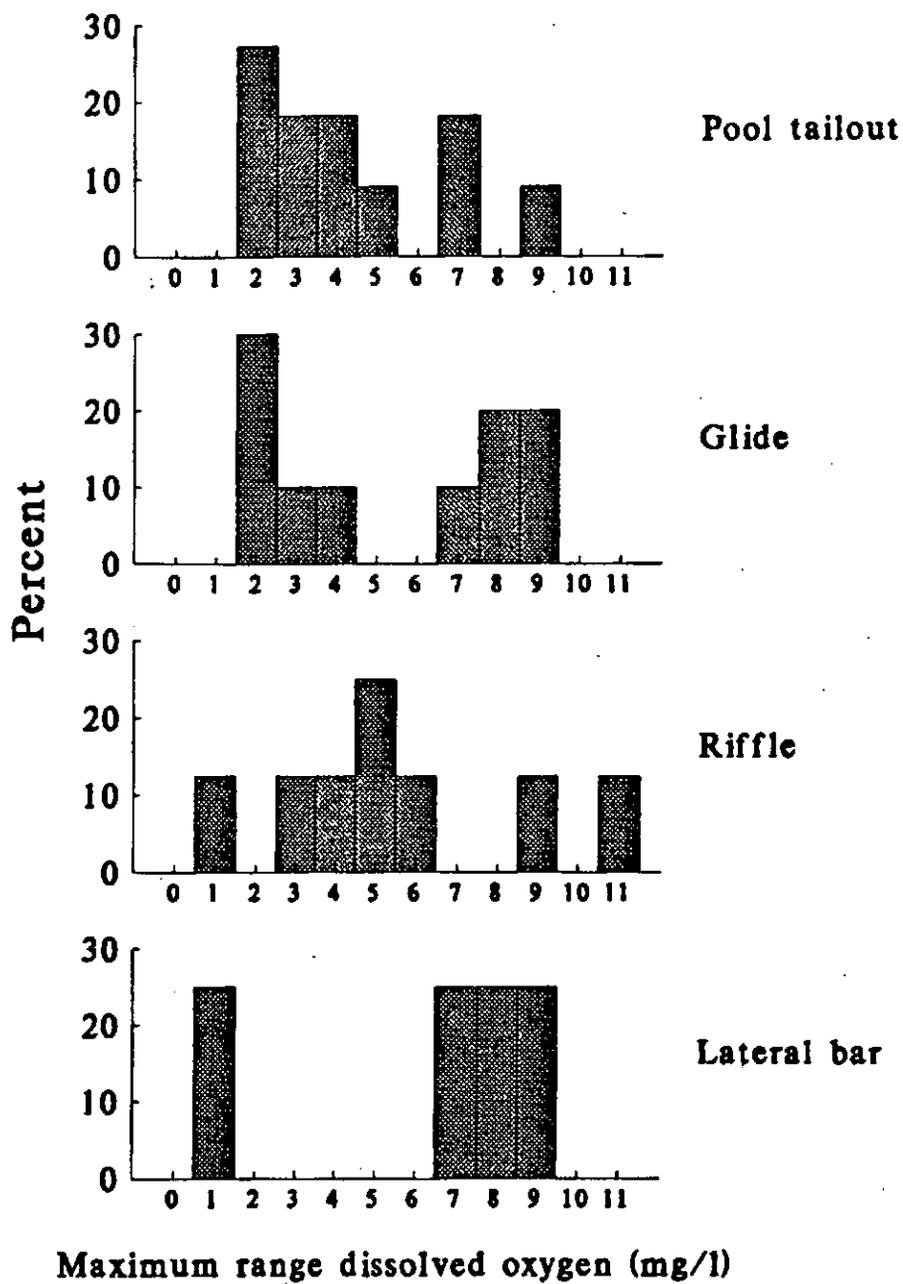
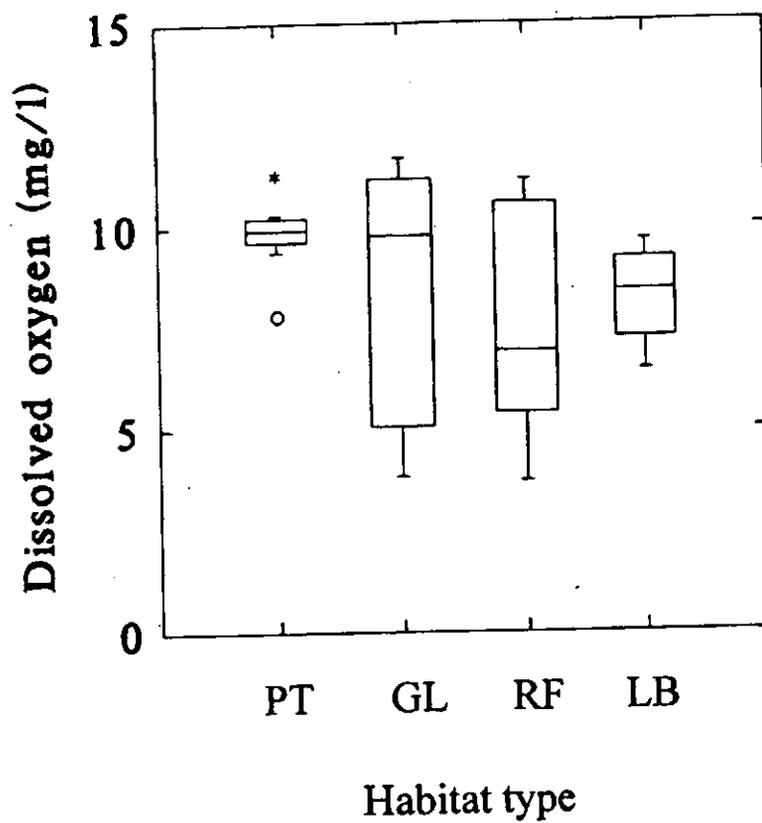
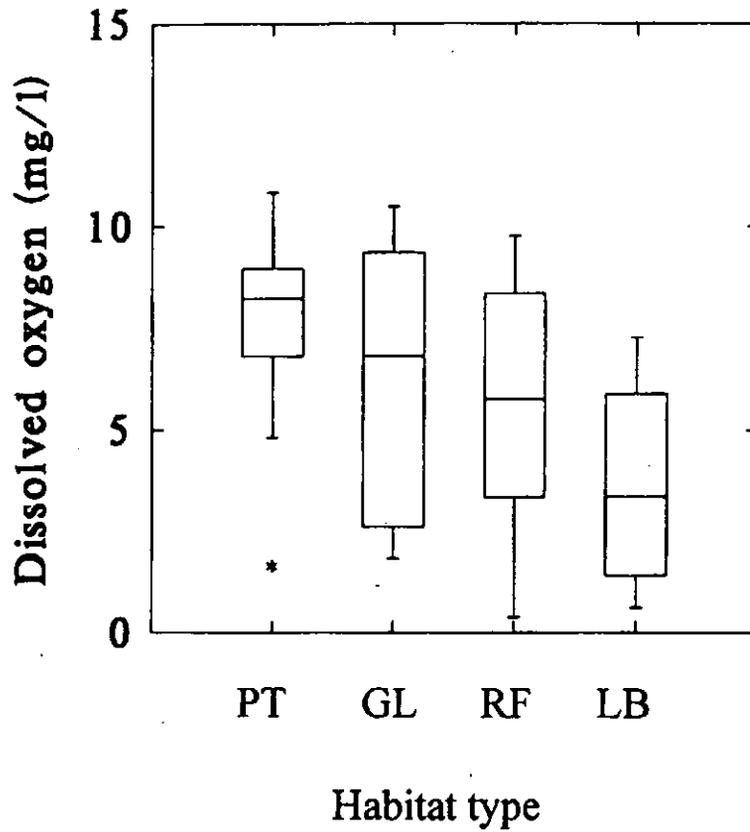


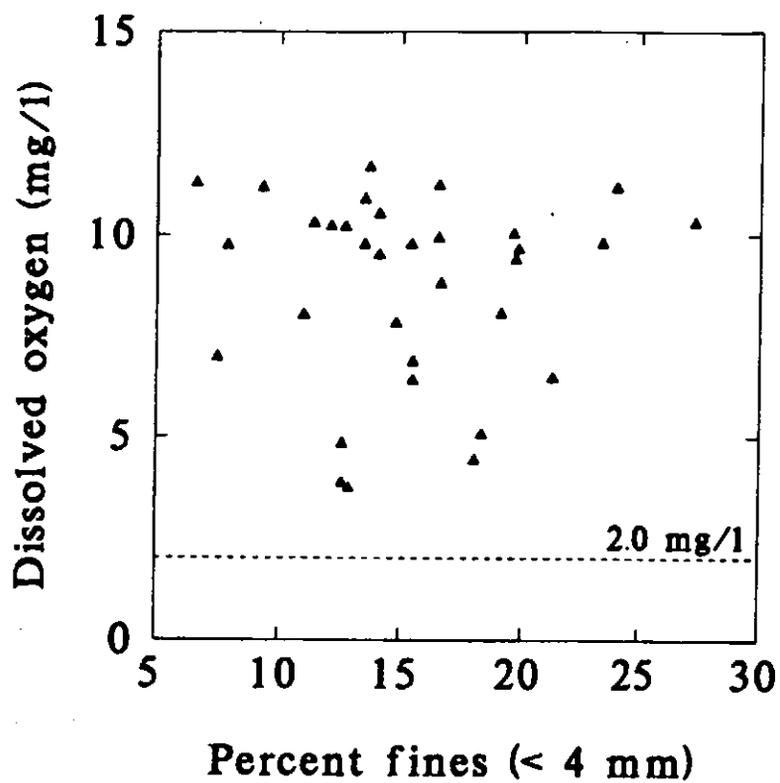
Figure I-B-6. Median and interquartile ranges (boxes) of DO levels at the calculated time of hatching for 4 habitat types. PT=pool tailout, GL=glide, RF=riffle, and LB=lateral bar.



**Figure I-B-7.** Median and interquartile ranges (boxes) of DO levels at the calculated time of emergence for 4 habitat types. PT=pool tailout, GL=glide, RF=rifle, and LB=lateral bar.



**Figure I-B-8.** Relationship between fine sediment (percent fines <4.0 mm) and dissolved oxygen at the time of hatching. Two mg/l is the level of dissolved oxygen below which chum salmon STE drops rapidly (Koski 1975).



### Discussion

Our data represent a unique window into undisturbed chum salmon egg pockets in a natural stream and advance our understanding of the DO levels experienced by wild salmon embryos. The high variability between and among reaches and habitat types and within individual egg pockets over time, describes a complex oxygen environment that resists simple generalizations. McNeil (1962) described a highly variable intergravel oxygen environment for pink and chum salmon spawning streams in Alaska. Spatial and temporal variability in McNeil's (1962) study appeared to be related to both broad scale interannual environmental controls and fine scale in channel conditions. More recently, Leman (1993) has described the spawning sites of chum salmon in the upper reaches of the Kamchatka River. Oxygen isopleths were observed and associated with groundwater ranged from 6.5-10.5 mg/l DO, and those influenced by subsurface river flow ranged from 4.8-6.5 mg/l DO. It is likely that some of the variability between our study reaches and egg pockets were related to similar influences. In our case we assume a groundwater influence would produce a lower DO regime, similar to what Koski (1975) encountered. Stream bed topography may affect the interchange of surface and subsurface waters (Vaux 1962). There is little chance, for example, that the lateral bar and some glide egg pockets were exposed to surface water interchange because of their vertical and horizontal location in the channel. Local flow patterns and elevation breaks in bed form do not create flow vectors to cause injection of oxygenated surface waters into the gravel.

The levels of DO we observed are within the range expected to produce good STE for chum salmon. Koski (1975) identified 2 mg/l as the threshold below which survival decreased rapidly. Wickett (1954) determined that 1.67 mg/l was the lethal level for chum salmon and more recent work has established that chum salmon have lower oxygen requirements than do coho or chinook (Fast and Stober 1984). Sub-lethal effects on size and fitness of fry that have had prolonged exposure to low DO have been reported for several species of salmonids including chum salmon (Brannon 1965; Mason 1969; Bams and Lam 1983; Koski 1975). However, Koski (1975) found no differences in the size of chum salmon fry emerging from redds with prolonged minimum DO concentrations less than 6.0 mg/l. It is likely that a portion of our egg pockets (as many as 10-15%) experienced DO concentrations that were low enough to cause later initial emergence or adverse effects on fry size.

Our failure to corroborate the relationship between fine sediment and DO (Koski 1975; Tagart 1984; Scrivenir and Brownlee 1989) may be due to a number of possibilities. First, in studies where the relationship has been described, it is usually weak (for example, see Scrivenir and Brownlee 1984, or Koski 1966). Secondly, the levels of fine sediments in our stream bed may not have been high enough to create the conditions of low permeability that result in reduced intergravel flow and delivery of oxygenated water. Koski (1975) for example described a relationship between fine sediment and DO where gravel composition consisted of 30-70% sand. Only 4 of our 33 data points had fines greater than 20%. Even though we used dry gravimetric methods and Koski (1975) used wet volumetric methods to analyze sediment samples, our samples were much "cleaner" (fewer fines) with only 4 to 6 of our 33 samples as fine as Koski's (1975) "cleanest". Kennedy Creek has an abundant supply of sand sized material in the stream banks and the gravel composition is moderately fine in texture (see Chapter I Part A and C).

### **Implications for Forest and Fish Management**

Our experience with dissolved oxygen in natural egg pockets in Kennedy Creek suggests that there may be broad temporal patterns associated with channel topography, but probably modified by many other biological and physical factors. As such we believe the best course of action to preserve multiple high quality spawning and incubation sites is to promote the development of a vigorous riparian forest and keep other watershed processes such as sediment supply and discharge regime in balance.

### **Acknowledgments**

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## Chapter 1.

### Incubation Environment of Chum Salmon (Oncorhynchus keta) in Kennedy Creek

#### Part C. Patterns of Scour and Fill in a Low-Gradient Alluvial Channel

David Schuett-Hames, N. Phil Peterson and Thomas P. Quinn

#### Abstract

The effects of scour and fill on chum salmon incubation habitat were studied in two reaches of Kennedy Creek, a third order, low-gradient alluvial channel in south Puget Sound, Washington. Scour occurred during two storm events having estimated return intervals (RI) of 1.4 yr and <1 yr. Significant differences in depth of scour were observed between the two study reaches and among habitat units (riffles, lower riffles, glides, pool tailouts and pool lateral bars) in each reach. Average depth of scour in Reach A (relatively simple, straight and narrow) was 0.075 m whereas in Reach B (complex, sinuous and wide site), scour was nearly twice as deep (0.14 m). Average scour depth and the percentage of monitors scoured to a depth of 0.2 m (median egg pocket depth) was greater in pool-associated habitats (pool tailouts and pool lateral bars) than in riffle-associated habitats (riffles, lower riffles, and glides). The relatively widespread scour to egg pocket depth during low magnitude events indicate that this may be a significant source of egg-to-fry mortality for salmonids spawning in low-gradient streams.

### Introduction

After spawning, female salmonids bury their eggs within stream substrates where the embryos complete development prior to emerging into the free flowing stream several months later. During this period, the embryos depend on the quality and stability of the intergravel environment for their health and survival. Optimum development requires an adequate flow of clean water within a suitable temperature range to supply oxygen, remove metabolic waste products, and prevent desiccation. In addition, the streambed must be stable enough to protect the embryos from mechanical shock and physical displacement. Many salmonid species spawn in fall, requiring the delicate embryos to reside in the streambed through the winter storm cycle of coastal regions of the Pacific Northwest. This period is punctuated by heavy precipitation causing frequent freshets. During these storms the discharge in salmon streams sometimes reaches a stage great enough to mobilize the streambed and place the developing embryos at risk of being shocked, crushed, or displaced.

Burial of eggs under the gravel is likely an adaptation to this hostile incubation environment. The female salmon spends considerable energy in preparing a series of egg pockets, consisting of depressions in the gravel about 20 cm deep. The stones in the bottom of the egg pockets are the large ones which are not washed away by the digging action and the current. The 10-12 cm zone below this depression is purged of fine particle sizes by the digging action of the female and it is in this "labyrinth" of interstitial voids that the eggs are deposited. The female salmon covers each successive egg pocket with gravels derived from immediately upstream. Aside from the primary role of creating interstitial space for the eggs and burying them to a depth of 20-30 cm, the digging action of the female coarsens the surface of the bed, which may increase the discharge required to initiate scour (Montgomery et al. in prep.).

By burying their eggs in the streambed, salmonids reduce the probability that scour will reach them. Larger salmon tend to dig deeper redds than smaller individuals (van den Berghe and Gross 1984; Crisp and Carling 1989). Nonetheless, scour of eggs and developing alevins can be a significant cause of mortality. McNeil (1966) recorded numerous instances of egg loss due to gravel movement in pink (*Oncorhynchus gorbusha*) and chum (*O. keta*) salmon spawning areas in southeast Alaska. Mortality regularly exceeded 50% and in one instance 90%. Tripp and Poulin (1986) estimated egg pocket scour as high as 80-90% in chum and coho (*O. kisutch*) spawning streams in the Queen Charlotte Islands of British Columbia. In southwestern Oregon 75% of the chinook redds were either scoured or deeply buried during a relatively small storm (Nawa et al. 1990).

Scour of substrate particles is a natural fluvial process associated with transport of bedload material and adjustment of channel morphology. Scour occurs when, as discharge increases, water velocity and shear stress increase until the threshold of motion is reached and substrate particles are entrained. Bedload movement occurs in two phases (Jackson and Beschta 1982). The first phase involves movement of sand size particles at moderate flows. The movement of larger bedload particles during high flows is highly irregular in time and space. Shear stress varies across the streambed, so portions of the bed move independently of one another and scour depths vary (Bathurst 1979).

With few exceptions, most studies of streambed scour have been designed to describe the fluvial geomorphic processes and dynamics of bedload transport. Depth of scour is generally believed to be controlled by magnitude and duration of stream discharge and streambed texture (Lisle 1989). However, other factors such as woody debris loading, sediment availability, particle

size and reach morphology, and the movement and sorting of gravel by spawning fish may also influence patterns of scour and fill. To better understand the ways in which these physical patterns and processes in streams affect the reproductive success of large salmonids, we initiated a study on Kennedy Creek to investigate; 1) the extent of scour in chum salmon incubation habitat, 2) the relationship between scour and discharge, and 3) the variations in scour and fill among channel units and reaches of different morphologies.

## Materials and Methods

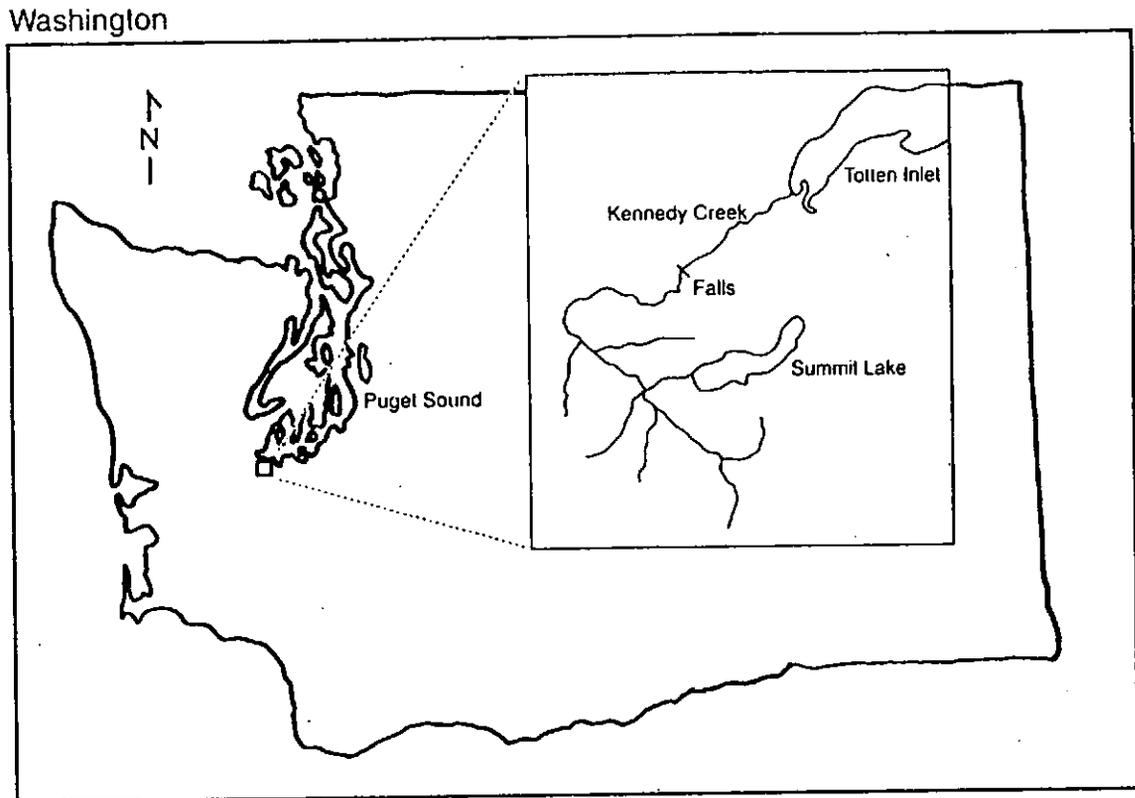
### Study Site

Kennedy Creek is a third-order drainage originating on the north slope of the Black Hills and flows about 16 km in a northerly direction into Totten Inlet in southern Puget Sound (Figure I-C-1). Elevation in the 5300 ha watershed ranges from sea level to 721 m. The uplands consist of moderately steep hillslopes underlain by marine volcanics of the Crescent formation. The main valley and some lower valley walls are mantled with undifferentiated glacial till and variable recessional outwash materials deposited during episodic continental glaciation.

The headwaters of Kennedy Creek consist of numerous high-gradient first and second order channels draining steep hillslopes flowing immediately into a large, flat valley created by glacio-fluvial erosion and deposition. The valley gradually narrows into a bedrock canyon near river km 4.4, where the stream flows over a large falls and through a narrow canyon that blocks upstream migration of anadromous salmonids. Below the gorge, the stream flows through a narrow V-shaped valley for about 1.5 km where the channel is occasionally restricted by bedrock outcrops. Gradually the channel becomes more sinuous and is less constricted. The study reaches were located at river km 1-2 in a section of the stream that was moderately confined by valley walls and slightly incised into non-cohesive highly erodible glacio-fluvial deposits.

The stream's climate is maritime with relatively wet, mild winters and cool dry summers. Annual precipitation averages 147 cm, mostly as rain from October through April. Discharge responds to precipitation and ranges from a mean low flow of 0.1 m<sup>3</sup>/s in August to a mean high flow of 4.8 m<sup>3</sup>/s in January, with a mean annual discharge of 1.7 m<sup>3</sup>/s. The highest peak flow recorded between 1960 and 1979 (the period of record for the USGS gaging station) was 39.1 m<sup>3</sup>/s and the mean annual peak flow (recurrence interval 2.33 years) is approximately 22.9 m<sup>3</sup>/s (Williams et al. 1985). Most forests in the watershed were harvested earlier in the century and now consist of second-growth stands of harvestable age Douglas fir (*Pseudotsuga menziesii*) in well-drained sites and red alder (*Alnus rubra*) in wetter sites. Harvest of second-growth timber in the basin is underway and a dense (3.6 km/km<sup>2</sup>) system of forest roads is in place.

Figure I-C-1. Location map of Kennedy Creek, Washington.



**Table I-C-1. Physical characteristics of study sites A and B.**

Attribute	Site A	Site B
Length (meters)	75.0	117.0
Coarse woody debris (pieces/100 m)	44	80
Mean bankfull width (meters)	16.0	20.9
Water surface slope	0.0065	0.0072
Mean bar height (average elevation from thalweg to bar surface in meters)	.51	1.61
Bed texture $D_{50}$	32.5	25.3

### Channel Reach Morphology

We identified several kinds of channel habitat in Kennedy Creek, two of which were selected for study. Type 1 reaches had the highest width-to-depth ratios, the greatest habitat complexity, abundant woody debris, and extensive gravel-bar deposits. They were often associated with meander bends and bare eroding banks. Type 2 reaches had moderate width-to-depth ratios, lower habitat complexity, smaller gravel bar deposits, and fewer pieces of woody debris. Reaches representative of Type 1 and 2, Reaches B and A respectively, were selected for study. Table I-C-1 provides information on these study sites. Five types of potential spawning habitat were identified in both reaches. Riffles had the fastest water velocities, shallow water depth, and turbulent water surfaces. Lower riffles were situated immediately upstream from pools and at the end of the riffles. Glides were deeper than riffles, had slower water velocities, and less turbulence. Pool tailouts were the shallow areas at the downstream end of pools. Pool lateral bars were submerged bars adjacent to pools. Pool bottoms were the only areas of the stream not used for spawning and we purposely did not include them for study.

### Scour and Fill Measurements

To measure scour and fill, a cross-sections was established at each of the five habitat types within both study reaches. After the salmon had finished spawning, scour monitors similar to Tripp and Poulin's (1986) design, Figure I-C-2, were inserted along the cross-sections at 2 m intervals and the streambed was surveyed for relative elevation. While these cross-sections included areas that had been used for spawning by chum salmon, they were selected to examine depth of scour in particular channel bedforms. To determine if scour and fill along these cross-sections differed from actual chum salmon spawning locations, 15 additional monitors (3 for each habitat type) were inserted within 0.5 m of egg pockets. After high flows, scour was determined by counting the number of balls floating on the end of the wire (estimated accuracy +/- 2 cm). Fill was documented by resurveying the cross-sections and comparing with previous elevations.

Peak flows were recorded using a crest-gage installed by the USGS. Stage heights were converted to discharge values using a rating curve prepared by the USGS. To determine the recurrence interval of peak flows, a flood frequency curve was constructed using USGS annual maximum peak flow data (Williams et al. 1985) from 1961-1979.

## Results

### Changes in Channel Morphology Associated with Salmon Spawning

In 1991-92 approximately 5,000 chum salmon per km spawned throughout the accessible length of Kennedy Creek. Numerous changes in channel morphology were associated with this activity in concert with minor freshets. Several distinct stages of the spawning activity are worth noting. The first fish arrived when flows were very low and as they migrated upstream, their caudal fins pushed particles aside. This action deepened the thalweg through shallow riffles and across riffle crests, creating a migration "passageway". Because of shallow water in the pool tailouts and riffles these fish often spawned at the upstream end of pools at the riffle pool boundary. During redd construction they moved material from the riffle down into the deeper water of the pool, creating a spawning "platform" with suitable water depth for spawning.

The second process, lowering the riffle crest, occurred after water levels began to rise and more salmon arrived. Under these conditions, chum salmon often spawned in pool tailouts on the upstream side of the riffle crest, the downstream bar impounding water in the pool. Their excavations lowered the height of the riffle crest and moved it downstream. This lowered the water level in the pool, expanding the size of the tailout area further upstream.

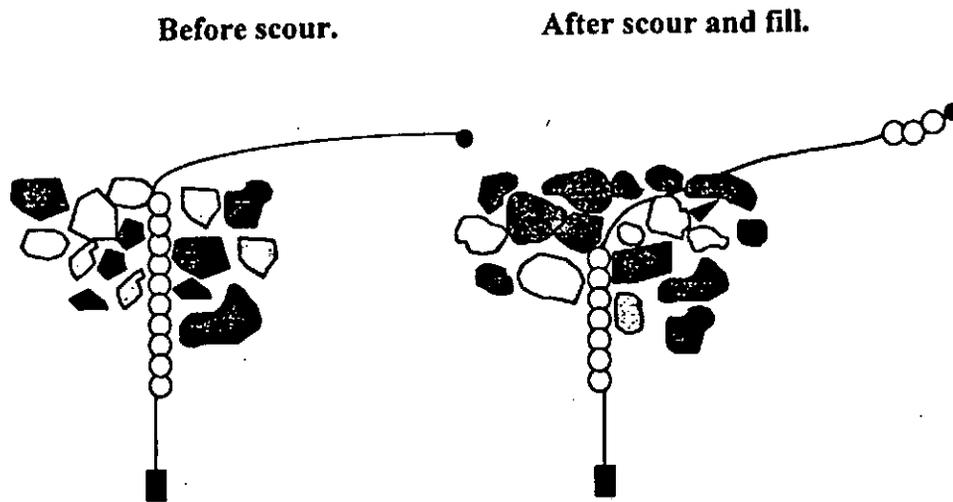
The third process, downstream extension of the riffle, occurred at higher flows when riffles were occupied by actively spawning salmon. Widespread excavation in conjunction with higher water velocities resulted in movement of material down through the riffle and into the upper end of the next pool. Initially the material deposited was sand separated from coarser substrate during redd construction. Later, high densities of spawning salmon excavated undulating dune-like bedforms throughout the riffle during freshets, resulting in large, deltaic deposits of gravel at the head of pools immediately downstream from the riffles. These areas were used as spawning sites by fish arriving later.

The fourth process, channel widening, occurred most frequently late in the spawning period when nearly all suitable spawning habitat was occupied. Newly arriving females often crowded the channel margins, constructing their redds by excavating along the toes of lateral gravel bars, eventually undermining them until they sloughed into the active channel. The new vertical face of the bar retreated repeatedly, sometimes by as much as 1-2 m. The result was a flat, submerged spawning area carved into a formerly dry, sloping bar.

### Changes in Channel Morphology Associated with Peak Flow Events

The largest discharge we recorded during the study period (winter 1991-92) was 16.9 m<sup>3</sup>/s on January 29, 1992. The recurrence interval (RI) for this event was calculated at 1.4 years. A smaller peak of 6.5 m<sup>3</sup>/s, RI < 1 year, occurred on February 22, 1992. Streambed scour and transport of gravel particles were observed during both events. An earlier freshet occurred on November 21, 1991 at the peak of spawning activity. During this freshet we observed some egg pocket scouring but it seemed to be concurrent with redd excavation by other fish. Gravel mounds and excavations made by the salmon were smoothed and the streambed was leveled during this freshet. The median particle size diameter ( $D_{50}$ ) for all cross-sections ranged from 35.8-17.8 mm. Cross-sections in Reach A had a slightly larger  $D_{50}$  (32.5 mm) than cross-sections in Reach B (25.3). Pool tailouts had the smallest  $D_{50}$  in each site.

**Figure I-C-2.** Scour monitor depicting 12 cm of scour and a similar amount of fill. Each ball is 4 cm in diameter.



Scour during peak flows occurred on all cross-sections in all habitat types. The average depth of scour for all cross-section monitors was 0.11 m (range 0.0-0.6 m). The average depth of scour in Reach B (0.14 m) was nearly double that of Reach A (0.08 m). Scour at 19.7% of the monitors reached a depth of 0.2 m, the median depth of chum salmon egg pockets (Chapter 1-A). Scour at 27.9% of the monitors in Reach B reached 0.2 m, compared to only 9.1% in Reach A.

The average depth of scour was greatest at lateral bars adjacent to pools (0.20 m) and pool tailouts (0.16 m) (Figure I-C-3). Average depth of scour at lower riffles (0.09 m) and glides (0.08 m) was intermediate, while scour at riffle cross-sections was lowest (0.02 m). Scour to median egg pocket depth followed a similar trend (Figure I-C-4). The percentage of monitors scoured to 0.2 m was greatest at the pool lateral bars (44.4%) and at pool tailouts (40.0%), lower at glides (16.7%) and lower riffles (15.8%) and did not occur at riffle cross-sections. The differences in the amount of depth to 0.2 m depth was different between habitat type ( $P < 0.05$ ).

The average depth of scour was over ten times greater during the January 29 peak flow (RI=1.4 yr), than during the February 22nd peak flow (RI<1 yr), 0.105 m and 0.006 m respectively. Scour to egg pocket depth (0.2 m; Figure I-C-5) occurred at 15 (19.7%) of the cross-section monitors during the larger event compared to only one (1.3%) during the subsequent event.

Scour at auxiliary egg pocket scour monitors (located near egg pockets, not on cross-sections), was similar or somewhat higher than on cross-sections for the same site and habitat type. A higher percentage of the auxiliary monitors scoured to egg pocket depth (33.3%) than did those on the cross-sections (19.7%). The locations of the auxiliary egg pocket monitors were not randomly selected and they were typically near the thalweg, while cross-section monitors were systematically spaced across the entire channel.

Streambed elevation increased an average of 0.025 m at cross-section monitors during the incubation period. Although the overall trend was for bed elevation to increase, only 57% of the monitor locations aggraded while 43% degraded. In Reach A, 67% of the monitor locations aggraded and in Reach B only 49% of the monitor locations aggraded. By habitat type, the trend in bed elevation change was for aggradation at riffles, lower riffles, and glides, while the pool tailouts and pool lateral bars tended to degrade.

### Discussion

We observed substantial variation in scour and fill at every spatial scale measured: between the two reaches, among habitat units within reaches, and among cross-sections and individual monitors on the same cross-section within habitat units. Other studies have reported similarly high temporal and spatial variation (e.g., Lisle 1989). Although this local variation must be considered in the interpretation of these kinds of data, we believe our results indicate that factors such as peak discharge, and channel reach and unit scale morphology affect the magnitude of scour and fill. Our observations of substantial scour and fill at or near bankfull flow, 1.4 and <1 year RI, are consistent with other studies (McNeil 1966; Reid et al. 1985; Beschta 1987; Sidle 1988; Lisle 1989; Nawa et al. 1990). In streams with high rates of sediment supply, extensive scour and bedload transport occur during peak flows with a 1-2 year RI.

Figure I-C-3. Depth of scour (m) in Reach A (simple) and Reach B (complex) in different types of channel units in Kennedy Creek.

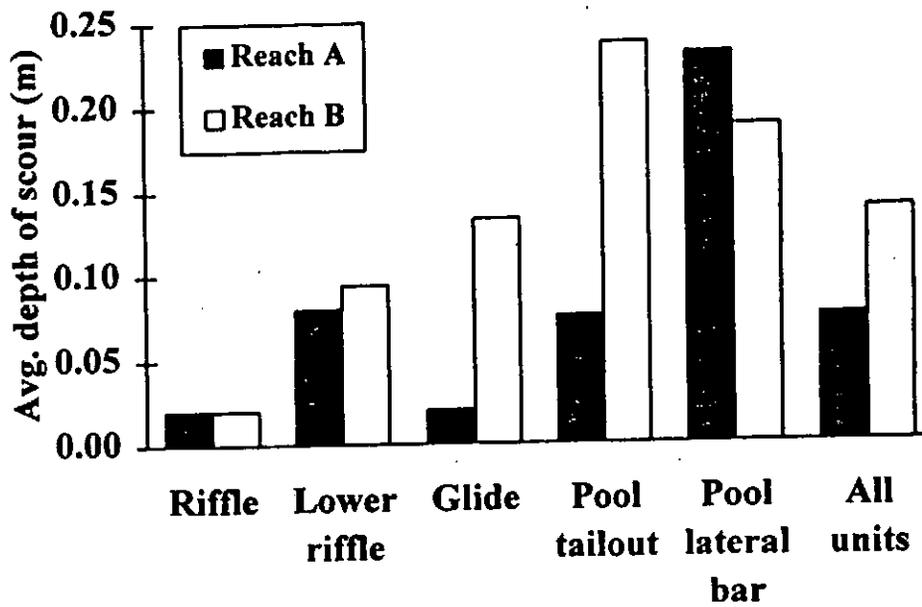


Figure I-C-4. Percentage of monitors scouring to egg pocket depth (20 cm) in different types of channel units in Reach A (simple) and Reach B (complex) in Kennedy Creek.

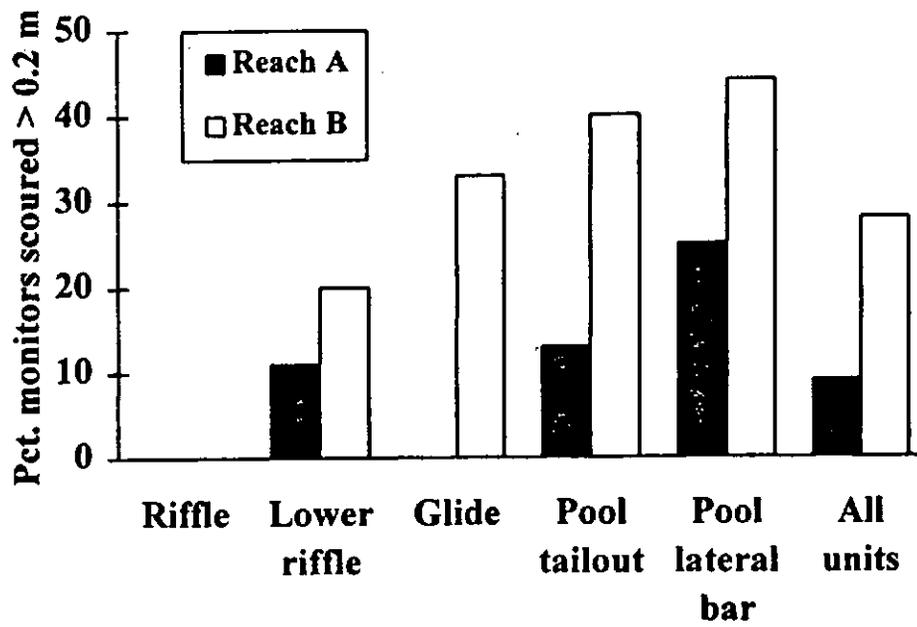
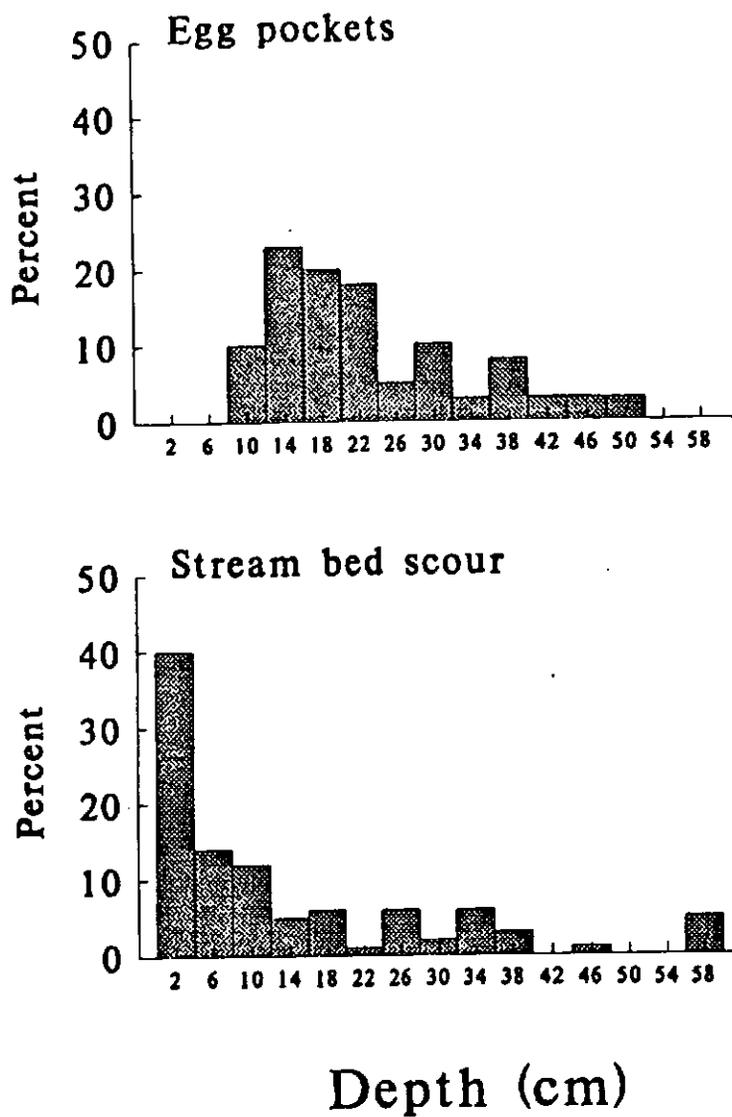


Figure I-C-5. Frequency distribution of egg pocket depths (n = 41) and depths of scour (n = 101) in Kennedy Creek.



The relationship between scour and discharge is not necessarily constant over time. Factors other than high flows, such as antecedent storm history, temporal proximity to a major channel disturbance (Sidle 1988), variation in bed compaction and armoring (Reid et al. 1985), variation in sediment size and availability, and the stability of upstream sediment storage sites (Beschta 1987), influence the discharge/scour relationship. The role of high densities of spawning chum salmon in altering the surface and sub-surface bed texture as well as the local bedforms may also be a significant factor in the magnitude and pattern of scour and fill at short RI peak flows. Therefore the discharge/scour relationship we have described for Kennedy Creek should be viewed in the context of current conditions and may change in the future.

Patterns of scour and fill, differed between riffle-like channel units (riffles, lower riffles, and glides), and pool-like channel units (pool tailouts and pool lateral bars). Active bed depth (the sum of the maximum scour and fill from beginning bed elevation) was greater in pool-like channel units than in riffle-like channel units. Scour was dominant in pool-like channel units while fill was dominant in riffle-like channel units. Processes causing scour and fill were also different between these two categories of channel units. In riffle-like units, scour to egg pocket depth was uncommon and usually associated with lateral migration of the thalweg, scour of new pools, or extensions of existing pools into the riffle. Scour to egg pocket depth in pool-like units was associated with the mobilization of material in pool lateral bars and tailouts or the movement of pool forming woody debris jams. It may be that much of the deeper scour we observed in Reach B was caused by shifting of coarse woody debris and/or redirection of erosive stream flow around it.

Andrews (1982) found that cross-sections in the East Fork River that were situated on riffle-like (wide and shallow) and pool-like (narrow and deep) channel locations responded differently to peak flows. These different responses are caused by differences in channel geometry and secondary currents that determine shear stress at different flows (Bathurst 1979). At high flows pools tend to be narrower and deeper than other parts of the channel, with convergent secondary currents that force high velocity streamlines to the bed near the center of the channel creating shear stress conducive to scour (Keller 1971). In contrast, riffles tend to be broader and shallower than average, with divergent secondary currents that promote mid-channel deposition (Richards 1982). Velocities and shear stress in riffles typically exceed those in pools at low to moderate flows due to steeper gradients and turbulence associated with shallow water depth and particle roughness (Richards 1982).

The pool tailouts and pool lateral bars in Kennedy Creek appear similar in size and shape before and after peak flows, obscuring their dynamic nature. We believe the dynamic nature of these areas is a consequence of relatively high availability of easily transportable bedload (sand and small gravel), that currently exists in Kennedy Creek. Past continental glacial deposits provide ample and non-cohesive material for recruitment into the channel from the stream embankments. Significant channel erosion occurred during the Thanksgiving Day storm of 1990 and many large bars deposited during that event are being reworked by subsequent peak flows and captured by the active channel. Deposits surrounding pools in Kennedy Creek appear to be functioning as transient sediment storage zones, evacuating on the ascending limb of the hydrograph and reforming and accumulating on the descending limb.

We hypothesize that the cycle of sediment accumulation and scour in the pool margins is due to the small diameter bedload in Kennedy Creek and changes in relative shear stress between pools and riffles associated with velocity reversal (Keller 1971). Small diameter bedload

continues to move through the riffles as storm flows recede and accumulates in pool margins because shear stress in the pools is no longer competent to transport it. The resulting deposits are scoured when shear stress in the pools increases during the next storm, and the cycle begins again.

Differences in the magnitude of scour and active bed depth between Sites A and B may be related to differences in reach scale morphology and the amount and location of coarse woody debris in the active channel. In Brice's (1984) classification scheme, Site A is a sinuous point bar channel, on the basis of the relatively narrow channel, absence of mid-channel bars, and the presence of bare point bars at bends. Site B in Brice's scheme would be a sinuous braided channel, on the basis of the wide channel, mid-channel bars, and side channels. However, some of these characteristics may be closely associated with the greater amount of woody debris in Reach B. In Montgomery and Buffington's (1993) classification scheme, both Site A and B are pool-riffle channels and as such have a wide array of response potential (including depth of scour or braiding) to changes in sediment supply, discharge, and obstructions.

The effect of scour on salmonid survival to emergence extends beyond actual physical displacement of incubating embryos. Scour and subsequent deposition of bedload material above the egg pockets is a major process by which fine sediments may have an impact (Lisle 1989). In the absence of scour, sand infiltrates a clean gravel bed only to a depth of about 10 cm (Beschta and Jackson 1979). Removal of the covering layers of gravel, exposes the egg pocket to intrusion of fine sediments, particularly in streams that have large quantities of sand in transport such as Kennedy Creek. During deposition of a gravel mixture rich in sand, the interstices in the gravel are more thoroughly filled with sand than is possible through *infiltration* alone, creating a formidable obstacle to emergence (Lisle 1989). In a sand rich system like Kennedy Creek, these effects may be equal to or greater than the primary scour effect.

### **Implications for Forest and Fisheries Management**

Streambed scour is a natural fluvial process with which salmonids have coexisted throughout their evolution. However, because their choice of spawning locations and the depth to which they can bury their eggs is limited, they are vulnerable to changes in frequency and magnitude of streambed scour. Since many productive salmon streams (pool riffle channels) can potentially respond to changes in basic channel inputs by increasing the depth of scour (Montgomery and Buffington 1993), a more thorough understanding of this subject is needed. Forest practices that create higher peak flows or more frequent sediment transporting discharges should be avoided to guard against increased depth of scour.

Fisheries managers should also consider that large numbers of spawning salmon may have a considerable effect on the character of their incubation environment, especially in years of relatively minor storm events. Changes to channel morphology from salmon spawning were of a similar magnitude and nature as those resulting from the small peak flows we observed. Salmon spawning is hastening the transition from the disturbed channel left after the large storm events of 1990 to a morphology in equilibrium with smaller, more frequent peak flow events. Fisheries management goals should consider the role of the animal itself in determining the long term productivity of stream habitat. The effect of selective fisheries, those that remove the larger individuals from a population, are an especially serious threat to stocks produced from streams with accelerated scour patterns. The progeny of larger females, that bury their eggs the deepest (van de Berghe and Gross 1984), may have the best likelihood of survival in these environments.

### **Acknowledgments**

Many individuals participated in aspects of this project. For assistance with field work, we thank Andrew Hendry, Larry Dominguez and Gordy George. We thank Paul Butler, Gino Lucchetti, C. Jeff Cederholm, David Montgomery for helpful comments on the study and for review of the manuscript. The research was funded by the Washington Department of Natural Resources, the U.S. Forest Service, the Washington Forest Protection Association, and the H. Mason Keeler Endowment to Thomas Quinn. We are also grateful to the Simpson Timber Company for permission to work on their land

## Chapter II.

### Winter Survival of Coho Salmon in Big Beef Creek

#### Part A. Survival and Growth of Overwintering Juvenile Coho Salmon Marked with Sequential Coded-Wire and Passive Integrated Transponder Tags

N. Phil Peterson, Earl F. Prentice and Thomas P. Quinn

##### Abstract

Wild juvenile coho salmon Oncorhynchus kisutch were marked with either sequential coded-wire (s-CW) tags or passive integrated transponder (PIT) tags in two successive years to assess possible differences between tag types in growth and survival from fall to spring in a natural stream. Survival, estimated from recovery of outmigrants, varied between years (25.4% in 1990-1991 and 42.1% in 1991-1992) but there was no difference in apparent survival between tag types in either year. Weight gain from fall until emigration from the stream the following spring also varied between years (0.021 and 0.028 g/d in 1990-1991 and 1991-1992, respectively; final weights: 4.55 g in 1990-1991 and 6.01 g in 1991-1992) but growth did not differ between tag types. Differences in survival and growth were not detected in even the smallest size class tagged (53 - 70 mm). We conclude that coho salmon as small as about 2.8 g and 65 mm fork length can be marked with s-CW or PIT tags without a difference in growth or survival.

### Introduction

Studies of fish growth, survival, migration and other forms of behavior routinely require marking of the fish, for which a wide variety of techniques are available (Parker et al. 1990). Marking often requires a compromise among features including cost of the mark itself, cost of data retrieval, minimum size of fish that can be marked, effects on growth and survival, longevity of the mark, visibility and other factors. One common mass-marking technique is the coded wire (CW; Northwest Marine Technology, Inc., Shaw Island, Washington) tag (Johnson 1990). These 1.1 mm long tags, inserted into the cranial cartilage of juvenile salmonids, generally are used to identify large groups of fish. The tags can also be manufactured to contain sequential codes (sequential or s-CW herein) for studies where individual recognition is required.

In Pacific salmon *Oncorhynchus* spp., recovery of information from the CW tag requires that the fish be killed. If the population is in jeopardy, this may be unacceptable. An alternative to the s-CW tag is the passive integrated transponder (PIT) tag (Prentice et al. 1990a). This tag (11 mm long, 2.1 mm diameter) is an integrated circuit chip and an antenna encapsulated in a glass tube and is injected ventrally into the fish's body cavity. The tag is detected and its code read electronically, making the data available to the user immediately without killing the fish. Laboratory studies revealed no effect of the PIT tag on growth, survival or swimming performance of juvenile chinook salmon *O. tshawytscha*, sockeye salmon *O. nerka* and steelhead trout *O. mykiss* about 70-100 mm long (Prentice et al. 1990a). Studies on the Columbia River indicated that the survival of PIT-tagged chinook salmon and steelhead was similar to controls or fish marked with freeze brands. However, the tests were of short duration (14 d) and survival of all groups was high (about 80-100%; Prentice et al. 1990a).

Concerns about the effects of land-use practices on salmonids (Salo and Cundy 1987; Meehan 1991; Naiman 1992) have encouraged researchers to define the factors affecting salmon growth and survival. Interannual variation in winter survival of coho salmon *O. kisutch* was correlated with the mean length of the fish at the end of the summer (Hartman et al. 1987) but no individual data were collected. To study the growth and survival of individual coho salmon from the end of the summer to the following spring, we required unique marks on small fish. This paper reports a comparison of the suitability of PIT and s-CW tags for assessing growth and survival of wild coho salmon in a natural environment.

### Methods

Our research was carried out in Big Beef Creek, an 18 km stream draining into Hood Canal from the Kitsap Peninsula, Washington. During 1-5 October, 1990 and 1991, wild coho salmon were seined from pools in Big Beef Creek below Lake William Symington. The salmon were anesthetized with MS-222, measured for weight ( $\pm 0.1$  g), and fork length ( $\pm 1$  mm). Equal numbers of fish from each pool were randomly assigned to receive either a s-CW or PIT tag each day. The PIT tags were inserted with a hand-held 12-gauge hypodermic needle and modified syringe (Prentice et al. 1990b). The s-CW tags were implanted with hand-held 24-gauge hypodermic needle and modified syringe after excision of the adipose fin. The s-CW tags were pre-loaded into a supply of needles each day. Adjacent tags (preceding and following the one implanted) were retained in solid silicone gel for later reading to accurately identify the tag of interest after recovery. Similar numbers of fish received each type of tag from each pool, though the overall numbers tagged varied among pools. All fish were returned to the pools where they had been collected, usually within 30-60 min of capture.

Coho salmon smolts generally leave Big Beef Creek between 15 April and 15 June (Washington Department of Fisheries, unpublished data). During that period, a permanent weir was operated above the mouth of the stream. Most coho salmon reside in the stream for one year, hence we checked all smolts for tags in 1991 and 1992. A Destron/IDI hand-held interrogator detected the PIT tags and the fish were also passed through a stronger, dual coil, in-line pipe detector (Biomark, Inc., Boise, Idaho), and then released. A missing adipose fin indicated the presence of an s-CW tag. Those fish were killed and the tags located with the aid of a magnetic detector (Northwest Marine Technology) and removed.

Individual growth was determined by the difference between fall and spring lengths and weights. Survival was estimated by the proportion of fish tagged in the fall that were recovered in spring. It is possible that some coho salmon migrated downstream before or after the smolt sampling period, thus we could not distinguish such unrecovered fish from mortalities. We assumed that such aberrations in migration timing would be rare and unbiased with respect to tag type, except as revealed by growth differences. We recovered seven age-2 smolts that had been marked in 1990 (three s-CW and four PIT tagged). Of the parr marked in 1991, no s-CW tagged individuals were recovered as age-2 smolts (they were not examined for PIT tags). Age-2 smolts were omitted from analysis because of their rarity and the difficulties in comparing their survival to that of age-1 smolts.

### Results and Discussion

The average fish size at the time of tagging differed between years (74.1 versus 76.8 mm,  $t = 6.73$ ,  $P < 0.001$ ; 4.2 versus 5.2 g,  $t = 13.29$ ,  $P < 0.001$ , in 1990 and 1991, respectively) but did not differ between tag types in a given year ( $P > 0.05$  for length and weight in each year). Overall apparent survival also varied between years (25.4% in 1990-1991 versus 42.1% in 1991-1992,  $X^2 = 43.77$ ,  $P < 0.001$ ). As a result of the interannual variation, we analysed each year's data on size and apparent survival separately (Table II-A-1). There were no differences in length or weight of smolts between tag groups in spring of either year ( $t$ -tests,  $P > 0.05$ ). Similarity in final size could mask a difference in growth rate if the tag groups differed in their dates of emigration. However, the median residence times (tagging date to capture date at the smolt trap) were 216 and 215 d for the s-CW and PIT tag groups in both years, respectively. Growth rate (weight gain/d) was also similar in both years: (21.0 and 20.9 mg/d for s-CW and PIT tagged fish in 1990-1991, and 28.4 and 27.7 mg/d in 1991-1992;  $t$ -tests,  $P > 0.50$ ). With the sample sizes and variances observed, we had a 90% chance of detecting differences of about 5 mg/d at  $\alpha = 0.05$  (Zar 1984).

The proportions of PIT and s-CW tagged fish recovered in spring did not differ in either year ( $X^2$  tests,  $P > 0.05$ ). Our ability to detect a difference in recovery was affected by the sample sizes and the magnitude of the difference. In 1991 and 1992 we recovered 28.1% and 42.5% of the s-CW tagged fish, and 22.6% and 41.8% of the PIT tagged fish, respectively. At our sample sizes, recovery of 21.5% or fewer in the PIT tagged group in 1991 and 35.0% in 1992 would have caused us to reject the null hypothesis of no effect at  $P < 0.05$ .

Table II-A-1. Survival (as estimated by percent of marked fish recovered), mean fork length (mm) and weight (g) of juvenile coho salmon marked in fall with passive integrated transponder (PIT) and sequential coded wire (s-CW) tags and recaptured the following spring in Big Beef Creek, Washington. Standard deviations are given in parentheses.

Years	Tag	Number tagged	Percent Recovered	Length		Weight	
				fall	spring	fall	spring
1990-91	PIT	358	22.6	74.6 (7.3)	96.4 (7.1)	4.17 (1.44)	8.99 (2.01)
	s-CW	359	28.1	73.6 (7.8)	96.5 (8.8)	4.15 (1.45)	9.07 (2.39)
1991-92	PIT	340	41.8	77.2 (7.2)	105.5 (7.7)	5.26 (1.46)	11.36 (2.53)
	s-CW	334	42.5	76.4 (7.5)	105.2 (7.5)	5.15 (1.49)	11.21 (2.45)

No difference in growth or recovery was detected between tag types but we were concerned that there might have been a difference in small fish that was masked when their results were combined with those of larger fish (presumably less affected by PIT tags). We therefore separated the data into three size-classes of fish: < 70, 70-79, and > 79 mm at the time of tagging (range 53 - 116 mm, though not all combinations of tag-type and year included this entire range). There were no differences in recovery between tag types in either year in any of the three size-classes ( $X^2$  tests,  $P > 0.05$  in all cases). Differences in weight gain of up to 1.1 g were observed between tag types within size classes, but the differences were not significant (standard deviations were about 1-3 g) and even the smallest size class showed no effect; s-CW-tagged fish gained 5.6 and 5.8 g in the two years, compared with 4.5 and 6.2 g for the PIT-tagged fish. Coho salmon as small as 58 mm and 2.4 g (PIT tag) and 56 mm and 2.3 g (s-CW tag) at the time of tagging were recovered as smolts but we cannot rule out an effect in such small fish owing to the sample size. Thus, for coho salmon larger than about 65 mm fork length and 2.8 g, no difference in growth or survival between tag types was apparent over seven months in a stream with significant natural mortality. This supports earlier findings (Prentice et al. 1990a) regarding the suitability of PIT tags for salmonids of this size.

Ideally, we would have compared the survival and growth of fish receiving each tag type to untagged controls. It would be impossible to know the exact number of untagged fish in the creek and this number would be needed to compare survival rates. It is possible to compare the mean size of tagged and untagged smolts but this assumes that the tagged fish were representative of the entire stream's production. Untagged smolts from Big Beef Creek were larger than the means of our tag groups in both years (112.6 and 116.1 mm in 1991 and 1992, respectively; David Seiler, Washington Department of Fisheries, personal communication). However, these figures do not demonstrate that tagging reduced growth, as we avoided collecting fish from certain areas (notably reaches above Lake William Symington) that produce unusually large smolts (Chapter III-B). The absence of these larger smolts in our samples precluded meaningful comparison between tagged and untagged fish.

The overall results showed no effect of tag type on growth and recovery but some adjustment of the data was necessary. We held 58 fish for 72 h and no PIT or s-CW tags were lost during this time period. However, 3% of the smolts recovered with missing adipose fins had no s-CW tags. Comparison of these fish with ones bearing tags indicated that the fins had been clipped and were not natural vestigial adipose fins. We adjusted the estimate of recovery/survival to reflect this level of tag loss. The adipose fins of the PIT tagged fish were not removed so no such adjustment was made. During the first 15 d of the 1991 smolt season, detection of PIT tags was hampered by exclusive use of a single, hand-held detection system. Subsequent use of a dual coil, in-line system indicated that the hand-held system detected 80% of the tags. In making survival comparisons, we expanded PIT tag recoveries during this 15 d period to account for undetected fish. This adjustment increased the estimated recovery by only four fish and did not alter the statistical conclusions.

In addition to the problems of tag loss and detection associated with the two types of tags, other attributes became apparent during the study. The s-CW tag was suitable for smaller fish than is the PIT tag (Buckley and Blankenship 1990). PIT tags were initially more costly (ca. \$3-5/tag versus about \$0.05 for s-CW tags in quantities of 100,000). The amount of time required to insert the tags was similar: about 5-15 s/tag after the fish had been anesthetized. PIT tag data were retrieved with an electronic device and were available for analysis immediately but the s-CW

tag had to be located, dissected from the fish and examined under a microscope (about 3 min/tag). Unless this was done at the time of capture, the fish had to be identified, preserved and stored for subsequent processing. Moreover, the manufacture of the s-CW tag is such that tags on either side of the one that was implanted must be retained and read to identify the individual fish. This additional procedure required purchase, retention and storage of large numbers of tags in an ordered sequence. On balance, the PIT tag seems particularly suitable if killing the fish is not acceptable and the initial cost of the tags is tolerable.

#### **Acknowledgments**

For assistance with field work, we thank Shelly Spalding, Andrew Hendry, David Brastow, Larry Dominguez, Gordy George and Coleman Byrnes; Steven Neuhauser and Clair Landry. We thank H.Lee Blankenship and Robert Bugert, and Sandra Downing for comments on the report. The research was funded by the Washington Department of Natural Resources, the U.S. Forest Service, the Bonneville Power Administration and the H. Mason Keeler Endowment to Thomas Quinn.

## Chapter II.

### Winter Survival of Coho Salmon in Big Beef Creek

#### Part B. The Influence of Habitat Complexity and Fish Size on Over-winter Survival and Growth of Individually-Marked Juvenile Coho Salmon in Big Beef Creek

N. Phil Peterson and Thomas P. Quinn

##### Abstract

Wild juvenile coho salmon were individually marked with passive integrated transponder and hand implanted sequential coded wire tags in October 1990 and 1991 to evaluate the effects of habitat complexity and fish size on winter survival in Big Beef Creek, a tributary to Hood Canal, Washington. Data on large woody debris (LWD) count and volume, habitat unit type and residual pool depths were collected at the habitat unit (individual pool) level in 1990, and at both the unit and stream reach level in 1991. Fish were subsequently recaptured as smolts with a permanent weir at the mouth of the stream. Overall survival differed between years (26 % in the 1990-91 season and 47 % in the 1991-92 season,  $X^2 = 61.08$ ,  $P < 0.01$ ). Survival also varied among habitat units in 1990-91 and among units and reaches in 1991-92. A strong longitudinal gradient in survival was observed in both years; fish that resided farthest from the estuary had the highest probability of survival. No pattern between survival and end-of-summer habitat character was apparent in either year at the habitat unit level, but survival was positively correlated with habitat complexity (number of habitat units) and LWD volume ( $r^2 = 0.76$ ,  $r^2 = 0.85$  respectively) at the reach level (defined as the 500 m downstream from the tagging site) in 1991-92. Distance from the estuary co-varied with habitat complexity, preventing us from ascertaining which factor had the primary influence on survival. In addition to the habitat effects, larger fish generally survived at a higher rate than smaller individuals. Survivors were larger than non-survivors (length; 76 vs. 74 mm, weight; 4.5 vs. 4.0 g) at time of tagging in 1990-91, but not in 1991-92 (length; 78 vs. 77 mm, weight; 5.3 vs. 5.2 g).

### Introduction

Juvenile coho salmon (*Oncorhynchus kisutch*) generally spend one or two years in freshwater prior to seaward migration and it is generally believed that their populations are limited by the amount of freshwater rearing habitat available (Marshall and Britton 1990). Stream size seems to affect the slope of this relationship but it is generally agreed that carrying capacity is set during the summer low flow period (Smoker 1955) by the amount of pool space, (Nickleson et al. 1979). As a result of this kind of freshwater rearing space limitation, production functions for coho stocks are typically asymptotic. However, around the asymptote, there is often a substantial amount of variability, much of which may be attributed to interannual variation in winter survival. Winter freshets frequently cause streambank erosion, streambed scour and fill, and rearrange accumulations of woody debris. All of these physical effects are a part of the natural disturbance regime typical of channels in the Pacific Northwest and although they occur sporadically, they are seasonally predictable.

Juvenile coho salmon often move from summer nursery areas in streams to off-channel and flood plain habitats in winter (Cederholm and Scarlett 1982; Peterson 1982) but many coho overwinter in stream habitats (Scarlett and Cederholm 1984; Brown and Hartman 1988). Juvenile coho exhibit a decided preference during the winter for deep pools with substantial accumulations of woody debris (Bustard and Narver 1975; Murphy et al. 1986). Experiments by McMahon and Hartman (1989) and Shirvell (1990) suggested that preferences for locations in streams near woody debris is a response to low water velocities created in the lee of debris. While off-channel habitat improves overwinter survival and growth for a segment of the population, the instream woody debris that characterizes streams in unlogged, forested watersheds (Bilby and Ward 1989, 1991) may be nevertheless important for the majority of the population. However, the association of coho salmon with woody debris is not direct evidence that the debris reduces winter mortality.

Removal of mature streamside forests often alters the amount and character of woody debris in streams draining managed forests (Bisson et al. 1987). While loss of woody debris from streams may reduce the abundance of juvenile salmonids (Elliott 1986; Dolloff 1986), growth and production, particularly in summer, may also be strongly influenced by temperature (Holtby 1988), prey populations (Murphy et al. 1986; Bilby and Bisson 1987, 1992), fry density and freshets, and interactions among these factors (e.g., Scrivener and Andersen 1984). Holtby (1988) indicated that over-winter survival of 0+ coho in Carnation Creek, British Columbia could be explained in large part by the population's average individual size at the end of the summer, independent of habitat conditions. Without information on the survival and growth of individuals, it is difficult to estimate the population level changes that might result from habitat alteration, because low parr densities at the end of summer might be offset by increased overwinter survival associated with large body size.

Woody material and the habitat complexity associated with it are thus inter-related with fish size in the ecology of juvenile stream-dwelling salmonids in complex ways (Bisson et al. 1987; Hartman et al. 1987). To better understand the interaction between summer growth and physical habitat on the overwinter survival of juvenile coho salmon, we measured and individually marked coho salmon at the end of the summer growing season from various habitats within a stream and monitored their size and survival to emigration as smolts. Our specific hypotheses were that overwinter survival and growth would be positively correlated with body size and the complexity of the habitat unit and stream reach where the fish were collected at the end of the summer.

## Methods

### Study area

Big Beef Creek is located on the Kitsap Peninsula, Washington and flows into Hood Canal (Figure II-B-1). It has a basin area of approximately 38 km<sup>2</sup> and contains 18 km of main stream channel, 8 km upstream and 10 km downstream of Lake William Symington, an artificial impoundment of 198 ha constructed in 1965. Fish pass over the 10 m dam and into the basin above the lake via a pool and weir fishway. Big Beef Creek's watershed is lower than 400 m elevation and the stream's dominant storm flows are derived from winter rains between November and March. A maximum flow of 21 m<sup>3</sup>/second was recorded in 1971 and summer low flows near the mouth average 0.08 m<sup>3</sup>/second. The 50 year flood has been estimated at 56 m<sup>3</sup>/second (Madej 1975). Above Lake Symington the main stream channel is very flat (0.2%), and is connected to extensive riparian wetlands. Below Lake Symington the stream gradient lessens gradually from 1.5% in reaches below the dam to 0.5% near the mouth. Several small, relatively steep and intermittent tributaries enter Big Beef Creek in the 10 km below Lake Symington.

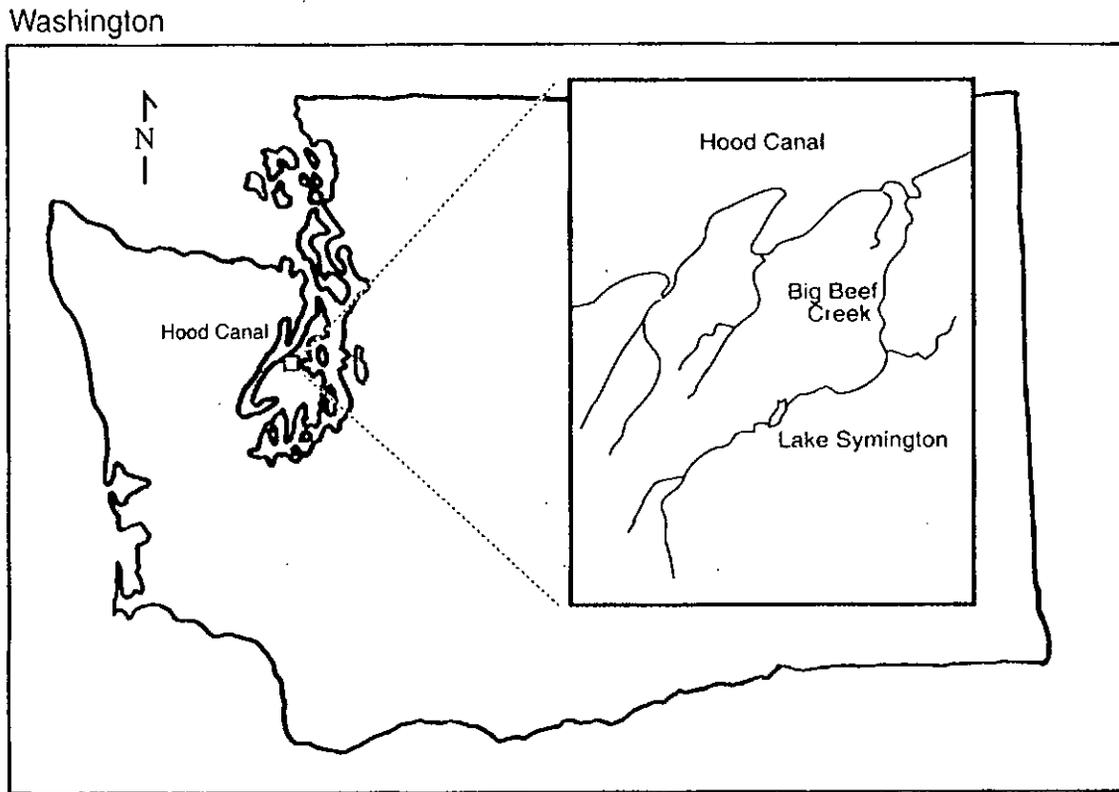
The basin's history of settlement began in the late 1800s. In some of the lower stream reaches, coarse sediment generated during the initial logging in the basin has accumulated in the stream channel and is gradually being transported through the system (Madej 1975). Numerous old cedar stumps on the stream banks provide evidence of the original conifer riparian forest which has regrown to red alder, (*Alnus rubra*), vine maple (*Acer circinatum*), and big leaf maple (*Acer macrophyllum*). Second growth western hemlock (*Tsuga heterophylla*), western red cedar (*Thuja plicata*), and Douglas fir (*Pseudotsuga menziesii*) make up a smaller but increasingly dominant component. In-channel large woody debris (LWD) reflects the existing riparian forest but some large pieces of cedar remain from pre-logging times.

### Fish tagging and recovery

Juvenile coho salmon were captured in the first week of October 1990 and 1991 by stick seine. Immediately after capture and anesthesia with MS-222, fish were implanted with either a sequential coded wire (s-CW) or a passive integrated transponder (PIT) tag, allowed 30-60 minutes to recover and then returned to the pool where they had been collected. A 12 gauge hand-held hypodermic needle and syringe were used to implant the PIT tag into the body cavity (Prentice et al. 1990a), and a 24 gauge needle and syringe were used to implant the s-CW tag into the fish's cranial cartilage. The adipose fin of all s-CW tagged fish was excised. A total of 728 and 955 fish were tagged in 1990 and 1991, respectively, evenly divided between s-CW and PIT tags. Fish were tagged from 14 pools in three stream reaches and 21 pools in five reaches in 1990 and 1991, respectively. Fork length, weight and home pool were recorded for each fish.

Marked fish were recovered the following spring at a permanent weir at the mouth of the stream. The weir was operated from April 7 to June 14, 1991 and to June 15, 1992. All individuals were electronically scanned for the presence of PIT tags. The codes from individuals carrying PIT tags were recorded and the fish were weighed and measured before being released. All adipose clipped fish were weighed and measured and then sacrificed for subsequent s-CW tag extraction and reading. Survival was calculated as the proportion of fish tagged in the fall that

Figure II-B-1. Location map of Big Beef Creek.



were recovered in the spring. Individuals migrating downstream prior to the smolt sampling period would be classified as mortalities. Some smolts migrate as early as the beginning of March (Seiler et al. 1984) but such fish are rare. Nevertheless, the survival estimates must be regarded as minimum estimates.

Parametric statistics were used to test differences in fish size (length and weight) for various treatment groups, including tag type, fish size, home pool and survival status. The survival of treatment groups was analyzed for deviations from expected values with chi square goodness of fit tests. Correlation analysis and stepwise multiple regression was used to relate fish survival to various habitat parameters.

### Habitat

A variety of habitat elements commonly used to describe streams in monitoring programs were measured at the habitat unit level (e.g., individual pool or glide) in 1990 and both the unit and the stream reach level in 1991. Habitat units were classified according to Bisson et al. (1982); most coho were taken from scour pools of various configurations, a plunge pool, and several glides. Bank full channel width, low flow pool dimensions and residual pool depth were measured for each unit (Lisle 1990). An inventory of all the CWD in the study reaches was conducted and the volume of each piece of wood within the bankfull channel and below the bankfull depth (corresponding to influence zones 1 and 2 of Robison and Bestcha 1991) was calculated using large calipers.

In 1991, each habitat unit was assigned an associated reach, the attributes of which were used for correlation with survival rates of associated unit populations. These reaches were defined as that 500 m section of stream immediately downstream from the corresponding habitat unit, based on the finding that most juvenile coho in two small Olympic Peninsula streams spent the winter within 500 m downstream of their location at the onset of winter (Scarlett and Cederholm 1984). However, some of the lowermost reaches were less than 500 m above the estuary and were only measured to the counting fence at the upper edge of the estuary. Owing to this variation in reach size measured, we standardized our reporting of habitat reach characteristics to 100 m length of stream (e.g., CWD volume/100 m). Most reaches shared some attributes since individual habitat units were usually less than 500 m apart. Over 3 km of stream was inventoried in reach level surveys in 1991. No habitat surveys were done for the units above the lake because we assumed the fish would over-winter in the lake or the numerous riverine wetlands.

### **Results**

Overall survival varied between years (26 % in the 1990-91 season and 47 % in the 1991-92 season,  $X^2 = 61.08$ ,  $P < 0.01$ ). We therefore analyzed each year's data separately for effects of tag type, size, and habitat. No differences in growth or survival could be attributed to effects of tag type in either year (Chapter II-A). As a result of this finding, and because the mean length and weight of fish at the time of marking differed between years (length;  $t = 8.49$ ,  $P < 0.01$ , weight;  $t = 14.82$ ,  $P < 0.01$ ) and at the time of smolting (length;  $t = 11.58$ ,  $P < 0.01$ , weight;  $t = 9.80$ ,  $P < 0.01$ ), we pooled data by tag type and analysed size and habitat effects within years.

Fish in larger size classes survived at a significantly higher rate than smaller fish in 1990-91 ( $X^2 = 15.40$ ,  $P < 0.01$ ) but not in 1991-92 ( $X^2 = 0.98$ ,  $P = 0.91$ ; Figure II-B-2). Similarly, the average size at tagging between non-survivors and survivors differed in 1990-91 (length;  $t = -$

3.15,  $P < 0.01$ , weight;  $t = -3.47$ ,  $P < 0.01$ ), but not in 1991-92 (length;  $t = -1.18$ ,  $P = 0.24$ , weight;  $t = -1.08$ ,  $P = 0.28$ ). In general, fish maintained their relative size ranking within the population, showing little tendency for small individuals to achieve size parity by time of smolting. Rather, the smaller fish at the end of the summer period were the smaller smolts. The exception, however, was the fish tagged upstream from Lake Symington. They were initially rather small but grew considerably more than their stream-dwelling cohorts over the winter period (Figure II-B-3).

Survival of fish from discrete habitat units varied in both years (1990-91;  $X^2 = 42.6$ ,  $P < 0.001$ , 1991-92;  $X^2 = 51.55$ ,  $P < 0.01$ ). Habitat variables measured in the individual pools or habitat units were poorly correlated with survival (e.g., Figure II-B-4). No correlations were found with any of the variables tested: residual pool depth, pool volume, CWD count, and CWD volume. The survival in 1991-92 however, correlated well with three attributes at the reach level; distance from the estuary ( $r^2 = 0.75$ ; Figure II-B-5), number of habitat units below the tagging site ( $r^2 = 0.81$ ; Figure II-B-6), and CWD volume ( $r^2 = 0.85$ ; Figure II-B-7).

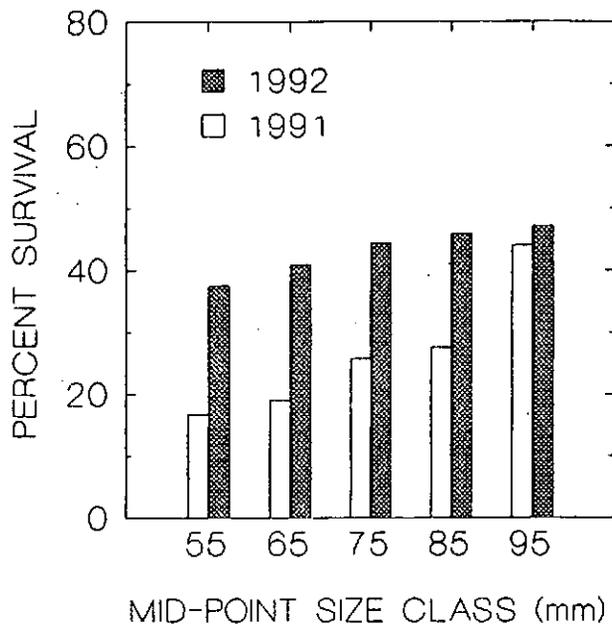
The median emigration dates were the 127th and 120th days of the year in 1991 and 1992, respectively (Figure II-B-8). There was no clear relationship between smolt length and emigration date (compare with Figure IV-6). The fish that had been tagged above the lake were captured at the weir one week later than the stream fish.

### Discussion

The salient findings of the study were the positive correlations between body size, distance from the estuary and end-of-summer habitat complexity with survival, and the variation in survival between years. Hartman et al. (1987) reported that the interannual variation in average survival of coho was related to body size but no data on individual fish were available. Our results indicated that the fish that were large at the end of the summer generally maintained their size advantage to the smolt stage. The exception to this pattern was the fish tagged above Lake William Symington. They were relatively small at the end of the summer but were larger than average as smolts, indicating higher growth than fish tagged below the lake. We cannot be certain where any of the fish actually spent the winter but such rapid growth would be consistent with pond or lake residence (Peterson 1982; Swales et al. 1988; Irvine and Ward 1989). The effect of size on survival was more pronounced in 1990-1991, when parr were small, than in 1991-1992 when they were larger. The effect of size also appeared to weaken within years at larger sizes.

The size advantage of parr at the end of the summer may have ramifications for their entire lives. Their size affected their likelihood of overwinter survival and size as smolts. Marine survival is positively correlated with size in coho salmon (Mathews and Ishida 1989; Holtby et al. 1990), as it also is with chum (Healey 1982) and sockeye salmon (Henderson and Cass 1991), cutthroat trout (Tipping and Blankenship 1993) and steelhead (Ward and Slaney 1988; Ward et al. 1989). We did not observe a relationship between smolt length and date of capture at the weir.

**Figure II-B-2.** Overwinter survival of juvenile coho salmon of different sizes at the end of summer in Big Beef Creek.



**Figure II-B-3.** Relationship between weight of coho salmon parr at the end of the summer 1991 and their weight as smolts in 1992. Individual parr tagged above and below Lake Symington are classified as "lake" and "stream" fish, respectively.

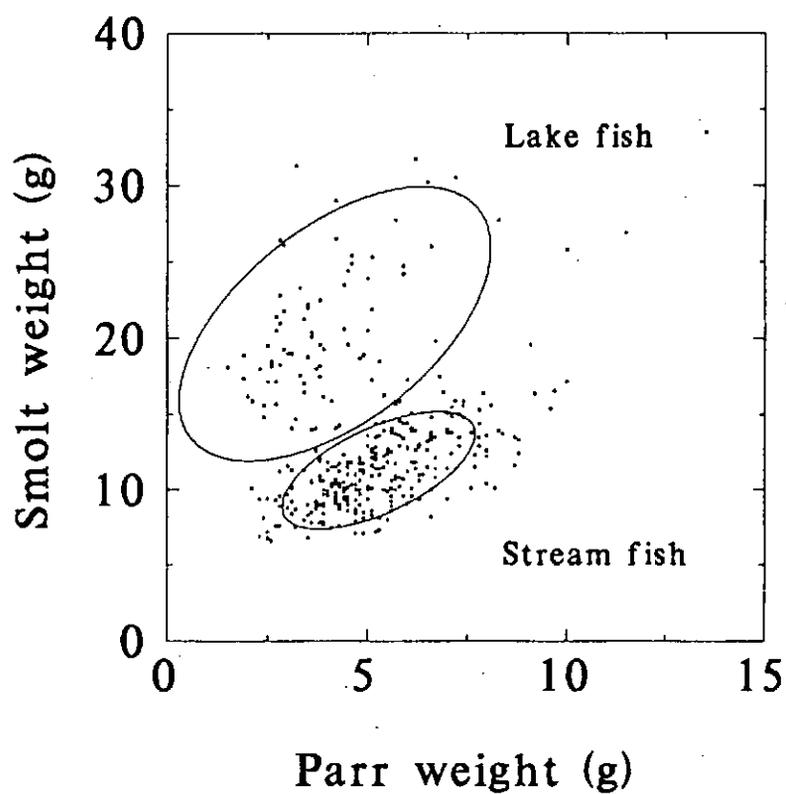


Figure II-B-4. Relationship between residual pool depth (end of summer habitat) and percent recovery (estimated survival) of juvenile coho salmon in Big Beef Creek.

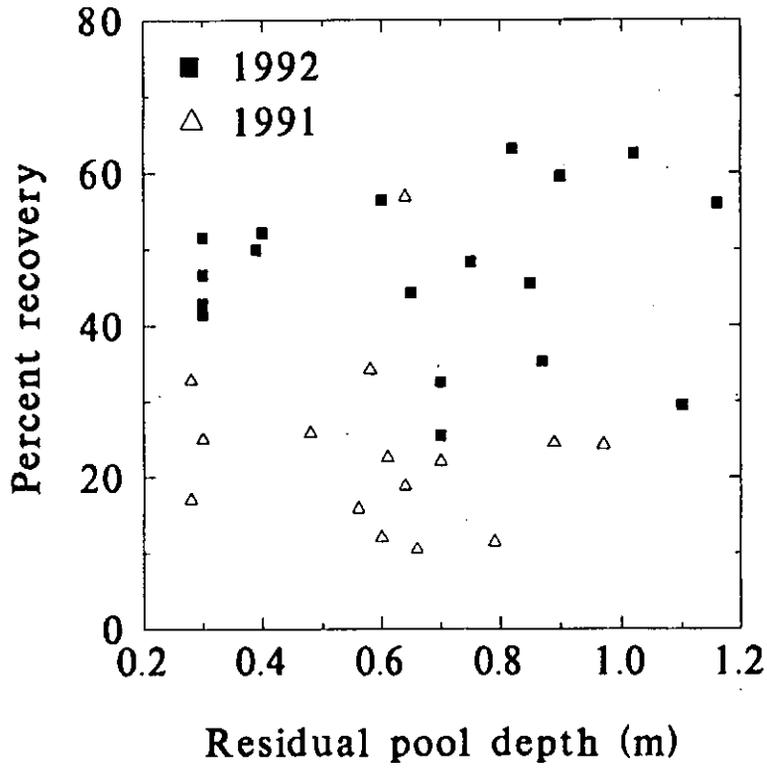


Figure II-B-5. Relationship between overwinter survival of juvenile coho salmon and the distance from the estuary of the unit in which they were caught at the end of the summer.

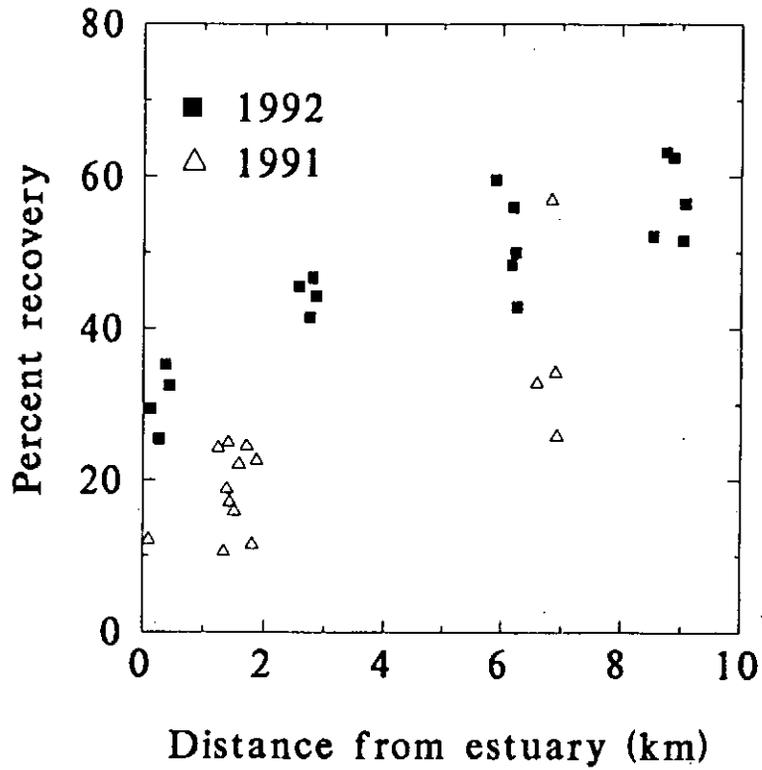
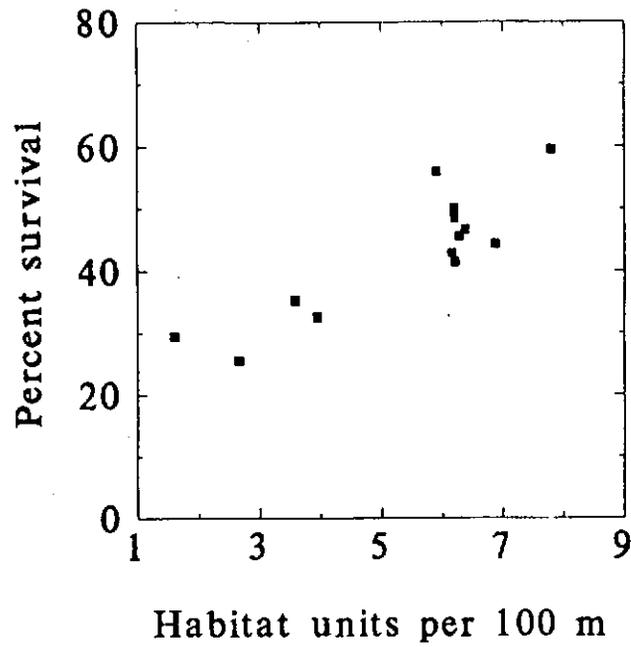
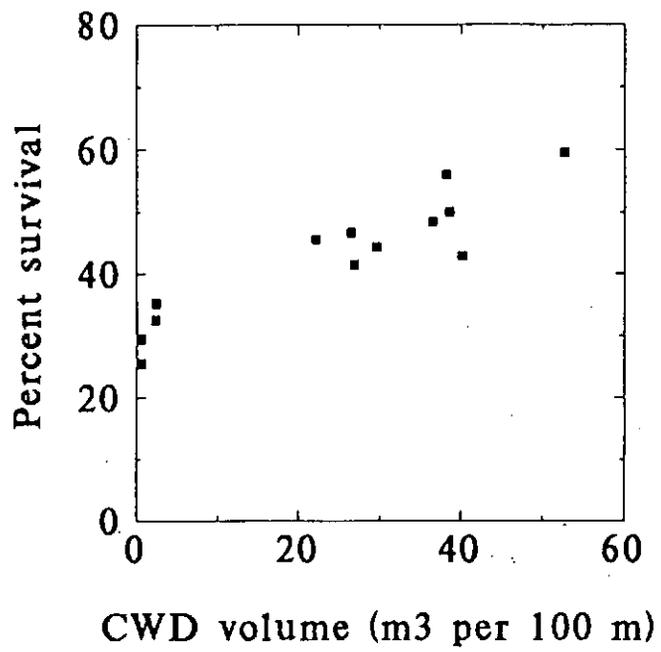


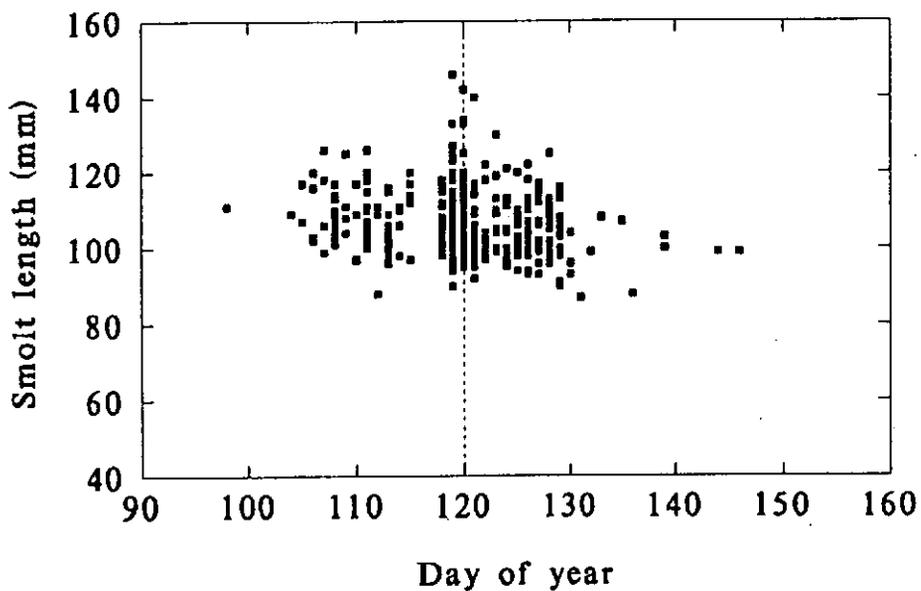
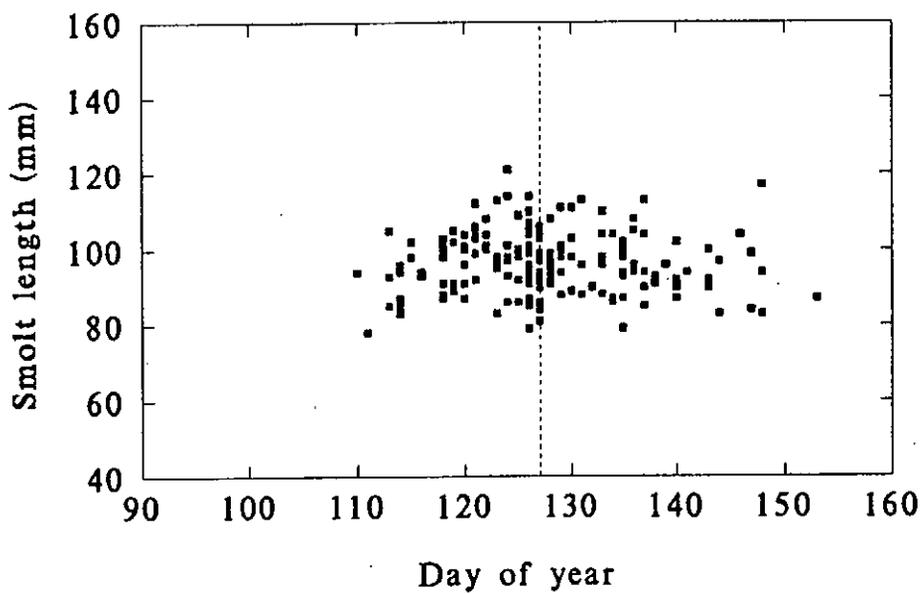
Figure II-B-6. Relationship between overwinter survival of juvenile coho salmon and the number of habitat units per 100 m in the reach downstream of the unit in which they were caught at the end of the summer.



**Figure II-B-7.** Relationship between overwinter survival of juvenile coho salmon and the volume of coarse woody debris per 100 m in the reach downstream of the unit in which they were caught at the end of the summer.



**Figure II-B-8.** Smolt length and date of migration of coho salmon tagged as parr in Big Beef Creek. Dashed lines indicate median migration dates. The two day gap in migration in 1992 resulted from retention of all fish without counting when tagging equipment malfunctioned.



However, there is evidence that large size is associated with early emigration from Big Beef Creek (though the first fish to leave are a few small individuals; Chapter IV), consistent with other studies of coho salmon (Irvine and Ward 1989) and anadromous brown trout (Bohlin et al. 1993). Marine survival is also strongly related to the time of seawater entry (e.g., coho: Bilton et al. 1982; Morley et al. 1988), which is related to smolt size.

The second major finding was the relationship between habitat complexity at the end of the summer and overwinter survival. The affinity of coho salmon for woody debris increases in winter (Bustard and Narver 1975; Heifetz et al. 1986; Murphy et al. 1986; Taylor 1988) but we do not assume that the salmon spent the winter in the habitat units where they were captured and released. Indeed, the correlation with survival was not with the complexity of the fish's immediate environment but rather with the 500 m below the capture point. It is well-known that coho salmon tend to move downstream in fall and overwinter in side-channels, ponds and sloughs (Carnation Creek: Brown and Hartman 1988; interior British Columbia: Swales et al. 1986; coastal Washington: Peterson 1982; coastal Oregon: Nickelson et al. 1992). We do not know where the tagged fish spent the winter but off-channel and side-channel habitat is limited in Big Beef Creek. The structural complexity in the stream may have enabled the coho salmon to maintain position, survive the winter and smolt from main-channel habitat.

One important factor that confounded our interpretation of the role of habitat complexity in overwinter survival was the tendency for simpler reaches to be situated near the mouth of the stream. Channelization work done in 1969 contributed to the simplified habitat in the lowermost 800 m of Big Beef Creek. Even though the stream quickly began to reconfigure itself into the former channel pattern (Cederholm 1972), the lack of CWD may be a persistent effect. It is possible that the fish moving downstream in fall from the lower (simpler) reaches left the stream entirely before they were able to find suitable habitat whereas fish starting farther upstream had a better chance of finding habitat before they reached the mouth of the stream. Emigration in winter would lead fry into the mainstem of a large river but would take them directly into Hood Canal in the case of Big Beef Creek. Such fry might not survive but in any case would not be captured at the fence in spring and so would be classified as mortalities.

It would require a study in a stream with a different configuration of habitat units or a detailed study of the movements of individual fish to disentangle the relationship between survival, proximity to the stream's mouth, and habitat complexity. However, in the absence of such information it seems prudent to assume that some aspect of complex habitat units enhanced the overwinter survival of coho salmon.

#### **Acknowledgments**

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### Chapter III.

#### Experimental Studies of The Roles of Brushy Debris for Stream Fishes

##### Part A. Summer Distribution, Survival and Growth of Juvenile Coho Salmon Under Varying Experimental Conditions of Brushy In-stream Cover

Shelley Spalding, N. Phil Peterson and Thomas P. Quinn

###### Abstract

Woody debris is an important feature of streams, and its presence and abundance have been correlated with the abundance, growth, and survival of juvenile salmonids. To investigate the proximate mechanisms linking brushy woody debris to salmonid fishes, we allowed juvenile coho salmon (*Oncorhynchus kisutch*) to colonize an outdoor experimental stream channel containing riffle-pool units with differing amounts of instream brushy woody debris over a 1-month period in summer. We then fixed densities and monitored growth and survival over a 15-week period. Coho salmon distribution, growth, and survival varied greatly but were not consistently related to brushy debris complexity.

### Introduction

Streams in unlogged, forested watersheds are characterized by abundant woody debris (Bilby and Ward 1989, 1991). As a result of the removal of mature streamside forests and regrowth dominated by alder, the amount and character of woody debris in streams draining managed forests often differs from that in unmanaged forests (Bisson et al. 1987). Other practices such as stream cleaning and log handling (Sedell et al. 1991), as well as storm-related debris flows have also contributed to the loss of woody debris from streams. The combined effect of woody debris reduction on streams has been substantial. Large material can affect the stream's depth, flow and routing of sediment and finer organic material (Elliott 1986; Bisson et al. 1987; Andrus et al. 1988; Bilby and Ward 1989, 1991; Carlson et al. 1990). Brushy material may provide cover from predators and visually isolate salmonids from each other, affecting levels of aggression (Mesick 1988; Dolloff and Reeves 1990), and it may also trap fine material.

Field studies often relate the density of juvenile stream-dwelling salmonids to either woody debris (e.g., Dolloff and Reeves 1990; Bugert et al. 1991), pools or hydraulic conditions associated with large pieces of wood (e.g., Bisson et al. 1988; Shirvell 1990; Taylor 1991; Fausch and Northcote 1992), or food resources associated with it (Nielsen 1992). However, it is not always clear whether the wood has affected the survival of fish or their distribution. Laboratory studies have demonstrated that salmonids, particularly coho salmon *Oncorhynchus kisutch* show an affinity for pools (Bugert and Bjornn 1991; Taylor 1991) or complex cover (McMahon and Hartman 1989), but the link between these responses and survival in the field is weak. While loss of woody debris from streams may reduce the abundance of juvenile salmonids (Elliott 1986; Dolloff 1986), growth and production, particularly in summer, may also be strongly influenced by temperature (Holby 1988), prey populations (Murphy et al. 1986; Bilby and Bisson 1987, 1992), fry density and freshets, and interactions among these factors (e.g., Scrivener and Andersen 1984).

Woody material is related to the ecology of juvenile stream-dwelling salmonids in complex ways (Bisson et al. 1987; Hartman et al. 1987). Only large woody material will structure the stream and form pools in alluvial channels, but both large and smaller, brushy wood may provide protection from predators, though this has not been clearly demonstrated (Bisson et al. 1987). To the extent that woody material provides relief from predation, it may enable fish to spend more time pursuing prey or to pursue them more effectively (Dill 1983; Metcalfe et al. 1987; Angradi 1992). Instream structure may also create velocity patterns providing energetically efficient foraging stations for salmonids (Fausch 1984, 1993), and wood need not be very large to affect local velocities. Woody material may also be related to prey abundance and growth (Nielsen 1992).

Woody debris thus may directly affect fish behavior and population characteristics and it may affect the channel which in turn affects the fish. The relative importance of these functions may vary with the size and characteristics of the debris (e.g., velocity barrier, overhead cover, visual isolation; McMahon and Hartman 1989; Fausch 1993). Time of year strongly affects affinity for cover. Coho salmon, for example, are much more attracted to cover in winter than summer (Bustard and Narver 1975; Murphy et al. 1986; Taylor 1988), coincident with a general tendency to seek off-channel rearing areas (Bustard and Narver 1975). Within species, age may affect cover use. Juvenile Dolly Varden and coho salmon showed increasing affinity for deep water and cover as they grew (Dolloff and Reeves 1990). Finally, there are important differences in responses to cover among salmonid species (Bustard and Narver 1975; Taylor 1988, 1991;

Bisson et al. 1988; Dolloff and Reeves 1990; Bugert and Bjornn 1991; Fausch 1993) To clarify the role of brushy woody debris in the summertime ecology of juvenile coho salmon, we conducted experiments in semi-natural experimental stream channels. Specifically, we tested the hypotheses that distribution, growth and survival are affected by the complexity of brushy material in otherwise similar, unstructured pools. We first conducted a distribution experiment, allowing fry to move throughout two channels with riffle-pool units differing in debris complexity. We then isolated the units, equalized the densities of fry, and conducted a growth and survival experiment.

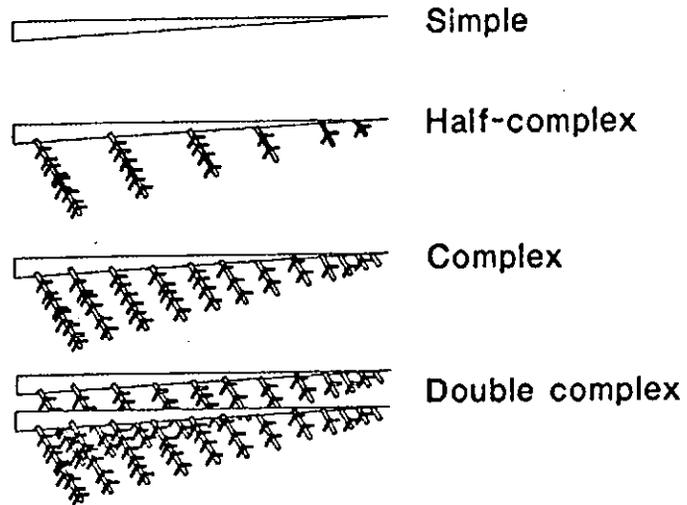
### Methods

Experiments were conducted in a semi-natural experimental stream receiving water from Big Beef Creek in Kitsap County, Washington. The average flow at the inlet was  $0.02 \text{ m}^3/\text{s}$  but additional water entered from springs emanating from the hillside and groundwater yielded an average of  $0.05 \text{ m}^3/\text{s}$  at the outlet during the experiment. The experimental stream was 34 m long and 9 m wide, divided longitudinally to create two parallel channels, designated A and B. Each channel consisted of seven riffle-pool units, designated 1-7 for position from upstream to downstream. The riffles were 2.4 m wide, 1.8 m long, and 0.05 m deep, and flowed into 3 x 3-m pools with a maximum depth of 0.5 m. The substrate was gravel similar in size to that in Big Beef Creek (geometric mean diameter = 35 mm). The seven units in each channel could be separated by screens set on wooden sills or left open to permit fish movement among units but fish could not move from one channel to the other.

The canopy and streamside vegetation were composed of red alder *Alnus rubra*, western red cedar *Thuja plicata* and salmonberry *Rubus spectabilis*. Canopy closure, measured with a spherical densiometer, averaged greater than 90% for all pools. All food came from natural aquatic and terrestrial production. Drifting aquatic invertebrates were sampled six times from each pool with a 1 m long by 0.5 m wide drift net with 240 micron mesh, placed at the the bottom of the riffle at dusk and removed 3 h later. Depth and velocity were measured at the net openings at the beginning and end of each sampling period. Qualitative samples of terrestrial invertebrates were taken during 3-h periods with 36 x 23-cm pans (containing water and a detergent surfacant to prevent insects from escaping) placed on stakes above the surface of the pool, 10 cm downstream of the riffle. Water temperature was recorded and averaged with a datalogger every 30 min in 10 of the 14 units.

Douglas fir "Christmas trees" were used to provide replicable debris to simulate tree tops or material left after logging operations (i.e., not large, channel-forming debris). The needles were removed from the trees and they were sheared in half along the long axis and cut to a length of 1.5 m from the natural top. The trees were then modified to create four different degrees of cover complexity (Figure III-A-1). In the "simple" treatment, all the branches were removed from the tree, leaving only a trunk that tapered from a spike to a diameter of about 10 cm. In the "half-complex" treatment, branches were alternately removed or retained every 15 cm up the trunk. In the "complex" treatment, all branches (except those on the sheared side) were left on, and in the "double complex" treatment, two complex trees were stacked and tied together. One treatment tree was staked into each pool, 0.5 m below the tail of the riffle and 2 cm below the water surface. The sheared side faced upward so that no branches extended above the water; no other cover was present in the units. The location of the treatment units within the streams was determined by generated random numbers.

**Figure III-A-1.** Diagrammatic representation (side view) of the four forms of brushy debris introduced into experimental riffle-pool units.



To initiate the distribution experiment, we collected 807 newly emerged coho salmon fry (mean size of a subsample of 60 on May 8 was 43.6 mm total length and 1.02 g) from Big Beef Creek from April 23 to May 8, 1991. We released 52 or 53 fry into each unit, except that the uppermost unit in each stream received an additional 32 fry to ensure adequate colonization of all treatments after the anticipated downstream-distribution of fry. Live boxes were installed below the bottom units to trap out-migrant fry. Eighteen fry emigrated between May 6-11 and were placed in the uppermost unit of their stream. The decision to return them to the streams was based on concern that high rates of emigration or mortality might result in inadequately populated units for experimental design and statistical analyses, once the redistribution period had ended. However, only one other fry was trapped and relocated upstream during the remainder of the experiment. The distribution experiment ended on May 22, when barriers were placed between all units and the fry were removed, counted and sorted into 5 mm size classes.

On May 23, we placed 56-57 coho salmon fry (mean size: 48.2 mm and 1.26 g) from the distribution experiment in each of the 14 units for the growth and survival experiment. All fry were measured, and equal numbers from each size class were placed into each unit. Unlike the distribution experiment, screened barriers prevented movement between units. At the end of this experiment on September 3, all fish were removed from the units, measured, and weighed. A few sea-run cutthroat trout *O. clarki* fry colonized the stream channels during the growth and survival experiment. These trout were initially much smaller than the salmon (they apparently entered the units through the mesh screen), but by the end of the experiment were comparable in size to the salmon. Accordingly, our analysis of density-related growth of coho salmon included the trout, but the computation of survival rates ignored them. Finally, daytime observations were made of predation from a blind situated at the downstream end of the channel on 36 occasions for a total of 154 h during the growth and survival experiment.

### Results

At the end of the distribution experiment, 788 of the 807 fry stocked were recovered and their density varied among units ( $X^2 = 31.78$  and  $62.64$  for channels A and B, respectively,  $df = 6$ ,  $P < 0.001$  in both cases, Table III-A-1). The densities of fry in the four treatments also differed from random ( $X^2 = 15.70$ ,  $df = 3$ ,  $P < 0.001$ ). Units with simple brushy debris had higher than average density (68.5 fry per unit) but densities in the other treatments were similar (50.7, 54.7 and 49.5 fry per unit in the half complex, complex and double complex treatments, respectively). The high average density observed in simple treatments may have been in part related to the locations of those units; units at the top of one and bottoms of both channels had higher than expected densities and two of these were simple units.

In the growth and survival experiment, fry survival averaged 74% overall and ranged from 63 to 91% in individual units (Table III-A-2). Heterogeneity was not detected among units within any of the four treatments ( $P > 0.38$  in all cases). The numbers of fish surviving in the units were then pooled and no variation among treatments was detected ( $X^2 = 1.66$ ,  $P = 0.65$ ). The slight variation in survival among treatments showed no trend with respect to the amount of cover (79, 70, 69 and 76% for the double complex, complex, half-complex and simple treatments, respectively).

Coho salmon growth in the units was comparable to that observed in wild salmon in Big Beef Creek that season. The experimental fry averaged 3.8 g on September 2 and fry in the creek averaged 4.2 g on October 5 ( $n = 717$ , Peterson and Quinn, unpublished data). Growth varied

among units; ranging from 3.0 to 4.9 g (Table III-A-2). Weights of individual coho varied in units within treatments ( $F = 16.39$ ,  $P < 0.001$ ) and among treatments ( $F = 3.52$ ,  $P = 0.015$ ). However, growth variation among treatments was not related to the degree of cover complexity (mean fry weights: simple, 3.7 g, half-complex, 4.1 g, complex, 3.7 g, double-complex, 3.7 g). Growth was negatively related to coho fry density (Spearman's rank correlation,  $\rho = -0.853$ ,  $P < 0.001$ ), consequently the variation in coho salmon biomass among units (141.3 to 188.1 g) was less than the variation in mean fry weight (1.33-fold vs. 1.63-fold).

The mean number of cutthroat trout was 3.5 per unit but only two units had more than 5 (13 and 19 trout). The abundance of trout showed no pattern with respect to cover complexity. They grew to an average of 3.7 g and were a significant component of the fish biomass in the two units where they were numerous. However, analysis of total fish density and coho biomass showed the same density-dependent pattern indicated by analysis of coho density alone (Spearman's rank correlation,  $\rho = -0.842$ ,  $P < 0.001$ ; Figure III-A-2).

Daytime peak temperatures rose from about 10 to 12° C during the distribution experiment and from 12 to 20° C during the growth and survival experiment. Temperatures in the units followed similar diel and seasonal patterns but the lowermost unit in the A channel tended to be 1 to 2° lower than the upstream units. However, temperatures in the units seemed to play no role in distribution or growth. The dry weight of invertebrate drift did not differ between the two channels (t-test,  $P = 0.76$ ) or among units (ANOVA,  $P = 0.62$ ). Qualitative assessment of invertebrate fall-in indicated that this food resource was also similar among units.

Three avian predators were seen at the channel during the 154 h of observations. Belted kingfishers (*Ceryle alcyon*) made 10 strikes on coho fry in the channel and at least three were successful. A green-backed heron (*Butorides striatus*) was seen on two occasions and eight fry were killed. Two visits by great blue herons (*Ardea herodias*) were observed but no attacks took place. This species is common in the area but were more often seen in the estuary downstream from the channel.

### Discussion

We found no evidence that the distribution of coho salmon fry was affected by brushy debris, nor did the presence of brushy material influence survival or growth. Similarly, Grette (1985) found no relationship between the amount of woody debris cover and the summer distribution of coho salmon fry in Olympic Peninsula streams. Temperature and food abundance were similar among units and hence can be ruled out as factors that might have confounded or biased the results (Wilzbach 1985). The woody debris typically described in field studies is larger than that used in this experiment. Attraction to such large material may reflect the ability of wood to structure the flow, depth and productivity of stream habitats more than affinity of coho salmon for woody debris per se, or any benefits in growth or foraging efficiency associated with the wood. Shirvell (1990) concluded that velocity refuge provided by woody structures was the primary factor determining coho salmon and steelhead trout positions. Average velocities in our pools (about 15 cm/sec) may have been too low for the debris to have served as velocity refuges.

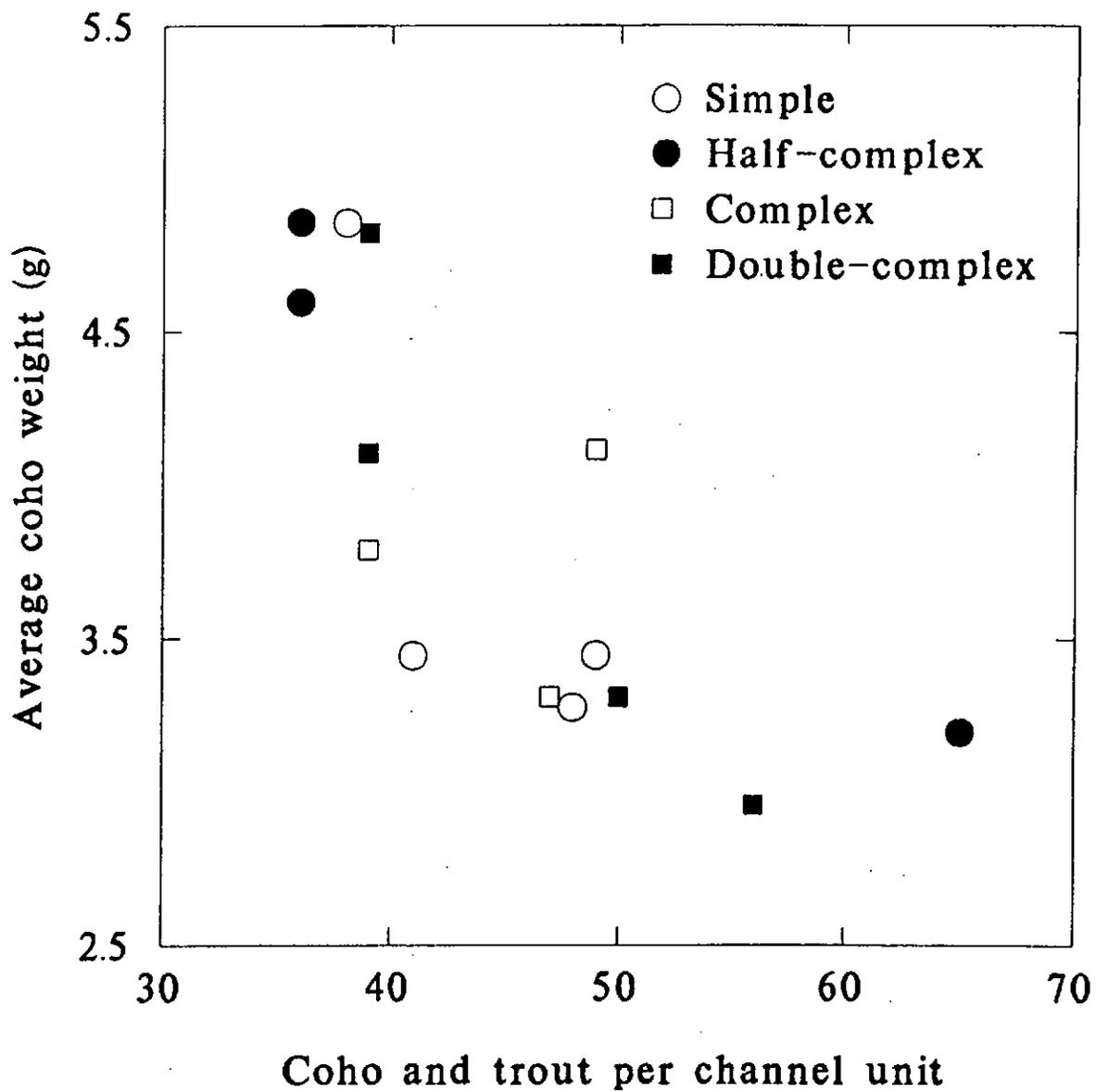
**Table III-A-1.** Distribution of coho salmon fry after 29 days in experimental stream channels. Units were 4.8 m long sections designated A or B for the two sides of the channel and 1-7 for position from upstream to downstream. Units are grouped by treatment type (nature of the brushy debris provided): simple (tree trunk only), half-complex (trunk with some limbs), complex (full tree), and double-complex (two trees).

Unit	Number stocked	Number recovered	% change	Average % change
Simple				
A4	53	45	-15.1	
A7	53	81	+52.8	
B1	87	109	+25.3	
B6	52	39	-25.0	+11.8
Half-complex				
A3	53	46	-13.2	
B2	53	48	-9.4	
B7	52	58	+11.5	-3.8
Complex				
A1	89	68	-23.6	
A5	53	51	-3.8	
B4	52	45	-13.5	-15.5
Double-complex				
A2	53	33	-37.7	
A6	53	72	+35.8	
B3	52	42	-19.2	
B5	52	51	-1.9	-5.7

**Table III-A-2.** Growth and survival of coho salmon fry after 15 weeks in experimental riffle-pool units. Units are grouped by treatment type (nature of the brushy debris provided): simple (tree trunk only), half-complex (trunk with some limbs), complex (full tree), and double-complex (two trees).

Unit	Number Stocked	Number Recovered	% survival	Mean coho weight	Coho biomass	Number trout	Total biomass
Simple							
A4	56	47	83.9	3.3	154.0	1	158.2
A7	57	47	82.5	3.4	162.0	2	168.3
B1	56	36	64.3	4.9	174.8	2	185.8
B6	56	41	73.2	3.4	141.3	0	141.3
Total	225	171	76.0	3.7	632.1	5	653.6
Half-complex							
A3	56	35	62.5	4.6	160.9	1	165.5
B2	57	36	63.2	4.9	174.9	0	174.9
B7	56	46	82.1	3.2	147.0	19	206.3
Total	169	117	69.2	4.1	482.8	20	546.7
Complex							
A1	56	36	64.3	4.1	148.2	13	202.7
A5	56	44	78.6	3.3	145.7	3	154.2
B4	56	38	67.9	3.8	144.0	1	149.4
Total	168	118	70.2	3.7	437.9	17	506.3
Double-complex							
A2	56	51	91.1	3.0	150.9	5	167.8
A6	57	48	84.2	3.3	158.9	2	167.8
B3	56	39	69.6	4.8	188.1	0	188.1
B5	56	39	69.6	4.1	160.1	2	160.1
Total	225	177	78.7	3.7	658.0	9	683.8
Overall Total	787	583	74.1	3.8	2210.8	51	2390.4

Figure III-A-2. Relationship between density of juvenile salmonids and average weight of coho salmon after 15 weeks of rearing under different conditions of cover complexity in experimental riffle-pool units.



In addition to the relatively small size of the wood and low velocity in the experimental stream, the results were probably influenced by the season. The affinity of coho salmon for woody debris increases in winter (Bustard and Narver 1975; Heifetz et al. 1986; Murphy et al. 1986; Taylor 1988) and our experiments were carried out in summer. Moreover, attraction to cover seems to increase as coho salmon grow (e.g., Dolloff and Reeves 1990), and our experiments were initiated early in their first year. It is also possible that the experimental units did not accurately mimic natural conditions, having aberrant growth and survival rates that invalidated the results. However, coho salmon growth in the units was comparable to that observed in wild salmon in Big Beef Creek that season. We observed density dependent growth in the units, indicating competition for food, but we have evidence of this in Big Beef Creek as well. Densities in the units (4.6 fry/m<sup>2</sup> pool) were higher than those generally observed in Puget Sound streams during the summer (e.g., Nielsen 1992).

The survival rate of 74% from 23 May until 2 September may also be higher than might be expected in natural streams but there was nevertheless significant predation. Successful attacks by kingfishers and green herons were observed and other predators (great blue herons, river otters, raccoons and common mergansers) were also observed near the experimental channels during the summer. The 154 h of observation constituted approximately 10% of the daytime period (assuming about 15 h daylight per day) during the 103 days of the study. The minimum of 11 successful attacks, if expanded 10-fold, accounted for over half the 202 fish that disappeared during the study. Undoubtedly some predation occurred at night and during crepuscular periods when no observations were made.

The fact that mortality was unaffected by cover complexity must be interpreted in the context of the size and configuration of the pools (50 cm deep). The affinity of coho salmon for pools (e.g., Bisson et al. 1988; Bugert et al. 1991; Taylor 1991) suggests that we might have detected changes in distribution and/or survival had the pools been shallower. Subsequent experiments in the channels with 50 and 25 cm pools indicated that coho salmon distribution and survival was strongly influenced by an interaction between depth and cover (Lonzarich 1994). Moreover, Atlantic salmon (*Salmo salar*) and brook trout (*Salvelinus fontinalis*) were only attracted to overhead cover in shallow (24-29 cm), not deep (43-50 cm) pools (Gibson and Power 1975).

Brushy debris in the experimental channels (and natural streams) may be relatively ineffective in providing escape refuge from the most common predators we observed. The nature of attacks by kingfishers and herons (surprise and stealth, respectively) may make them difficult for stream fishes to prevent. Angradi's (1992) rainbow trout experiments indicated that threats from avian predators resulted in only brief suspension of feeding, followed by rapid resumption of normal behavior and no net loss of food intake. The survivorship benefits associated with wary behavior and maintenance of a feeding station near cover may be outweighed by the inferior growth opportunities, relative to feeding stations in more open areas of the stream. Fish predators, on the other hand, may pose more constant threat and cover may play a different role for small fish in the presence of piscivores (Gilliam and Fraser 1987; Angradi 1992). In light of these experiments, our results indicate that the primary benefit conveyed by woody debris in streams for summer survival of coho salmon is as an agent of pool development, a role not played by smaller, brushy material.

### Acknowledgments

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### Chapter III.

#### Experimental Studies of The Roles of Brushy Debris for Stream Fishes

##### Part B. Experimental Evidence for the Relationship of Depth and Structure to the Distribution, Growth and Survival of Stream Fishes

David G. Lonzarich and Thomas P. Quinn

###### Abstract

Experiments in a semi-natural stream, containing four depth and structure treatments, quantified the effects of these components of complexity on habitat selection, growth and survival of five fish species common to coastal streams of Washington. When fishes were permitted to freely select among the various habitat types, most species and age-classes avoided shallow pools lacking structure. In some cases depth or physical structure alone appeared to explain these distributions. However, assemblage and population level responses (i.e., coho salmon, Oncorhynchus kisutch) were strongly influenced by the combined effects of depth and structure. A subsequent experiment revealed that predation losses (likely by birds) of water-column species using the simplest habitat type were as much as 50% higher than in the other treatments. However, there were no differences in survival of the benthic species, coastrange sculpin (Cottus aleoticus), among the different treatments. Nor were there significant differences in growth for any species among treatments. These results illustrate the influence of both water depth and physical structure on the fitness of fishes from coastal streams in Washington and the possibility of guild-specific differences in predation risk; that is, benthic species may be less susceptible than water-column species to avian predators. The results also underscore the potential biological consequences of human disturbance to streams, which often result in the loss of pool depth and structure.

## Introduction

Water depth and physical structure are important determinants of habitat selection in stream fishes. For example, in streams of the Pacific northwestern United States, numerous field studies have demonstrated strong relationships between salmonid density and biomass, and physical structure of woody debris (e.g., McMahon and Hartman 1989; Shirvell 1990; Bugert et al. 1991). Likewise, fishes often show strong size-specific partitioning by depth (e.g., Schlosser 1982; Power 1984). This latter relationship has led to the hypothesis that depth provides refuge from avian predators (Power 1987; Schlosser 1987a, b; Schlosser 1988). Laboratory studies have shown that avian predation risk is influenced by water depth (Harvey and Stewart 1991). Other hypotheses of the ecological role of complexity include the suggestion that physical structure provides visual isolation that can minimize competitive (Mortenson 1977; Dolloff 1986) and/or predator-prey interactions (Schlosser 1987b; Harvey 1991) much as the littoral zone functions in lakes and coastal systems. Physical structure may also minimize the negative effects associated with high water velocity by providing refuge from high flows that can affect energetics (Dill and Fraser 1984; Shirvell 1990) or survival from flood events (Angermeier and Karr 1984; Pearsons et al. 1992). If depth or structure allowed fishes to devote less time to vigilance against predators or competitors, more energy could be devoted to feeding and growth.

It is likely that each of these hypothesized mechanisms plays some role in determining patterns of habitat selection among stream fishes. However, depth and structure may not have similar fitness consequences to both benthic and water-column species. Benthic species may be less susceptible to avian predation than water-column species by virtue of their cryptic coloration, sedentary behaviors and use of substrate as cover. Consequently, benthic species may suffer lower habitat-specific mortality due to avian predators, and respond very differently than water-column species to differences in structural complexity and deep water.

The significance of the relationship between habitat complexity and the ecology of stream fishes is especially important in areas where streams have been altered by human disturbance. For example, streams in watersheds that have been extensively logged often contain shallower pools and less woody debris than pristine watersheds (e.g., Bilby and Ward 1991; Fausch and Northcote 1992). In the Pacific Northwest, salmon and trout appear to be negatively effected by the loss of structure and depth in streams within logged watersheds (Murphy and Hall 1981; Li et al. 1987; Fausch and Northcote 1992). Although the mechanisms behind these patterns appear to be fairly well articulated, they remain poorly quantified. Field observations have illustrated that predation by terrestrial predators can be significant (Alexander 1979; Wood 1987, Dolloff 1992). Moreover, laboratory experiments have shown that stream fishes respond to the presence of avian predators, in part by modifying behaviors and/or altering their use of habitats (e.g., Dill and Fraser 1984). Very little attention has been given to the effects of predation on stream fish assemblages.

The objectives of this study were to define patterns of habitat selection and to measure the growth and survival of benthic and water-column fishes associated with habitats that differed in depth and physical structure. Two sets of experiments were conducted using species representative of coastal streams of Washington. The first experiment tested the hypothesis that there were no assemblage- or species-level patterns of habitat selection on the basis of differences in depth and structure. The second experiment tested the hypothesis that fitness as measured by growth and survival was equal among different habitat treatments.

### Materials and Methods

Experiments were conducted in semi-natural stream channels at the University of Washington field station at Big Beef Creek, Washington. These channels have the advantages of both a natural stream and a controlled experimental environment. The channels consists of two side-by-side streams each measuring 3 x 34 m, fed by water from Big Beef Creek approximately 400 m upstream. Each channel contained seven units (for a total of 14) that included one 3 x 3 m riffle and one 3 x 5 m pool with small gravel substrate (diameter=3-10 cm). The units could be isolated by removable barriers constructed with 4 mm mesh screen. Invertebrates were able to colonize the units from upstream and aurally for more than one year before the study began. Flow was regulated in each channel throughout the study at approximately 0.014 m<sup>3</sup>/s. The channels were situated along a natural riparian corridor with a mixture of deciduous and conifer trees, and shrubby understory. Among the birds that frequently used the stream corridor were two piscivores, belted kingfisher (*Ceryle alcyon*) and great blue heron (*Ardea herodias*).

There were four experimental treatments: deep water (maximum depth 50 cm) with structure (Treatment I), deep water without structure (Treatment II), shallow water (maximum depth 25 cm) with structure (Treatment III), shallow water without structure (Treatment IV). The structure was provided by one similar-sized Douglas fir (approximately 1 m tall and 1 m in diameter of the branches at the base).

The fishes were collected from Big Beef Creek and included species and sizes typical of coastal streams of Washington: coho salmon (*Oncorhynchus kisutch*; 55-85 mm SL), steelhead trout (*O. mykiss*, young-of-the-year [YOY]=50-80 mm SL and 1+=100-130 mm SL), cutthroat trout (*O. clarki*, 1+=120-150 mm SL), three-spined stickleback (*Gasterosteus aculeatus*, 40-50 mm SL), and coastrange sculpin (*Cottus aleuticus*; 50-110 mm SL). Fishes were placed in the channels at relative densities similar to those found in Big Beef Creek. Mean densities per channels were 89.3 coho salmon, 27.1, 0+ steelhead trout, 11.1, 1+ steelhead trout, 2.1, 1+cutthroat trout, 47.0 coastrange sculpin and 6.0 three-spined stickleback.

#### Habitat Selection Experiment

A series of four, 2 week experiments were conducted between 13 July-10 September and 12 October-26 October 1992. Treatments were randomly assigned to the different units in each channel for the first experimental trial and then alternated in each subsequent trial. Fishes were added in equal numbers to the first, third and lowermost unit of each channel. At the end of 2 wk, the units were isolated using the fences and fishes were sampled within each unit using a backpack electroshocker or small seine. Fishes collected were identified to species, and then measured and weighed. Mean number of fishes collected, number of individuals per species/age-class, species richness and Shannon diversity (H) (Zar 1984) per treatment were analyzed using Kruskal-Wallis non-parametric two-way ANOVA's (Zar 1984) at P < 0.05 level of significance unless otherwise stated.

Two important assumptions of this experiment were that fishes were able to explore all available habitat types within a channel, and that prey abundance did not differ significantly among units. In a previous experiment (Chapter III-A), coho salmon moved freely across all the units in a channel. On the basis of these results, we assumed that steelhead and cutthroat trout would have similar access to the different units. We were less confident that coastrange sculpin would explore the entire channel so we conducted a preliminary experiment to determine movement patterns in the channels. On 4 July, we placed 30 marked coastrange sculpin in one channel for 2

wk. One group of 15 (marked by an upper caudal fin clip) was placed in the uppermost unit and another (marked by a lower caudal fin clip) was placed in the lowermost unit. Thirteen coastrange sculpin were recovered 14 days later; two of seven fish introduced into the bottom treatments were collected in the upper three units, while two of six fish introduced into the upper unit were found in the lower three units. We were thus satisfied that coastrange sculpin would have access to the entire channel.

The assumption that prey were not distributed differentially among units in the two channels was important because of the potential confounding effect variable prey densities could have on efforts to assess the influence of habitat complexity on fish distribution. Surveys were conducted in summer 1991 (Chapter III-A) and 1992 (Lonzarich unpubl. data) to document patterns of insect drift and aerial fallout into each of the units. These results showed only slight differences in food availability among units. The assumption of prey distribution was further supported by results from a study of coho salmon growth in the channels conducted in summer 1991, which showed similar gains in biomass of fishes among the different units (Chapter III-A).

#### Growth and Survival Experiment

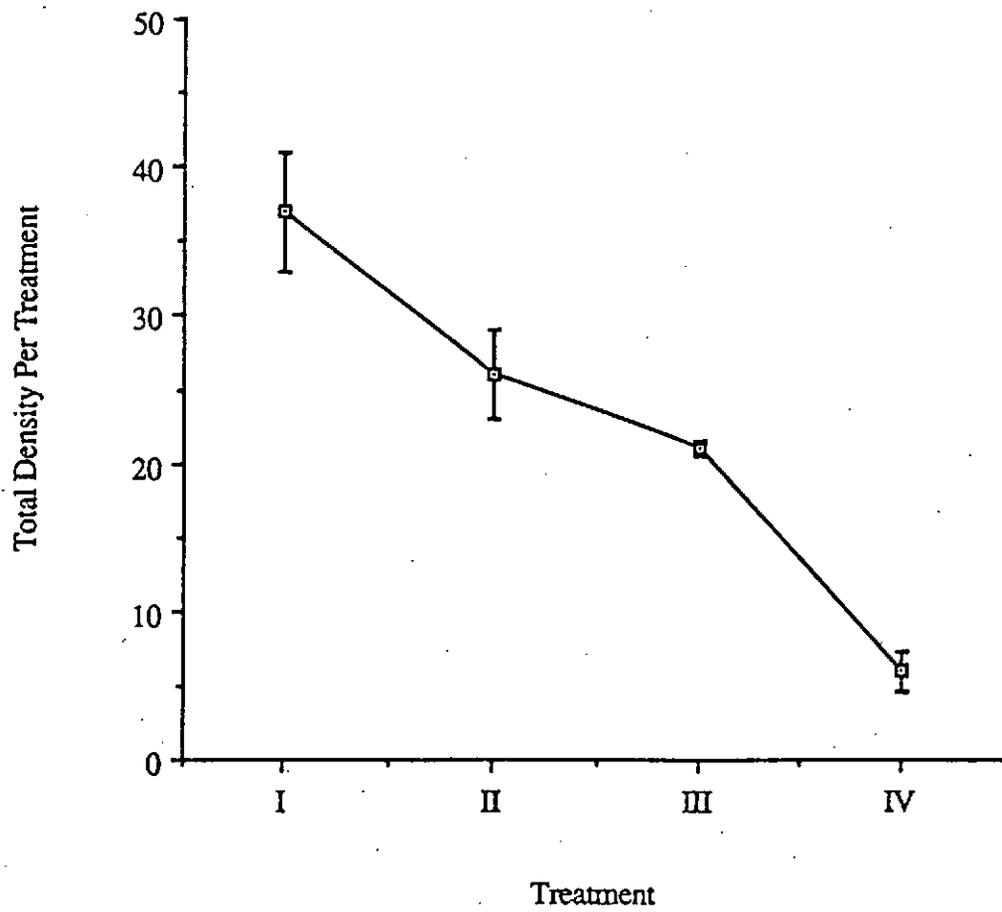
A one month experiment was conducted between 12 September and 12 October 1992 using coho salmon, 0+ and 1+ steelhead trout and coastrange sculpin. Three-spined stickleback and cutthroat trout were not used in this experiment because we were unable to obtain sufficient numbers for all treatments. Treatments were randomly assigned to the different units in each channel, and each treatment consisted of three replicates. Each of the units was isolated to prevent fishes from moving among treatments. Twenty coho salmon, 10 YOY steelhead trout, three 1+ steelhead trout and 10 coastrange sculpin were weighed and placed in each unit. At the conclusion of the experiment, the fishes were removed from each unit, counted, weighed and measured. Among-treatment differences, mean percent mortality and population growth (differences in total biomass for each species/age-class over the course of the experiment) were compared using Kruskal-Wallis ANOVA.

### **Results**

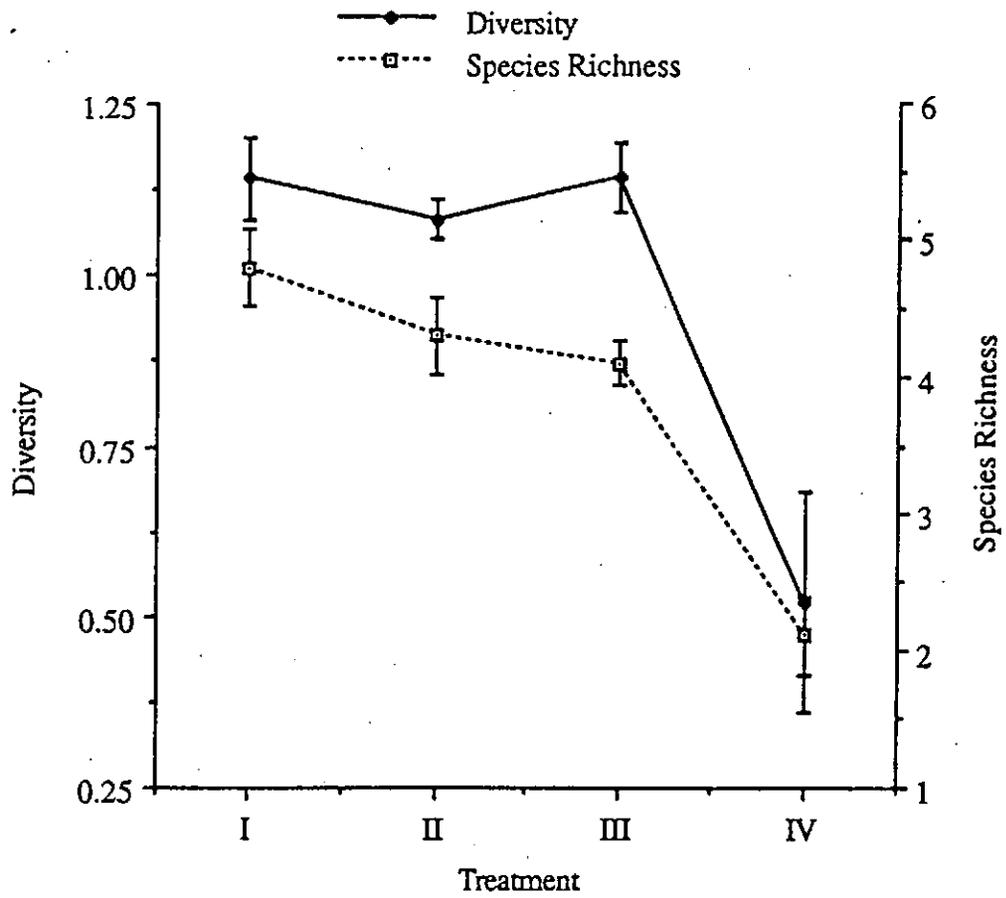
#### Habitat Selection

Total assemblage density, diversity and species richness declined from the most complex (Treatment I) to the least complex (Treatment IV), but the patterns of variation in these factors differed slightly. For example, mean total density declined consistently with complexity from a high of 43 fishes in the most complex treatment to five in the least complex (Figure III-B-1). However, this pattern contrasted with an apparent threshold response in diversity and species richness (Figure III-B-2). The mean values for diversity ( $H = 1.07-1.12$ ) and species richness (4.3-4.9) in the first three treatments were not significantly different, but both variables declined by more than two-fold in Treatment IV (Figure III-B-2).

**Figure III-B-1.** Mean total fish density ( $\pm$  S.E.) per treatment for habitat selection experiment. I = Deep with structure; II = Deep without structure; III = Shallow with structure; IV = Shallow without structure (n = 9).



**Figure III-B-2.** Mean Shannon diversity and species richness ( $\pm$  S.E.) per treatment for habitat selection experiment (see Figure III-B-1 for explanation).



Species- and age-specific responses to the different complexity treatments varied, but with the exception of stickleback, each group exhibited strong patterns of habitat selection, and much greater use of the most complex treatment than the least complex (Figure III-B-3). Coastrange sculpin used the two deep-water habitats more frequently than shallow habitats by a nearly three to one ratio but the presence of structure did not influence their distribution (53% in Treatments I and III, and 47% in Treatments II and IV;  $P > 0.50$ ). Yearling cutthroat trout and steelhead trout almost never occupied shallow water treatments (100% of all cutthroat trout and 83% of all steelhead trout were found in Treatments I and II), and exhibited a steady decline from the most complex to least complex habitat. Habitat selection by YOY steelhead trout appeared to be based largely on the presence of structure, as fish were nearly three times more abundant in the two structured treatments than the two unstructured treatments. However, there were only slight differences in the distribution of YOY steelhead trout with depth (58% in Treatments I and II and 42% in Treatments III and IV;  $P > 0.50$ ). Coho salmon exhibited a threshold response. Slight differences were found in the proportion of individuals found in Treatments I - III (27% - 40%), but habitat use declined dramatically in Treatment IV (6%).

#### Growth and Survival

Mean population biomass increased in each of the four treatments for all species and size classes (Figure III-B-4), but there were no strong treatment-specific patterns in growth for any taxa. Coho salmon (16%) and YOY steelhead trout (21.5%) showed the greatest gains in growth; coastrange sculpin were next (10.8%), followed by steelhead trout (9.9%). There was little variation in growth among treatments in coho salmon and YOY steelhead trout, but for yearling steelhead trout and the coastrange sculpin, net population growth appeared lower in Treatment II than any of the other three treatments. This may have resulted from size-specific predation leading to the loss of large individuals from some replicates over the course of the experiment. In these units, total biomass at the conclusion of the experiment was less than that at the beginning, producing a net negative growth rate and low overall growth rate for that treatment. Even with this lower growth rate in Treatment II, there was still no consistent relationship between growth and complexity for any of the four fish groups.

Survival, measured as the percentage of fish remaining in a channel unit treatment at the conclusion of the experiment, varied among treatments and fish group (Figure III-B-5). Survival declined across treatments in each of the three water-column groups. Coho salmon survival was greatest in the deep water-structure treatment (89%), nearly twice that in Treatment IV. Both YOY and 1+ steelhead trout showed better survival in Treatment I (means 71% and 89%, respectively) than Treatment IV (29% and 33%, respectively). As with coho salmon, there was a trend towards lower survival in Treatments II and III, but the differences with Treatment I were not significant ( $P < 0.20$ ). In contrast to this consistent decline in survival for the three water-column fishes, survival of coastrange sculpin did not vary among treatments ( $P > 0.50$ ); survival ranged from 60-100%.

**Figure III-B-3.** Mean proportional habitat use ( $\pm$  S.E.) by species and age-class per treatment in the habitat selection experiment.

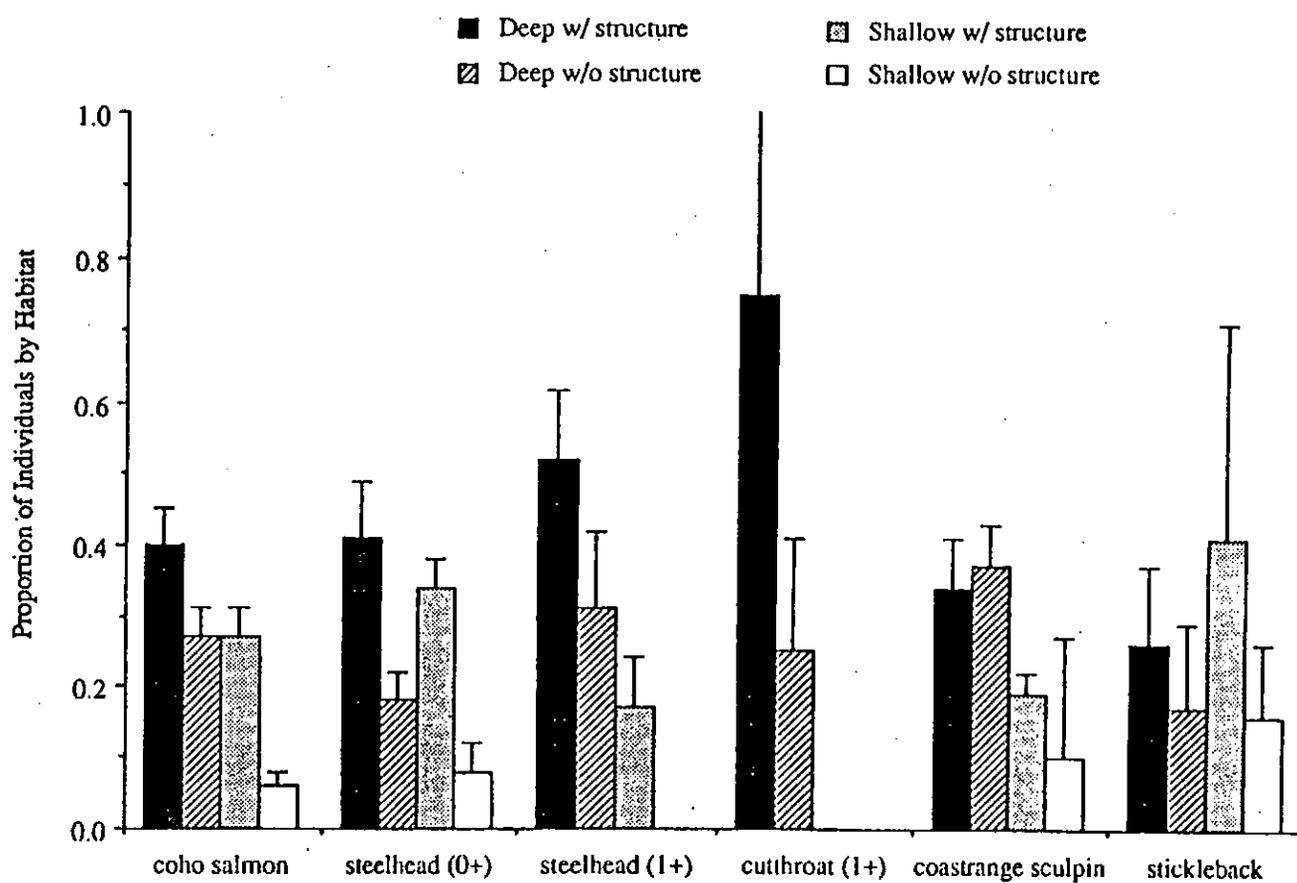


Figure III-B-4. Mean species-specific growth by treatment in the growth-survival experiment (n=3).

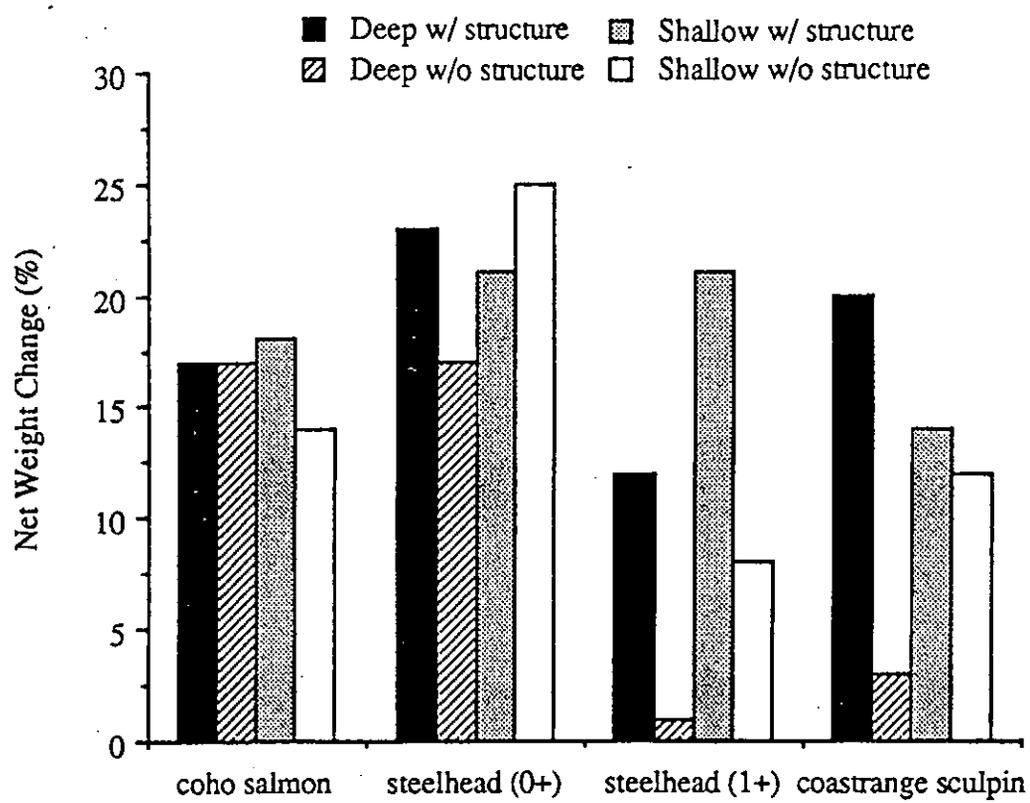
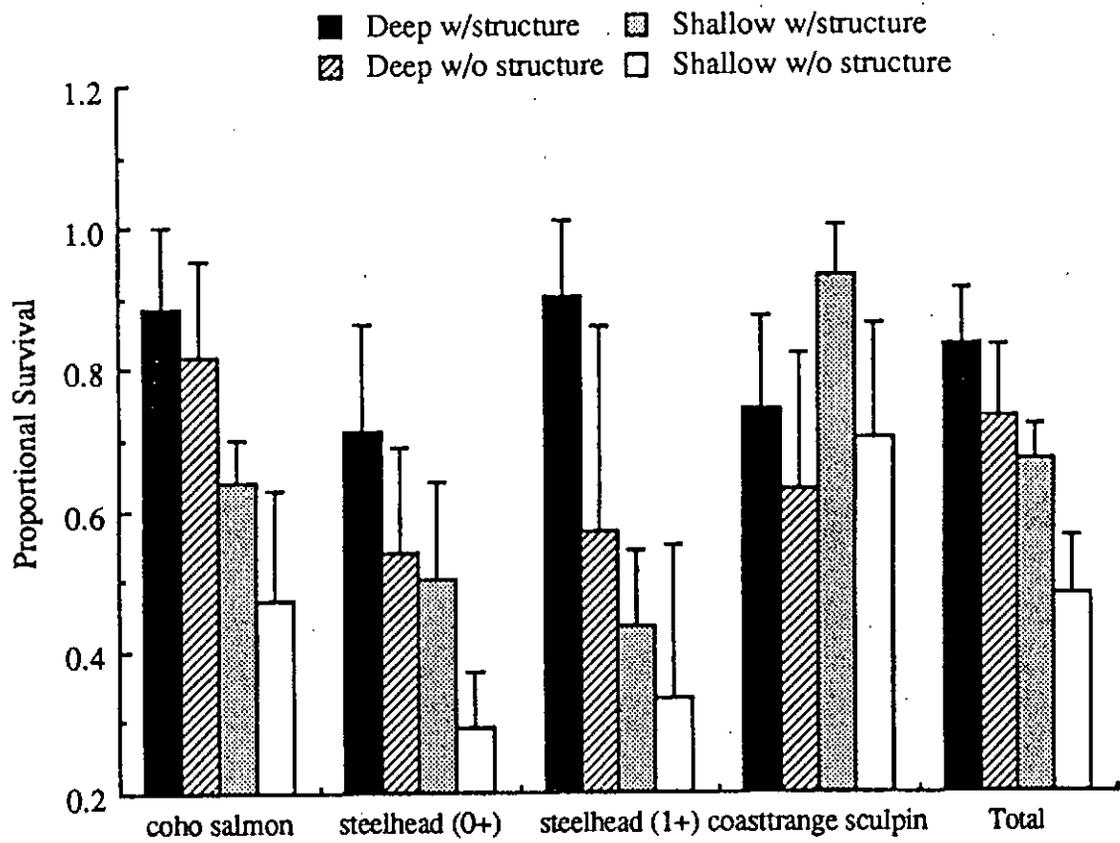


Figure III-B-5. Mean species-specific survival by treatment in the growth-survival experiment (n=3).



### Discussion

These experiments showed strong patterns of habitat selection by all water-column species examined, except three-spined stickleback, and differential survival that was related to habitat complexity. Like the other groups, coastrange sculpin showed a strong pattern of habitat selection but depth appeared more important than structure in determining their distribution. However, unlike the other species, coastrange sculpin showed no significant differences in survival among the different treatments. Furthermore, similarities in mean net growth rate among treatments for both water-column and benthic species suggested that fishes were not selecting habitat treatments based on factors that might have influenced their growth rates.

Fishes generally select habitats that provide opportunities to maximize energy gains or survival (Werner et al. 1983; Schmitt and Holbrook 1985). In small, low gradient coastal streams of the Pacific Northwest, habitats differ in quality on the basis of differences in depth, velocity, cover and food resources. Depth may provide spatial refuge from avian predators, while cover can provide refuge from predators (both birds and fish), high velocities and competitors. Recently, Fausch (1993) experimentally examined the relative importance of these different attributes of in-stream cover to stream-dwelling salmonids in a British Columbia stream. Independently manipulating different components of cover, Fausch (1993) found that steelhead trout selected treatments containing overhead cover but showed no preference for habitats providing visual isolation or refuge from high water velocities. Coho salmon, in contrast, showed no preference for any of the different cover treatments, suggesting that cover alone may not adequately explain patterns of habitat use in this species. The experiments conducted in the present study illustrated variable, species-specific differences in habitat selection. In some cases, depth or physical structure alone appeared to explain these distributions. However, assemblage and population level responses (i.e., coho salmon) and survival of water column species, were strongly influenced by the combined effects of depth and structure.

The differences in habitat selection and survival of benthic and water-column species were consistent with the hypothesis that benthic species should be less susceptible to predation than water-column species. This view appears to be supported by Dolloff (1992) who documented predation by river otter (*Lutra canadensis*) on fishes in an Alaskan stream. On the basis of fish otoliths retrieved from otter scat, Dolloff inferred that predation on coho salmon may have been six times higher than predation on coastrange sculpin. It was not clear from this study, however, if this pattern reflected differences in susceptibility or differences in the relative proportions of the two prey species in the stream community.

Although the results from the present study are available only for one cottid species, they may have broader implications because cottids are a relatively species rich, widespread and abundant family in Pacific Northwest streams. If benthic species are less susceptible to avian predators than water-column species, then degradation of stream habitats may lead to shifts from diverse assemblages comprised of benthic and water-column species to assemblages that are dominated by benthic species. Such shifts in assemblage structure might also alter the trophic dynamics of stream food webs.

Although avian predation was not quantified directly, the loss of fishes from the experimental units was very likely attributable to predation by belted kingfisher and great blue heron because none of the fishes used in the experiments were large enough to prey on other fishes. The importance of avian predation on stream fishes has formed a central element of recent habitat selection hypotheses (Power 1984; Schlosser 1987b). However, avian predation has

rarely been estimated in natural streams (but see Alexander 1979; Wood 1987; Dolloff 1992), and only once been experimentally examined (Harvey and Stewart 1991) and then only with water-column fishes.

In warm water streams, piscivorous fishes may strongly influence the distribution of other fishes, especially small individuals (Moyle and Li 1979; Power 1987; Schlosser 1988). These predators can force small fishes into habitats, producing high densities that may lead to intense competition (Schlosser 1987a). In small coastal streams of Washington there are few fish species large enough to act as predators on fishes for any extended period (although the larvae of most species may be exposed to fish predators). The potential predators are often salmonids, and their abundance is affected by fishing pressure as well as instream community dynamics. Avian predation, however, may have strong direct and indirect effects. The results presented here illustrate to some extent the relationship between habitat complexity and predation risk. The indirect effects could be manifested through increased vigilance and reduced feeding opportunities (Mittelbach and Chesson 1987; Angradi 1992) but the risk of predation could also lead to shifts in habitat use that may eventually produce increased competition among individuals in habitats that confer lower predation risk (Fraser and Cerri 1982; Werner et al. 1983; Schlosser 1987a). If densities increase in these habitats to the point at which competitive interactions become intense, fishes then must make a tradeoff between the costs associated with predation risk and those associated with competition.

Land-use activities and associated disturbances tend to alter the complexity of habitats in many streams. Stream fishes often have strong affinities for complex habitats and these habitats confer significant fitness benefits. The results of these experiments illustrate that the relative significance of two important components of complexity, depth and structure, may vary among different species. These results also illustrate the influence that terrestrial predation may play in determining the habitat fishes select and the fitness consequences associated with such choices. However, we emphasize that these results do not discount the potential importance of other mechanisms (e.g., competition, flow), and that predation has potentially strong indirect effects that merit further study. Nonetheless, these results strengthen the view that habitat complexity is an important attribute of streams, which must be preserved to maintain the integrity of stream fish communities.

#### Acknowledgments

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## Chapter IV.

### Factors Affecting the Freshwater and Marine Growth and Survival of Coho Salmon from Big Beef Creek

Thomas P. Quinn

#### Abstract

The coho salmon population in Big Beef Creek, Washington has been monitored since 1966. Since this time the estimated annual adult escapement has ranged from 5536 to 395 and smolt abundance has ranged from 64,803 to 10,872. The abundance of smolts was apparently unaffected by the number of spawners at escapements greater than about 400 females. The number of smolts was positively correlated with 60 day peak flows during the winter when they were spawned and was also positively correlated with the discharge during the 60 day low flow period in their first summer of stream residence. Neither parent escapement nor smolt abundance (both used as surrogates for parr density) was correlated with smolt size, and size was also not correlated with summer or winter flow regimes. Smolt size varied over the run; very small (about 80 mm fork length) smolts left first, followed by relatively large (about 120 mm) smolts, and then progressively smaller smolts towards the end of the season. The marine catch distribution of this population, inferred from coded wire tag recoveries, was primarily off the southwest coast of Vancouver Island, British Columbia and, to a lesser extent, the Washington coast and Puget Sound. Very few recoveries were reported from the Strait of Georgia, despite substantial fisheries in that region. Marine survival averaged 20.1% (range: 9.8 - 32.3%) but was not strongly correlated with sea surface temperature, salinity or an index of upwelling off the coast. However, adult body size was positively correlated with salinity during the final summer at sea. The exploitation rate on this population averaged 77%. The sex ratio of returning adults was biased in favor of males, even without counting jacks (54.3% versus 45.7.8% of adult returns) and males were smaller on average than females in all years.

### Introduction

The population biology of salmon frequently involves an interplay between density-dependent and density-independent factors, acting at various life history stages. This interplay can lead to compensatory or depensatory effects. Survival during the embryonic stage may be related to the density of spawners (McNeil 1964), flooding (McNeil 1966; Thorne and Ames 1987), and fine material in the spawning substrate (Chapman 1988; Scrivener and Brownlee 1989). For stream-dwelling species such as coho salmon (*Oncorhynchus kisutch*), survival in freshwater may be positively related to the volume of water during summer low-flow periods (Smoker 1955) or negatively related to winter floods (Tschaplinski and Hartman 1983).

In addition to such abiotic factors as flow conditions, the density and growth of stream-dwelling fry is affected by their territorial behavior and the abundance of food and space (Chapman 1962, 1966; Nielsen 1992). Size at the end of the summer may be associated with good over-winter survival (Hartman et al. 1987; this report, Chapter II-B) and large size of smolts. Marine survival is positively correlated with size among sockeye salmon (*O. nerka*) populations (Koenings et al. 1993); within a season in chum (*O. keta*: Healey 1982), sockeye (Henderson and Cass 1991) and coho salmon (Mathews and Ishida 1989; Holtby et al. 1990) and cutthroat trout (*O. clarki*: Tipping and Blankenship 1993) and steelhead (*O. mykiss*: Ward and Slaney 1988; Ward et al. 1989). However, marine survival may be more strongly related to the time of seawater entry than body size (e.g., coho: Bilton et al. 1982; Morley et al. 1988). Nevertheless, migration date is itself related to fish size (e.g., coho: Irvine and Ward 1989; anadromous brown trout, *Salmo trutta*: Bohlin et al. 1993), further complicating the relationships.

In addition to the effect of size on marine survival, however, there are many oceanographic factors that correlate with salmon survival and growth. Poor survival and growth were associated with the 1983 El Nino event in coho and chinook salmon populations that rear off the Oregon coast, though northward-migrating populations showed no effect (Johnson 1988). Coastal upwelling seems to exert a positive effect in the survival of coho salmon, though the evidence is not always strong and the mechanisms not entirely clear (Scarnecchia 1981; Holtby et al. 1990; reviewed by Pearcy 1992). In a species such as coho salmon with little variation in marine residence period, increased growth by females will be associated with larger size at maturity and higher fecundity (van den Berghe and Gross 1989; Fleming and Gross 1990), which may result in greater competition among the next generation of fry.

The links between density-dependent and density-independent processes in salmon life histories are strong and it is impossible to understand the results of human activities (e.g., landuse or fishing) without considering the entire life cycle (Holtby and Scrivener 1989). Many insights into the biology of salmon in general and coho salmon in particular have been derived from the studies at Carnation Creek, British Columbia (e.g., Bustard and Narver 1975; Hartman et al. 1987; Holtby and Scrivener 1989; Holtby and Healey 1986, 1990; Holtby et al. 1990) and the purpose of this paper is to test the generality of some of these results. Specifically, long-term data on coho salmon from Big Beef Creek, Washington were analysed to determine: 1) trends over time in adult return and smolt production, 2) correlations between smolt size and abundance with density, and summer and winter flows during the incubation and juvenile rearing periods, 3) the relationship between smolt size and date of emigration, 4) correlations between marine growth and survival with smolt size, abundance, and sea surface temperature, salinity and coastal upwelling, and 5) the sex ratio and relative sizes of male and female coho salmon.

## Materials and Methods

### Site Description

Big Beef Creek flows into Hood Canal from Kitsap Peninsula, Washington (Figure IV-1). Its basin area is approximately 38 km<sup>2</sup>. There are 18 km of main stream channel, 8 km upstream and 10 km downstream of Lake William Symington, a shallow (mean depth 3 m) 198 ha impoundment constructed in 1965 (Williams 1970). Fish pass over the 10 m dam and into the basin above the lake via a pool and weir fishway. Big Beef Creek's watershed is lower than 400 m elevation and the stream's dominant storm flows are derived from winter rains between November and March. A maximum flow of 21 m<sup>3</sup>/second was recorded in 1971 and summer low flows near the mouth average 0.08 m<sup>3</sup>/second. The 50 year flood has been estimated at 56 m<sup>3</sup>/second (Madej 1975). Above Lake Symington the main stream channel is very flat (0.2%), and is connected to extensive riverine wetlands. Below Lake Symington the stream gradient lessens gradually from 1.5% below the dam to 0.5% near the mouth. Several small, relatively steep and intermittent tributaries enter Big Beef Creek in the 10 km below the lake. Monthly mean daily maximum summer temperatures in 1966 were 12.5° C above the lake and 16.6° in the lower region of the stream (Williams 1970). Winter temperatures are moderated by springs feeding the upper stream and by the lake, seldom dropping below 4°.

The basin's history of settlement began in the late 1800s. In some of the lower stream reaches, coarse sediment generated during the initial logging in the basin has accumulated in the stream channel and is gradually being transported through the system (Madej 1975). Numerous old cedar stumps on the stream banks reflect the original conifer riparian forest which has regrown to red alder, (*Alnus rubra*), vine maple (*Acer circinatum*), and big leaf maple (*Acer macrophyllum*). Second growth western hemlock (*Tsuga heterophylla*), western red cedar (*Thuja plicata*), and Douglas fir (*Pseudotsuga menziesii*) make up a smaller but increasingly dominant component. In-channel coarse woody debris (CWD) reflects the existing riparian forest but some large pieces of cedar remain from pre-logging times. The lowermost km of the creek was channelized in 1969 to divert runoff away from the artificial spawning channel constructed at that time (Cederholm 1972).

Williams (1970) reported that the stream and lake contained 13 fish species, including four salmonids (coho and chum salmon, steelhead and cutthroat trout), three cottids (*Cottus asper*, *C. aleoticus* and *C. confusus*), two lamprey species (*Lampetra planeri* [renamed *L. richardsoni*] and *Entosphenus tridentatus*), threespine stickleback (*Gasterosteus aculeatus*), blackside dace (*Apocope oscula*) (= *Rhinichthys osculus*?), and two non-native species (yellow perch, *Perca flavescens*, and brown bullhead, *Ictalurus nebulosus*). Seiler et al. (1981) also reported a third lamprey species, *L. ayersi*, in the creek and the non-native largemouth bass (*Micropterus salmoides*) has been reported in the lake (David Seiler, pers. comm.). Coho salmon have been the most numerous salmonid species in recent years but chum salmon were formerly also very abundant (Seiler et al. 1981, 1984), and use spawning and rearing habitats above and below the lake. The great majority of coho smolts have been reported to emigrate from the system after their first year (94.2% and 88.4% in 1966 and 1967, respectively; Williams 1970). Some coho salmon emigrate as fry and the number seems to vary greatly among years (Seiler et al. 1981, 1984).

### Sources of Data

From 1966 through 1969, the adult coho salmon population was estimated by stream surveys. A permanent weir was built at the mouth of Big Beef Creek in 1970 and few if any spawn below the weir. However, the weir was not designed to operate during peak flows because complete enumeration was not the objective (Seiler et al. 1981). The stream surveys and weir counts from 1970 to 1977 should be regarded as minimum estimates, as unknown numbers of fish were unsurveyed or passed upstream when the weir was not operating. In 1978 the weir was modified to operate under essentially all flow conditions and the counts may be regarded as highly accurate from this year forward. During the weir's operation, the sex of adult salmon has been recorded and every tenth fish was measured (fork length).

Smolts have been captured with fan traps at the same location as the adult weir since 1978 and these represent accurate counts. Prior to 1978 their abundance was estimated from a combination of screen-panel leads and a live box in the creek and an inclined plane trap on a side-channel of the creek (C.J. Cederholm, Washington Dept. of Natural Resources, pers. comm.). These trapping operations were less complete than the fan traps installed later, both because they did not operate under all water conditions and because some salmon spawned below the traps. No smolt sampling took place in 1968 and 1972-1974. From mid-March to early April the smolts were anesthetized with MS-222 and counted and a subsample was measured (fork length). Since 1977 most smolts from mid-April through early June have been marked with coded wire tags after removal of the adipose fin. Subsamples of the smolts were also measured on a weekly basis. In addition to the smolts, coho salmon fry also emigrate from Big Beef Creek. Their abundance seems to vary among years but they tend to emigrate earlier than the smolts (Seiler et al. 1984). Smolt trapping operations have often commenced in mid-April, after most fry often leave. The fry counts are thus not regarded as consistent. Moreover, fry are not tagged and there is no estimate of their marine survival. Because the fry and not been consistently and fully enumerated or tagged, they have been omitted from the analysis in the body of this report.

We used stream discharge data acquired by Lestelle et al. (1993) from records of the United States Geological Survey. Specifically, we analysed the relationships between coho salmon size and abundance and the mean flow on the 60 consecutive days with lowest summer (July 1 - October 31) and highest winter (December 1 - February 28) flows. Continuous stream temperature data were not available.

Coded wire tag data were examined to estimate the distribution of Big Beef Creek coho salmon. Such information was needed to select the recording station for correlation of oceanographic variables with marine growth and survival. Use of tag data for this purpose has two limitations. First, catch is a biased estimator of distribution unless effort is comparable. Second, the catches only indicated the location of coho salmon during their second (and final) summer at sea. Bearing these limitations in mind, more tags were recovered from the southwest side of Vancouver Island, British Columbia, than any other major geographical area. For this reason, and to facilitate comparison between our data and the data on the marine survival of Carnation Creek coho salmon reported by Holtby et al. (1990), we analysed data on sea surface temperature and salinity recorded at Amphitrite Point lighthouse, on the southwest coast of Vancouver Island at the northern edge of Barkley Sound. We did not use the data from Kains Island, the other recording station used by Holtby et al. (1990), because its location (northwestern Vancouver Island) is apparently beyond the range of most Big Beef Creek coho salmon. Holtby et al. (1990) used an index of coastal upwelling at 48° N and 125° W (off the northern coast of

Washington). We hypothesized that survival would be primarily influenced by conditions during the first summer at sea and adult size would be primarily influenced by conditions during the second summer. To avoid complications resulting from the tendency of male coho salmon to return as jacks (after only one summer at sea) or adults (two summers at sea), we only analysed the data on body size of females (who spend two summers at sea before maturing). We hypothesized that the correlations with growth and survival would be negative with temperature, positive with salinity, and positive with upwelling (Scarnecchia 1981; Holtby et al. 1990; Pearcy 1992).

## Results

### Freshwater Survival and Growth

The estimated escapements of adult coho salmon to Big Beef Creek from 1966 to 1991 varied from 5536 in 1966 to 395 in 1990 and have been generally lower in recent than in previous years (Figure IV-2). Smolt runs have ranged from 64,803 in 1967 (the first year of smolt counting) to 10,872 in 1987 (Figure IV-3). While the data are not equally accurate in all years for the reasons presented in the Materials and Methods section, they have been analysed at face value. Escapements up to about 1000 salmon seemed to produce increasingly large numbers of smolts but no increase in smolt production was evident from parent escapements greater than about 1000 (Figure IV-4). Smolt abundance was positively correlated with the discharge during both the winter high flow period in the year when the fish were spawned and the summer low flow period when the fry were residing in the stream (Table IV-1; Figure IV-5). No surveys of newly emerged fry or parr at the end of the summer were conducted on a regular basis so survival during the distinct freshwater phases (i.e., egg-to-fry, summer, and winter) could not be evaluated.

Because there were no direct estimates of fry or parr density, we used the number of females in the parent escapement and the number of smolts produced as surrogate variables representing intraspecific competition in the stream. The mean smolt size was not correlated with either measure of density, nor was it correlated with either summer or winter flow conditions. Smolt size varied over the duration of the run but the pattern was complex. The first migrants were a few very small (about 80 mm) individuals, leaving in late March. These fish were followed (in early April) by the largest smolts of the season. A general decline in smolt size was then observed in almost all years towards the end of the migration period in early June (Figure IV-6).

### Marine Distribution, Survival and Growth

The coded wire tag data base revealed an estimated 43,193 recoveries (expanded for sampling effort). Excluding those in Big Beef Creek itself, 36,152 fish were recovered, ranging from Alaska (5) to California (2). However, by far the largest number of recoveries was from the southwest side of Vancouver Island (34.2%) with another 5.6% from the northwest side of Vancouver Island. Coho were recovered throughout the summer in these areas. Only 7.4% were recovered from the coast of Washington north of Willapa Bay and even fewer were taken south of this area. Many coho were recovered from Puget Sound (17.7%) but most of these were in October, suggesting that the fish may not have resided there all summer. The timing of returns to the Strait of Juan de Fuca (13.7%) and Hood Canal (16.8%) suggested that the fish were caught as they were returning (i.e., primarily in September-October and October-November, respectively). In contrast, the Strait of Georgia produced only 0.5% of the marine recoveries.

The average marine survival, calculated from returns to Big Beef Creek and recoveries of tagged salmon in fisheries but not including returns of jacks, was 20.1% (range: 9.8 to 32.3%) for brood years 1976 to 1978. The average estimated exploitation rate was 77.1% (range: 49.4 to 92.3%). However, there was no clear trend (i.e., upward or downward) in survival or fishing over time. Interannual variation in marine survival showed a weak positive correlation with smolt abundance but no relationship with mean smolt size (Table IV-1). Of the three physical variables (temperature, salinity and upwelling) examined for the first summer of marine residence, only temperature showed any relationship with survival and that was weakly negative. None of the variables in the second summer at sea were correlated with survival.

Mean size of adult females showed a nearly significant positive correlation with salinity in the first summer at sea and a significant positive correlation with salinity in the second summer at sea (Figure IV-7). Adult size was not correlated with temperature or upwelling in either summer, nor was it correlated with smolt size or abundance. There were also clear patterns in adult size and sex ratio. Females were larger than males (excluding jacks), on average, in all 14 years (mean fork lengths: females: 58.17 cm, males: 53.46 cm,  $t = 10.69$ ,  $P < 0.001$ ). Moreover, males (excluding jacks) were more numerous in the escapement than females in 14 of 16 years and there was a significant difference at  $P < 0.05$  (chi-square test) in 11 of 16 years. The overall return of 10,141 males and 8,562 females also differed from 50:50 ( $X^2 = 139.72$ ,  $P < 0.001$ ). The jacks were counted in 12 of the 16 years and in those years females comprised 34.83% of the returning fish, compared to 42.93% adult males and 22.25% jacks (return years 1980-1991,  $n = 15,652$  fish).

### Discussion

We hypothesized that smolt production from Big Beef Creek would be adversely affected by high flows in the winter when the embryos were incubating, with the belief that such flows might scour the gravel and destroy embryos or expose them to predation (McNeil 1966; Holtby and Healey 1986; Thorne and Ames 1987). We observed the opposite relationship (i.e., higher smolt production two years following high winter peak flows). The lake and swamps above it may moderate flows enough to prevent scour in the spawning gravels, explaining the absence of negative correlation with smolt yield, but it is not clear why high flows would positively correlate with smolt production. There may be some correlation between winter and fall flows such that very dry falls (possibly delaying adult migration and spawning) might co-occur with lower than average flows in winter as well.

Relatively high flows during the summer low flow period were correlated with smolt production. This is consistent with data from Bingham Creek, a tributary of the Chehalis River (Lestelle et al. 1993). It is also consistent with the generalization that juvenile coho salmon form feeding territories in streams and that constriction of space in low flow conditions results in emigration or predation, regulating density in the available space. Low flows may also isolate fish in pools that either dry up entirely or subject them to high risk of predation. We have no consistent data on downstream migration by fry but the apparent limit of 20,000 - 50,000 smolts over a range of adult escapements also argues for a freshwater carrying capacity. In some years the number of migrating fry was substantial (e.g., 21,437 fry and 40,076 smolts in 1981; Seiler et

Figure IV-1. Map of Big Beef Creek, Washington.

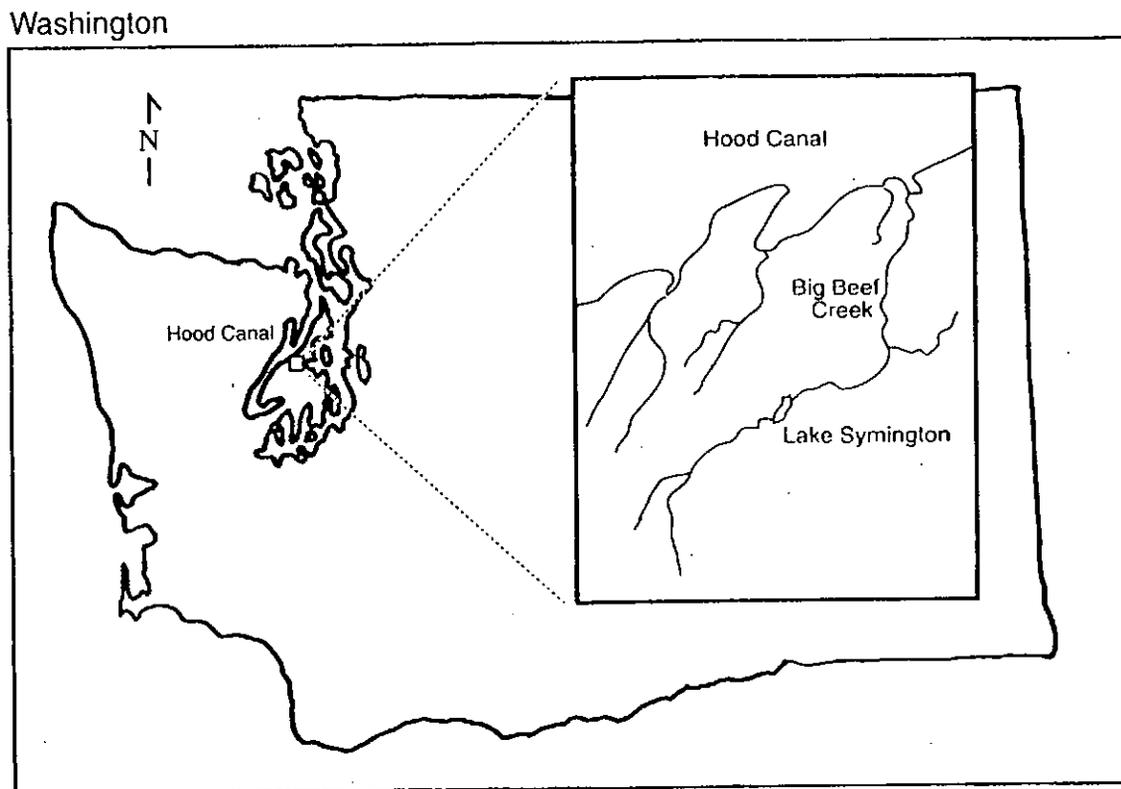


Figure IV-2. Abundance of adult coho salmon returning to Big Beef Creek.

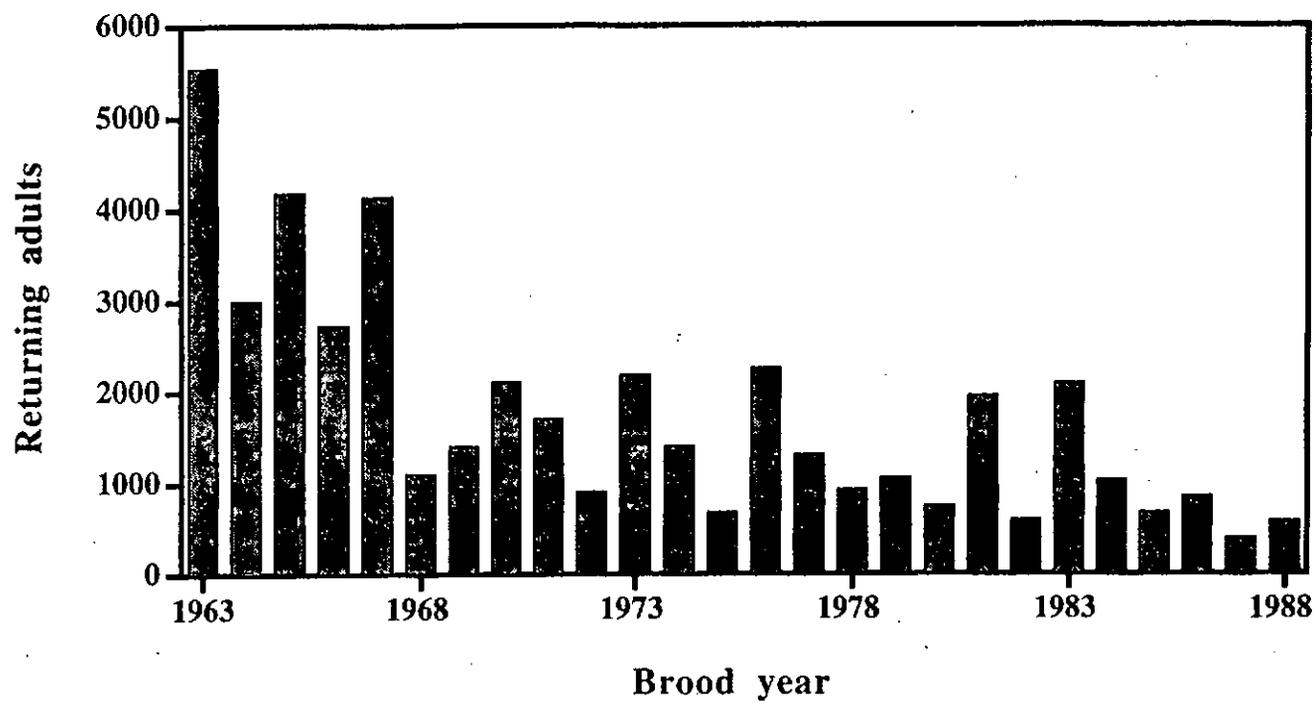
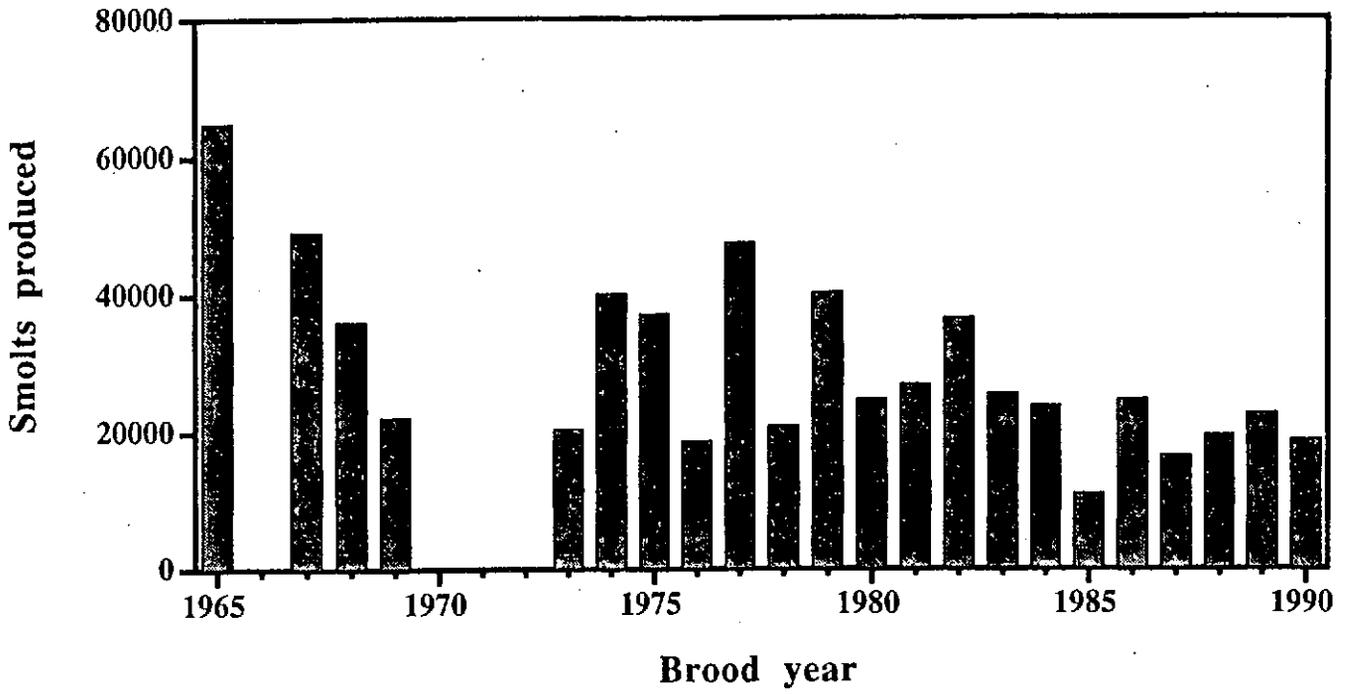


Figure IV-3. Abundance of coho salmon smolts leaving Big Beef Creek.



**Figure IV-4.** Relationship between number of coho salmon smolts emigrating from Big Beef Creek and the number of females in the parent escapement (smolts assumed to be all age 1+).

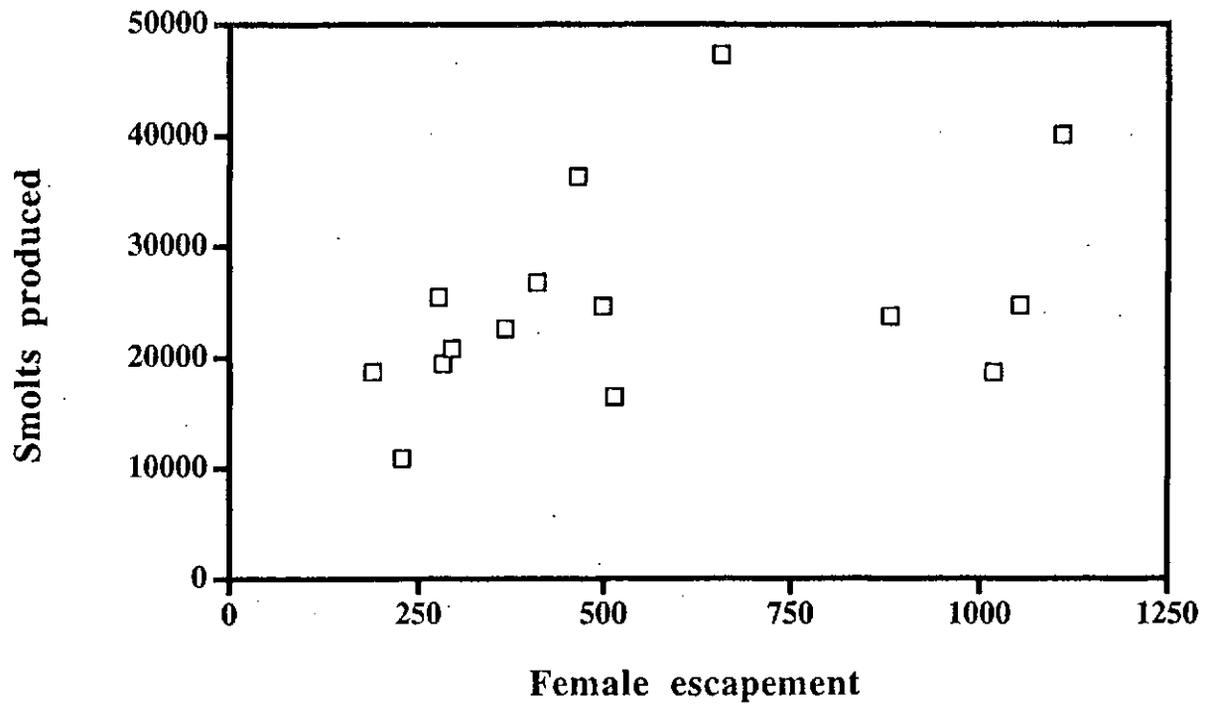


Figure IV-5. Relationship between the mean discharge of Big Beef Creek during the 60 day lowest flow period of the summer and the subsequent year's smolt run size.

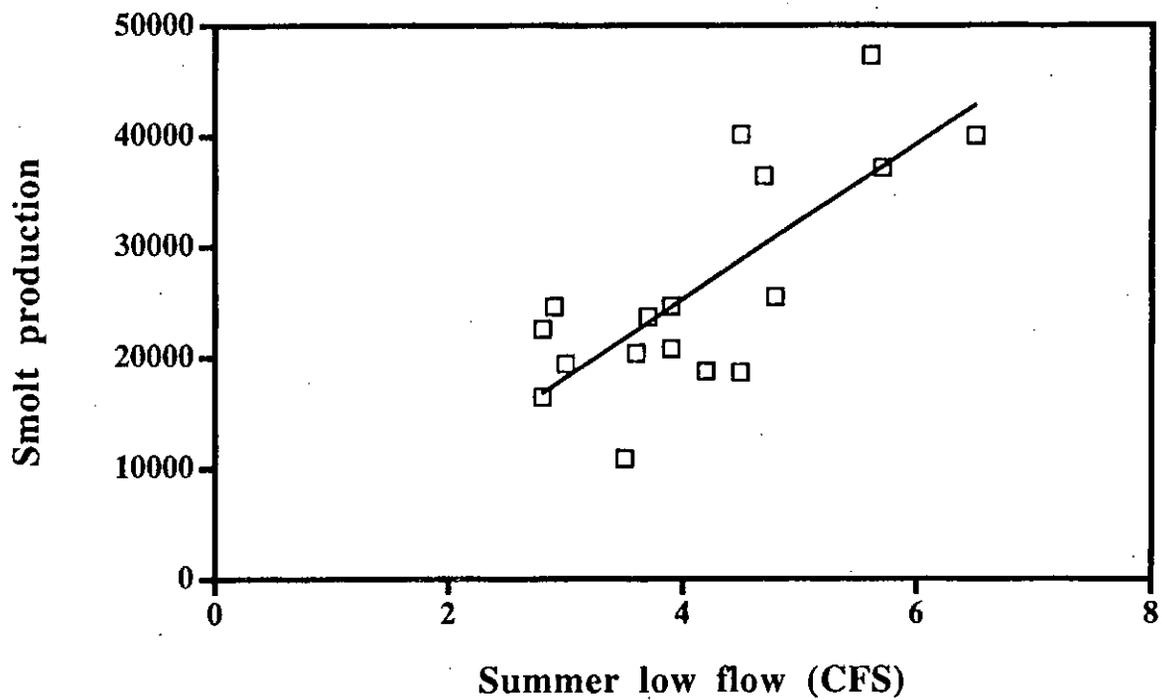
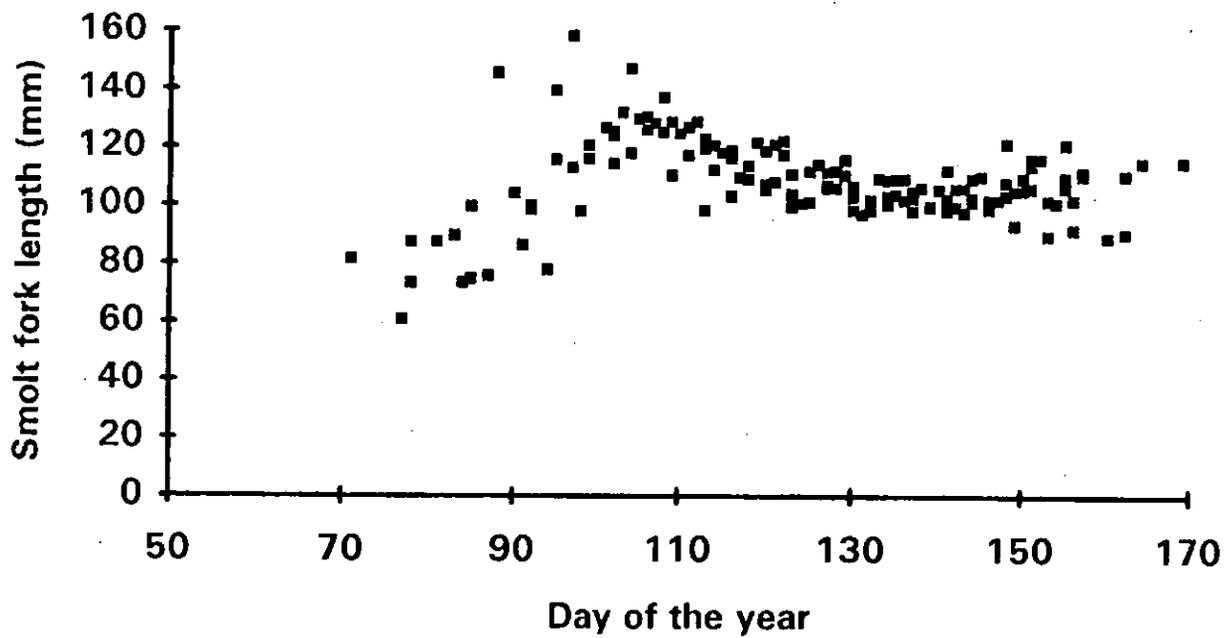
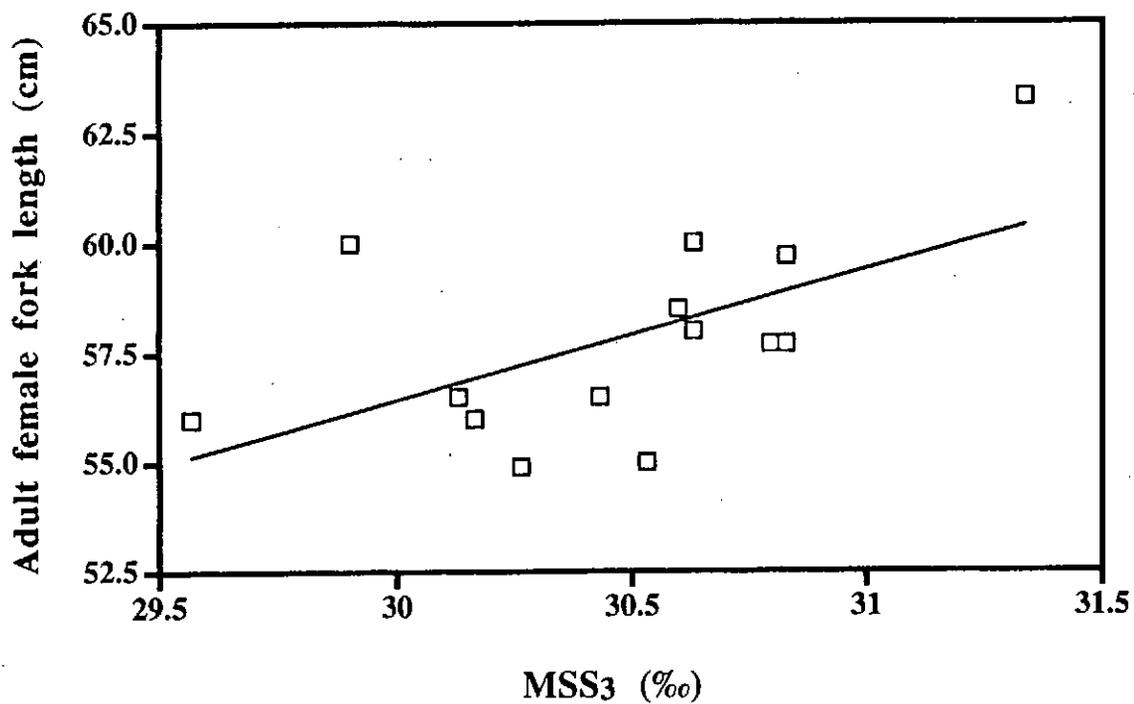


Figure IV-6. Mean fork length of Big Beef Creek coho salmon smolts over the duration of the migratory period. Each point represents the weekly mean size in a given year. Exact dates and duration of sampling varied among years.



**Figure IV-7.** Relationship between mean sea surface salinity from June through August, recorded at Amphitrite Point, British Columbia, and the mean length of female coho salmon returning to Big Beef Creek in the fall of that year.



**Table IV-1.** Relationships, calculated by linear regression, between physical and biological factors (independent variables) and the abundance or size of Big Beef Creek coho salmon. N refers to the number of years of data, BY refers to brood year, BY+x refers to the xth year after the brood year. Summer and winter flow refer to the lowest and highest average flows on 60 consecutive days from July 1 - October 31 and December 1 - February 28, respectively. MST and MSS refer to mean summer (June - August) sea surface temperature and salinity at Amphitrite Point, B.C.; MSU refers to mean summer upwelling index.

Dependent variable	Independent variable	Predicted relationship	Observed relationship	r <sup>2</sup>	P	N
Smolt abundance	number of females	positive	positive	0.142	0.167	15
	winter flow in BY	negative	positive	0.238	0.040	18
	summer flow in BY	positive	positive	0.564	0.0005	17
	winter flow in BY+1	negative	negative	0.063	0.332	17
Smolt length	number of females	negative	negative	0.059	0.401	14
	number of smolts	negative	negative	0.008	0.757	14
	summer flow in BY	positive	negative	0.006	0.804	13
	winter flow in BY+1	negative	negative	0.078	0.333	14
Marine survival	number of smolts	positive	positive	0.185	0.142	13
	smolt length	positive	positive	0.017	0.671	13
	MST in BY+2	negative	negative	0.167	0.166	13
	MSS in BY+2	positive	positive	0.036	0.536	13
	MSU in BY+2	positive	negative	0.024	0.649	11
	MST in BY+3	negative	positive	0.030	0.569	13
	MSS in BY+3	positive	negative	0.043	0.499	13
	MSU in BY+3	positive	none	0.000	0.976	10
Female length	smolt length	positive	negative	0.046	0.479	13
	MST in BY+2	negative	positive	0.032	0.540	14
	MSS in BY+2	positive	positive	0.236	0.078	14
	MSU in BY+2	positive	negative	0.038	0.545	12
	MST in BY+3	negative	positive	0.034	0.526	14
	MSS in BY+3	positive	positive	0.324	0.033	14
	MSU in BY+3	positive	negative	0.039	0.559	11

al. 1984). There have been no ongoing habitat surveys so we cannot rule out the possibility that the stream's carrying capacity is changing. In the first 11 years of smolt data (spanning brood years 1965-1979) there were seven years with more than 30,000 smolts and only four with fewer than 30,000. In contrast, only one of the 11 most recent brood years (1980-1991) produced over 30,000 smolts (36,346 in brood year 1982). This downward trend in smolt production may have several causes and cannot be confidently interpreted without data on habitat changes, water quality in the lake, status of non-native species, temperature and other factors that have not been recorded.

Variation in smolt size over the course of the run has been observed elsewhere. Irvine and Ward (1989) noted that a few small coho smolts left at the beginning of the run in the Keogh River, B.C., followed by an abrupt transition to large smolts, and a gradual decline in smolt size. This was the pattern that we observed (though sampling did not occur early enough in all years to record the small smolts). We did not detect a group of very large smolts emigrating at the end of the season that Irvine and Ward (1989) recorded in some years. Such size-dependent migratory timing is known for other anadromous salmonids (e.g., brown trout, *Salmo trutta*) and is hypothesized to reflect a balance between optimal size and time of entry into the ocean (Bohlin et al. 1993).

Irvine and Ward (1989) reported that two year old coho tended to emigrate earlier than one year olds and a similar pattern has been reported in sockeye salmon from Bristol Bay, Alaska (Crawford and Cross 1992) and Atlantic salmon, *S. salar* (Saunders 1967). However, the migratory timing of Carnation Creek coho smolts did not vary between age groups (Holtby et al. 1989). Coho smolts are not routinely aged at the Big Beef Creek fence but two year olds are uncommon (Williams 1970; Peterson and Quinn, unpublished data) so the trends in size over the season are probably not primarily by age differences. Irvine and Ward (1989) reported that the origin of coho within the watershed did not affect their emigration date, except to the extent that fish rearing in a lake tended to be larger than stream fish and emigration date varied with size. Coho rearing in Lake William Symington tend to be larger than average for the system (Williams 1970; Chapter II - B). Smolts that had been tagged as parr above the lake emigrated somewhat later than stream parr, in spite of the fact that they were larger, on average, as smolts, than the stream parr. Thus the generalizations about size and timing apparently did not over-ride the differences in timing associated with habitat.

Smolt age, size, habitat within the stream system, and date of emigration are intricately linked and have direct and indirect effects on marine survival and adult life history. Survival is related to size and emigration date in a complex manner (Mathews and Ishida 1989). Hatchery studies (e.g., Morley et al. 1988) indicate that date of emigration may have a greater consequence for survival than size and that small coho released early survive better than larger ones. As pointed out by Holtby et al. (1990), however, the relative importance of size for survival may vary with the mean size of the fish in the study population as well as with local oceanic conditions. The smolt groups released from Quinsam Hatchery by Morley et al. (1988) averaged about 14-30 g, compared with only 3-11 g for Carnation Creek coho (Holtby et al. 1990). Carnation Creek smolts were smaller than those from Big Beef Creek (mean of annual means: 84.6 mm for age one smolts, 100.7 for age two smolts from Carnation Creek [n = 14 years] vs. 108.7 mm [15 years] for all Big Beef Creek smolts). Based on our tagging study (Chapter II-B), coho size at the end of the summer varied among habitats, and both habitat and size affect overwinter survival. Size affects marine survival and it also affects emigration date, which is strongly related to survival.

Events in freshwater and at the smolt stage not only affect survival but also adult life history. Experimental studies have revealed that the proportion of jacks often increases with smolt size (e.g., Brannon et al. 1982) but is also affected by release date (Morley et al. 1988). Finally, size and date of smolt emigration affected mean adult size (Morley et al. 1988; Mathews and Ishida 1989). The reproductive output of females (egg size and egg number) and their competitive ability are functions of their size (van den Berghe and Gross 1984, 1989; Fleming and Gross 1990; but see also comments by Holtby and Healey 1986). The competitive ability of males is strongly related to size in coho (Gross 1985; Fleming and Gross 1994) and other species of salmon (e.g., sockeye, *O. nerka*, Quinn and Foote 1994).

The sex ratio and size difference between males and females observed here follow the pattern described for many coho salmon populations by Holtby and Healey (1990). They noted that when males outnumber females, males also tend to be smaller than females. The phenomenon of male-biased sex ratios had been noted previously (e.g., University of Washington hatchery population: Brannon et al. 1982) but no unified explanation had been forwarded. Holtby and Healey (1990) proposed that males of some populations may have more risk-averse foraging tactics than females, resulting in both higher survival and lower growth rates than females. The greater size of females than males is not a general characteristic of salmon, however. Males tend to be larger than females for a given age in populations of sockeye (e.g., Iliamna Lake populations: Blair et al. 1993), chum (Beacham and Murray 1985; Salo 1991), pink (Beacham and Murray 1985) and chinook (Roni 1992). Greater male size at maturity likely reflects both the greater sexual selection on size in males than females (Quinn and Foote 1994) and the greater energetic demand of gonad production in females, diverting energy from somatic growth in the later period of marine residence. It is not clear why females are often larger than males in coho but not other species of salmon. Finally, selective fisheries may play some role in biased size and sex ratios.

Unlike stream systems, where competition for limited food or space clearly influences ecological interactions among salmonids and other fishes, the evidence for density-dependent marine survival and growth is less clear. Salmon growth (and consequently age structure) can be affected by high densities in certain very large stock-complexes (e.g., sockeye salmon from Bristol Bay, Alaska: Rogers and Ruggerone 1993) or regions with extensive artificial propagation (e.g., chum salmon from Japan: Ishida et al. 1993). However, there were no data available for correlation of adult size with the total abundance of coho and chinook salmon in Washington and British Columbia. Thus we cannot rule out density-dependent growth of coho salmon from Big Beef Creek but it was not evident in the data sets examined. Marine survival showed a weak positive correlation with smolt abundance, suggesting some possible predator-saturation shortly after emigration, or perhaps conditions favorable to Big Beef Creek coho were also favorable for other nearby populations (i.e., Hood Canal) and this suite of populations saturated local predators.

Nickelson (1986) concluded that the marine survival of Oregon coho salmon was density-independent but was influenced by upwelling. While the direct links to salmon are unclear, there is convincing evidence that the last century has seen long-term climate changes with coincident changes in salmon production in the North Pacific Ocean (Beamish and Bouillon 1993). In general, when conditions are favorable for survival in northern regions (e.g., Alaska), they are unfavorable in southern regions (Francis and Sibley 1991). It seems reasonable, however, that there might be a geographically intermediate zone where correlations with upwelling and other

oceanographic conditions might be weak or non-existent. We detected no significant correlations between temperature, salinity or upwelling and marine survival, though there was a weak negative relationship between temperature in the first summer and survival. The absence of correlations is influenced by the relatively small sample size (13 years for most comparisons). Moreover, temperature and salinity were measured off the southwest coast of Vancouver Island at Amphitrite Point. This area corresponds to the center of coded wire tag recoveries in the second summer at sea but it may not be the feeding area for Big Beef Creek coho in their first summer. In any case, there is no convincing evidence that oceanographic conditions off the coast exerted a strong influence on survival, nor that marine survival has declined in recent years.

There was evidence that growth (of females) was correlated with sea surface salinity, especially in the second summer at sea. Holtby et al. (1990) also found significant correlations of salinity with early marine growth and survival as well. There is interannual variation in the abundance of salmon prey resources (Frost 1983; Brodeur and Ware 1992) and salmon diet (Brodeur 1992). However, the diets of salmon at sea are rather broad and they seem to feed opportunistically on fishes, crustaceans and soft-bodied organisms in the epipelagic zone. Fisher and Percy (1988) reported that upwelling was positively correlated with survival of Oregon coho salmon but that growth was good under differing levels of upwelling. They concluded that survival of a year class is set very early in the marine residence period and is affected by predation rather than starvation or poor growth. Many animals eat salmon, and significant predation from spiny dogfish (Beamish et al. 1992) and pinnipeds such as harbor seals (Olesiuk 1993) may occur in some situations. However, there is no single predator or other agent that is known to account for the observed mortality. Complex interactions between oceanographic conditions, prey resources, salmonid growth, and the changing distribution and abundance patterns of predators presumably control the magnitude and interannual variation in marine mortality.

#### Acknowledgments

Many individuals, too numerous to name, collected the data on which this report is based. I thank David Seiler (Washington Department of Fish and Wildlife) and L. Blair Holtby (Department of Fisheries and Oceans, Canada) for sharing their data from Big Beef Creek and Carnation Creek, respectively. Chris Sheridan, Michael McNabb, Miguel Pascual and Steve Ralph helped assemble and analyse the data sets. The research was funded by the Washington Department of Natural Resources, the U.S. Forest Service, and the H. Mason Keeler Endowment to Thomas Quinn.

## Chapter V.

### Dynamics of Stream Fish Assemblages and the Application of a Habitat-Species Index to Washington Streams

David G. Lonzarich

#### Abstract

This study examined the patterns of variability in Washington stream fish communities. Seasonal surveys were conducted in one stream from each of three regions of Washington between July 1990 and September 1992: Porter Creek (Chehalis River system), Bear Creek (Lake Washington system) and Taneum Creek (Yakima River sub-basin, Columbia River system). In addition, two other streams in each system were surveyed in one summer season only for a total of nine streams. The three primary study streams had large differences in the seasonal timing and magnitude of flooding but exhibited many similarities in assemblage and population dynamics. Moreover, the fish communities were relatively stable over time, in spite of substantial variation in flow conditions. Overall flow regime did not appear to control the communities as strongly as had been predicted. The results are consistent with the view that the magnitude of flooding (different between Bear and Porter creeks) may be less important than the timing of floods (similar in Bear and Porter creeks) as a force influencing assemblage dynamics in these systems.

Using all sites in each of the nine streams surveyed in 1992, habitat complexity was significantly correlated with species richness. The relationship of complexity to species evenness was somewhat variable but generally positive. Density was not correlated with habitat complexity for any of the three species collected in all three streams. However, the density of the two most abundant pool-dwelling species, coho salmon and speckled dace, showed strong positive relationships with % pool area. Assemblage structure in the most complex sites was also much more stable than the structure in relatively simple sites.

## Introduction

Flow disturbances are important mechanisms that profoundly influence the ecology of stream organisms. Floods can shape recruitment success (Schlosser 1982, 1985; Harvey 1987), adult mortality (Fisher et al. 1982; Meffe 1984; Erman et al. 1988; Lamberti et al. 1991), and cause changes in habitat conditions. Moreover, because floods can influence population densities and the composition of stream assemblages, they may play an important role in mediating biotic interactions such as competition and predation (Meffe 1984; Greenberg 1988; Hemphill 1991; Strange et al. 1992). However, because flow regimes and disturbance histories in streams vary geographically and are also related to human activities, the dynamics of stream fish populations and the mechanisms regulating assemblage structure may experience great spatial variability (Horwitz 1978).

A growing appreciation has developed for the relative influences of biological factors and disturbance in stream ecosystems (e.g., Peckarsky 1983; Resh et al. 1988; Poff and Ward 1989; Yount and Niemi 1990). Schlosser's (1987a) conceptual model made predictions about processes of community regulation in different stream environments. This hypothesis, analogous to benign-harsh models (e.g., Menge 1976; Peckarsky 1983), predicts that fish assemblages in harsh environments are more likely to be regulated by abiotic, stochastic processes (e.g., floods, recruitment variability) whereas populations in more benign environments are generally controlled by biotic factors such as competition and predation. In streams, harshness is defined by a variety of factors such as the frequency and severity of floods that are ultimately linked to the geomorphic and hydrologic characteristics of specific drainages. While Schlosser (1987a) specifically discussed gradients of harshness along the stream continuum, the expectations of this model may apply among streams as well (Resh et al. 1988; Poff and Ward 1989).

Resh et al. (1988) and Poff and Ward (1989) provided quantitative frameworks for describing patterns of variability in flow regimes and discussed the potential implications of the variability in the timing and magnitude of flooding on the ecology of stream assemblages. Poff and Ward (1989) explicitly related biological processes to the predictability, magnitude and timing of flow disturbances. In streams with harsh flow conditions, fish populations may fluctuate greatly due to variable recruitment success (Schlosser 1985; Schlosser and Angermeier 1990; Clark 1991; Strange et al. 1992) or over-winter mortality (e.g., Erman et al. 1988) depending on the timing of flood events. Populations may be more stable in streams with muted and temporally predictable flows (Poff and Ward 1989). In the Pacific Northwest, there is extensive variation in the disturbance regime among streams due to the region's diverse topography and climate. The coastal region often experiences extreme variation in the flow conditions within streams but the seasonal timing of floods in these systems is often very predictable. Floods typically occur during fall and winter long after most resident fishes (i.e., non-anadromous species) have spawned. Their effects on recruitment may thus be slight compared to streams where high flows coincide with larval recruitment (Schlosser 1985). In contrast to this pattern, some lowland streams of this region experience little seasonal variation in flow, and mountainous streams can experience high flows following snow-melt in the late spring. The consequences of these different flow regimes maybe manifested at different levels in stream assemblages and in different ways among streams.

Studies of the impact of floods on stream fishes generally fall into three categories: manipulative laboratory experiments, natural experiments, and comparative surveys. Manipulative experiments attempt to mimic flood conditions in artificial streams (e.g., Harvey

1987). The advantage of this approach is that the role of floods can be isolated from other extraneous factors. A potential drawback, however, is that such research is conducted at spatial and temporal scales that are too small to answer many important questions. Natural experiments include those studies that monitor changes in stream assemblages before and after floods occur (e.g., Lamberti et al. 1991; Pearsons et al. 1992). A third approach is based on a comparison of biota in streams having different flow regimes (Resh et al. 1988). Describing the relationship between stream disturbance regimes and the dynamics of fish populations is very important to the management of stream resources. The latter approach is based on a comparison of biota in streams having different flow regimes (Resh et al. 1988). While the utility of this approach is potentially limited by correlated factors that can mask the effects of disturbance, it provides the opportunity to establish the basis for variability in the dynamics of populations and assemblages.

#### **Management of streams and the role of disturbance.**

Progress in conserving stream fish resources is hampered by difficulties in relating habitat disturbances to stream biota, and by a poor understanding of the variable roles abiotic and biotic factors play in the regulation of fish populations across different physical and climatic settings. In the Pacific Northwest, forest practices have been linked to the decline in wild salmon production, yet investigations aimed at linking forestry impacts to salmonid production have produced mixed results. While some studies have linked certain consequences of logging to salmon biology (e.g., sediment load: Scrivener and Brownlee 1989; elevated temperatures: Holtby 1988), others have indicated that streams adjacent to clear-cuts have higher primary productivity and faster growing coho salmon than unlogged controls (e.g., Bilby and Bisson 1992). Thus, the complex interactions between land-use practices and salmon are not fully understood, despite the long-term studies conducted on the Alsea River, Oregon, and Carnation Creek, British Columbia, and other investigations. This can be partly traced to the fact that the effects of land-use practices often confound each other (e.g., Murphy and Hall 1981). Moreover, salmon populations are prone to large annual fluctuations due to marine mortality and fishing pressure, and fishing is a significant factor in the abundance of resident game species as well.

Problems associated with the use of species-based indices of habitat degradation in the Pacific Northwest have spurred interest in the relationship between stream assemblages and habitats in this region. There are several reasons to suspect that stream fish assemblages may be better indicators of land-use impacts than single salmonid species (Karr 1981; Naiman et al. 1992). Communities integrate various features of environmental quality, such as food and habitat. The physical degradation of streams can cause changes in the food web and the composition and distribution of habitats. Further, resident members of stream communities are exposed only to watershed-borne limiting factors, in contrast to salmon.

Characteristics of stream fish assemblages (i.e., diversity, biomass, trophic composition) have been used to evaluate the physical and chemical quality of rivers (Karr 1981; Fausch et al. 1990). The success of such efforts rests on the idea that stream fishes need specific habitat configurations or water quality conditions. Moreover, assemblage-habitat relationships must be stable over time. Long-term monitoring of fish assemblages, therefore is a prerequisite for the study of such indices. Because the dynamics of stream assemblages may be related to the natural disturbance regimes that are specific to different drainages, such studies must be conducted across a range of stream environments.

In this study, I examined the variability in fish assemblages in three streams of Washington state. After examination of the streams' annual flow regimes, the following predictions were made: (1) that seasonal and annual dynamics of fish assemblage structure would vary inversely with the seasonal flow fluctuations, and (2) species-specific patterns of overall and YOY density and biomass over a three year period should be least variable in the stream with the lowest seasonal variation in flow conditions. In addition to an examination of these predictions, I investigated the relationship between physical habitat attributes and various assemblage properties to evaluate assemblage-based indices in assessing habitat degradation in Washington streams.

## Materials and Methods

### Study Sites

Seasonal fish surveys were conducted in one stream from each of three climatic regions of Washington between July 1990 and September 1992 (Figure V-1). These streams flowed directly into a large river or lake, and were characterized by low gradient, unconstrained channels and gravel-cobble substrates. The most significant difference among the streams was their flow regimes (Figure V-2). Bear Creek (Sammamish River drainage) is a ground water and lake fed stream whose seasonal flow variation rarely exceeds one order of magnitude. Porter Creek (Chehalis River drainage) is rain-fed with sharp seasonal variations that generally peak in the winter two to three orders of magnitude above summer flows. Taneum Creek (Yakima River drainage) is rain- and snow-melt fed with sharp seasonal fluctuations that generally peak in late spring. Because long term flow data were unavailable for this stream, I used USGS data from Manastash Creek which is a similar sized drainage located within 10 km of Taneum Creek. High flows in Manastash Creek are as much as two orders of magnitude above summer flows. These differences were also reflected in terms of flow predictability and constancy (Colwell 1974; Resh et al. 1988). Predictability (P) describes the among year predictability of high flow events and values of P range between 0 (low annual predictability) and 1 (high annual predictability). Constancy (C) is a measure of seasonal constancy in stream flow and values of C vary between 0 (high seasonal variability) and 1 (constant flow). Both P and C were highest in Bear Creek (C = 0.5, P = 0.75), followed by Porter Creek (C = 0.37, P = 0.60) and then Manastash Creek (C = 0.28, P = 0.60). In addition to the general differences in flow among streams, peak flows varied greatly over the course of the study. Winter flows in 1990-1991 were much higher than flows in winter 1991-1992. For example, the instantaneous peak flow in Porter Creek was nearly 50% higher in winter 1990-91 ( $55.7 \text{ m}^3/\text{s}$ ) than 1991-1992 ( $38.6 \text{ m}^3/\text{s}$ ). Because the flow regimes of these streams differ, I hypothesized that fish population densities in Bear Creek would be less variable than Porter and Taneum creeks. However, it is not easy to isolate the effects of flow from other physical factors that could cause population fluctuations, such as local geomorphology and landuse practices, and from fishing. However, this study's goal was to provide information on spatial and temporal variability in the dynamics of stream assemblages in this region.

To increase the spatial coverage of the study, single season (summer) surveys were conducted in two secondary study streams in each of the three regions (Figure V-1). These

Figure V-1. Map of Washington state showing the location of the nine streams surveyed in this study.

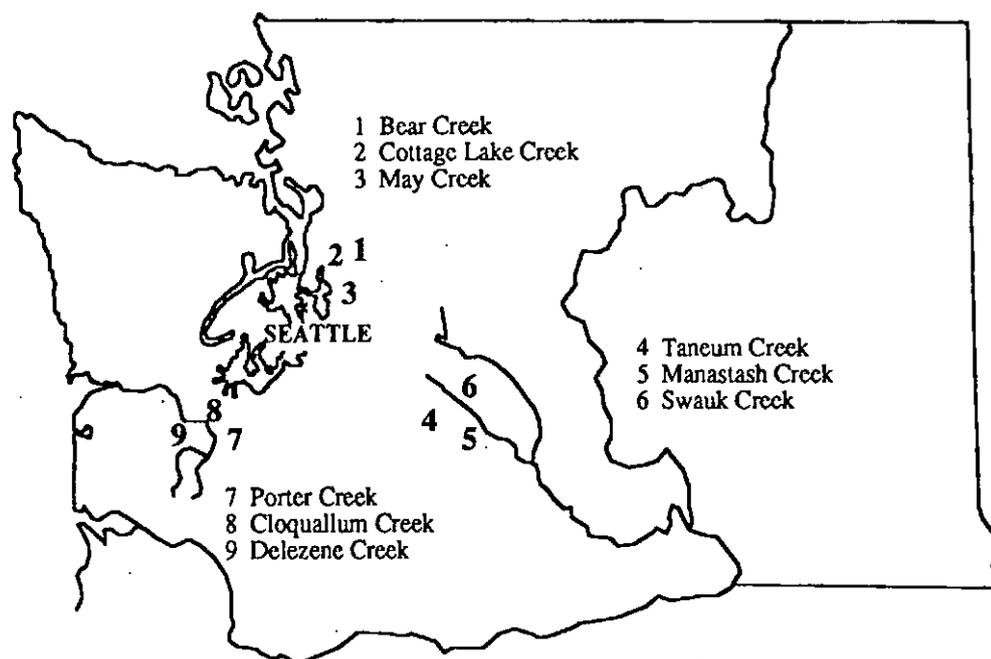
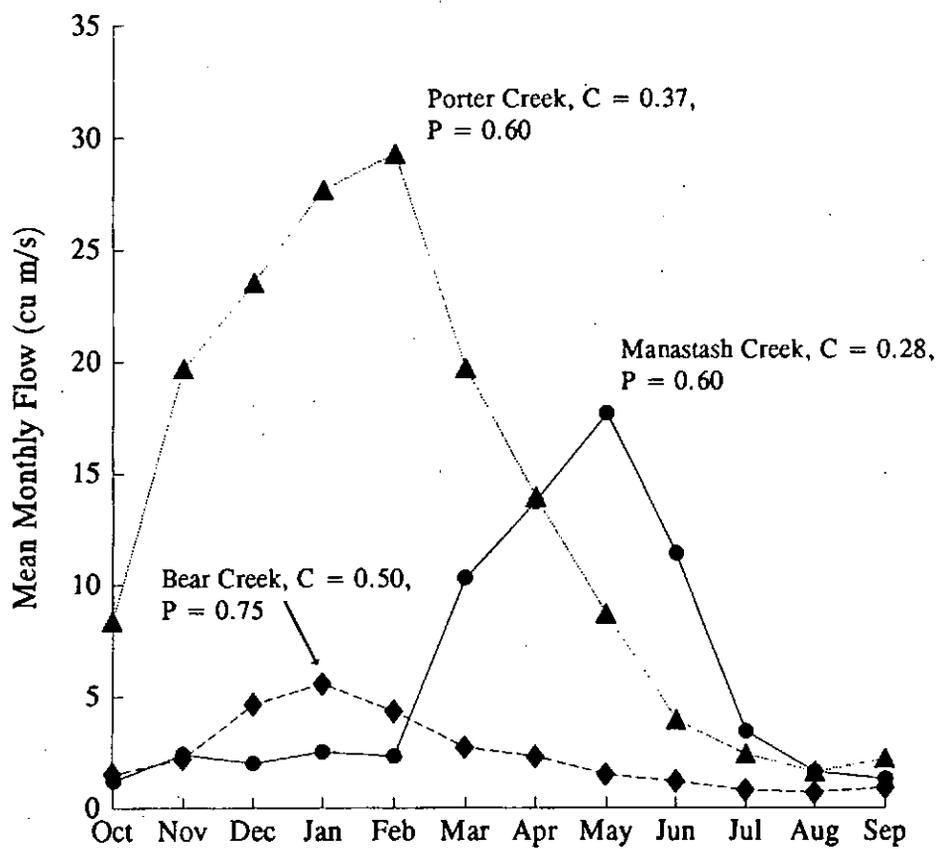


Figure V-2. Flow regimes for Taneum, Bear, and Porter creeks as represented by mean monthly flows ( $m^3/s$ ), predictability (P) and constancy (C). See text for definitions.



streams were selected on the basis of their proximity to and physical similarities with the long-term sites (e.g., basin size, gradient, valley segment types, habitat conditions). These surveys were designed to compare community structure (i.e., species composition, size structure, habitat use) with the primary streams to ascertain the generality of the results from the primary streams.

In each of the nine streams, three reaches were selected on the basis of similarities in habitat structure. Each reach contained at least one pool, riffle and glide, and varied between 21 - 35 m in length. I did not feel that repeated sampling of sites (without removal) would bias the results because similar studies have been conducted without evidence that sites were depleted of fishes (e.g., Schlosser 1982, D. Stouder, University of Washington, pers. comm.). However, to minimize the risk of any negative effects, most, if not all, fishes collected in this study were returned to upstream sections after each sampling.

Electrofishing surveys were conducted seasonally at each primary stream between summer 1990 and summer 1992. During low flow periods, population estimates were made using a three-pass technique and the formula described by Junge and Libosvářský (1965). At high flows, and in the secondary streams (sampled only in summer 1992), relative densities were obtained using only one-pass. To determine the effectiveness of single-pass surveys in estimating the relative abundance of species, I compared the relative abundance of species and age-groups derived from population estimates with the relative abundance derived from numbers collected after the first pass of each population survey using the Percent Similarity Index (PSI, Wolda 1981). The overall similarity between first pass data and the estimated population data was very high (mean = 89%, range 80 - 96%).

For each survey, all individuals or at least 30 of each species were weighed and measured. For several species, young-of-the-year (YOY) and age 1+ conspecifics were treated separately because they differed in microhabitat use (Lonzarich, unpublished data). On the basis of these data, I determined the relative abundance, density, biomass and condition factor of each species and age-group. Temporal variability in the structure of fish assemblages in Porter, Bear and Taneum creeks was examined by (1) computing the coefficient of variation (CV) for species and overall assemblage densities (Grossman et al. 1990), and (2) comparing the similarity of assemblages across the eight seasons.

### Habitat Surveys

Physical habitat features of each site were determined by measuring depth, velocity, substrate, cover, percent composition of habitat units, habitat volume and area, riparian cover and composition. Habitat complexity was measured during each survey by measuring the area of habitat types within individual sites (pool, backwater pool, riffle, glide) using a slight modification of the classification system described by Bisson et al. (1981). I recognized four habitat types: riffles, glides, scour pools and backwater pools. Using area measurements for each habitat, I used the Brilliuon evenness index (Pielou 1974) to calculate the complexity of stream reaches. Because habitat complexity was negatively correlated with the total area of individual sites ( $r^2 = -0.40$ ,  $P < 0.01$ ), I corrected the evenness value for each site, multiplying it by the total area. Habitat complexity was also evaluated on the basis of depth, bottom and surface velocity and substrate, following the methods of Gorman and Karr (1978). Depth, current and substrate were measured at regular intervals along transects perpendicular to the stream channel. The distance between transects ranged from 1 - 3 m and the distances between points on a transect ranged from 0.5 - 1.0 m depending on stream size. Between 50 and 100 points were sampled within

individual sites. Depth was measured to the nearest cm and water velocity was measured using a Marsh-McBirney Model 200 flow meter. Substrate was placed into one of six size categories: (1) boulder (> 125 cm), (2) cobble (15 - 125 cm), (3) large gravel (5 - 15 cm), (4) small gravel (0.1 - 5 cm), (5) sand, and (6) silt.

Habitat complexity was determined using two different methods. Following Gorman and Karr (1978), depth and current measurements were categorized, and together with the substrate data, were used in the computation of a Shannon-Wiener Index (Zar 1984) for each sample site. Site complexity was also defined using the combined coefficients of variation for continuous depth and velocity (surface and bottom) data. All three measures of habitat complexity were compared to the species evenness, species richness and % YOY for each site by linear regression ( $P < 0.05$ ). Square-root transformations were performed on all data that deviated from normality.

## Results

### Primary Streams

#### Assemblage Dynamics

There were many similarities in the dynamics of fish populations and assemblages in Porter, Bear and Taneum creeks although the species compositions in the three streams differed somewhat (Table V-1). Assemblage stability, as reflected by combined and individual species coefficient of variation (CV) values, was generally highest (lowest CVs) in Bear Creek and lowest (highest CVs) in Taneum Creek although few significant differences were detected (Table V-2). Among the species collected in all three streams, CVs for torrent sculpin and speckled dace varied among streams, but CVs for coho salmon and trout were similar. The mean for all benthic species (i.e., sculpins, longnose dace) from the three streams (CV = 0.41) was lower than the mean for all water-column species (salmon, trout and speckled dace, CV = 0.84,  $P < 0.01$ ).

The CV revealed little variation in assemblage composition over the nine seasons in the three primary streams. However, temporal trends in the structure of assemblages in these streams were very different. Using percent similarity for overall assemblage structure as an index of seasonal variation, seasonal changes in assemblage structure for each stream were assessed using summer 1990 and summer 1991 data as the baseline (Figure V-3). For summer 1990 assemblage data, similar patterns were apparent for Bear and Porter creeks. These assemblages experienced pronounced seasonal shifts in structure during the winter, but high similarity values during the subsequent summer low flow months. This seasonal variation was manifested differently over the two winters. In the first winter the relative abundance of benthic species, especially cottids, increased (summer 1990 relative abundance = 62%, winter 1991 = 84%). During the second year, however, there were relatively more water-column species (i.e., YOY coho salmon) in winter than summer (summer 1991 relative abundance = 67%, winter 1992 = 46%). Taneum Creek sites, in contrast, experienced a major shift in assemblage structure following the summer 1990 sampling season, but little variation over five seasons between summer 1991 and summer 1992. The most pronounced change between summer 1990 and 1992 was an increase in the relative abundance of torrent sculpin (14% to 34%) and slight decrease in piute sculpin (66% to 54%).

**Table V-1.** Common species collected in primary study streams on at least more than one occasion between summer 1990 and summer 1992.

Common name	Scientific name	Bear Cr.	Porter Cr.	Taneum Cr.
torrent sculpin	<i>Cottus rhotheus</i>	X	X	X
reticulate sculpin	<i>C. perplexus</i>		X	
piute sculpin	<i>C. beldingi</i>			X
coho salmon	<i>Oncorhynchus kisutch</i>	X	X	
rainbow trout	<i>O. mykiss</i>	X	X	X
cutthroat trout	<i>O. clarki</i>	X	X	
speckled dace	<i>Rhinichthys osculus</i>	X	X	X
longnose dace	<i>R. cataractae</i>		X	
reidside shiner	<i>Richardsonius</i>	X	X	
	<i>balteatus</i>			
three-spine	<i>Gasterosteus</i>	X		
stickleback	<i>aculeatus</i>			
brook lamprey	<i>Lampetra richardsoni</i>	X	X	

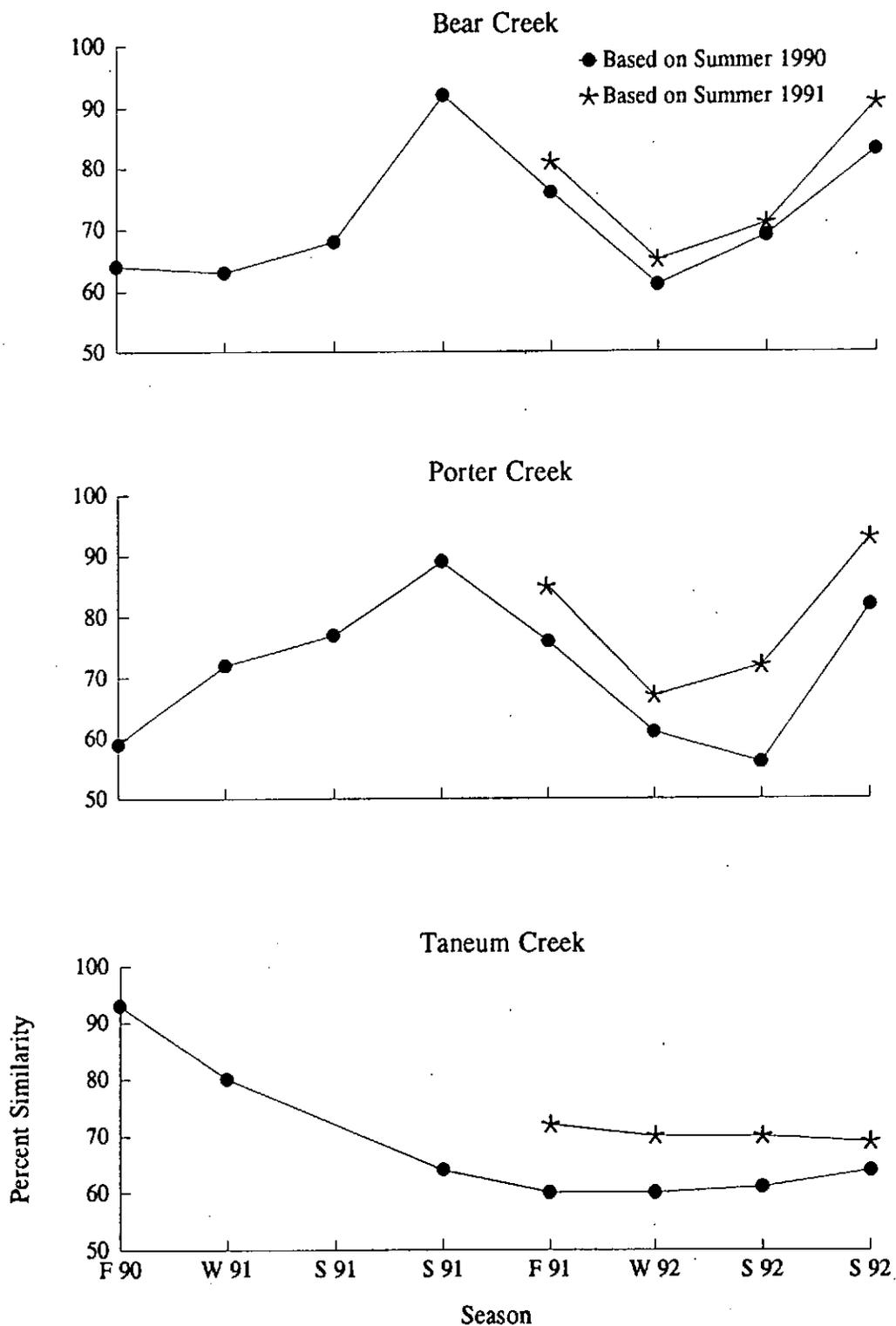
**Table V-2.** Coefficients of variation based on the relative abundance of individual species in each stream. Combined means for combined sites in each stream were not significantly different ( $P > 0.05$ ).

	SITE 1	SITE 2	SITE 3	COMBINED SITES
<b>Porter Creek</b>				
torrent sculpin	0.28	0.13	0.21	0.19
reticulate sculpin	0.41	0.28	0.57	0.29
longnose dace	0.76	0.80	0.69	0.55
speckled dace	1.12	0.95	0.76	0.60
coho salmon	1.08	1.17	1.03	1.07
rainbow trout	0.35	0.63	0.49	0.40
<b>MEAN</b>	0.67	0.66	0.63	0.65
<b>Bear Creek</b>				
torrent sculpin	0.33	0.28	0.34	0.29
speckled dace	0.60	0.72	0.66	0.59
coho salmon	0.50	0.74	1.07	0.69
cutthroat trout	0.46	0.64	0.62	0.30
<b>MEAN</b>	0.47	0.59	0.67	0.58
<b>Taneum Creek</b>				
torrent sculpin	0.60	0.33	0.59	0.55
piute sculpin	0.27	0.32	0.15	0.18
speckled dace	2.18	1.18	1.25	1.08
rainbow trout	0.65	0.65	0.63	0.46
<b>MEAN</b>	0.92	0.62	0.66	0.73

**Table V-3. Mean population densities (fish/m<sup>2</sup>) in Porter, Bear and Taneum creeks, based on the mean of three sites in each stream.**

	Summer 1990	Summer 1991	Summer 1992
<b>Porter Creek</b>			
torrent sculpin	0.40	0.79	0.85
reticulate sculpin	0.24	0.37	0.29
longnose dace	0.12	0.18	0.20
speckled dace	0.05	0.09	0.25
coho salmon	0.05	0.06	0.21
rainbow trout	0.13	0.14	0.14
<b>TOTAL</b>	<b>0.98</b>	<b>1.63</b>	<b>1.67</b>
<b>Bear Creek</b>			
torrent sculpin	0.66	1.02	0.60
speckled dace	0.22	0.47	0.36
coho salmon	0.24	0.31	0.13
cutthroat trout	0.10	0.08	0.09
<b>TOTAL</b>	<b>1.22</b>	<b>1.80</b>	<b>1.17</b>
<b>Taneum Creek</b>			
torrent sculpin	0.12	1.48	0.58
piute sculpin	0.78	1.57	0.94
speckled dace	0.04	0.01	0.05
rainbow trout	0.13	0.27	0.18
<b>TOTAL</b>	<b>1.06</b>	<b>3.33</b>	<b>1.74</b>

**Figure V-3.** Percent similarity of assemblages in three streams over a period of eight seasons. Similarity values are based on the use of summer 1990 and summer 1991 as reference dates.



### Population Patterns

Summer densities varied only slightly among the three streams (Bear Creek = 1.1 - 1.9; Porter Creek = 1.0 - 1.9; and Taneum Creek = 1.0 - 2.3 individuals per  $m^2$ , Table V-3). There were no consistent temporal trends in the density of any species in Bear and Taneum creeks; however, individual species and overall assemblage densities in these two streams were higher in summer 1991 than similar periods in 1990 and 1992.

Densities of YOY fishes varied significantly among years in the three streams, being most variable in Taneum Creek and least variable in Bear Creek. In Bear Creek, summer densities of YOY cottids and speckled dace varied by 50 and 35%, respectively over the three summers. In Porter Creek, densities of YOY fishes varied as much as four-fold (e.g., coho salmon) but this variability was no greater than that observed for older age-groups of speckled dace, trout, longnose dace, etc. By contrast, variability in YOY densities of both piute sculpin and torrent sculpin in Taneum Creek was much greater than the variability found in older age-groups (Figure V-4). Summer 1991 YOY densities of these two cottids were as much as 30 times greater than population densities in either 1990 or 1992. In contrast, the greatest disparity in population densities for all other species and adult cottids was no more than five-fold.

Mean densities of YOY fishes differed greatly among the three streams. For YOY torrent sculpin, densities were generally highest in Bear Creek and lowest in Porter Creek. Among the different salmonid species, the mean density of coho salmon was two times higher in Bear than in Porter Creek. In contrast, YOY trout densities were higher in Porter and Taneum creeks than in Bear Creek (Figure V-4). Recruitment of YOY minnows in the three streams was limited to speckled dace in Bear and Taneum creeks. Young-of-the-year speckled dace or longnose dace were never collected from Porter Creek sites. Annual variability in dace recruitment was much lower in Bear Creek than in Taneum Creek; while densities of YOY dace were always much higher in Bear Creek.

Biomass estimates for each population from length-weight regression models revealed several significant patterns (Figure V-5). Most pronounced among these was the increasing trend in summer biomass for both Porter and Taneum creeks from 1990 to 1992, and the absence of variation at either the assemblage or species level in Bear Creek. In Taneum Creek, mean biomass of fishes increased nearly four-fold between summer 1990 and 1992. Dramatic increases in the biomass of rainbow trout ( $0.7 \text{ g/m}^2$  to  $5.4 \text{ g/m}^2$ ) and torrent sculpin ( $0.4 \text{ g/m}^2$  to  $1.9 \text{ g/m}^2$ ) contributed most to this trend. Porter Creek experienced a comparatively slight upward trend in biomass over the three summers due largely to increased biomass of torrent sculpin, coho salmon and speckled dace.

To explore the relationship between flow characteristics and assemblage dynamics, regression analyses were performed using flow predictability and constancy as independent variables against all population and assemblage data. Neither flow predictability nor constancy were correlated with any of the biological characteristics measured.

**Figure V-4.** Mean densities of YOY and older ("adult") fishes in Bear, Porter and Taneum creeks for summers 1990 - 1992. Species listed include torrent sculpin (TS), reticulate sculpin (RS), piute sculpin (PS), longnose dace (LD), speckled dace (SD), cutthroat trout (CT), rainbow trout (RT) and coho salmon (CS).

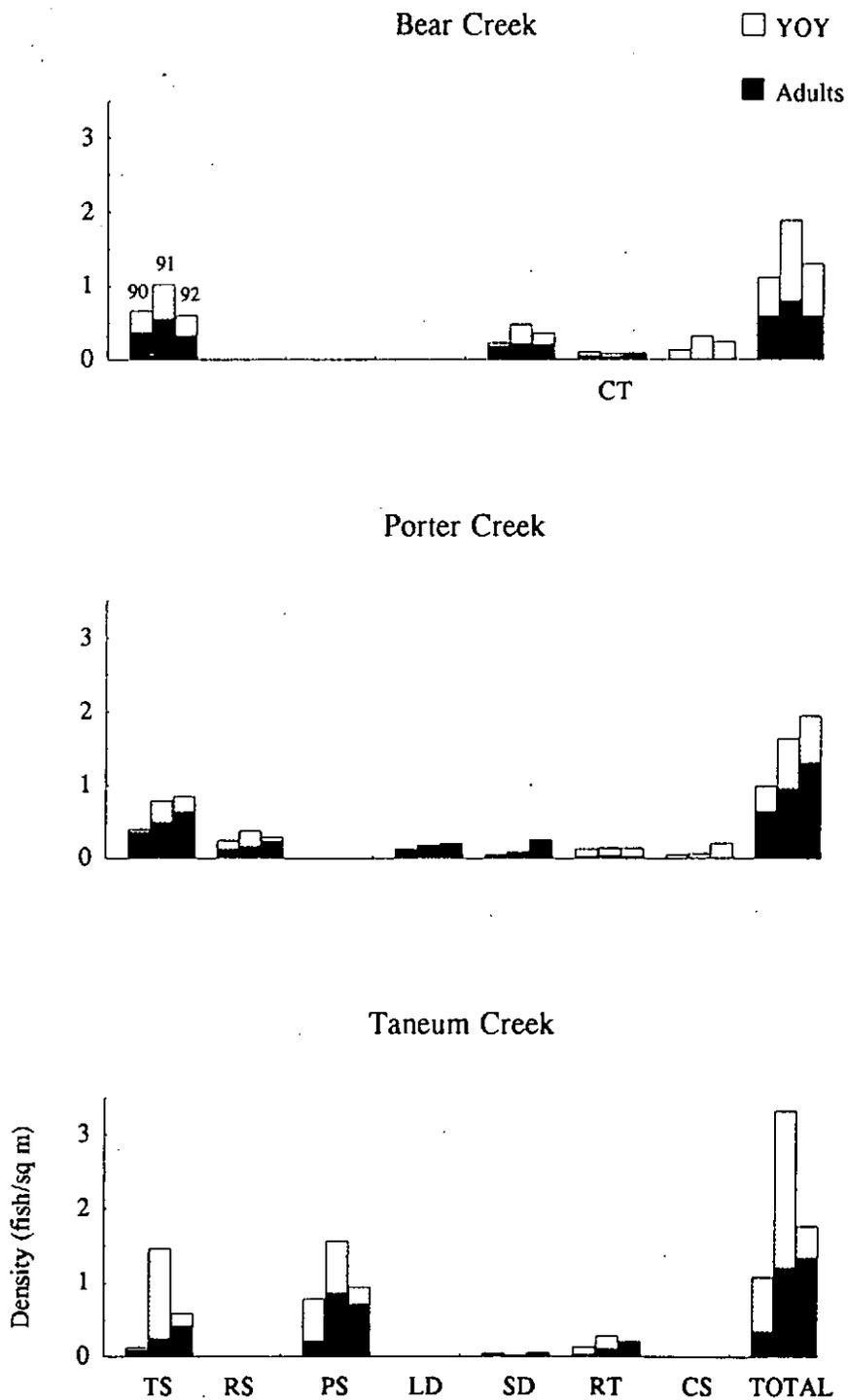
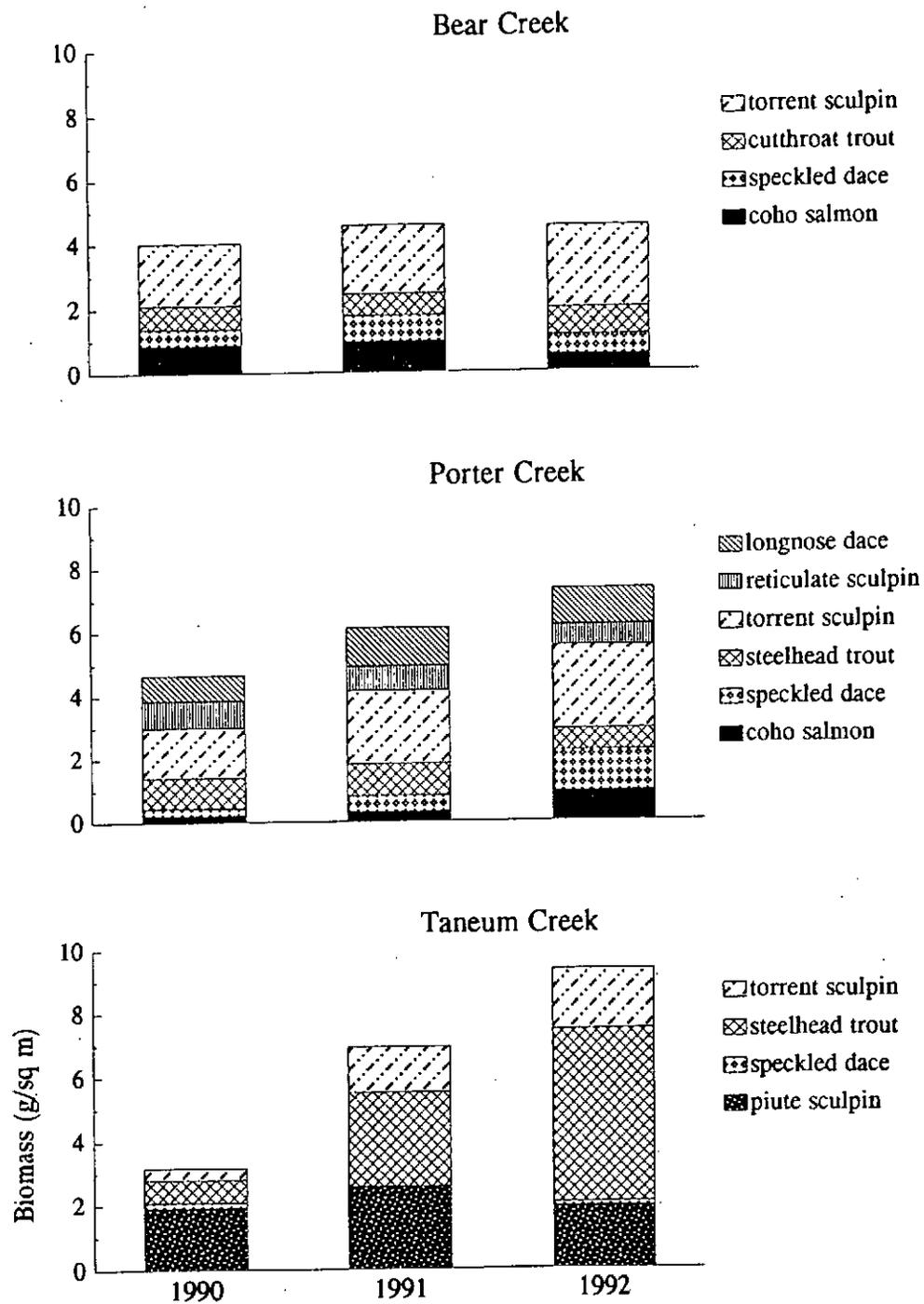


Figure V-5. Mean estimated biomass for fishes in primary streams as determined from summer population surveys.



### Secondary Streams

Comparisons of the fish faunas in the nine streams surveyed during summer 1992 showed little similarity in structure even within geographic regions (Table V-4). In the Lake Washington drainage, May and Cottage Lake creek assemblages each shared only a 61% similarity with the Bear Creek fauna. In all three streams, assemblages were dominated by torrent sculpin (relative abundance = 50 - 62%) and coho salmon (13 - 29%). However, the composition of other species in the streams differed in several respects. Speckled dace was only collected in Bear Creek (29%), and the May Creek sites included two cottids (reticulate and coastrange sculpin, *C. aleuticus*) not found in the other two streams. Rainbow trout were collected in May and Cottage Lake creeks but not Bear Creek. Benthic species accounted for 50% of all individuals collected in Bear Creek, and 62 and 69% of the individuals collected in May and Cottage Lake creeks, respectively.

Similarity in the faunas of the three Chehalis River drainage streams ranged between 62 and 68%. The species composition was similar, but the relative abundance of species varied considerably in the three streams. Torrent sculpin was the most common species in all three streams (45 - 62% of all individuals collected). Benthic species comprised 66% of the Porter Creek fauna and as much as 83% in Cloquallum Creek.

Yakima River drainage streams showed the greatest variability in assemblage structure, exhibiting both the lowest and highest similarity values of all the streams compared. The faunas of Manastash and Taneum creeks were very similar (83%) but each was extremely different from Swauk Creek (26 and 31%). Differences in the faunas of these streams reflected differences in both species composition and relative abundance. Swauk Creek contained 11 different species or ecologically distinct age-groups, whereas Taneum and Manastash creeks each contained only six. Piute sculpin (53%), and torrent sculpin (29%), dominated the faunas of Taneum and Manastash creeks, but in Swauk Creek these two cottids were relatively rare (7% and 17%, respectively). Swauk Creek was dominated by minnows and catostomids, which collectively comprised 71% of all individuals collected. Rainbow trout was relatively scarce in all three streams (7 - 16%). Finally, benthic species comprised 80 and 83% of the Taneum and Manastash fauna but only 45% of the Swauk Creek fauna.

The relative abundance of YOY fishes varied among the nine streams but there was no consistent pattern of variation across the three geographic regions (Table V-4). In six of the nine streams, YOY recruits accounted for approximately 50% of all individuals collected. In contrast, YOY fish represented less than 30% of the total collected in Porter, Taneum and Manastash creeks.

**Table V-4.** Biological characteristics of nine streams surveyed in summer 1992. Number of taxa include species and age-groups of species which exhibit ontogenetic shifts in habitat use (Chapter 2). YOY = young-of-the-year; BENTHIC = Benthic species.

DRAINAGE	STREAM	% YOY	NO. TAXA	% BENTHIC
Lake Washington				
	Bear Creek	51	11	50
	Cottage Lake Creek	49	7	62
	May Creek	44	9	69
Chehalis				
	Porter Creek	27	10	66
	Cloquallum Creek	42	10	83
	Delezene Creek	50	8	74
Yakima				
	Taneum Creek	28	6	80
	Swauk Creek	69	11	45
	Manastash Creek	18	6	83

### Habitat - Faunal Relationships

No consistent, strong relationships between physical habitat complexity and components of fish assemblage structure (i.e., species richness, species evenness and assemblage stability) were detected within or across the three major drainages using the complexity measures developed by Gorman and Karr (1978) and modified by Angermeier and Schlosser (1989, Figure V-6). However, several patterns were detected using the habitat complexity index developed by T. Beechie (University of Washington) and modified in this paper. Using all sites in each of the nine streams surveyed in 1992, habitat complexity was significantly correlated with species richness ( $r^2 = 0.40$ ,  $P < 0.05$ , Figure V-7). The relationship of complexity to species evenness was somewhat variable but generally positive. When all nine streams surveyed in summer 1992 were examined collectively, there was no correlation between complexity and evenness, however, in six of the nine streams surveyed there was an increase in species evenness with increasing site complexity. If the three streams that showed no relationship (May, Cottage and Cloquallum creeks) are dropped from the analysis, the habitat-evenness correlation becomes highly significant ( $r^2 = 0.54$ ,  $P < 0.01$ ). Density was not correlated with habitat complexity for any of the three species collected in all three streams. However, the density of the two most abundant pool-dwelling species, coho salmon ( $r^2 = 0.74$ ,  $n = 6$ ,  $P < 0.05$ ) and speckled dace ( $r^2 = 0.64$ ,  $n = 9$ ,  $P < 0.05$ ), showed strong positive relationships with % pool area (Figure V-8).

Comparisons made across the three summers in the primary streams revealed similar relationship between species evenness and habitat complexity (Figure V-9). During each of the three summers, species evenness was significantly correlated with habitat complexity in the primary streams although the relationship diminished consistently over time. This variability in the evenness-complexity relationship can be principally attributed to annual differences in the biota of the streams as physical habitat complexity in the survey sites changed little among years. Species richness was also correlated with complexity over the three summers in the primary streams.

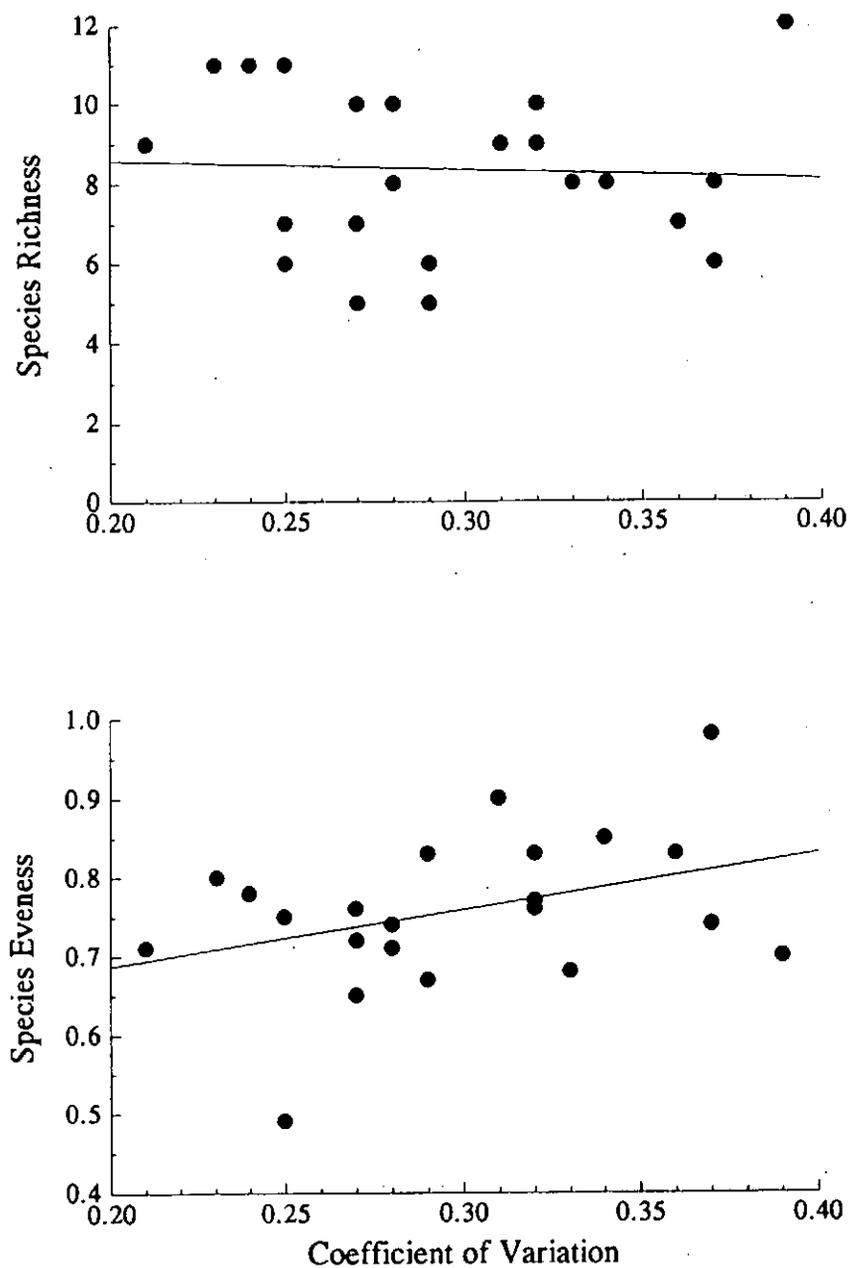
Temporal stability in the structure of assemblages in the three primary streams was also strongly correlated with habitat complexity (Figure V-10). Using only species that were common to all three streams, significant negative relationships were detected when habitat complexity was plotted against the coefficients of variation for total assemblage density (i.e., the total of all individuals in an assemblage) and for species relative abundance. These results indicated that assemblage structure in the most complex sites was much more stable than the structure in relatively simple sites.

## Discussion

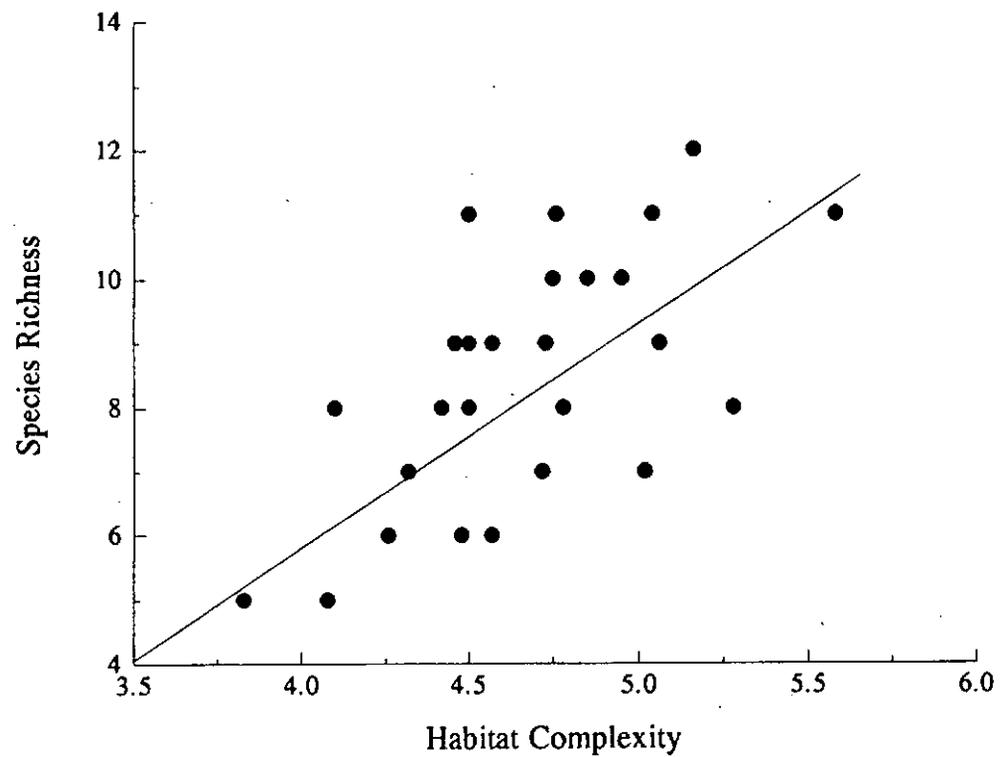
### Assemblage Dynamics

In this study, streams with large differences in the seasonal timing and magnitude of flooding exhibited many similarities in assemblage and population dynamics. Coefficients of variation for overall assemblage densities and species relative abundance in Porter and Bear creeks were indistinguishable from one another but both were significantly lower than the CVs for Taneum Creek. For all three of these streams, CVs (0.47 - 0.92) were on the lower range of values reported by Grossman et al. (1990) in a review of multi-year stream surveys conducted across the United States. The high values recorded (range 75 - 135%) were thought to reflect

**Figure V-6.** Species richness and species evenness plotted against the coefficient of variation for combined habitat variables (total depth, substrate, bottom and surface velocity). Regression lines do not differ from zero ( $P > 0.05$ )



**Figure V-7.** Relationship between habitat complexity (T. Beechie, unpubl. manuscript) and species richness for all nine streams surveyed in summer 1992 ( $r^2 = 0.40$ ,  $P < 0.01$ ). Species richness included ecologically distinct age-classes as well as taxonomic species.



**Figure V-8.** Relationship between % pool area and mean densities of coho salmon ( $r^2 = 0.74$ ,  $P < 0.05$ ) and speckled dace ( $r^2 = 0.64$ ,  $P = 0.01$ ). Data combined for surveys conducted between summer 1990 and 1992.

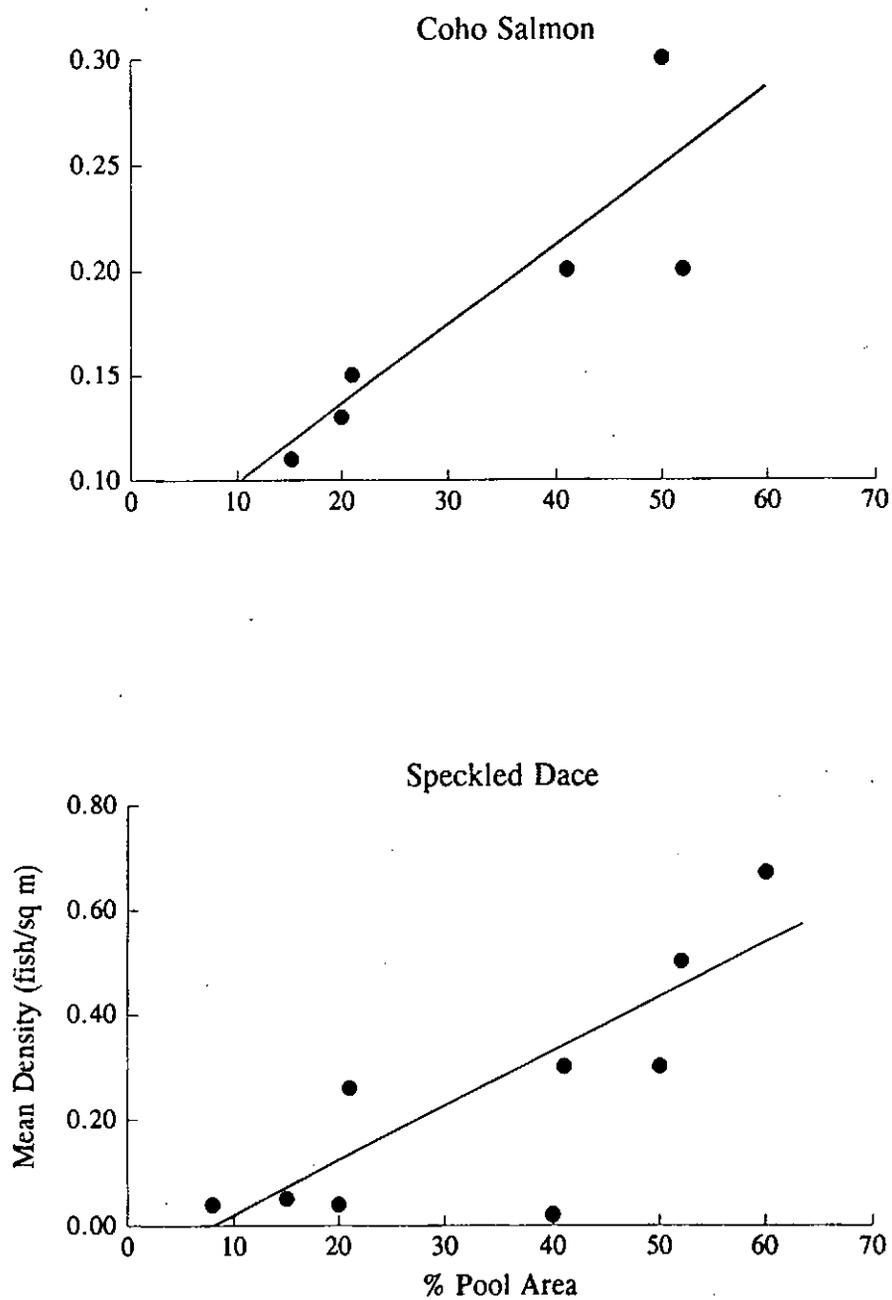
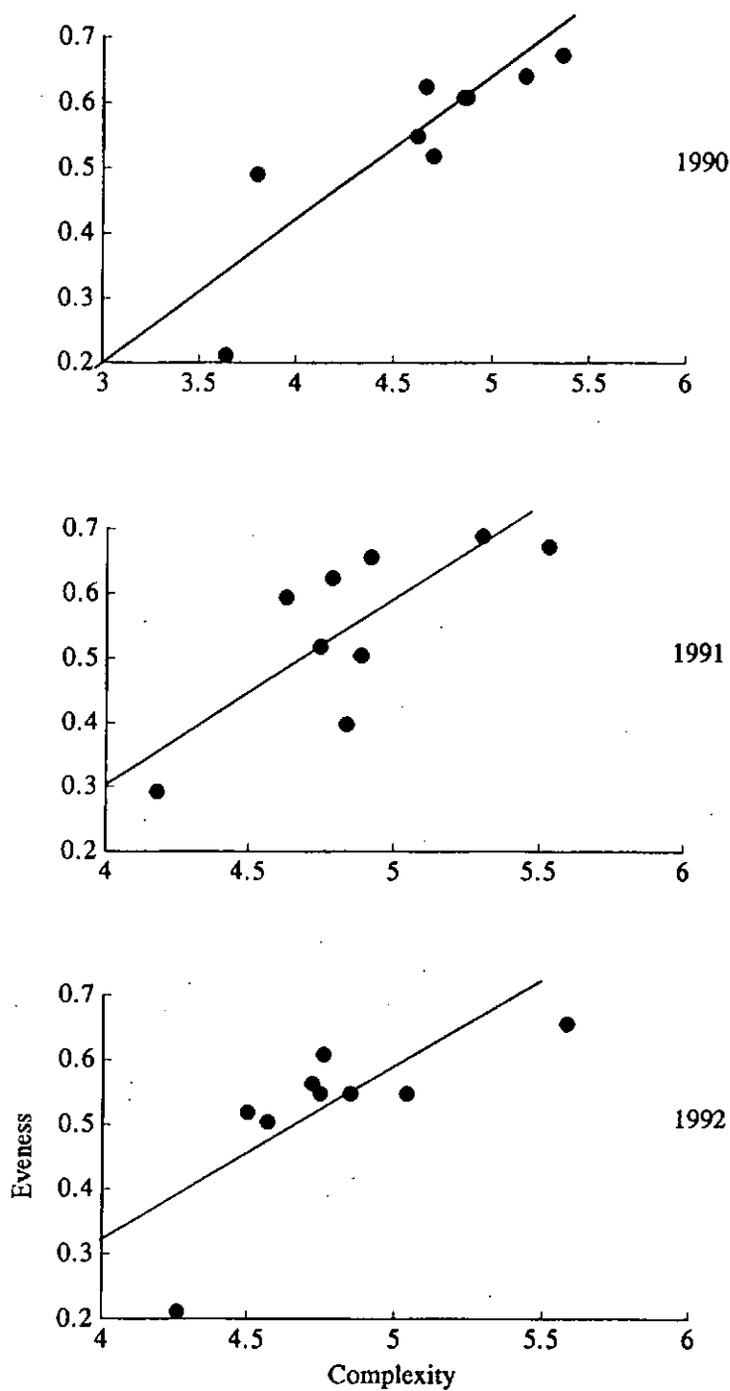
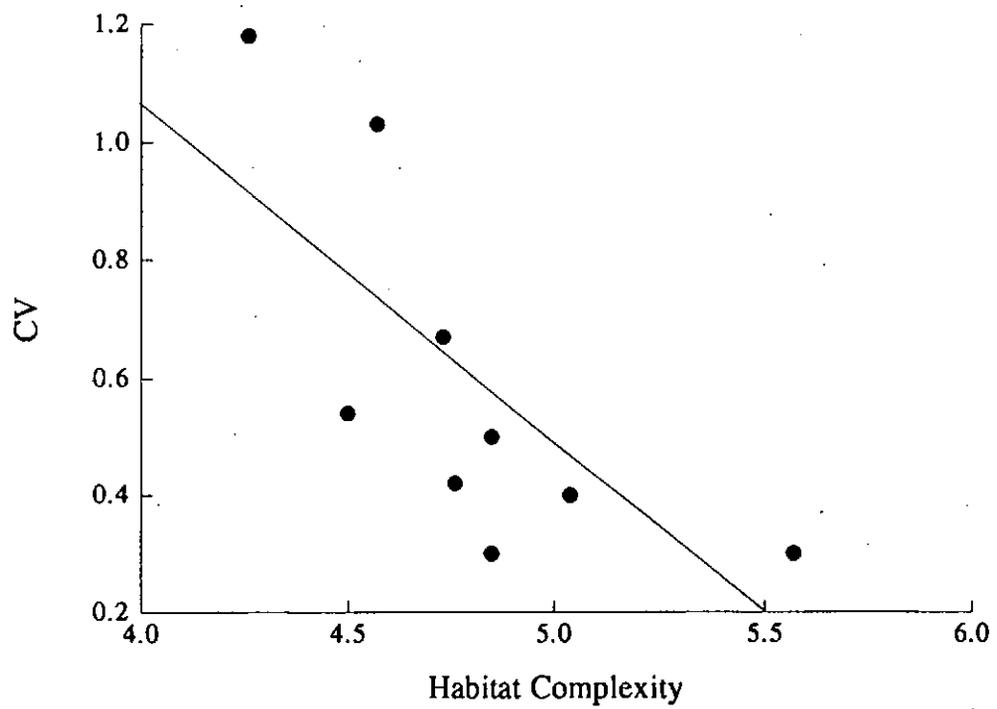


Figure V-9. Relationship between habitat complexity and species evenness for primary streams in summers 1990 ( $r^2 = 0.70$ ,  $P < 0.01$ ), 1991 ( $r^2 = 0.57$ ,  $P < 0.05$ ) and 1992 ( $r^2 = 0.50$ ,  $P < 0.05$ ).



**Figure V-10.** Relationship between habitat complexity and coefficients of variation for each of the three surveyed assemblages in the three primary streams ( $r^2 = 0.55$ ,  $P < 0.05$ ).



unstable assemblage structure, although the authors acknowledged that the lack of comparative data restricted their interpretations.

Using the criteria established by Grossman et al. (1990), assemblages in Porter and Bear creeks appeared to experience low to moderate temporal variation, while those in Taneum Creek were more variable. Percent similarity values, which were relatively high for Porter and Bear creeks and low for Taneum Creek, further support this conclusion by suggesting stable assemblage structure in the two former streams but low assemblage stability in the latter. Although the short duration of this study may limit the strength of these interpretations, the study encompassed a broad range of flow conditions; far above (fall 1990) to well below (fall - winter 1991-92) long-term averages. Moreover, the three-year study spanned at least one generation of these short-lived species (Wydoski and Whitney 1979) and thus satisfied one of the criteria described by Connell and Sousa (1983) for assessing assemblage stability. Therefore, the findings of this study may reflect patterns of assemblage variability in these systems. The significance of these results lies in their implications to the regulation of stream populations. For assemblages showing temporal stability, there may be strong density dependent components (e.g., competition, predation) to population regulation (Ross et al. 1985). Therefore, the patterns of variability observed in these different assemblages may indicate the importance of biotic controls over populations.

### **Population Processes**

It is difficult to determine precisely the reason for the greater stability of assemblages in Porter and Bear creeks. However, these results are consistent with the view that the magnitude of flooding (different between Bear and Porter creeks) may be less important than the timing of floods (similar in Bear and Porter creeks) as a force influencing assemblage dynamics in these systems. As factors influencing stream populations, winter floods may lead to high mortality if channel scouring crushes fish with mobilized bed-material (Erman et al. 1988) or if flows displace fish downstream (Sedell et al. 1990; Pearsons et al. 1992). In a California mountain stream, Erman et al. (1988) found that mortality caused by intense winter flooding led to a three-fold decrease in piute sculpin densities. In the present study, conservative estimates of over-winter survival (which also includes movement) for juvenile and adult cottids for all three streams ranged between 27 and 82%. Over-winter survival of water-column species may be lower than this. However, no mortality estimates were made because these populations are likely more vagile than cottid populations. The similar dynamics of Bear and Porter creek populations may reflect similar mortality risks across very different winter flow regimes, but the correlation between mortality and flow regimes must be quantified more precisely.

Variability in the structure of Taneum Creek fish assemblages was most strongly linked with recruitment fluctuations in the two cottid populations (as measured by the densities of YOY fish in summer surveys). Flooding during the late spring snow melt may have caused this variability as high flows coincide with at least the early part of the spawning season for the two species in this stream (Wydoski and Whitney 1979). High flows have been linked with recruitment variability in fishes (e.g., Seegrist and Gard 1972; Schlosser 1985; Schlosser and Angermeier 1990; Pearsons et al. 1992). High water velocities can affect recruitment success by causing egg and larval mortality. Consistent with this hypothesis, cottid recruitment was relatively stable in Bear and Porter creeks where peak flooding (fall and winter) and spawning (late spring) occur in different seasons.

Despite this evidence, other factors may be responsible for recruitment fluctuations and assemblage dynamics in Taneum Creek. For example, assemblage stability (as measured by CVs) was negatively correlated with habitat complexity, and complexity was lower in Taneum than in Porter or Bear creeks. Recruitment fluctuations may also be affected by annual differences in stream temperatures and food availability (Schlosser and Angermeier 1990). Given that recruitment variation can profoundly influence the dynamics and structure of stream assemblages (Schlosser 1985; Schlosser and Ebel 1989), we agree with Schlosser and Angermeier (1990) that identifying the mechanisms responsible for this variation, and the precise consequences to fishes, should be a major goal of stream research.

### **Habitat - Faunal Relationships**

The classification of stream habitats using physical and chemical parameters has had a long history as a tool in the management of stream biota (Naiman et al. 1992). In cold water streams, examinations of habitat degradation have often focused upon the relationship between physical habitat quality (e.g., percent pool area, large woody debris) and salmonid growth and survival (e.g., Modde et al. 1991; Bilby and Bisson 1992). Where correlations between these factors exist, managers can predict the consequences of changes in stream habitat to salmonid production. For various reasons, however, this relationship can be very complex or difficult to demonstrate (Murphy and Hall 1981).

We expected that increasing reach complexity (as reflected by the evenness of habitat units along a stream reach) would correlate with higher species richness and evenness. This hypothesis was based on the assumption that fishes in these streams exhibit a high degree of habitat specialization (Wydoski and Whitney 1979; Lonzarich 1994). Habitat complexity, as defined by Beechie, was a good predictor of several biological characteristics in the streams surveyed, including not only species richness and evenness but also assemblage stability. Although this latter relationship was not anticipated, it should not have been surprising (see Fausch and Bramblett 1991; Pearsons et al. 1992). Among the factors potentially responsible for this relationship is structural complexity which may provide refuge from high water velocities and lead to greater survival. Channel stability may also be greater in complex reaches and minimize the effects of bed-material transport and other material on fish survival.

One somewhat surprising result of my examination of habitat-faunal relationships was the poor correspondence of faunal characteristics to the complexity index (Gorman and Karr 1978; later modified by Angermeier and Schlosser 1989). Because this index is based on the heterogeneity of depth, velocity and substrate within stream reaches, it should have more accurately predicted faunal characteristics than the index developed by Beechie (unpubl. manuscript) which incorporates the area and types of habitats in a reach.

The stability of the faunas in the three streams surveyed and the often strong habitat-faunal relationships suggest that stream habitat degradation may have predictable consequences for the biota of streams in this region. In streams where reach complexity declines, lower species richness, evenness and possibly assemblage stability may be expected. In this study, such patterns were detected despite differences in the flow regimes of Bear, Porter and Taneum creeks. The temporal constancy of these relationships in the three primary streams further validates the utility of this complexity index as a management tool. Yet, the weakness of the relationship between complexity and species evenness using all nine streams surveyed in 1992 suggests that more extensive testing and development of this model may be required. One potential weakness of the

index is that complexity is based only on the evenness of habitat units along a stream reach. In this respect it is somewhat different from definitions of complexity that have been used elsewhere (Gorman and Karr 1978; Pearsons et al. 1992) which often make reference to the three-dimensional structure or physical complexity of channel units, typically pool habitats. It is possible that the index might be improved by incorporating information on the structural complexity of channel units within a stream reach. Although not evident in the results of this analysis, another potential limitation of the index is that Washington contains several unique zoogeographic regions which influence the number of species that can be found in any given site. There are various ways to handle this, such as using species evenness or only comparing streams within zoogeographic regions.

Finally, any analysis of stream fish communities must acknowledge the roles of natural marine mortality for anadromous species and fishing mortality for both resident and anadromous game species. Coho salmon are subjected to heavy fishing pressure and it is not safe to assume that the carrying capacities of streams are reached on a regular basis. Cutthroat and rainbow/steelhead trout may be resident or anadromous and their populations may also reflect fishing pressure to some extent.

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### Concluding Remarks

The various investigations that comprised Project 19 revealed the intricate adaptations of Pacific salmon and non-salmonid fishes to the physical conditions in Washington streams. These adaptations do not mean that the fishes are insensitive or invulnerable to physical processes. Quite the contrary; while salmon are inherently productive species and the non-salmonid stream fishes are able to persist under rigorous conditions, relatively slight alterations in physical characteristics of streams can adversely affect them. The detection of such effects, however, can be masked or magnified by density-dependent processes and a background of climatic variation. The existence of climatic variation affecting salmon in freshwater or at sea, or compensatory and dependant processes, does not obviate the need for habitat protection. Indeed, adverse oceanic conditions or droughts during freshwater rearing will lower the productivity of a populations, making ideal physical habitat even more essential.

Our ability to understand these complex relationships in Washington has been limited by the absence of long-term habitat information and details of population biology to accompany data sets such as that gathered by the Washington Department of Fisheries (now Fish and Wildlife) at Big Beef Creek. However, rather than argue against maintaining such data sets, we strongly believe that they should be continued and augmented with appropriate habitat information and stream temperature records. We also praise the staff that have been responsible for these investigations.

Finally, we decry the circumstances that set in motion our own "long-term" study and then cut it short. The extent to which scientists in this state are forced to rely on data from the Alsea River, Oregon and Carnation Creek, British Columbia is nothing short of embarrassing. The need for comprehensive research in this state has long been recognized and the absence of such work has not resulted from a dearth of qualified or motivated scientists. The leaders of the natural resource agencies, Native American tribes, environmental activists, forest products industry, and other stakeholders owe it to the citizens of this state and to the resources themselves to commit sufficient funds for high quality (though not necessarily high cost) research over a long period of time. Unless such work is undertaken, we will be condemned to high levels of uncertainty when attempting to assess the consequences of past actions and predict the future of salmon in Washington.

## References

- Adams, J. M., and R. L. Beschta. 1980. Gravel bed composition in Oregon coastal streams. *Canadian Journal of Fisheries and Aquatic Sciences* 37:1514-1521.
- Alderdice, D. F., W. P. Wickett, and J. R. Brett. 1958. Some effects of exposure to low dissolved oxygen levels on Pacific salmon eggs. *Journal of Fisheries Research Board of Canada* 15:229-249.
- Alexander, G.R. 1979. Predators of fish in coldwater streams. Pages 153-171 in *Predator-prey systems in fisheries management*. Stroud, R.H. and Clepper, H.E., editors. Sport Fishing Institute, Washington D. C.
- Andrews, E. D. 1982. Bank stability and channel width adjustment, East Forks River, Wyoming. *Water Resources Research* 18:1184-1192.
- Andrus, C.W., B.A. Long, and H.A. Froehlich. 1988. Woody debris and its contribution to pool formation in a coastal stream 50 years after logging. *Canadian Journal of Fisheries and Aquatic Sciences* 45: 2080-2086.
- Angermeier, P.L., and Karr, J.R. 1984. Relationships between woody debris and fish habitat in small warmwater streams. *Transactions of the American Fisheries Society* 113: 716-726.
- Angermeier, P.L., and I.J. Schlosser. 1989. Species-area relationships for stream fishes. *Ecology* 70: 1450-1462.
- Angradi, T.R. 1992. Effects of predation risk on foraging behavior of juvenile rainbow trout (*Oncorhynchus mykiss*). *Canadian Journal of Zoology* 70: 355-360.
- Baltz, D.M., P.B. Moyle and N.J. Knight. 1982. Competitive interactions between benthic stream fishes, riffle sculpin, *Cottus gulosus*, and speckled dace, *Rhinichthys osculus*. *Canadian Journal of Fisheries and Aquatic Sciences* 39:1502-1511.
- Bams, R. A. and C. N. H. Lam. 1983. Influences of deteriorating water quality on growth and development of chum salmon (*Oncorhynchus keta*) larvae in a Japanese-style keeper channel. *Canadian Journal of Fisheries and Aquatic Sciences* 40:2098-2104.
- Bathurst, J. C. 1979. Distribution of boundary shear stress in rivers. Pages 95-116. In D. D. Rhodes and G. P. Williams (editors) *Adjustment of the fluvial system: a proceeding of the Tenth Annual Geomorphology Symposia Series*.
- Beacham, T.D. and C.B. Murray. 1985. Variation in length and body depth of pink salmon (*Oncorhynchus gorbuscha*) and chum salmon (*O. keta*) in southern British Columbia. *Canadian Journal of Fisheries and Aquatic Sciences*. 42: 312-319.
- Beamish, R.J., B.L. Thomson and G.A. McFarlane. 1992. Spiny dogfish predation on chinook and coho salmon and the potential effects on hatchery-produced salmon. *Transactions of the American Fisheries Society* 121: 444-455.
- Beamish, R.J. and D.R. Bouillon. 1993. Pacific salmon production trends in relation to climate. *Canadian Journal of Fisheries and Aquatic Sciences* 50: 1002-1016.
- Beschta, R. L. 1987. Conceptual models of sediment transport in streams. Pages 387-419. In C. R. Thorne, J. C. Bathurst, and R. D. Hey, editors. *Sediment transport in Gravel-Bed Rivers*. John Wiley and Sons, Ltd.
- Beschta, R. L. and W. L. Jackson. 1979. The intrusion of fine sediments into a stable gravel bed. *Journal of Fisheries Research Board of Canada* 36:204-210.

- Bilby, R.E., and P.A. Bisson. 1987. Emigration and production of hatchery coho salmon (*Oncorhynchus kisutch*) stocked in streams draining an old-growth and a clear-cut watershed. *Canadian Journal of Fisheries and Aquatic Sciences* 45: 1397-1407.
- Bilby, R.E., and P.A. Bisson. 1992. Allochthonous versus autochthonous organic matter contributions to the trophic support of fish populations in clear-cut and old-growth forested streams. *Canadian Journal of Fisheries and Aquatic Sciences* 49: 540-551.
- Bilby, R.E., and J.W. Ward. 1989. Changes in characteristics and function of woody debris with increasing size of streams in western Washington. *Transactions of the American Fisheries Society* 118: 368-378.
- Bilby, R.E., and J.W. Ward. 1991. Characteristics and function of large woody debris in streams draining old-growth, clear-cut, and second-growth forests in southwestern Washington. *Canadian Journal of Fisheries and Aquatic Sciences* 48: 2499-2508.
- Bilton, H.T., D.F. Alderdice and J.T. Schnute. 1982. Influence of time and size at release of juvenile coho salmon (*Oncorhynchus kisutch*) on returns at maturity. *Canadian Journal of Fisheries and Aquatic Sciences* 39: 426-447.
- Bisson, P.A., J.L. Nielsen, R.A. Palmason, and L.E. Gore. 1982. A system of mapping habitat types in small streams, with examples of habitat utilization by salmonids during low stream flow. Pages 62-73 in N.B. Armantrout, editor. *Aquisition and utilization of aquatic habitat information*. Western Division, American Fisheries Society.
- Bisson, P.A., R.E. Bilby, M.D. Bryant, C.A. Dolloff, G.B. Grette, R.A. House, M.L. 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 E.O. Salo and T.W. Cundy, editors. *Streamside management - forestry and fishery interactions*. Institute of Forest Resources, University of Washington, Seattle.
- 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. *Transactions of the American Fisheries Society* 117: 262-273.
- Bjornn, T.C. 1969. Survival to emergence of trout and salmon fry in various gravel-sand mixtures. Pages 80-88 in *Proceedings, forum on the relation between logging and salmon*. American Institute of Fishery Research Biologists, and Alaska Department of Fish and Game, Juneau, Alaska.
- Blair, G.R., D.R. Rogers and T.P. Quinn. 1993. Variation in life history characteristics and morphology of sockeye salmon (*Oncorhynchus nerka*) in the Kvichak River system, Bristol Bay, Alaska. *Transactions of the American Fisheries Society* 122: 550-559.
- Bohlin, T., C. Dellefors, and U. Faremo. 1993. Optimal time and size for smolt migration in wild sea trout (*Salmo trutta*). *Canadian Journal of Fisheries and Aquatic Sciences* 50: 224-232.
- Brannon, E.L. 1965. The influence of physical factors on the development and weight of sockeye salmon embryos and alevins. *International Pacific Salmon Fisheries Commission Progress Report* 12.
- Brannon, E.L., C. Feldmann and L. Donaldson. 1982. University of Washington zero-age coho salmon smolt production. *Aquaculture* 28: 195-200.
- Brice, J.C. 1984. Planform properties of meandering rivers. Pages 1-15. In C. M. Elliot, editor. *River Meandering: proceedings of the conference "Rivers '83"*. American Society of Civil Engineers, New York.

- Brodeur, R.D. 1992. Factors related to variability in feeding intensity of juvenile coho salmon and chinook salmon. *Transactions of the American Fisheries Society* 121: 104-114.
- Brodeur, R.D., and D.M. Ware. 1992. Long-term variability in zooplankton biomass in the subarctic Pacific Ocean. *Fisheries Oceanography* 1: 32-38.
- Brown, T.G., and G.F. Hartman. 1988. Contributions of seasonally flooded lands and minor tributaries to the production of coho salmon in Carnation Creek, British Columbia. *Transactions of the American Fisheries Society* 117: 546-551.
- Buckley, R.M., and H.L. Blankenship. 1990. Internal extrinsic identification systems: overview of implanted wire tags, otolith marks, and parasites. *American Fisheries Society Symposium* 7: 173-182.
- Bugert, R.M., and T.C. Bjornn. 1991. Habitat use by steelhead and coho salmon and their responses to predators and cover in laboratory streams. *Transactions of the American Fisheries Society* 120: 486-493.
- 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. *Transactions of the American Fisheries Society* 120: 474-485.
- Bustard, D.R., and D.W. Narver. 1975. Aspects of the winter ecology of juvenile coho salmon (*Oncorhynchus kisutch*) and steelhead trout (*Salmo gairdneri*). *Journal of the Fisheries Research Board of Canada* 32: 667-680.
- Carling, P.A., and N.A. Reader. 1982. Structure, composition and bulk properties of upland stream gravels. *Earth Surface Processes and Landforms* 7: 349-365.
- Carlson, J.Y., C.W. Andrus, and H.A. Froehlich. 1990. Woody debris, channel features, and macroinvertebrates of streams with logged and undisturbed riparian timber in northeastern Oregon, U.S.A. *Canadian Journal of Fisheries and Aquatic Sciences* 47: 1103-1111.
- Cederholm, C.J. 1972. The short-term physical and biological effects of stream channelization at Big Beef Creek, Kitsap County, Washington. Master's thesis, University of Washington.
- Cederholm, C.J., and L.M. Reid. 1987. Impacts of forest management on coho salmon (*Oncorhynchus kisutch*) populations of the Clearwater River, Washington: a project summary. Pages 373-398. in E. O. Salo and T. E. Cundy, editors *Streamside management: forestry and fishery interactions*. Contribution No. 57 College of Forest Resources, University of Washington, Seattle, Washington.
- Cederholm, C.J., and W.J. Scarlett. 1982. Seasonal immigration of juvenile salmonids into four small tributaries of the Clearwater River, Washington, 1977-1981. Pages 98-110 in E. L. Brannon and E. O. Salo, editors. *Salmon and trout migratory behavior symposium*. School of Fisheries, University of Washington., Seattle, Washington.
- Chapman, D.W. 1962. Aggressive behavior in juvenile coho salmon as a cause of emigration. *Journal of the Fisheries Board of Canada* 19: 1047-1080.
- Chapman, D.W. 1966. Food and space as regulators of salmonid populations in streams. *American Naturalist* 100: 345-357.
- Chapman, D.W. 1988. Critical review of variables used to define effects of fines in redds of large salmonids. *Transactions of the American Fisheries Society* 117: 1-21.
- Clark, R.A. 1991. Influence of stream flows and stock size on recruitment of arctic grayling (*Thymallus arcticus*) in the Chena River, Alaska. *Canadian Journal of Fisheries and Aquatic Sciences* 49: 1027-1034.

- Coble, D.W. 1961. Influence of water exchange and dissolved oxygen in redds on survival of steelhead trout embryos. *Transactions of the American Fisheries Society* 90:469-474.
- Colwell, R.K. 1974. Predictability, constancy and contingency of periodic phenomena. *Ecology* 55: 1148-1153.
- Connell, J.H., and W.P. Sousa. 1983. On the evidence needed to judge ecological stability and persistence. *American Naturalist* 121: 781-823.
- Conover, W.J. 1980. *Practical non-parametric statistics*. John Wiley & Sons, New York.
- Crawford, D.L. and B.A. Cross. 1992. Bristol Bay sockeye salmon smolt studies for 1991. Technical Fishery Report 92-20. Alaska Department of Fish and Game, Juneau, Alaska.
- Crisp, D.T., and P.A. Carling. 1989. Observations on siting, dimensions and structure of salmonid redds. *Journal of Fish Biology* 34:119-134.
- Dill, L.M. 1983. Adaptive flexibility in the foraging behavior of fishes. *Canadian Journal of Fisheries and Aquatic Sciences* 40: 398-408.
- Dill, L.M., and A.H.G. Fraser. 1984. Risk of predation and the feeding behavior of juvenile coho salmon (*Oncorhynchus kisutch*). *Behavioral Ecology and Sociobiology* 16: 65-71.
- Dolloff, C.A. 1992. Predation by river otters (*Lutra canadensis*) on juvenile coho salmon (*Oncorhynchus kisutch*) and Dolly Varden (*Salvelinus malma*) in southeast Alaska. *Canadian Journal of Fisheries and Aquatic Sciences* 50: 312-315.
- Dolloff, C.A. 1986. Effects of stream cleaning on juvenile coho salmon and Dolly Varden in southeast Alaska. *Transactions of the American Fisheries Society* 115: 743-755.
- Dolloff, C.A., and G.H. Reeves. 1990. Microhabitat partitioning among stream-dwelling juvenile coho salmon, *Oncorhynchus kisutch*, and Dolly Varden, *Salvelinus malma*. *Canadian Journal of Fisheries and Aquatic Sciences* 47: 2297-2306.
- Eberhardt, L.L., and J.M. Thomas. 1991. Designing environmental field studies. *Ecological Monographs* 61: 53-73.
- Edington, J.R. 1984. Some observations of fine sediment and gravels of five undisturbed watersheds. Pages 109-114. *in* W. R. Meehan, T. R. Merrell, Jr., and T. A. Hanley, editors. *Fish and wildlife relationships in old-growth forests*. Proceedings of a symposium held in Juneau, Alaska, 12-15, April, 1982. American Institute of Fishery Research Biologists.
- Einstein, H.A. 1968. Deposition of suspended particles in a gravel bed. *American Society of Civil Engineering, Journal of Hydrology Division* 94(HY5):1197-1205.
- Elliott, S.T. 1986. Reduction of a Dolly Varden population and macrobenthos after removal of logging debris. *Transactions of the American Fisheries Society* 115: 392-400.
- Erman, D.C., E.D. Andrews, and M. Yoder-Williams. 1988. Effects of winter floods on fishes in the Sierra Nevada. *Canadian Journal of Fisheries and Aquatic Sciences* 45: 2195-2200.
- Everest, F.H., C.E. McLemore and J.F. Ward. 1980. An improved tri-tube cryogenic gravel sampler. U.S. Department of Agriculture, Forest Service Research Note PNW-350.
- Everest, F.H., R.L. Beschta, J.C. Scrivener, K.V. Koski, J.R. Sedell, and C. J. Cederholm. 1987. Fine sediment and salmonid production: a paradox. Pages 98-142 *in* Salo, E.O. and T.C. Cundy, editors. *Streamside management - forestry and fishery interactions*. College of Forest Resources, University of Washington, Seattle, Washington.
- Fausch, K.D. 1984. Profitable stream positions for salmonids: relating specific growth rate to net energy gain. *Canadian Journal of Zoology* 62: 441-451.

- Fausch, K.D. 1993. Experimental analysis of microhabitat selection by juvenile steelhead (*Oncorhynchus mykiss*) and coho salmon (*O. kisutch*) in a British Columbia stream. *Canadian Journal of Fisheries and Aquatic Sciences* 50: 1198-1207.
- Fausch, K.D., J. Lyons, J.R. Karr, and P.L. Angermeier. 1990. Fish communities as indicators of environmental degradation. *American Fisheries Society Symposium* 8: 123-144.
- Fausch, K.D., and R.G. Bramblett. 1991. Disturbances and fish communities in intermittent tributaries of western Great Plains river. *Copeia* 1991: 659-674.
- Fausch, K.D., C.L. Hawkes, and M.G. Parsons. 1988. Models that predict standing crop of stream fish from habitat variables: 1950-1985. Gen. Tech. Rep. PNW-GTR-213. Portland, OR:U.S. Department of Agriculture, Forest Service, Pacific Northwest Research Station. 52 p.
- Fausch, K.D., and T.G. Northcote. 1992. Large woody debris and salmonid habitat in a small coastal British Columbia stream. *Canadian Journal of Fisheries and Aquatic Sciences* 49: 682-693.
- Fraser, D.F., and R.D. Cerri. 1982. Experimental evaluation of predator-prey relationships in a patchy environment: consequences for habitat use in minnows. *Ecology* 63: 307-313.
- Fisher, J.P., and W.G. Pearcy. 1988. Growth of juvenile coho salmon (*Oncorhynchus kisutch*) in the ocean off Oregon and Washington, USA, in years of differing coastal upwelling. *Canadian Journal of Fisheries and Aquatic Sciences* 45: 1036-1044.
- Fisher, S.G., L.J. Gray, N. Grimm, and D.E. Busch. 1982. Temporal succession in a desert stream ecosystem following flash flooding. *Ecological Monographs* 52:93-110.
- Fleming, I.A., and M.R. Gross. 1990. Latitudinal clines: a trade-off between egg number and size in Pacific salmon. *Evolution* 71: 1-11.
- Fleming, I.A., and M.R. Gross. 1994. Breeding competition in a Pacific salmon (coho: *Oncorhynchus kisutch*): measures of natural and sexual selection. *Evolution* (in press).
- Francis, R.C. and T.H. Sibley. 1991. Climate change and fisheries: what are the real issues? *Northwest Environmental Journal* 7: 295-307.
- Frost, B.W. 1983. Interannual variation of zooplankton standing stock in the open Gulf of Alaska. Pages 146-157 in W.S. Wooster, editor. *Year to Year - Interannual Variability of the Environment and Fisheries of the Gulf of Alaska and the Eastern Bering Sea*. Washington Sea Grant, Seattle.
- Gibson, R.J., and G. Power. 1975. Selection by brook trout (*Salvelinus fontinalis*) and juvenile Atlantic salmon (*Salmo salar*) of shade related to water depth. *Journal of the Fisheries Research Board of Canada* 32: 1652-1656.
- Gilliam, J.F., and D.F. Fraser. 1987. Habitat selection under predation hazard: test of a model with foraging minnows. *Ecology* 68: 1856-1862.
- Gomez, B. 1983. Representative sampling of sandy fluvial gravels. *Sedimentary Geology* 34: 301-306.
- Gorman, O.T., and J.R. Karr. 1978. Habitat structure and stream fish communities. *Ecology* 59: 507-515.
- Grant, J.W.A., J. Englert and B.F. Bietz. 1986. Application of a method for assessing the impact of watershed practices: effects of logging on salmonid standing crops. *North American Journal of Fisheries Management* 6: 24-31.
- Greenberg, L.A. 1988. Interactive segregation between the stream fishes *Etheostoma simoterum* and *E. rufilineatum*. *Oikos* 51: 193-202.

- Grette, G.B. 1985. The role of large organic debris in juvenile salmonid rearing habitat in small streams. Master's thesis, University of Washington, Seattle, Washington.
- Gross, M.R. 1985. Disruptive selection for alternative life histories in salmon. *Nature* 313: 47-48.
- Grossman, G.D., J.D. Dowd, and M. Crawford. 1990. Assemblage stability in stream fishes. *Environmental Management* 14: 661-672.
- Grost, T.G., W.A. Hubert, and T.A. Wesche. 1991a. Field comparison of three devices used to sample substrate in small streams. *North American Journal of Fisheries Management* 11: 347-351.
- Grost, R.T., W.A. Hubert and T.A. Wesche. 1991b. Description of brown trout redds in a mountain stream. *Transactions of the American Fisheries Society* 120: 582-588.
- Hall, J.D., M.L. Murphy and R.S. Aho. 1978. An improved design for assessing impacts of watershed practices on small streams. *Internationale Vereinigung für Theoretische und Angewandte Limnologie Verhandlungen* 20: 1359-1365.
- Hartman, G., J.C. Scrivener, L.B. Holtby, and L. Powell. 1987. Some effects of different streamside treatments on physical conditions and fish population processes in Carnation Creek, a coastal rain forest stream in British Columbia. Pages 330-372 in E. O. Salo and T. W. Cundy, editors. *Streamside management: forestry and fishery interactions*. College of Forest Resources, University of Washington, Seattle.
- Harvey, B.C. 1987. Susceptibility of young-of-the-year fishes to downstream displacement by flooding. *Transactions of the American Fisheries Society* 116: 851-855.
- Harvey, B.C. 1991. Interactions among stream fishes: predator-induced habitat shifts and larval survival. *Oecologia* 87: 29-36.
- Harvey, B.C., and A.J. Stewart. 1991. Fish size and depth relationships in headwater streams. *Oecologia* 87: 336-342.
- Healey, M.C. 1982. Timing and relative intensity of size-selective mortality of juvenile chum salmon (*Oncorhynchus keta*) during early sea life. *Canadian Journal of Fisheries and Aquatic Sciences* 39: 952-957.
- Heifetz, J., M.L. Murphy, and K.V. Koski. 1986. Effects of logging on winter habitat of juvenile salmonids in Alaskan streams. *North American Journal of Fisheries Management* 6: 52-58.
- Hemphill, N. 1991. Disturbance and variation in competition between two stream insects. *Ecology* 72: 864-872.
- Henderson, M.A., and A.J. Cass. 1991. Effect of smolt size on smolt-to-adult survival for Chilko Lake sockeye salmon (*Oncorhynchus nerka*). *Canadian Journal of Fisheries and Aquatic Sciences* 48: 988-994.
- Hilborn, R. and C.J. Walters. 1981. Pitfalls of environmental baseline and process studies. *Environmental Assessment Review* 2: 265-278.
- Holtby, L.B. 1988. Effects of logging on stream temperatures in Carnation Creek, British Columbia, and associated impacts on the coho salmon (*Oncorhynchus kisutch*). *Canadian Journal of Fisheries and Aquatic Sciences* 45: 502-515.
- Holtby, L.B., T.E. McMahon and J.C. Scrivener. 1989. Stream temperatures and inter-annual variability in the emigration timing of coho salmon (*Oncorhynchus kisutch*) smolts and fry and chum salmon (*O. keta*) fry from Carnation Creek, British Columbia. *Canadian Journal of Fisheries and Aquatic Sciences* 46: 1396-1405.

- Holtby, L.B., B.C. Andersen, and R.K. Kadowaki. 1990. Importance of smolt size and early ocean growth to interannual variability in marine survival of coho salmon (Oncorhynchus kisutch). *Canadian Journal of Fisheries and Aquatic Sciences* 47: 2181-2194.
- Holtby, L.B., and M.C. Healey. 1986. Selection for adult body size in female coho salmon (Oncorhynchus kisutch). *Canadian Journal of Fisheries and Aquatic Sciences* 43: 1946-1959.
- Holtby, L.B., and M.C. Healey. 1990. Sex-specific life history tactics and risk-taking in coho salmon. *Ecology* 71: 678-690.
- Holtby, L.B. and J.C. Scrivener. 1989. Observed and simulated effects of climatic variability, clear-cut logging and fishing on the numbers of chum salmon (Oncorhynchus keta) and coho salmon (O. kisutch) returning to Carnation Creek, British Columbia. *Canadian Special Publication of Fisheries and Aquatic Sciences* 105: 62-81.
- Horwitz, R.J. 1978. Temporal variability patterns and the distributional patterns of stream fishes. *Ecological Monographs* 48: 307-321.
- Irvine, J.R., and B.R. Ward. 1989. Patterns of timing and size of wild coho salmon (Oncorhynchus kisutch) smolts migrating from Keogh River watershed on northern Vancouver Island. *Canadian Journal of Fisheries and Aquatic Sciences* 46: 1086-1094.
- Ishida, Y., S. Ito, M. Kaeriyama, S. McKinnell and K. Nagasawa. 1993. Recent changes in age and size of chum salmon (Oncorhynchus keta) in the North Pacific Ocean and possible causes. *Canadian Journal of Fisheries and Aquatic Sciences* 50: 290-295.
- Jackson, W. L. And R. L. Beschta. 1982. A model of two-phase bedload transport in an Oregon Coast Range stream. *Earth Surface Processes and Landforms* 7:517-527.
- Johnson, J.K. 1990. Regional overview of coded wire tagging of anadromous salmon and steelhead in northwest America. *American Fisheries Society Symposium* 7: 782-816.
- Johnson, S.L. 1988. The effects of the 1983 El Nino on Oregon's coho (Oncorhynchus kisutch) and chinook (O. tshawytscha) salmon. *Fisheries Research* 6: 105-123.
- Junge, C., and J. Libosvářský. 1965. Effects of size selectivity on population estimates based on successive removals with electrofishing gear. *Zool. Listy*. 14: 171-178.
- Karr, J.R. 1981. Assessment of biotic integrity using fish communities. *Fisheries* 6: 21-26.
- Koenings, J.P., H.J. Geiger, and J.J. Hasbrouck. 1993. Smolt-to-adult survival patterns of sockeye salmon (Oncorhynchus nerka): effect of smolt length and geographic latitude when entering the sea. *Canadian Journal of Fisheries and Aquatic Sciences* 50: 600-611.
- Keller, E. A. 1971. Areal sorting of bed-load material: the hypothesis of velocity reversal. *Geological Society of America Bulletin* 82:753-756.
- Koski, K V. 1966. The survival of coho salmon (Oncorhynchus kisutch) from egg deposition to emergence in three Oregon streams. Master's thesis. Oregon State University, Corvallis, Oregon.
- Koski, K.V. 1975. The survival and fitness of two stocks of chum salmon (Oncorhynchus keta) from egg deposition to emergence in a controlled-stream environment at BigBeef Creek. Ph.D. dissertation, University of Washington, Seattle.
- Lamberti, G.A., S.V. Gregory, L.R. Ashkenas, R.C. Wildman, and K.M.S. Moore. 1991. Stream ecosystem recovery following a catastrophic debris flow. *Canadian Journal of Fisheries and Aquatic Sciences* 48: 196-208.

- Leman, V.N. 1993. Spawning sites of chum salmon, Oncorhynchus keta: microhydrological regime and viability of progeny in redds (Kamchatka River basin). *Journal of Ichthyology* 33: 104-117.
- Lestelle, L.C., M.L. Rowse, and C. Weller. 1993. Evaluation of natural stock improvement measures for Hood Canal coho salmon. Point No Point Treaty Council, Technical REport 93-1: 179 p.
- 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, editors. University of Oklahoma Press, Norman, Oklahoma.
- Lichatowich J., and S. Cramer. 1979. Parameter selection and sample sizes in studies of anadromous salmonids. Oregon Dept of Fish and Wildlife Report Series, Fisheries Number 80-1.
- Lisle, T. E. 1989. Sediment transport and resulting deposition in spawning gravels, north coastal California. *Water Resources Research* 25:1303-1319.
- Lisle, T. E. and R. E. Eads. 1991. Methods to measure sedimentation of spawning gravels. USDA, U.S. Forest Service Research Note. PSW-411.
- Lisle, T. E. and J. Lewis. 1992. Effects of sediment transport on survival of salmonid embryos in a natural stream: a simulation approach. *Canadian Journal of Fisheries and Aquatic Sciences* 49:2337-2344.
- Lonzarich, D.G. 1994. Stream fish communities in Washington: patterns and processes. Ph.D. dissertation, Univ. of Washington.
- Lotspeich, F.B., and F.H. Everest. 1981. A new method for reporting and interpreting textural composition of spawning gravel. United States Department of Agriculture, U.S. Forest Service, Research Note PNW-369, 11 pp.
- Madej, M. A. 1975. Response of a stream channel to an increase in sediment load. Master's thesis, University of Washington, Seattle, Washington.
- Marshall, D.E., and E.W. Britton. 1990. Carrying capacity of coho salmon streams. *Canadian Manuscript Report of Fisheries and Aquatic Sciences* 2058: 32 p.
- Mason, J.C. 1969. Hypoxial stress prior to emergence and competition among coho salmon fry. *Journal of the Fisheries Research Board of Canada*. 26:63-91.
- Mathews, S.B., and Y. Ishida. 1989. Survival, ocean growth, and ocean distribution of differentially timed releases of hatchery coho salmon (Oncorhynchus kisutch). *Canadian Journal of Fisheries and Aquatic Sciences* 46: 1216-1226.
- McMahon, T.E., and G.F. Hartman. 1989. Influence of cover complexity and current velocity on winter habitat use by juvenile coho salmon (Oncorhynchus kisutch). *Canadian Journal of Fisheries and Aquatic Sciences* 46: 1551-1557
- McNeil, W.J. 1962. Variations in the dissolved oxygen content of intragravel water in four spawning streams of southeastern Alaska. United States Fish and Wildlife Service Special Scientific Report - Fisheries. 402: 15 p.
- McNeil, W.J. 1964. Redd superimposition and egg capacity of pink salmon spawning beds. *Journal of the Fisheries Research Board of Canada* 21: 1385-1396.
- McNeil, W.J. 1966. Effect of the spawning bed environment on reproduction of pink and chum salmon. *Fishery Bulletin* 65: 495-523.

- McNeil, W.J., and W.H. Ahnell. 1960. Measurement of gravel composition of salmon streambeds. Fisheries Research Institute, University of Washington, Circular 120.
- Meehan, W.R., editor. 1991. Influences of forest and rangeland management on salmonid fishes and their habitats. American Fisheries Society Special Publication 19.
- Meffe, G.K. 1984. Effects of abiotic disturbance on coexistence of predatory-prey species. *Ecology* 65: 1525-1534.
- Menge, B.A. 1976. Organization of the New England rocky intertidal community: role of predation, competition and environmental heterogeneity. *Ecological Monographs* 46: 355-393.
- Mesick, C.F. 1988. Effects of food and cover on numbers of Apache and brown trout establishing residency in artificial stream channels. *Transactions of the American Fisheries Society* 117: 421-431.
- Metcalfé, N.B., F.A. Huntingford, and J.E. Thorpe. 1987. The influence of predation risk on the feeding motivation and foraging strategy of juvenile Atlantic salmon. *Animal Behaviour* 35: 901-911.
- Mittelbach, G.G., and P.L. Chesson. 1987. Predation risk: indirect effects on fishes. Pages 315-332 in *Predation: direct and indirect impacts on aquatic communities*. W. C. Kerfoot and A. Sih, editors. University Press of New England, Hanover, NH.
- Modde, T., R.C. Ford, and M.G. Parsons. 1991. Use of habitat based stream classification system for categorizing trout biomass. *North American Journal of Fisheries Management* 11: 305-311.
- Montgomery, D.R., and J.M. Buffington. 1993. Channel classification, prediction of channel response, and assessment of channel condition. Report for TFW-SH10-93-002, 84 p, Department of Geological Sciences and Quaternary Research Center, University of Washington, Seattle, Washington.
- Morley, R.B., H.T. Bilton, A.S. Coburn, D. Brouwer, J. Van Tine, and W.C. Clarke. 1988. The influence of time and size at release of juvenile coho salmon (*Oncorhynchus kisutch*) on returns at maturity: results from studies on three brood years at Quinsam Hatchery, B.C. *Canadian Technical Report of Fisheries and Aquatic Sciences* 1620: 120 p.
- Mortenson, E. 1977. Density-dependent mortality of trout fry (*Salmo trutta* L.) and its relationship to the management of small streams. *Journal of Fish Biology* 11: 613-617.
- Mosley, M.P., and D.S. Tindale. 1985. Sediment variability and bed material sampling gravel-bed rivers: *Earth Surface Processes and Landforms* 10: 465-482.
- Moyle, P.B., and H.W. Li. 1979. Community ecology and predator-prey relationships in warmwater streams. Pages 171-181 in *Predator-prey systems in fisheries management*. R.H. Stroud and H.E. Clepper, editors. Sport fishing Institute, Washington D. C.
- Murphy, M.L., and Hall, J.D. 1981. Varied effects of clear-cut logging on predators and their habitat in small streams of the Cascade Mountains, Oregon. *Canadian Journal of Fisheries and Aquatic Sciences* 38: 137-145.
- 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. *Canadian Journal of Fisheries and Aquatic Sciences* 43: 1521-1533.
- Naiman, R.J., editor. 1992. *Watershed management: balancing sustainability and environmental change*. Springer-Verlag, New York.

- Naiman, R., D.G. Lonzarich, T. Beechie, and S. Ralph. 1992. General principles of stream classification and the assessment of conservation potential in rivers. Pages 93-124 in River conservation and management. P.J. Boon, P. Calow and G.E. Petts, editors. John Wiley and Sons, Chichester, England.
- Nawa, R. K., C. A. Frissell, and W. J. Liss. 1990. Life history and persistence of anadromous salmonid stocks in relation to stream habitats and watershed classification. Project F-122R. Oregon Department of Fish and Wildlife. Oregon State University, Corvallis, Oregon.
- Nehlsen, W., J.E. Williams and J.A. Lichatowich. 1991. Pacific salmon at the crossroads: stocks at risk from California, Oregon, Idaho and Washington. *Fisheries* 16(2): 4-21.
- Nielsen, J.L. 1992. Microhabitat-specific foraging behavior, diet, and growth of juvenile coho salmon. *Transactions of the American Fisheries Society* 121: 617-634.
- Nickelson, T.E. 1986. Influences of upwelling, ocean temperature, and smolt abundance on marine survival of coho salmon (*Oncorhynchus kisutch*) in the Oregon production area. *Canadian Journal of Fisheries and Aquatic Sciences* 43: 527-535.
- Nickelson, T.E., W.M. Beidler, M. Willard, and M.J. Willis. 1979. Streamflow requirements of salmonids. Oregon Department of Fish and Wildlife; Final Report; Federal Air Project: AFS - 62. 20 p.
- Nickelson, T.E., J.D. Rogers, S.L. Johnson and M.F. Solazzi. 1992. Seasonal changes in habitat use by juvenile coho salmon (*Oncorhynchus kisutch*) in Oregon coastal streams. *Canadian Journal of Fisheries and Aquatic Sciences* 49: 783-789.
- Olesiuk, P.F. 1993. Annual prey consumption by harbor seals (*Phoca vitulina*) in the Strait of Georgia, British Columbia. *Fishery Bulletin* 91: 491-515.
- Parker, N.C., A.E. Giorgi, R.C. Heidinger, D.B. Jester, E.D. Prince, and G.A. Winans, editors. 1990. Fish-marking techniques. *American Fisheries Society Symposium* 7.
- Pearcy, W.G. 1992. Ocean ecology of North Pacific salmonids. Washington Sea Grant Program, University of Washington, Seattle, Washington.
- Pearsons, T.N., H.W. Li, and G.A. Lamberti. 1992. Influences of habitat complexity on resistance to flooding and resilience of stream fish assemblages. *Transactions of the American Fisheries Society* 121: 427-436.
- Peckarsky, B. 1983. Biotic interactions or abiotic limitations? A model of community structure, Pages 303-334 in *Dynamics of lotic ecosystems*. T.D. Fontaine and S.M. Bartell, editors. Ann Arbor Science, Ann Arbor, Michigan.
- Peterson, N.P. 1982. Immigration of juvenile coho salmon (*Oncorhynchus kisutch*) into riverine ponds. *Canadian Journal of Fisheries and Aquatic Sciences* 39: 1308-1310.
- Pielou, E.C. 1974. *Population and Community Ecology: Principles and Methods*. Gordon and Breach, New York.
- Poff, N.L., and J.V. Ward. 1989. Implications of streamflow variability and predictability for lotic community structure: a regional analysis of streamflow patterns. *Canadian Journal of Fisheries and Aquatic Sciences* 46: 1805-1818.
- Power, M.E. 1984. Depth distribution of armored catfish: predator induced resource avoidance. *Ecology* 65: 523-528.
- Power, M.E. 1987. Predator avoidance by grazing fishes in temperate and tropical streams: importance of stream depth and prey size. Pages 333-352 in *Predation: direct and*

- indirect impacts on aquatic communities. W.C. Kerfoot and A. Sih, editors. University Press of New England, Hanover, NH.
- Prentice, E.F., T.A. Flagg, and C.S. McCutcheon. 1990a. Feasibility of using passive integrated transponder (PIT) tags in salmonids. *American Fisheries Society Symposium* 7: 317-322.
- Prentice, E.F., T.A. Flagg, C.S. McCutcheon, D.F. Brastow, and D.C. Cross. 1990b. Equipment, methods, and an automated data-entry station for PIT tagging. *American Fisheries Society Symposium* 7: 335-340
- Quinn, T.P., and C.J. Foote. 1994. The effects of body size and sexual dimorphism on the reproductive behaviour of sockeye salmon (*Oncorhynchus nerka*). *Animal Behaviour* (in press).
- Reckendorf, F. and M. Van Liew. 1989. Sampling of sediment intrusion into artificial redds in the Tucannon watershed, Washington. In *Proceedings of Sixth Symposium on Coastal and Ocean Management/ASCE*, July 11-14, 1989, Charleston, South Carolina.
- Reeves, G.H., F.H. Everest and J.D. Hall. 1987. Interaction between the reddsider shiner (*Richardsonius balteatus*) and the steelhead trout (*Salmo gairdneri*) in western Oregon: the influence of water temperature. *Canadian Journal of Fisheries and Aquatic Sciences* 44: 1603-1613.
- Reid, L.M., and T. Dunne. 1984. Sediment production from forest road surfaces. *Water Resources Research* 20: 1753-1761.
- Reid, I., L.E. Frostick, and J.T. Layman. 1985. The incidence and nature of bedload transport during flood flows in coarse-grained alluvial channel. *Earth Surface Processes and Landforms* 10: 33-44.
- Resh, V.H., A.V. Brown, A.P. Covich, M.E. Gurtz, H.W. Li, G.W. Minshall, S.R. Reice, A.L. Sheldon, J.B. Wallace, and R. Wissmar. 1988. The role of disturbance in stream ecology. *Journal of the North American Benthological Society* 7: 433-455.
- Richards, K. S. 1982. *Rivers: form and process in alluvial channels*. Methuen & Co. Ltd., London, 361 p.
- Rinne, J.N. 1988. Grazing effects on stream habitat and fishes: research design considerations. *North American Journal of Fisheries Management* 8: 240-247.
- Rogers, D.E., and G.T. Ruggerone 1993. Factors affecting marine growth of Bristol Bay sockeye salmon. *Fisheries Research* 18: 89-103.
- Roni, P. 1992. Life history and spawning habitat in four stocks of large-bodied chinook salmon (*Oncorhynchus tshawytscha*). Master's thesis, University of Washington, Seattle, Washington.
- Ross, S.T., W.J. Matthews, and A.A. Echelle. 1985. Persistence of stream assemblages: effects of environmental change. *American Naturalist* 126: 24-40.
- Salo, E.O. 1991. Life history of chum salmon. Pages 231-309 in C. Groot and L. Margolis, editors. *Pacific salmon life histories*. University of British Columbia Press, Vancouver.
- Salo, E.O., and T.W. Cundy, editors. 1987. *Streamside management: forestry and fishery interactions*. College of Forest Resources, University of Washington, Seattle.
- Saunders, R.L. 1967. Seasonal patterns of return of Atlantic salmon in the northwest Miramichi River, New Brunswick. *Journal of the Fisheries Research Board of Canada* 24: 21-32.
- Scarlett, W.S., and C.J. Cederholm. 1984. Juvenile coho salmon fall-winter utilization of two small tributaries of the Clearwater River, Jefferson County, Washington. Pages 227-242

- in J. M. Walton and D. B. Houston, editors. Proceedings of the Olympic Wild Fish Conference, Peninsula College, Port Angeles, Washington.
- Scarnecchia, D.L. 1981. Effects of streamflow and upwelling on yield of wild coho salmon (*Oncorhynchus kisutch*) in Oregon. *Canadian Journal of Fisheries and Aquatic Sciences* 38: 471-475.
- Schlosser, I.J. 1982. Fish community structure and function along two habitat gradients in a headwater stream. *Ecological Monographs* 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. 1987a. 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 D. C. Heins, editors. University of Oklahoma Press, Norman, Oklahoma.
- Schlosser, I.J. 1987b. The role of predation in size and age-related habitat use by stream fishes. *Ecology* 68: 651-659.
- Schlosser, I.J. 1988. Predation risk and habitat selection by two size classes of stream cyprinid: experimental test of a hypothesis. *Oikos* 52: 36-40.
- Schlosser, I.J., and K.K. Ebel. 1989. Effects of flow regime and cyprinid predation on a headwater stream. *Ecological Monographs* 59: 41-57.
- Schlosser, I.J., and P.L. Angermeier. 1990. The influence of environmental variability, resource abundance, and predation on juvenile cyprinid and centrarchid fishes. *Polish Archives of Hydrobiology* 37: 265-284.
- Schmitt, R.J., and S.J. Holbrook. 1985. Patch selection by juvenile black surfperch (*Embiotocidae*) under variable risk: interactive influence of food quality and structural complexity. *Journal of Experimental Marine Biology and Ecology* 85: 269-285.
- Scrivener, J.C., and B.C. Andersen. 1984. Logging impacts and some mechanisms that determine the size of spring and summer populations of coho salmon fry (*Oncorhynchus kisutch*) in Carnation Creek, British Columbia. *Canadian Journal of Fisheries and Aquatic Sciences* 41: 1097-1105.
- Scrivener, J.C., and M.J. Brownlee. 1989. Effects of forest harvesting on spawning gravel and incubation survival of chum (*Oncorhynchus keta*) and coho salmon (*O. kisutch*) in Carnation Creek, British Columbia. *Canadian Journal of Fisheries and Aquatic Sciences* 46: 681-696.
- Sedell, J.R., F.N. Leone and W.S. Duval. 1991. Water transport and storage of logs. *American Fisheries Society Special Publication* 19: 325-368.
- Sedell, J.R., G.H. Reeves, F.R. Hauer, J.A. Stanford, and C.P. Hawkins. 1990. Role of refugia in recovery from disturbances: modern fragmented and disconnected river systems. *Environmental Management* 14: 711-724.
- Seegrist, D.W., and R. Gard. 1972. Effects of floods on trout in Sagehen Creek, California. *Transactions of the American Fisheries Society* 101: 478-482.
- Seiler, D., S. Neuhauser, and M. Ackley. 1981. Upstream/downstream salmonid trapping project, 1977-1980. Washington Department of Fisheries, Progress Report 144: 197 p.
- Seiler, D., S. Neuhauser, and M. Ackley. 1984. Upstream/downstream salmonid trapping project, 1980-1982. Washington Department of Fisheries, Progress Report 200: 152 p.

- Sheridan, W. L., M. P. Perensovich, T. Faris, and K V. Koski. 1984. Sediment content of streambed gravels in some pick salmon spawning stream in Alaska. Pages 153-165. in W.R. Meelhan, T.R. Merrell, Jr., and T.A. Hanley, editors. Fish and wildlife relationships in old-growth forests. Proceedings of a symposium held in Juneau, Alaska, 12-15, April, 1982. American Institute of Fishery Research Biologists.
- Shirvell, C.S. 1990. Role of instream rootwads as juvenile coho salmon (*Oncorhynchus kisutch*) and steelhead trout (*O. mykiss*) cover habitat under varying streamflows. Canadian Journal of Fisheries and Aquatic Sciences 47: 852-861.
- Shirvell, C.E. 1989. Habitat models and their predictive capability to infer habitat effects on stock size. Canadian Special Publication of Fisheries and Aquatic Sciences 105: 173-179.
- Shumway, D.L., C.E. Warren, and P. Doudoroff. 1964. Influence of oxygen concentration and water movement on the growth of steelhead trout and coho salmon embryos. Transactions of the American Fisheries Society 93:342-356.
- Sidle, R.C. 1988. Bed load transport regime of a small forest stream. Water Resources Research 24:207-218.
- Silver, S.J., C.E. Warren, and P. Doudoroff. 1963. Dissolved oxygen requirements of developing steelhead trout and chinook salmon embryos at different water velocities. Transactions of the American Fisheries Society 92: 327-343.
- Smoker, W.A. 1955. Effects of streamflow on silver salmon production in western Washington. Ph.D. dissertation, University of Washington, Seattle.
- Strange, E.M., P. B. Moyle, and T. C. Foin. 1992. Interactions between stochastic and deterministic processes in stream fish community assembly. Environmental Biology Fishes 36: 1-15.
- Swales, S., R.B. Lauzier and C.D. Levings. 1986. Winter habitat preferences of juvenile salmonids in two interior rivers in British Columbia. Canadian Journal of Zoology 64: 1506-1514.
- Swales, S., F. Caron, J.R. Irvine, and C.D. Levings. 1988. Overwintering habitats of coho salmon (*Oncorhynchus kisutch*) and other juvenile salmonids in the Keogh River system, British Columbia. Canadian Journal of Zoology 66: 254-261.
- Tagart, J.V. 1984. Coho salmon survival from egg deposition to fry emergence. Pages 173-182 in Proceedings of the Olympic Wild Fish Conference. Walton, J.M and D.B. Houston, editors. Peninsula College and Olympic National Park, Port Angeles, Washington.
- Taylor, E.B. 1988. Water temperature and velocity as determinants of microhabitats of juvenile chinook and coho salmon in a laboratory channel. Transactions of the American Fisheries Society 117: 22-28.
- Taylor, E.B. 1991. Behavioural interaction and habitat use in juvenile chinook, *Oncorhynchus tshawytscha*, and coho, *O. kisutch*, salmon. Animal Behaviour 42: 729-744.
- Thorne, R.E., and J.J. Ames. 1987. A note on the variability of marine survival of sockeye salmon (*Oncorhynchus nerka*) and effects of flooding on spawning success. Canadian Journal of Fisheries and Aquatic Sciences 44: 1791-1795.
- Tipping, J.M., and H.L. Blankenship. 1993. Effect of condition factor at release on smolt-to-adult survival of hatchery sea-run cutthroat trout. Progressive Fish Culturist 55: 184-186.
- Tripp, D.B., and V.A. Poulin. 1986. The effects of logging and mass wasting on salmonid spawning habitat in streams on the Queen Charlotte Islands. British Columbia Ministry of Forests and Lands, Land Management Report 50, Victoria, B.C.

- 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. *Canadian Journal of Fisheries and Aquatic Sciences* 40: 452-461.
- van den Berghe, E.P., and M.R. Gross. 1984. Female size and nest depth in coho salmon (Oncorhynchus kisutch). *Canadian Journal of Fisheries and Aquatic Sciences* 41: 204-206.
- van den Berghe, E.P., and M.R. Gross. 1989. Natural selection resulting from female breeding competition in a Pacific salmon (coho: Oncorhynchus kisutch). *Evolution* 43: 125-140.
- Vaux, W.G. 1962. Interchange of stream and intra-gravel water in a salmon spawning riffle. U.S. Fish and Wildlife Service Special Scientific Report, Fisheries 405.
- Walters, C.J., and J.S. Collie. 1988. Is research on environmental factors useful to fisheries management? *Canadian Journal of Fisheries and Aquatic Sciences* 45: 1848-1854.
- Ward, B.R., and P.A. Slaney. 1988. Life history and smolt-to-adult survival of Keogh River steelhead trout (Salmo gairdneri) and the relationship to smolt size. *Canadian Journal of Fisheries and Aquatic Sciences* 45: 1110-1122.
- Ward, B.R., P.A. Slaney, A.R. Facchin, and R.W. Land. 1989. Size-biased survival in steelhead trout (Oncorhynchus mykiss): back-calculated lengths from adults' scales compared to migrating smolts at the Keogh River, British Columbia. *Canadian Journal of Fisheries and Aquatic Sciences* 46: 1853-1858.
- Wentworth, C.K. 1922. A scale of grade and class terms for clastic sediments. *Journal of Geology* 30:377-392.
- Werner, E.E., J.F. Gilliam, D.J. Hall, and G.G. Mittelbach. 1983. An experimental test of the effects of predation risk on habitat use in fish. *Ecology* 64: 1540-1548.
- Wickett, W.P. 1954. The oxygen supply to salmon eggs in spawning beds. *Journal of Fisheries Research Board of Canada* 11:933-953.
- Williams, J.R., H.E. Pearson, and J.D. Wilson. 1985. Streamflow statistics and drainage-basin characteristics for Puget Sound Region, Washington: Volume I. Western and southern Puget Sound. U.S. Geological Survey.
- Williams, K.R. 1970. Some ecological investigations of Big Beef Creek, 1966-67. Master's thesis, University of Washington, Seattle, Washington.
- Wilzbach, M.A. 1985. Relative roles of food abundance and cover in determining the habitat distribution of stream-dwelling cutthroat trout (Salmo clarki). *Canadian Journal of Fisheries and Aquatic Sciences* 42: 1668-1672.
- Wolda, H. 1981. Similarity indices, sample size and diversity. *Oecologia* 50: 296-302.
- Wood, C.C. 1987. Predation of juvenile Pacific salmon by the common merganser (Mergus merganser) on eastern Vancouver Island. 2. Predation of stream-resident juvenile salmon by merganser broods. *Canadian Journal of Fisheries and Aquatic Sciences* 44: 950-959.
- Wydoski, R.S., and R.R. Whitney. 1979. Inland fishes of Washington. University of Washington Press, Seattle, Washington. 220 pp.
- Young, M.K., W.A. Hubert, and T.A. Wesche. 1989. Substrate alteration of spawning brook trout in a southeastern Wyoming stream. *Transactions of the American Fisheries Society* 118: 379-385.
- Young, M.K., W.A. Hubert, and T.A. Wesche. 1990. Fines in redds of large salmonids. *Transactions of the American Fisheries Society* 119: 156-162.

- Young, M.K., W.A. Hubert, and T.A. Wesche. 1991a. Biases associated with four stream substrate samplers. *Canadian Journal of Fisheries and Aquatic Sciences* 48: 1882-1886.
- Young, M.K., W.A. Hubert, and T.A. Wesche. 1991b. Selection of measures of substrate composition to estimate survival to emergence of salmonids and to detect changes in stream substrates. *North American Journal of Fisheries Management* 11: 339-346.
- Yount, J.D., and G.J. Niemi, editors. 1990. Recovery of lotic communities and ecosystems following disturbance: theory and application. *Environmental Management* 14:515-762.
- Zar, J.H. 1984. *Biostatistical analysis*. Prentice-Hall, Englewood Cliffs, New Jersey.