JUVENILE COHO SALMON HABITAT UTILIZATION AND DISTRIBUTION IN A

SUBURBAN WATERSHED: THE SALMON RIVER (LANGLEY,B.C.)

by

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Abstract

I investigated juvenile coho salmon (<u>Oncorhynchus</u> <u>kisutch</u>) distribution and habitat utilization in an agricultural/urban watershed, the Salmon River, Langley, B.C. The results of my empirical work confirmed the importance of instream woody debris and undercut banks in coho distribution. I examined experimentally how juvenile coho select among patches that differ in foraging profitability and in cover availability. Ideal free distribution (IFD) models were used as the practical basis for hypotheses about habitat choice by coho salmon. My experiments were conducted in artificial stream channels and involved two different types of cover, instream and overhead, and two spatial scales. The two scales (patches within individual pools and pools within stream reaches) were used to detect the effect of different levels of sampling and information processing by the fish. Juvenile coho responded positively to food abundance both within and between pools, but they did not do it as predicted by the IFD model. Cover presence further deviated coho distribution from an IFD. Within pools, coho foraged in open patches away from cover, but preferred pools with cover when choosing between separate units. None of the alternative dispersion models that I considered, derived from the IFD, fully explained the observed dispersion patterns. Coho's ability to maximize food intake rate was not only affected by the physical complexity of their habitat, but also by intraspecific competition and interference. Subsequently, I investigated experimentally coho's response to food and different densities of woody debris in natural stream reaches. If food was abundant, coho favoured pools with sparse cover, which offers accessible refuge and leaves unobstructed foraging patches where prey and perhaps also predators are easy to detect. Pools with either high densities or total lack of woody debris attracted proportionately less fish. Earlier in the summer, fry were indifferent towards cover, but as they became older their association with instream woody debris increased. Experiments I conducted during winter indicated that water velocity and temperature affected juvenile coho downstream

movement. The proportion of fish that tried to leave the experimental channels increased with water discharge and decreased with water temperature.

Based on the results of my empirical and experimental work, and on information derived from comparative case studies, I evaluated the potential impact of agriculture and urbanization on coho salmon habitat. Activities associated with these types of land developments tend to: a) reduce stream channel complexity; b) eliminate off-channel fish habitat; c) increase both the magnitude and the frequency of peak flows; d) augment water sediment transport; e) alter riparian vegetation; and, f) degrade water quality.

A multilayered management plan, aimed at increasing coho salmon production, was developed. The plan's management strategies were devised reflecting on the different spatial scales that watershed components have and on the connectivity processes that exist among them.

Table of Contents

List of Tables

List of Figures

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Dedication

A la memoria de mi amada madre.

CHAPTER 1

INTRODUCTION

This thesis examines how juvenile coho salmon respond to the distribution and abundance of resources, such as food and cover. Although, the empirical and experimental components of my study have a relatively small scale (individual pools and stream reaches), the interpretation of my results, conclusions and management recommendations have been developed with a watershed perspective in mind.

The different species of salmonids comprise local populations, referred to as stocks, that are adapted to the specific environmental conditions of their watersheds of origin (Ricker 1972). In the particular case of anadromous populations (those that spawn and in some species rear in freshwater, but complete their growth and maturation in the sea) their spawning in natal streams maintains a high level of reproductive isolation among them, thus maintaining the genetic variability of the species (Thorpe et al. 1981). This high level of genetic variation among the populations of a species is what provides the basis for future evolution (Futuyma 1979), and an "insurance" of adaptation to environmental change (White and Nekola 1992). Therefore, it is important that preservation of wild stocks be a component of current management practices if fishery resources are to be maintained or restored.

Many stocks of anadromous salmonids (<u>Oncorhynchus</u> spp.) in western North America are currently under risk of becoming extinct, while others have declined from 50 to 85% of their average historic abundance (DFO 1990, Nehlsen et al. 1991, Northcote and Burwash 1991, DFO 1992). Although several hypotheses have been advanced to explain these declines (overfishing, freshwater habitat loss, interactions with hatchery fish, and ocean habitat changes), freshwater habitat loss has been associated with every one of the 214 salmonid stocks that Nehlsen et al. (1991) identified as either facing high to

moderate risk of extinction or being of special concern. These authors recognized different factors that had a negative impact on wild stocks, but concluded that habitat degradation was one of the leading causes of their decline. Although, new evidence suggests that competition with hatchery fish for limited ocean resources represents a serious threat for some stocks (Walters 1993), it is reasonable to consider that a combination of all the mentioned factors, with their relative importance varying from year to year, is behind the decline in salmonid abundance.

Habitat degradation and loss are side effects of different types of human activities. The initial changes to the aquatic component of a watershed begin with the early alterations that man introduces to its terrestrial component. Mining and logging have historically preceded a number of other land use activities in coastal watersheds of the Pacific Northwest. These extraction operations indirectly affected stream morphology and hydrology by modifying the soil and its vegetation cover. Agriculture later developed in many deforested lands, and more recently urban settlements began to cover ever larger portions of basin catchment areas.

To understand how land use activities such as agriculture, urban development, mining or logging may affect fish production, it is necessary to know the habitat requirements of the different species, and to identify the general environmental changes brought about by human activities in each watershed. Because juveniles of different salmonid species have specific nursery habitat requirements and different lengths of freshwater residence, they are not equally susceptible to all development activities. For example, sockeye salmon (Oncorhynchus nerka) have been harmed at two different stages of their life cycle. First, during the phase of egg incubation in stream gravel by siltation from improper logging practices and, historically, by gravel displacement resulting from river log driving (Michael Healey, pers. comm.); and second, during their lake rearing phase by dam construction (Nehlsen et al. 1991). Chum salmon (Oncorhynchus keta) have been largely affected by degraded water quality and siltation of spawning bed gravel

2

in many watersheds (Nehlsen et al. 1991). The relatively long period of residence of coho salmon (<u>Oncorhynchus</u> <u>kisutch</u>) in small coastal streams (Sandercock 1991) make this species particularly susceptible to habitat alterations caused by logging (Hall and Lantz 1969, Thedinga et al. 1989, Hicks et al. 1991), agriculture (Birtwell et al. 1988, Hicks et al. 1991) and urban development (Henderson 1991, Lucchetti and Fuerstenberg 1993).

1.1. The concept of habitat

The abundance and the pattern of distribution of animals is believed to be determined by the availability and spatial distribution of resources (Larkin 1977, Milinski 1979 & 1984, Milinski and Parker 1991). The uneven distribution of resources, in both space and time, creates patches of better or poorer habitat among which individual organisms distribute themselves.

Habitat can be simply defined as the "place" where an organism lives, and includes the range of environmental conditions, both abiotic and biotic, it requires to live, grow and reproduce (Odum 1971). Its spatial scale is not fixed; but rather determined by its range of action (home range). Thus, the habitat of a large organism, or a relatively mobile one (i.e., birds), contains within its physical boundaries the smaller scale habitats of smaller, or less mobile, organisms. This kind of organization implies a hierarchy of habitats that are nested in space. A river represents a particularly good system to further illustrate this point. The entire watershed makes up the environment of smaller scale subsystems, such as stream sections, which in turn constitute the environment of habitat systems at lower scale levels, such as stream reaches. Each stream reach is made up of smaller components, pools and riffles, and these habitats contain patches or microhabitats of different types (Frissell et al. 1986).

The importance of habitat patches in studies of animal ecology is now widely recognized, not only because many ecological processes are strongly influenced by

patchiness, but also because of problems associated with human-induced disturbances and habitat conservation strategies (May and Southwood 1990). In the particular context of conservation and management of animal populations, the relevance of animal distribution in a patchy environment arises from the fact that habitat protection, and enhancement, is usually conducted at a small scale within a larger mosaic of habitats that are affected by different human activities (Bernstein et al. 1991b). If we do not know how animal populations distribute among these different habitat patches (both protected and exploited ones) it is very difficult to design an effective conservation plan. For example, a strategy that protects habitat patches that are only used by adults, and allows development activities to take place in patches of nursery habitat, will not be very successful in the long term.

Many of the current conservation issues revolve around loss of habitat. Estuaries, marshes, small streams, as well as old-growth forests are among the many ecosystems that have been drastically modified by human activities, resulting in a net reduction of suitable habitat for a large number of species (Henderson 1991, Franklin 1992, Foster 1993, Turner and Meyer 1993, Williams 1993). Because habitat requirements of many organisms varies with time, and not all habitats that are occupied contribute the same proportion of reproductive individuals to the total population, loss of some critical types of habitat may have a disproportionately large impact on the subsistence of a local population (Goss-Custard 1985). To understand the consequences of such loss of habitat for a particular species, it is useful to have a model of how individuals distribute between habitat patches. This approach permits a realistic assessment of the impact of habitat degradation on animal populations (Bernstein et al. 1991b).

1.2. Animal distribution and rate maximizing models

The factors governing animal distribution among habitat patches have been studied by foraging theorists since the early 1970s. Simple intake rate-maximization models, such as the marginal value theorem (Charnov 1976), were among the earlier models to predict successfully the behaviour of individual foragers under experimental conditions. Rate maximizing models were developed to illustrate how behavioural decisions by some individuals affected other individuals in the population. These models predict the outcome of the conflict each forager has between its preference for the most profitable patch of habitat and its potentially lowered individual feeding rate induced by the presence of competitors in that patch. The first model of this type, independently developed by Orians (1969), Fretwell and Lucas (1970), and Parker (1970), is known as the "ideal free distribution" (IFD) model. The original IFD model, and the different versions derived from it, describe how a population of rate-maximizing competitors is distributed among habitat patches. These models have been used by many researchers as a starting point for understanding the mechanisms governing animal patch choice (Milinski 1979 & 1984, Fraser and Sise 1980, Whitham 1980, Harper 1982, Godin and Keenleyside 1984, Gillis and Kramer 1987, Abrahams 1989, Abrahams and Dill 1989, Inman 1990, Bernstein et al. 1991a, Grand and Grant 1994, Tyler and Gilliam 1995). The different IFD models are based on certain assumptions about the behaviour of foraging competitors; they anticipate the strategies foragers will follow in achieving specific goals, and predict both qualitative and quantitative results that can be compared to those of experiments or field observations.

Earlier studies have tested various IFD models under continuous food input to predict, with different degrees of success, the distribution of foraging fish (Milinski 1979 & 1984, Fraser and Sise 1980, Godin and Keenleyside 1984, Gillis and Kramer 1987, Abrahams 1989, Tyler and Gilliam 1995). But none has applied IFD predictions to understand how juvenile fish select rearing habitat in response to more than one resource

type. The models I decided to use, as a general background against which to examine my observations about individual behaviour, include the "classical" IFD model (Orians 1969, Fretwell and Lucas 1970, Parker 1970), and its modified versions: the "ideal despotic distribution" (IDD) model (Fretwell and Lucas 1970), the free distribution with perception limits model (PL) (Abrahams 1986), and the free distribution of unequal competitors model (UC) (Parker and Sutherland 1986) (for review of these models see section 4.1.1.).

Animal dispersion models - like those mentioned above - help in assessing the potential impact of habitat loss by improving our understanding of how individuals distribute between different patches of habitat. The identification of the most valuable types of habitat (i.e. spawning, rearing , wintering, etc.) is usually based on data from field surveys. This process assumes that animal distribution always reflects the spatial occurrence of different types and quality of habitat. However, this oversimplification may have serious practical consequences from a conservation point of view. There are circumstances in which the most populated habitat is not the best available one. Territorial behaviour, for example, may force large numbers of subordinate individuals to occupy suboptimal habitat. In other cases the distance between good patches of habitat or the detection of resources, may affect the relationship between distribution of consumers and distribution of resources. An interpretation of distribution of habitat patches that uses exclusively field survey data, and does not incorporate information on these kinds of behavioural processes that affect animal dispersion, may be very misleading in the preparation of effective management plans. Furthermore, it is difficult to understand the key features that create good quality habitat from an entirely empirical approach.

1.3. Study goal and objectives

The goal of this study was to evaluate the impacts that land use in agricultural and urbanized watersheds of the Lower Fraser Valley may have on their salmonid populations through habitat alteration.   I focused my study on one particular species of Pacific salmon, coho salmon (Oncorhynchus kisutch), because: a) it has demonstrated a gradual but steady decline in regional abundance during the last 25 years, and has undergone the greatest decrease in abundance among all species of Pacific salmon present in the Fraser River Basin [current abundance approaches 12.5% of that reported at the beginning of this century (Northcote and Burwash, 1991)];   b) it supports, in the Georgia Strait, one of the country's most valuable recreational fisheries, and an important commercial troll fishery [total annual catch during the last 30 years between 500,000 and 1,000,000 fish (Walters 1993)];   c) the Fraser River is the single largest producer of coho salmon in the province, and coho in many of the small streams of the Lower Fraser Sub-basin, that account for approximately 75% of the system's total production (Henderson 1991), has almost become an "urban species";   and, d) coho salmon's habitat requirements in forested coastal watersheds and the impact of logging have been relatively well studied, whereas little attention has been given to the study of the impact of urbanization on this species.

I focused my research on one particular watershed, the Salmon River, Langley. This system became the natural choice for a study of this kind, because: a) it represents a highly productive salmonid system that has suffered a slow but irreversible change from a forested to an agricultural to an increasingly urbanized landscape;   b) it still sustains a relatively large coho population;   and, c) it has been the subject of previous studies that examined the composition of its aquatic fauna, its annual productivity, the evolution of land use patterns in the watershed, the quality of its surface and underground water, etc., which can provide very valuable information on which fish-land use management decision could be based (McMynn and Vernon 1954, Hartman 1968, Eggleston and Lavkulich

7

1973, Hall and Weins 1976, Luttmerding 1980, Paish 1980 & 1981, DeLeeuw 1982, Watts 1992, Fausch 1993, Cook 1994, Corporation of the Township of Langley 1994).

My objectives were: a) to examine juvenile coho salmon distribution and habitat utilization in the Salmon River Watershed during both summer and winter; b) to examine experimentally, under controlled conditions, the mechanisms behind juvenile coho salmon selection of habitat patches (patches differed in foraging quality, and other factors that were identified after completion of empirical work (from part *a*) as having an important or a controversial role on the distribution of coho salmon); c) to investigate further, this time with experiments done in natural stream reaches, the influence of a selected set of habitat factors on the distribution of juvenile coho salmon among suitable rearing patches in streams; d) to determine experimentally the effect of a selected set of factors on the downstream movement of juvenile coho salmon during winter; e) to evaluate the potential impact of land use activities associated with agriculture and urban development on coho salmon nursery habitat, based on the results of my empirical and experimental work and on information derived from comparative case studies; and, f) to discuss the most adequate management approach to preserving coho salmon habitat and the methodologies for mitigating the negative effects of some land uses on the stream system.

In chapter two, I describe the distribution and general features of coho salmon bearing streams in the Lower Fraser Sub-basin; I introduce the Salmon River Watershed as a case study, outline its physical characteristics, summarize the pattern of land use and forest cover removal within it, and report on its fish resources. In chapter three, I present the results of a survey of coho salmon distribution and habitat use in the Salmon River, during both summer and winter. In chapter four, I examine how juvenile coho salmon select among habitat patches that differed in foraging profitability and in the availability of other resources. The experiments for this phase of my study were conducted in artificial channels, and IFD theory was used as the practical basis for hypotheses about habitat

choice. In chapter five, I further examine the influence of cover and food abundance on the distribution of juvenile coho salmon with the use of experiments conducted in natural stream reaches. These experiments were designed after taking into account the results of my earlier channel experiments, and the conflicting information on habitat preference of coho salmon that I found in the literature. In chapter six, the results and conclusions from experiments that explored the effect of changes in flow and food availability on the downstream movement of juvenile coho salmon during winter are presented. In chapter seven, using the results obtained in the previous chapters I discuss the effects that agriculture and urbanization may have on coho salmon distribution in the Salmon River. I then discuss general aspects of coho salmon habitat management and conservation, and provide specific recommendations for the Salmon River Watershed in particular.

CHAPTER 2

SALMONID HABITAT IN THE LOWER FRASER VALLEY

2.1. The Fraser River Basin

The Fraser River is among the large rivers of Canada. It is 1,375 km long, and it has a mean annual flow of 3,972 m^3/sec, and drainage basin area of 234,000 km^2. The river originates in the Rocky Mountains, near the foot of Mt. Robson, along the border between British Columbia and Alberta. It initially flows in a north-west direction, between the Rocky Mountains to the east and the Cariboo Mountains to the west, and then turns toward the south as it approaches the city of Prince George. In its middle reaches, the Fraser River runs through the dry and high interior plateau that extends between the Cariboo Mountains to the east and the Coast Mountains to the west. Further south it enters the Fraser Canyon to cross the southern Coast Mountains. After this last mountain crossing the river turns west toward the Strait of Georgia, and in its last 160 km - between Hope and Vancouver - it flows through the Lower Fraser Valley, in the Lower Fraser Sub-basin (Dorcey 1991). Before reaching its mouth, the river splits into two: the Main Arm, which carries approximately 85% of the flow (SOE Report 1992), and the North Arm.

2.2. The Lower Fraser Valley

The Lower Fraser Valley comprises a triangular area of approximately 4,000 km^2 (less than 2% of the total drainage area of the Fraser Basin), confined by the Coast Mountains to the north, the Cascades, along the border with the United States, to the south, and the waters of the Strait of Georgia to the west (Figure 1). As it flows westward through this valley the Fraser River receives a number of tributaries that drain

areas progressively more developed and urbanized. For example, in the eastern Lower Fraser Valley, the Harrison and the Chilliwack Rivers run through forested mountain lands. In the central section, tributaries such as the Salmon River drain agricultural land with zones of low density residential development. Closer to the city of Vancouver most tributaries, such as the Brunette River, flow through urban and industrial zones (Fox 1976, Dorcey 1991).

2.2.1. Climate

The climate in the Lower Fraser Valley is dominated by maritime air masses travelling eastward that are affected by the presence of the Coast Mountains to the north and the Cascade Mountains to the east. Temperatures in the lowlands are relatively moderate with an annual average of approximately 10°C. Mean monthly temperatures range from 1°C in January to 17°C in July (with a maximum recorded daily range of -20°C to 35°C) (SOE Report 1992). Precipitation is highest in autumn and winter, while a dry period of several weeks is common during the summer. This may produce drought conditions in some parts of the valley, particularly those with coarse soils, that have made irrigation necessary to maintain the more intensive farming that is developing in the region (Moore 1990, SOE Report 1992). Most of the precipitation falls as rain in the lowlands, increasing slightly in a northeasterly direction from 1,093 mm/yr in White Rock to about 1,716 mm/yr in Hope (1951-1980, see Dakin 1993). Snowpack accumulates in the surrounding mountains persisting, in many occasions, until the beginning of the summer. Although the flow regime of small tributary streams in the valley is governed by the seasonal precipitation pattern of the area, mainstem river flow increases in the spring because it is largely controlled by snowmelt and glacier melt in the central and northern areas of the basin (Moore 1991).
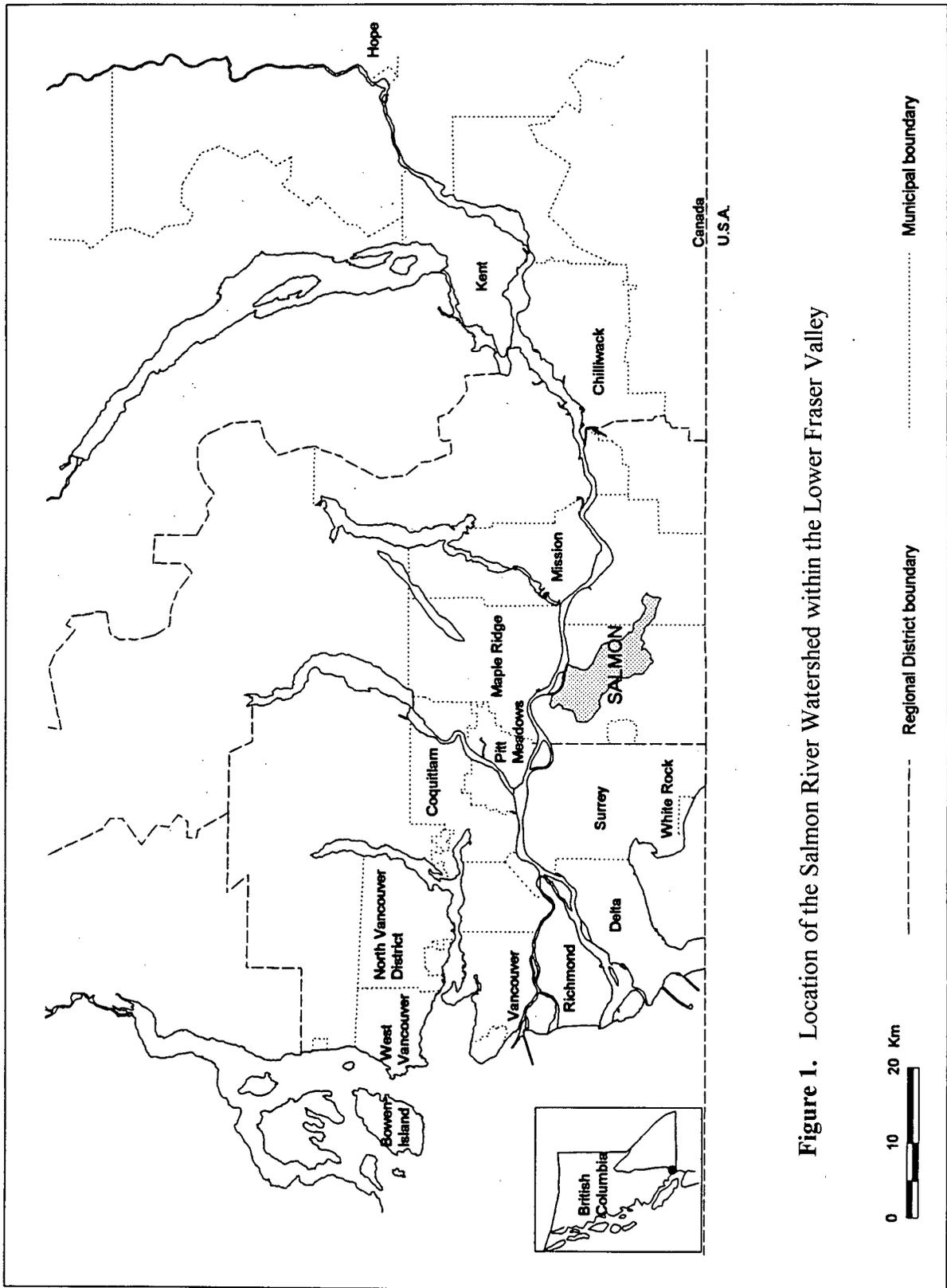
Figure 1. Location of the Salmon River Watershed within the Lower Fraser Valley

············· Municipal boundary

— · — · — Regional District boundary

0   10   20 Km

12

2.2.2. Land use and urbanization in the Lower Fraser Valley

During the 1980s the Lower Fraser Valley had one of the fastest population growth rates in the country and this trend has continued in the 1990s (approximately 33% population growth rate between 1987 and 1994, GVRD 1995). By 1994 approximately 1.96 million people lived in the area, which was equivalent to 50% of the total population of the province (GVRD 1995). Most of the inhabitants of this valley (close to 1.77 million) lived in the country's third largest metropolitan area the Greater Vancouver Regional District (GVRD), which includes the city of Vancouver and the surrounding municipalities (Moore 1990, GVRD 1995).

The mountains to the north, the ocean to the west and the United States border to the south have determined that the urban sprawl of Greater Vancouver could only occur in one direction, eastward into the Lower Fraser Valley. The result is a steady process of urbanization that is turning agricultural into residential and commercial lands.

The Fraser River Valley is one of the most important agricultural regions of the province. Although it represents only 7% of the province's prime agricultural land it accounts for over 55% of the total agricultural economic production (Statistics Canada 1987). Moore (1990), in her report on the urbanization process in the Lower Fraser Valley, explained that of the 4,354 ha urbanized during the 1980-87 period approximately 44% (1,900 ha) was land previously classified as undisturbed (mainly woods, shrubland, and grasslands); 26% (1,127 ha) of the developed land derived from agricultural land (mainly grazing land); an additional 22% (952 ha) had been previously classified as "land in transition" and "idle" (a combination of different land classes including former rangelands and undisturbed land that were ready to be converted into residential lands when municipal rezoning allowed it). A small proportion (8% = 370 ha) of the land urbanized during that period was formerly used for forestry activities, extraction (i.e. gravel pits, rock quarries, etc.), and small scale farming (i.e. horticulture).

The reduction of agricultural lands (including rangeland), coupled with the increased demand for horticulture and specialty crops created by the larger population, has modified the profile of the average farmer in the valley. There has been a slow but steady shift toward more intensive farming (Statistics Canada 1987 & 1988, Moore 1990), which has higher environmental costs (pollution associated with the use of agro-chemicals and high manure production) and a lower sustainability in the long term (as exposed top soils are washed and blown away).

2.2.3. Fish resources

The Fraser River is one of the large salmonid producing systems in the world (Northcote and Larkin 1989). It accounts for almost a third of the total average annual salmon catch in British Columbia (Henderson 1991). Its diversity of fish species, however, is relatively low when compared to other large rivers in North America. For example, the Fraser has 53 species (including temporary marine invaders and 7 introduced species), whereas the Columbia River has 85, the St. Lawrence 99 and the Mississippi 241. Its relatively poorer fauna is probably the result of only recent de-glaciation (approximately 13,000 years ago) (Northcote and Burwash 1991).

Eight of the nine salmonid species present in the Fraser River Basin occur in the Lower Fraser River Sub-basin (Table 1) (bull trout, Salvelinus confluentus, is the exception) (Northcote et al. 1978). Despite differences in their life cycles, all salmonids share several freshwater requirements. They all need: a) free access to spawning grounds; b) clean spawning gravels relatively free of sediments to incubate the eggs, with a good infiltration of oxygen carrying water; c) relatively low (6 to 10°C) and constant water temperatures that allow adults to spawn and eggs to develop; d) clean and well oxygenated flowing waters with protected areas of slow velocity; e) drifting invertebrates to prey upon; and, g) shelter from predation (Adams and Whyte 1990, Henderson 1991, Groot and Margolis 1991)

Table 1. List of salmonid species present in the Lower Fraser River.

Common Name	Scientific Name
Pink salmon	Oncorhynchus gorbuscha
Chum salmon	Oncorhynchus keta
Sockeye salmon	Oncorhynchus nerka
Coho salmon	Oncorhynchus kisutch
Chinook salmon	Oncorhynchus tshawytscha
Steelhead / rainbow trout	Oncorhynchus mykiss
Cutthroat trout	Oncorhynchus clarki
Dolly Varden	Salvelinus malma

Many of the above mentioned habitat conditions have been completely eliminated or degraded by the human activities throughout the Lower Fraser Valley. General fish habitat problems in the Lower Fraser River have been summarized by Northcote and Burwash (1991), and those that specifically affect Pacific salmon have been reviewed by Henderson (1991).

2.3. The Salmon River Watershed

The Salmon River flows for 33 km in a northwesterly direction before entering the Fraser River at Fort Langley (Figures 1 and 2), 60 km east of Vancouver. Its watershed, with an area of approximately 8,070 ha and an elevation that ranges from 2 to 137 m, is largely within the Township of Langley, and only a small portion of the headwaters are located in the District of Matsqui. Its main tributary, Coghlan Creek, joins it about 14 km upstream from the Fraser River (Watts 1992). The entire watercourse can be subdivided into 3 sections (upper, middle and lower reaches, Figure 3) taking into account its

gradient, substrate type, channel configuration, and water velocity. The upper reaches (with an average gradient of 3%, slow water velocity, very low summer flows, flat stream slopes and a substrate dominated by fine sand and organic silt) begin upstream from 48th. Ave. for the Salmon River (extending for approximately 11 km), and upstream from 256th. St. for Coghlan Creek (with an estimated length of 2.5 km). The middle reaches (characterized by a steeper gradient, 5%, a rather constant summer flow derived from underground sources, distinct habitat units such as pools and riffles, and a substrate dominated by coarse sand, gravel and cobble) correspond to approximately 12 km of the Salmon River between 48th. Ave. and 72nd. Ave., and the lower 5 km of Coghlan Creek between 256th. St. and the confluence with the Salmon River. The river in this middle part runs through narrow and steep ravines, with slopes ranging from 15 to 60 percent (Luttmerding 1980) and has well developed riparian vegetation that shades the watercourse. The lower reaches (characterized by a low gradient -0.5 to 3%, and uniform channel) begin downstream from 72nd. Ave and continue to the confluence with the Fraser River, next to Fort Langley . The sequence of distinct pools and riffles present in the middle reaches disappear in this section. It acquires all the characteristics of a floodplain river, including a meandering deep channel with almost flat banks, slow flowing turbid waters, and a fine sediment substrate.

The lower reaches of the river have been dyked to prevent flooding of adjacent farm land. Historically these area was probably a large seasonally flooded wetland. Several small tributaries that discharged into the Salmon River across this floodplain have also been dyked, and in some cases (such as Davidson Creek) straightened into a network of channels to improve the drainage and make adjacent land use easier. Where these creeks bisected the dykes along the mainstem they have been gated. Another important
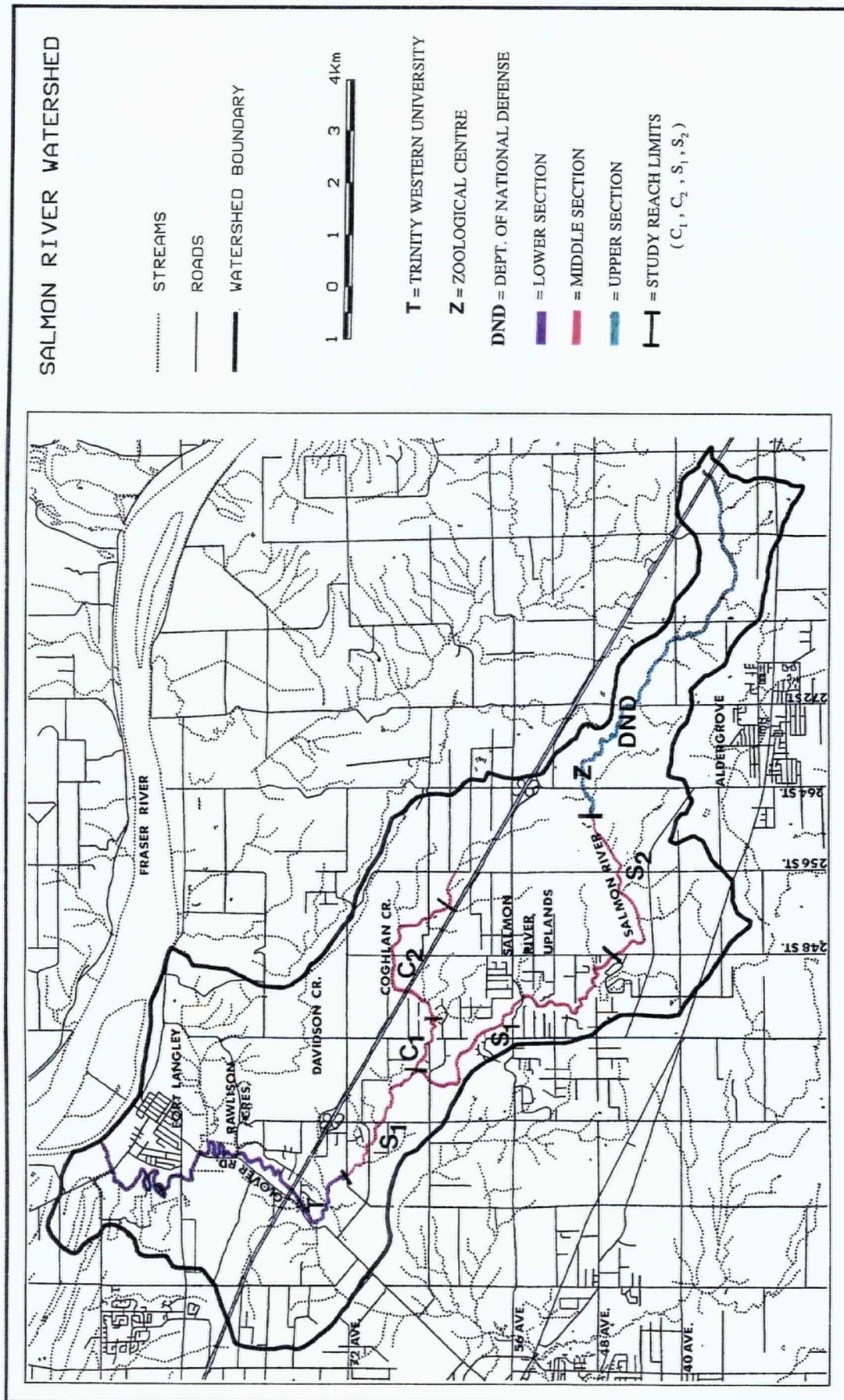
Figure 2. Location of the Salmon River, its main tributaries, and the residential areas within the watershed in the Township of Langley

modification to the natural drainage of this river was the installation of a flood gate and a pumphouse at the mouth of the river in 1949. The purpose of this complex was to prevent flooding of the watershed's floodplain during the spring freshets of the Fraser River. The gates are closed and the pump is in operation from late March to July interfering with the spring migration of coho and trout smolts. Smolts have to go through the pump to get to the Fraser, which according to the Department of Fisheries and Oceans estimates introduces a 25 to 31% mortality on the migrating fish (Paish 1981)

2.3.1. Surficial materials

The Salmon River drains a basin with a variety of soils. The land depression encircling Fort Langley that corresponds to an abandoned Fraser River meander is characterized by fluvial deposits; the rest of the watershed presents underlying zones of stony marine sediments, sandy and gravelly glacio-fluvial materials, and glacio-marine clay deposits (for additional information see Eggleston and Lavkulich 1973). The nature and distribution of these deposits determines the characteristics of the stream bed materials, affects water chemistry, groundwater distribution and stream flow, besides influencing the spatial pattern of land use in the watershed.

The coarse textured outwash sands and gravels of glacio-fluvial origin underlying the central area of the watershed form the Hopington or Salmon River Aquifer. This groundwater reservoir, the largest within the watershed, is a significant contributor to the stream baseflow during the summer months and an important source of ground-water for many households in the area (Cook 1994).

2.3.2. Water discharge and water quality

Discharge records for 1970-1993 from the Salmon River gauging station (#08MH090, Water Resources Branch, Environment Canada) indicate that the lowest flows (about 0.10 to 0.35 m^3/s) occur during the summer months (July to October),

whereas the late fall and early winter (November to February) experiences the highest flows of the year (between 13 and 25m³/s). The flow regime of this stream is driven by autumn-winter rainfall. The average annual precipitation measured at a weather station situated south of the Salmon River in Langley Prairie, was 1,554 mm/yr based on a 30 year record (Watts 1992).

The quality of the water in the Salmon River is relatively good for fish production when compared to other tributaries of the Lower Fraser River . But considering the degradation of some of those systems, this does not mean that there are no reasons for concern in this watershed. Water pH levels recorded during my field work in the system ranged from 6.7 to 7.8. Levels that are within those recommended for drinking water (6.5 to 8.5). Dissolved oxygen was recorded by S. Thornton for Westwater during the low flow period to determine whether adequate oxygen levels exist during the summer for salmonids. Dissolved oxygen should be above 5.0 mg/l, below this concentration salmonid egg mortality increases, and the metabolic rates as well as the swimming performance of salmon and trout are negatively affected (Adams and Whyte 1990). The three river sections showed different dissolved oxygen levels and contrasting daily variation patterns. In the headwaters of the Salmon River (measured at 272 St.) the levels of dissolved oxygen were too low (1.9 mg/l) for salmonid survival. The situation in the middle reaches (measured at Williams Park) was very different, with dissolved oxygen levels always close to saturation levels (between 10 and 11 mg/l) and not showing any daily fluctuation. But in the lower reaches of the river (measured at Glover Rd. and Rawlison Crescent) oxygen concentrations were high during the day (approximately 8 - 9 mg/l) and dropped dramatically at night (3.8 mg/l), well below the lower tolerance level of salmonids. In the lower reaches the daily fluctuation was clearly due to the photosynthetic cycle. During day hours, rooted plants and algae produced and released more oxygen than that respired by the aquatic community; whereas once photosynthesis ceased the oxygen concentration in water was brought down by the ongoing respiration.

Eutrophication from farmland run-off was identified by Hall and Wiens (1976) as causing elevated BOD (Biochemical Oxygen Demand) that reduced oxygen concentration in some small tributaries in the upstream portion of the middle reaches. They also observed that nitrate levels, although below suggested drinking water limits (10 mg/l), were higher than in the mainstem of the Fraser River, particularly during the low flow period. Cook (1994), in a very detailed study of the water quality and land use in the watershed, concluded that both nitrate and phosphate were contaminating the waters of a large portion of the Hopington Aquifer. The most likely sources of pollution, according to her study, were septic systems, fertilizers and manure. Hall and Wiens (1976) also recorded high levels of fecal coliforms, indicating human fecal contamination, in the lower reaches of the river. Additionally, the levels of certain trace metals, such as copper and zinc, have been observed to be high in the Salmon River compared to other streams in the region (Hall and Wiens 1976). Their increased concentration at higher flows suggest that they originate from non-point sources. Although, most water problems in the watershed are associated with non-point sources of pollution, two clear sources of nitrate and fecal bacteria contamination exist: Trinity Western University and the Greater Vancouver Zoological Centre (ex Vancouver Game Farm).

Water temperature in the Salmon River is suitable for salmonid fishes, except for some particular stream sections. During 1991, I recorded mean summer (May-September) temperatures of: 12.1°C in the upper reaches, 9.3°C in the middle reaches, and 14.2°C in the lower reaches. However, the same August temperatures were dangerously high for salmonids at both the uppermost reaches (19.2°C), above 48th. Ave. (see Figure 2), and the lower reaches (18.9°), by 88th Ave. Mean water temperatures during the January-February periods of 1992 and 1993 were: 4.8°C (1992) and 3.8°C (1993) by 48th Ave., 7.3°C (1992) and 4.4°C (1993) in the middle reaches, and 4.4°C (1992) and 2.8°C (1993) in the lower section.
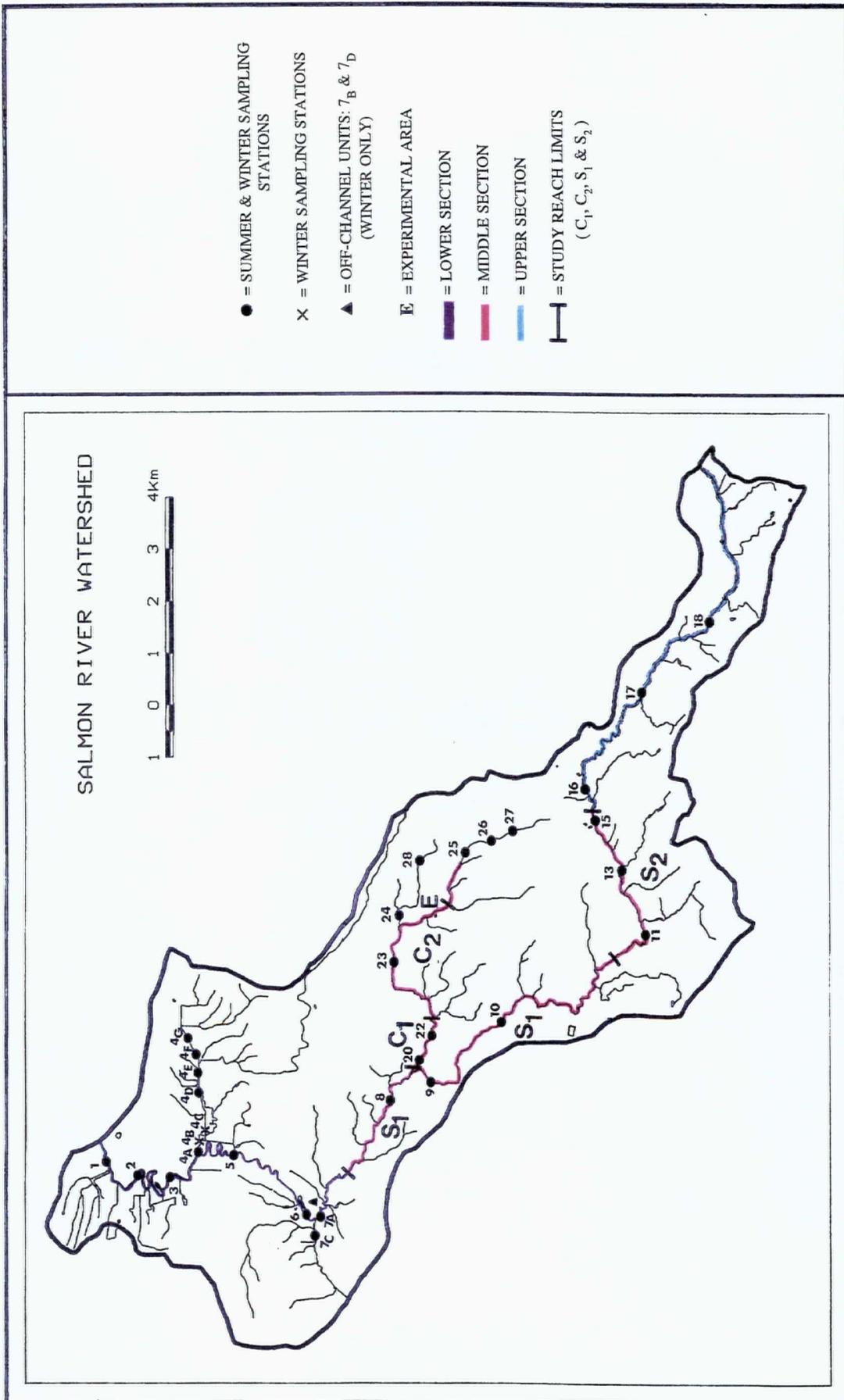
Figure 3. Location of sampling stations on the Salmon River. (Map source: Watts 1992)

21

2.3.3. Man-induced changes to the vegetation of the watershed

Fort Langley, the first permanent European settlement on the Lower Mainland of the province, was established in 1827 near the confluence of the Salmon and Fraser Rivers (Crawford 1993). Originally, most of the Salmon River basin must have been covered by coniferous forest (Land Surveyors Notebooks 1873 -1874). But by the 1870s large stands of coniferous trees had already been logged and/or burned down, and were replaced by mixed deciduous regeneration forests (Land Surveyors Notebooks 1873-1874). A historic vegetation map of the watershed (Pauline Landry, for Westwater Research Centre), based on information from land surveyors' notebooks (Land Surveyors Notebooks 1873-1874), shows that most of the floodplain was covered by prairie grass and shrubs. Shrub describes a community including willow (Salix spp.), crabapple (Malnus fusca), and hardhack (Spiraea douglassi). The middle reaches of Davidson Creek ran through a red alder (Alnus rubra) and willow forest; whereas its upper reaches and a section of the lower Salmon River (between 72nd. Ave. and Rawlison Crescent) crossed a mixed deciduous regeneration forest of red alder, willow, cherry (Prunus spp.), black cottonwood (Populus trichocarpa), and crabapple, with some second growth western hemlock (Tsuga heterophylla) and Douglas fir (Pseudotsuga menziesii). Most of the middle reaches of both the Salmon River and Coghlan Creek ran through mixed coniferous stands of: western red cedar (Thuja plicata), hemlock, Douglas fir, grand fir (Abies grandis), and Sitka spruce (Picea sitchensis), accompanied - particularly in riparian zones - by alder, willow, vine maple (Acer circinatum), broadleaf maple (Acer macrophyllum), and dogwood (Cornus nuttallii).

Logging and farming began in the floodplain in the late 1800s, and subsequently spread to the upper regions of the basin (McMynn and Vernon 1954). Much of the riparian vegetation in agricultural lands was removed, and although in some areas stream side trees have been reestablished they have a much lower density than natural stands.

Cattle access to the river and its small tributaries (i.e. Davidson Creek) has prevented riparian vegetation recovery and has caused bank erosion in many areas.

The central part of the watershed, which has less productive soils, was cleared and developed later (McMynn and Vernon 1954). In this middle section, both the Salmon River and Coghlan Creeek have a relatively pristine appearance. But at a closer examination it is possible to observe that riparian forest alteration and clearing occurred in some areas due to different land use activities in the vicinity of the channel. However, extensive riparian removals are relatively uncommon. Most of the mixed deciduous and coniferous woods of this region have been gradually removed for farming and, more recently, residential development. Many of the small tributaries and ephemeral watercourses in the middle reaches of the watershed, near the residential development known as Salmon River Uplands, have been severely altered by urbanization. Even at Williams Park the natural vegetation has been removed, and sections of the stream bank have been stabilized with rock filled gabions. In many locations of the river, upstream passage of fish has been reduced or impeded where roads cross the stream channel and elevated culverts were placed in the channel.

Farming activities in the vicinity of the Salmon River upper section have also caused riparian alterations. The narrow and shallow channel in the upper reaches is more vulnerable to riparian alterations than the large floodplain channel near Fort Langley. In this part of the watershed the mixed forest cover has been slowly eliminated and cattle grazing prevents the regeneration of the riparian vegetation. Other land uses in this section of the watershed is likely to have an equivalent if not greater negative impact on the stream system. The upper reaches of the Salmon River run through a zoological garden and a military base, and some residential areas (Aldergrove) are extending closer to the headwaters of the system. The Greater Vancouver Zoological Centre straddles the creek, and its animal waste and bank erosion contribute to the degradation of the aquatic habitat. Further upstream in the DND (Department of National Defense - CFS) lands,

23

degradation continues as a result of military training exercises and vegetation removal. These headwaters of the Salmon River resemble a roadside ditch. Although no salmonids currently use this part of the watershed, land use impacts on these reaches affect the hydrology and the quality of fish habitat further downstream.

The upper section of Coghlan Creek appears to be slightly less damaged, and provide better salmonid habitat. However, during low summer flows water extraction for irrigation may potentially cause serious problems to fish (Paish 1981).

A complete description of land use dynamics from 1980 to 1990 and its potential effect on fish habitat is provided by Watts (1992). I will briefly mention the conclusions of that study that are the most relevant in the context of the current dissertation. In this predominantly agricultural watershed (4,038 ha of farmland or 50% of the whole watershed), residential and undeveloped lands have expanded (3% and 4% respectively) at the expense of farmland (-9%). Because Watts classified as undeveloped both wood lots and "idle" land ("wait-listed" for urbanization), the actual potential for residential development in these lands is higher than it may seem at a first glance. Moreover, compared to the general situation in the whole watershed, increases in undeveloped land within a 500 m wide riparian buffer zone are higher (6%), suggesting a higher potential for urbanization in the vicinity of the watercourse. According to Watts (1992), changes in land use are even more dramatic within the riparian buffer zone in the middle reaches of the river near Williams Park. There, on Coghlan Creek and the Salmon River, agricultural land decreased by 32% and 22% respectively. Undeveloped land increased by 34% on Coghlan Creek and by 6% on the Salmon River, while residential areas augmented 15% and 17% respectively.

I conducted an examination of historic and recent aerial photographs of the Salmon River watershed to determine changes in forested area, including riparian buffer zones, that have occurred during the last 40 years. I summarized the distribution of forest cover in 1:25,000 scale vegetation maps of the watershed for the years 1954, 1963, 1978

24

and 1989. Area estimation from these maps was done by comparing the weight (to the nearest 1 mg) of a piece of map paper of known area, to the weight of each paper piece that represented every forest patch in the watershed. By calculating the percentage of watershed area that was covered by forests in 1954 (37.4%, see Table 2), it is evident that most of the deforestation occurred before then.

Table 2. Forest cover in the Salmon River Watershed for different years between 1954 and 1989), based on a total area of 8070 ha (% of the total watershed). Riparian buffer strip total width = 280 m.

Year	Forested Area	Not Forested Area	Forested Buffer	Not Forested Buffer
1954	3,018 (37.4%)	5,052 (62.6%)	826.2 (45.9%)	973.8 (54.1%)
1963	3,164 (39.2%)	4,906 (60.8%)	810 (45%)	990 (55%)
1978	2,486 (30.8%)	5,584 (69.2%)	795.6 (44.2%)	1,004.4 (55.8%)
1989	2,856 (35.4%)	5,213 (64.6%)	784.8 (43.6%)	1,015.2 (56.4%)

From 1954 to 1979 forest cover in the whole watershed declined slightly, and then increased somewhat by 1989 (Table 2). The latter increase probably reflects farmland removed from production followed by establishment of an alder scrub forest. This is supported by the increase in undeveloped land reported by Watts (1992). However, riparian forest cover has steadily declined from 1954 to 1989 (Table 2) as evidenced by the diminishing amount of forested buffer. Yet, the percentage change in the proportion of the riparian that is forested is not large (5%). Although this seems in conflict with the increase in undeveloped land detected by Watts (1992) within the buffer zone he analyzed, it is possible that the majority of this land was "idle" waiting for subdivision and immediate residential development and no forest growth was allowed.

Changes to the vegetation cover, and particularly to the riparian forest, will affect the stream system by modifying the water collection, retention, and delivery mechanisms

of the entire watershed ecosystem. Because the different components of a watershed (i.e. geomorphology, channel morphology, hydrologic pattern, water quality, riparian communities, stream habitat, etc) are inter-connected (Stanford and Ward 1992), human induced changes to the terrestrial components will reflect on the characteristics and the functions of the aquatic component. Therefore, land uses in the uplands of a basin may alter fish habitat in its middle or lower reaches as a result of the system's connectivity.

Despite increased land development and riparian alterations, the Salmon River still sustains a rich fish fauna. The number of coho salmon it produced annually during the early 1980s was estimated to represent almost 5% of the total coho production of the Fraser River Sub-basin (Farwell et al. 1987). Marshall and Britton (1990), comparing it to other systems of equivalent size, ranked it among the top coho streams in the province, with an estimated yield of 2,430 smolts/km ($\cong$ 70 smolts/100m^2).

2.3.4. Fish species diversity

There are 18 species of fish in the Salmon River Watershed (Hartman 1968) (Table 3). Some occur in the watershed only occasionally, whereas others are very common throughout the year. Few species distribute over the entire watershed (the exceptions being stickleback, Pacific lamprey, and western brook lamprey), the remainder are either restricted to the lower reaches of the system (largescale sucker, longnose sucker, brown bullhead, squawfish, carp, peamouth chub, brassy minnow, and redside shiner), or to the middle and upper reaches (salmonids). The Salish sucker, a species listed as endangered, is found in only three other streams in the province; within the Salmon River it is found exclusively in the upper reaches. I found this species to be relatively abundant in the deep pools of the upper Salmon River.

The species in Table 3 can be grouped into three classes: a) species with economic and recreational value (salmon and trout); b) endangered species (Salish sucker); and c) species that are neither endangered nor have market value, but contribute

to the biodiversity of the stream system. Because salmonids have a relatively narrow range of environmental tolerance compared to most other species of fish present in the Salmon River, they will be the first ones to be affected by changes to the stream. Ensuring that salmonid habitat is not degraded or lost in the stream, will normally be enough to guarantee that conditions in the entire watershed remain relatively unchanged and the other species will benefit as a result. However, special attention (deserving a separate detailed study of its own) has to be paid to Salish sucker habitat. The requirements of this endangered species are not well known, and it should not be assumed that a general stream conservation plan would be enough to protect its populations.

Effective habitat protection strategies have to be based on properly identified habitat factors (factors with an important controlling role in the ecology of the animal using the habitat), and a good understanding of the mechanisms that control (with spatial and temporal variations) the response of animals to these factors. In the following sections I briefly describe what is considered to constitute good coho salmon habitat and describe its general spatial distribution within the Salmon River Watershed.

2.3.5. Coho habitat requirements

Juvenile coho salmon rear during their first year, or more, of life in freshwater before migrating to sea as smolts (Sandercock 1991). In some populations a proportion of the fry rear in lakes, where they occupy the nearshore littoral zone (Mason 1974). The majority, however, rear in small coastal streams and small tributaries of larger rivers (such as it is the case of the Salmon River) where they set up territories shortly after emergence (Sandercock 1991). Coho salmon tend to be more territorial in stream reaches with faster flowing waters, whereas in some slow flowing areas it is not uncommon to find them forming loose aggregates and cruising for food (Mundie 1969). Those that "take residence" normally occupy a small space with slow moving waters, from where they make short excursions to feed or to chase intruders away. Subordinate individuals, which

are chased and displaced by resident coho, tend to be less aggressive and grow more slowly due their lack of access to good feeding areas (Chapman 1962).

Highly productive coho salmon streams are small enough to provide a large proportion of marginal slow areas to midstream faster flowing waters, and have a relatively similar proportion (1:1 ratio) of alternating pools and riffles (Ruggles 1966, Sandercock 1991). Coho prefer zones with reduced water velocity. They favour pools over other types of habitat and use instream structures as protection from high water flows. In this manner, they may minimize their energy expenditures to maintain position while feeding on drifting prey (Mundie 1969, Everest and Chapman 1972, Fausch 1993). Coho are visual predators and seldom feed from the bottom. They prefer to capture invertebrates that drift either suspended in the water column or on the surface (Hoar 1958, Hartman 1965, Nielsen 1992).

In addition to providing allochthonous prey items and shelter from water velocity, instream and riparian cover provide other benefits. Low-hanging overhead cover such as undercut banks and rootwads may decrease the amount of light reaching the water surface, thereby, making fish less visible to potential predators (Murphy and Hall 1981, Helfman 1981). Instream cover can also provide refuge from predators and simultaneously increase visual isolation among competitors. Visual isolation may reduce aggressive interactions among competitors and could, therefore, lead to an increase in the number of fish occupying a given area (Dolloff 1986, Mesick 1988, Bugert et al. 1991, Fausch 1993).

Table 3. Species of fish present in the Salmon River Watershed (adapted from Hartman 1968, and Watts 1992). (-)= species that occur infrequently. (end.)= endangered

Common Name	Scientific Name
Coho Salmon	Oncorhynchus kisutch
Steelhead Trout	Oncorhynchus mykiss
Cutthroat Troat	Oncorhynchus clarki clarki
Dolly Varden (-)	Salvelinus malma
Prickly Sculpin	Cottus asper
Largescale Sucker	Catostomus macrocheilus
Salish Sucker (end.)	Catostomus sp.
Longnose Sucker (-)	Catostomus catostomus
Northern Squawfish	Ptycocheilus oregonensis
Peamouth Chub	Mylocheilus caurinus
Redside Shiner	Richardsonius balteatus
Brassy Minnow	Hybognathus hankinsoni
Brown Bullhead (-)	Ameiurus nebulosus
Carp (-)	Cyprinus carpio
Threespine Stickleback	Gasterosteus aculeatus
Starry Flounder (-)	Platichthys stellatus
Pacific Lamprey	Lampetra tridentata
Western Brook Lamprey	Lampetra richardsoni

Although the description presented above corresponds to the most accepted version of the role of cover as a summer habitat component. Contradictory conclusions are common in the literature about its actual importance and coho's response to its abundance and spatial distribution (Bisson et al. 1982, Dolloff 1986, Dolloff and Reeves

1990, Shirvell 1990, Peters et al. 1993, Bugert et al. 1991, Bugert and Bjorn 1991, Fausch 1993, Spalding et al. 1995). Therefore, in the following chapter I examine its relationship and controlling role on coho salmon densities. Later, in Chapter 4, I go one step further and examine experimentally the response of coho salmon to this habitat factor.

In autumn, as water temperatures decline and coastal streams experience their first freshets due to increased rainfall, juvenile coho salmon redistribute either into deeper pools or to off-channel habitat (Bustard and Narver 1975b, Cederholm and Scarlett 1982, McMahon and Hartman 1989, Nickelson et al. 1992a). Over-wintering coho salmon prefer reduced water flow and abundant cover, such as fallen logs, rootwads and undercut banks. Conditions they normally find in small first order tributaries (Cederholm and Scarlett 1982, Scarlett and Cederholm 1984, Brown and Hartman 1988), sidepools (or alcoves), sloughs and wetlands (Bustard and Narver 1975b, Brown 1985, Tschaplinski and Hartman 1983), off-channel riverine ponds (Peterson 1982a and 1982b, Swales and Levings 1989), beaver ponds (Bryant 1984, Nickelson et al. 1992a), and even small lakes (Swales et al. 1988).

2.3.6. Distribution of coho habitat within the watershed

Although studies on salmonid habitat in the Salmon River started as early as 1954, with McMynn and Vernon, and continued with Hartman (1965, 1968), there was no quantitative survey of the system and its habitat features until DeLeeuw (1982) looked at the effect of a major flood event that occurred during the winter of 1979. Nonetheless, it was Watts' (1992) research that has provided an overall evaluation of habitat in the entire watershed, as well as a systematic description of the morphology, cover abundance and susbstrate composition for selected reaches in the middle section of the stream.

The central part of the watershed, including both the middle reaches of the Salmon River and most of Coghlan Creek, offers the best nursery habitat for salmonids in the watershed (Watts 1992). It was in this part of the system that Hartman (1965) recorded

the highest coho salmon densities (his density estimates, however, should be considered with care because of serious sampling methodology limitations). Unfortunately he did not include in his survey the uppermost reaches of the mainstem, which are currently quite degraded and for the most part seem to be unoccupied by salmonids. Few fish have been found in the lower section of the system, this is particularly true in winter (Hartman 1965). In general, the floodplain portion of this watershed has been considered to play a minor role in coho salmon production. It has been mainly regarded as a mere migration corridor used by smolts leaving the system and by adults travelling toward the spawning grounds. Because of this view, no attention has been paid to the potential role that its small tributaries and abundant drainage channels and ditches may play as coho salmon overwintering habitat. Evidence from other systems indicates that coho salmon overwinter in side channels, riverine ponds, small tributaries and other kinds of off-channel habitat if these are available (Peterson 1982b, Cederholm and Scarlett 1982, Scarlett and Cederholm 1984).

2.3.7. Human activities and coho salmon habitat: the connection

Since the mid 1800s the Salmon River Watershed has been progressively modified by human actions. By 1954 its forest covered area was only slightly larger than it is today, indicating that a largely forested basin lost, in less than 100 years, most of its natural vegetation and gradually became a landscape of anthropogenic patches. Corn and hay fields, vegetable patches, horse racing rings, roads, buildings, grazing pastures, commercial greenhouses, a zoo, a military training camp, gravel pits, chicken farms, golf courses, dairy farms, highways, gas stations, a university campus, and many more components of today's watershed landscape are the result of human land use activities. Thus, the catchment area within an agricultural/urban watershed can be described as a mosaic of terrestrial patches that are drained by a network of streams. Water flowing through this network inter-connects otherwise separate biological communities, and

31

integrates the influence of a variety of natural and man made processes that occur within the watershed (Stanford and Ward 1992). The acknowledgement of the spatial and temporal variability of the components of lotic systems and their strong connectivity, is central both to the understanding of impacts of human activities on fish habitat and to the planning of adequate management actions.

Man places organisms and structures on the land, elements that did not evolve with the rest of the watershed's components. The result is that most of these "introductions" somehow interfere with many of the natural connectivity processes. In this manner, land use activities interfere with important connections and create new causal links that did not exist before. Thus, they may alter entire series of processes that connect regional (basin scale) to local (fish habitat scale) watershed components.

Using Frissell et al's (1986) conception of watersheds as series of hierarchically nested habitats (see section 1.1), helps to visualize how its components can be inter-connected even when they have vastly different spatial scales. I applied this hierarchical model of organization and the concept of functional connectivity (Stanford and Ward 1992) to relate man induced alterations to components at the watershed or stream segment scale with changes in components at the stream reach scale. I began by examining elements that rank relatively low in the hierarchical organization and occur at a relatively reduced scale (i.e. fish habitat scale processes), and finished integrating them into a higher level and larger scale context (i.e. entire watershed, stream sections). First, I confirmed the controlling roles of some habitat components on juvenile coho salmon (food and cover) and, subsequently, I examined the mechanisms through which those components influence coho salmon distribution and abundance at the individual pool and stream reach level. At the end, I evaluate how human interference on the natural connectivity of the watershed affects those (and other relevant) habitat factors controlling coho salmon distribution and, therefore, alters coho's total abundance in the watershed.

CHAPTER 3

JUVENILE COHO SALMON IN THE SALMON RIVER WATERSHED: THEIR DISTRIBUTION AND HABITAT USE

3.1. Introduction

I sampled the Salmon River both in summer and winter to determine rearing habitat selection and utilization by juvenile coho salmon. The results of my field work were used, in part, to identify factors that controlled the distribution of coho salmon parr. Some of the mechanisms behind coho's response to these factors were later examined experimentally both in artificial and natural channels (see Chapters 4, 5, and 6). The empirical information was subsequently applied, in combination with the results of my experiments, to elaborate management guidelines that recognize the hierarchical organization of the watershed and the connectivity among its components.

3.2. Summer distribution and habitat use

3.2.1. Methods

In 1991, during the period of low flow (August-September), a total of thirty-eight pools, glides and riffles were sampled at 24 different stations (see Figure 3). Sampling stations were selected as follows. On a map, the entire Salmon River and its tributaries were divided into equal segments, representing 100 m long reaches; these segments were assigned individual identification numbers. Afterwards, 24 sampling sites were picked using a random number table. Two separate channel units (one upstream and one downstream from the actual access route to the stream) were sampled at each site. However, this was only possible throughout most of the middle reaches of the watershed where the stream channel is very heterogeneous, showing well defined pools and riffles.

In the more homogeneous channel of the lower and upper reaches, one single type of unit was sampled per station. At five sites, I sampled three units in the same locality to compensate for nearby sites that were not accessible (i.e. absent or uncooperative landowner). This random sampling design allowed different types of fish habitat to be represented in close proportion to their occurrence in the river.

The middle reaches of the system were divided into four different study units (S1, S2, C1 and C2, Figure 3) to detect any pattern in the distribution of coho throughout the section that has been reported as having the best salmonid habitat (Watts 1992). These four reaches were defined to match those studied by Watts (1992), the only difference being that the boundaries of S1 in this study extend downstream passing Williams Park down to the 232nd. St. bridge.

Before sampling, I blocked the ends of each unit with 0.5 cm mesh nets to prevent any fish from entering or leaving the section. I electrofished the units in an upstream direction using a battery-powered backpack electroshocker (at 250-400 V) and applied a removal method for estimating fish population size (Bohlin et al. 1989). In all cases at least three electrofishing passes were made (for detailed information on electrofishing procedures see Bohlin 1989, and Lobón-Cerviá 1991). Fish caught in different passes were kept in separate holding tanks and were not returned to the stream until the census was over. Recovery intervals of 45 to 60 min. were left between passes to allow fish redistribution in the unit.

I used this fishing method in twenty-seven hydraulic units at thirteen sampling stations (see Appendix A), whereas in the stream's lower reaches (Stations 1, 2, 3, 4 and 5, in which depth made electrofishing impossible) or in the headwaters (Stations 16, 17, 18, 26, 27 and 28, where muddy waters impeded fish detection) I used wire mesh minnow traps. They constitute an effective passive gear for trapping small fish, and have been used in many studies for estimating fish population size in lakes (Tonn and Magnuson 1982, Tonn 1985, He and Lodge 1990). The minnow traps (length = 45cm, diameter =

23cm, and mesh size= 0.6 cm) were left in the stream overnight (for a total of 18 hours) and baited with salmon roe. I placed the roe in small perforated plastic bags to prevent fish from eating it. In total, for the 24 sampling stations, I caught 2,204 juvenile coho, which were anesthetized using CO_2 (0.3 l of club soda in 4 l of water) before measuring their fork length (to the nearest 1 mm) and their weight (recorded to the nearest 0.01 g).

In my study I identified different types of habitat using the classification method developed by Bisson et al. (1982). This method not only considers the more general depth and current velocity characteristics of the stream channel, but it also incorporates information about the predominant flow pattern, the substrate composition and even the presence of large obstructions (i.e., logs). I distinguished the following habitat types:

1) *Riffles*: shallow units (less than 20 cm deep), with relatively high water velocity (between 20 and 50 cm/s), and in which the large sized components of the substrate, such as boulders and cobbles, tend to break the water surface throughout the entire unit.

2) *Pools*: units that normally have a minimum depth of 30 cm, are shallower at both ends, and have slow current velocities. They are further divided into:

   2.1) *backwater pools*: they are carved into one of the banks of the stream by eddies behind large obstructions such as rootwads or boulders. Normally, they are very shallow (less than 30 cm), with extremely low water velocity, and a substrate dominated by fine-grained materials.

   2.2) *trench pools*: they are normally large and long slots carved in the bedrock. They tend to be in the middle of the channel and have a U shaped cross-section, with a coarse-grained substrate. Their current velocities are the swiftest of any pool type and the direction of the flow is very uniform.

   2.3) *lateral scour pools*: they differ from trench pools in that they are deeper on one side, because the flow is mainly directed to it by some partial channel obstruction or bend. Often, a water undercut bank is present in these pools. The distribution of fines in the substrate is uneven, they predominate over larger gravel on the shallower side.

   2.4) *plunge pools*: they are created by the water passing over a complete or nearly complete channel obstruction, and dropping vertically into the channel below. The waterfall that is formed carves a depression in the

substrate thus creating a relatively deep pool (more than 100cm). Both the pattern of flow and the substrate particle size are highly variable.

3) *glides*: they possess attributes of both riffles and pools. They are moderately shallow (10-30 cm deep, although they can be deeper), with the distinguishing features of relatively constant depth along the unit and a relatively fast and even flow that lacked pronounced turbulence. They have stable banks and a typical substrate that is dominated by gravel and cobbles.

Different types of instream and bank elements may be used by fish as cover from current velocity or shelter from predation. The two main types of cover I considered were: instream and overhead cover. The first one is normally represented by submerged logs (large woody debris), twigs and branches (fine woody debris), rootwads, or boulders. Whereas overhead cover includes any overhanging terrestrial vegetation and undercut bank, and is largely dependent on the conditions of the riparian zone. The amount of each individual cover type was calculated on a percentage base. For this purpose, contours of all cover structures found in the sampled units were drawn on gridded paper (based on measurements taken in the field) within a simple sketch of the hydraulic unit they occupied (which was drawn at the same scale). A simple subtraction of grid squares provided a rough estimate of the proportion of the area of each hydraulic unit occupied by cover. This measurement of cover abundance, considering its lack of precision, was subsequently ranked according to the following scale: 5 = cover present in 100 to 81% of the unit (a condition that was not observed); 4 = cover in 80 to 60% of the unit; 3 = cover in 60 to 40% of the unit; 2 = cover in 40 to 20% of the unit; 1 = cover in 20 to 1% of the unit; and 0 = no cover. Additional physical instream variables were measured to be used in the scale representation of the different units and to further characterize available fish habitat. The following list is largely based on the variables used by Watts (1992):

1) *Length* (m): total length of the pool, riffle or glide.

2) *Wetted width* (m): mean width of the water surface perpendicular to the channel's length. It is averaged from measurements taken over two to four transects, depending on the length of the channel unit (i.e., pool, riffle, etc.).

3) *Channel width* (m): width of the channel from rooted vegetation to rooted vegetation (terrestrial) or mean high water level if vegetation is absent. Measured using same transects as in wetted width.

4) *Area* (m^2): computed by multiplying length by wetted width.

5) *Depth* (m): average depth for entire section, calculated from series of measurements taken along same transects used to measure width (at 1/3, 1/2 and 2/3 of wetted width).

6) *Volume* (m^3): computed by multiplying depth, wetted width and length.

7) *Velocity* (m/sec): measured to estimate water discharge in a channel unit. A propeller-type flow meter was used to measure water velocity at same sites where depth was measured.

8) *Substrate composition* (%): visual estimate of percent composition of streambed. The following particle classes were identified: fines (sand and silt = up to 0.1 cm), small gravel (0.1 to 4 cm), large gravel (4 to 10 cm), cobble (10 to 30 cm), boulder (larger than 30 cm).

9) Temperature (°C): measured using a glass mercury thermometer. Several readings were obtained at mid-water column in each one of the transects used to measure wetted width. If different readings were obtained, the value that I report corresponds to the mean temperature for the entire unit.

3.2.2. Data analysis

Fish total numbers in each unit were estimated by the "Catch Per Unit of Effort" method (CPUE) developed by Leslie & Davies (Krebs 1989). It is a population depletion method that assumes a liner relationship between the number of animals caught per unit of effort (i.e. time) and the initial size of the population being sampled. A regression line is calculated using the "least squares" method (Zar 1984), and its slope and intercept are estimates of the probability of each individual of being caught (catchability) and the initial population size respectively (Krebs 1989, Bohlin et al. 1989, Lobón-Cerviá 1991). This model makes a series of assumptions about the population, such as: a) the population is closed (there are no immigration, emigration, births or deaths affecting it during the sampling period); b) the probability of catching an individual remains constant throughout the sampling period (which means that animals neither learn how to avoid being caught, nor become increasingly attracted by the capture device, as it is many times the case with baited traps); and, c) all individuals in the population have the same probability of being caught (Krebs 1989, Bohlin et al. 1989, Lobón-Cerviá 1991). Both the number of fish collected during each pass and the effort required in each opportunity were entered in a computer program that used Leslie's CPUE formula to estimate total number of fish in each habitat type (N) ("CATCH" program available in Krebs, 1989). Densities were calculated by dividing the estimated total number of fish in a hydraulic unit by that unit's area. Fish rearing densities between two different river sections or habitat types were compared using t-tests.

A word of caution should be said about the accuracy of removal methods. One of the major sources of inaccuracy of these methods is the estimated individual's "catchability". The sample is normally dominated by fish with a catchability above the population average, which results in an underestimation of the population size (Bohlin et al. 1989). Although territorial salmonids in small clearwater streams seem ideal subjects for the application of the removal method, because their individual catchability approaches

the assumptions of equality and independence, Bohlin and Sundström (1977) found that in populations of trout the unequal catchability they observed introduced a 15% underestimation of the population size.

Although removal methods always tend to underestimate the population size, more precise estimates of "N" (with smaller error) than using regression based estimators such as Leslie's can be obtained using maximum likelihood estimators, because they allow for different catchability on the first pass (Schnute 1983, Lobón-Cerviá 1991). In this study, however, the maximum likelihood method produced population estimates that are comparable to those I obtained with Leslie's method (see Appendix C), therefore, my conclussions are the same regardless of the estimation method I use.

The mark-recapture method, an alternative approach to estimate population size, has been estimated to be 10 to 20% more accurate than the removal method at estimating juvenile coho salmon population size (Rodgers et al. 1992). It was not used in this study because it requires doubling or tripling the time needed to sample each unit. In addition, mark-recapture estimates may result in overestimation of the actual population size (Rodgers et al. 1992). A reason why some researchers advise against their use, especially when management decisions are going to be based on their results (Carl Walters, pers. comm.).

To quantify habitat use I chose the "coefficient of utilization" derived by Bisson et al. (1982) from Ivlev's electivity index:

$$\text{Utilization} = \frac{\text{habitat specific density } - \text{ average total density}}{\text{average total density}}$$

Where habitat specific density is the average density in the habitat type of interest and average total density is the average density over the entire stream reach, all habitats combined. This coefficient ranges in value from minus one, indicating total non-use of habitat type, to positive infinity as a greater proportion of the population resides in the

habitat type of interest. A value of zero indicates that the population occurs in the habitat type in proportion to that type's abundance in the stream (Bisson et al. 1982).

Principal components analysis (PCA) was used to study the relationships among the following habitat variables: large woody debris, fine woody debris, rooted vegetation, overhead cover, undercut bank, and percent fines in the substrate. Eigenvector coefficients (the loading of each variable on the different axes or eigenvectors) and structure coefficients (Pearson correlation coefficients among habitat variables and principal components) showed the associations between original variables and the principal components.

Stepwise multiple regression was used to study the association between coho salmon densities and the habitat variables mentioned above. In the stepwise method variables are added one by one to the model. For each variable an F statistic (which reflects the variable's contribution to the overall predictive power of the model) is estimated. If the probability value associated with F is significantly greater than a pre-specified level, the variable is added into the model. After the addition of each variable, the stepwise method re-examines all variables already included in the model and deletes any with a non-significant F statistic. Only after this analysis and the necessary deletions are made, a new variable can be added to the model. The stepwise procedure ends when all variables included in the model have significant F statistics and all those excluded have not (Zar 1984). The principal components from the PCA are not intercorrelated (they are orthogonal to each other), and can be used in the stepwise multiple regression analysis instead of the original habitat variables which may display some degree of collinearity. If the degree of collinearity among some variables is high, conclusions regarding the significance of those variables in the subsequent regression analysis are likely to be spurious. When collinearity is present, standard errors of partial regression coefficients are often large, and these coefficients become poor estimates of the relationships among the variables in the analysis (Zar 1984).

T-tests were used to detect any significant differences in mean coho salmon weight and length between different sections of the watershed. Although *t*-tests are robust enough to stand considerable departures from the theoretical assumptions that both samples come from normally distributed populations with equal variances, in those cases that unequal variances between samples were detected (using F tests) I applied Cochran and Cox's approximation of the probability level of the *t* statistic (Cochran and Cox 1957). Analysis of variance (ANOVA) was used to determine whether mean fish weight within a given river section differed significantly with habitat type. As part of this analysis, I performed multiple comparisons on coho salmon weights between the different habitat types applying Tukey's Studentized Range Test. This test controls for the Type I experimentwise error rate, which is the probability of falsely rejecting at least one null hypothesis during the course of comparing all the pairs of means (Zar 1984). I also used ANOVA to compare coho salmon rearing densities among different habitat types in S1, S2, C1, and C2 combined, and Tukey's Studentized Range Test for multiple comparisons on fish densities between habitats.

3.2.3. Results

No coho salmon were found at any of the stations in the upper reaches, beyond the elevated double culvert under access bridge to stable located on 48th. Ave. (referred to as S5 by Watts, 1992, and located approximately 22 km upstream from the river's mouth). However, coho salmon were present in the pool immediately downstream from it. Beyond this point (stations 16, 17 and 18) only sticklebacks and a few Salish suckers (13 individuals) were caught in minnow traps. In the upper reaches of Coghlan Creek (stations 26 and 27) and its small first order tributaries, such as Willow Creek (station 28) no coho salmon were trapped, only sticklebacks (see Figure 3 for sampling locations).

In the lower reaches of the Salmon, it is also possible to distinguish two different zones, the one between the railway crossing (near stations 6 and 7) and Rawlison Crescent

(by station 5) in which coho salmon densities ranged from 0.25 to 0.68 fish/m^2, and the floodplain area where no coho salmon were found. Species caught in the minnow traps were: sticklebacks, redside shiners, peamouth chubs, brassy minnows, juvenile northern squawfish, lamprey and largescale suckers.

In the middle reaches of the watershed coho salmon were abundant, but their rearing densities varied among reaches and among habitat types. Figure 4 shows that although coho preferred backwater pools and lateral scour pools to either trench pools or glides, there was an important variation in fish densities depending on whether their habitat was in S1, S2, C1, C2, or the lower reaches. Riffles were utilized the least by coho salmon, regardless of location. Their mean densities in riffles (0.36 coho/m^2) were significantly lower than densities in both lateral scour pools (2.97 coho/m^2) and backwater pools (3.08 coho/m^2) (F= 5.23, df = 4, p= 0.005; Tukey's test, α= 0.05, df = 19, ANOVA). But when compared to fish densities in trench pools and glides they were not statistically significant. Many of the differences that are evident in Figure 4 are not confirmed statistically, because there was a large amount of variation in density values within most types of habitats and the sample size was too small (20 units in the middle reaches). It is important, however, to notice that lateral scour pools and backwater pools sustained the highest mean density of coho of all the different kinds of habitat I surveyed (this is even more marked in reaches S1 and C1). Log transformed data gave similar results and, therefore, analyses included in this section are all on untransformed data.

In the lower reaches of the river, channel homogeneity limited the availability of habitat to only two main types, and their mean coho salmon densities were relatively low (0.40 coho/m^2) compared to most sites in the middle reaches (except for riffles). When different types of habitat were pooled together by reach, S1 was the reach with the highest coho salmon density, followed C2, S2 and C1 in decreasing order (Figure 5).
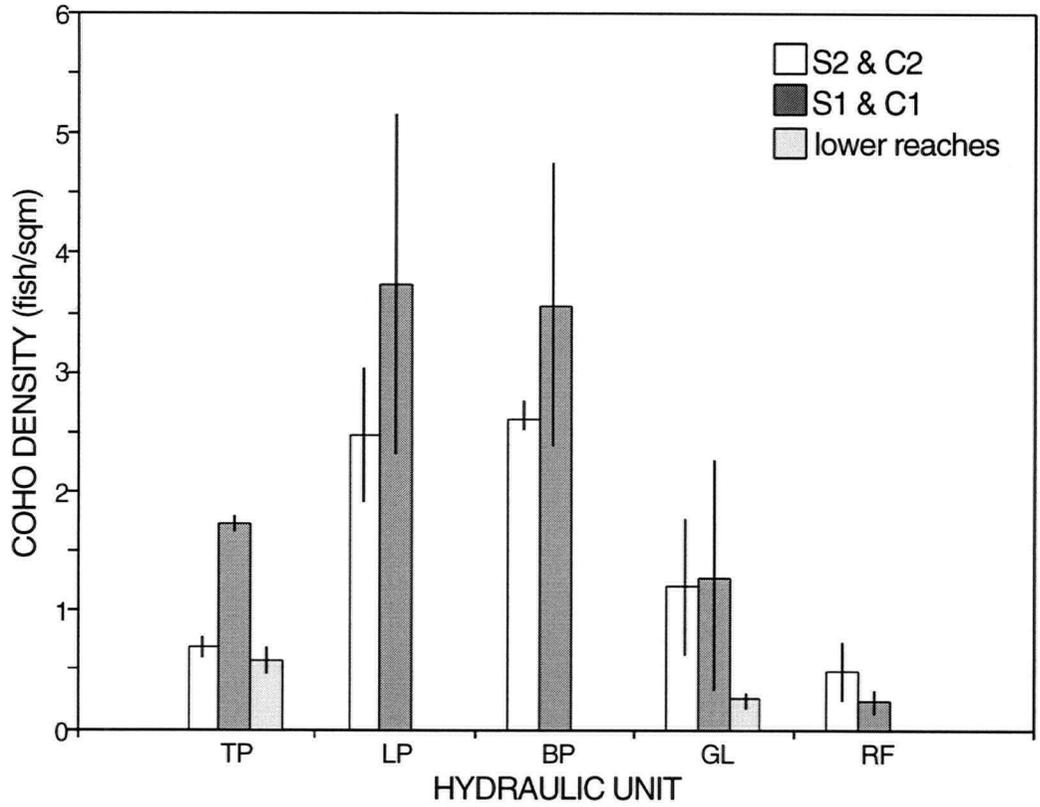
Figure 4. Juvenile coho salmon densities in different reaches (S1, S2, C1, C2 and lower section) and habitats (TP = trench pool, LP = lateral pool, BP = backwater pool, GL = glide, RF = riffle). Vertical lines indicate range.
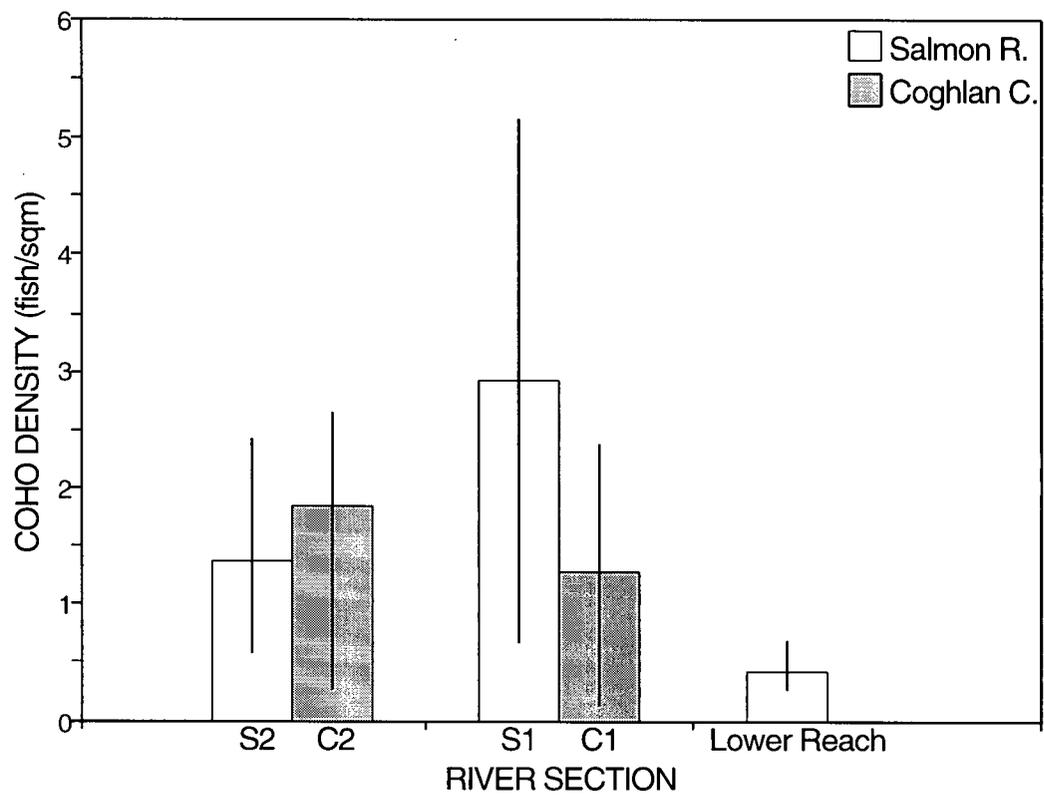
Figure 5. Juvenile coho salmon densities in different reaches of the Salmon River and Coghlan Creek. Vertical lines indicate range.

Habitat specific utilization coefficients (uc) confirmed what is shown in Figure 4, that most juvenile coho preferred lateral scour and backwater pools, whereas fewer chose riffles (uc of riffles= -0.86 in C1, and uc= -0.69 in C2). Habitat utilization, however, not only changed among watershed sections, but also between the Salmon River and Coghlan Creek. Thus, coho utilization of S1's backwater (uc = 2.0) and lateral scour pools (uc= 2.27) was higher than in C1 (uc= 0.51 and 0.47 respectively). Lateral scour pools were more utilized in C2 (uc= 0.92) than in S2 (uc= 0.38), and they were the most utilized type of unit in the watershed in reach S1 (uc= 2.27). Trench pools were not preferred by coho either in S2 (uc= -0.56) or the lower reaches of the Salmon (uc= -0.64), but had a slightly positive use index in the central part of the watershed (S1 uc= 0.14, and C1 uc= 0.05). Glides were not among coho's preferred hydraulic units (uc in C1= -0.03, in S1= -0.06, in C2= -0.24, and in the lower section of the watershed uc= -0.84).

The first three principal components accounted for 33, 26, and 17% (eigenvalues = 1.99, 1.60 and 1.04 respectively, n = 28) of the variance in habitat features. The first component described an axis of increasing fine woody debris (structure coefficient = 0.50, p= 0.0062), fine substrates (structure coefficient = 0.63, p= 0.0003), rooted vegetation (structure coefficient = 0.70, p= 0.0001), and overhanging vegetation (structure coefficient = 0.80, p= 0.0001). The second component was mainly associated with undercut bank (structure coefficient = 0.78, p= 0.0001) and fine woody debris (structure coefficient = 0.77, p= 0.0001). The third component described variation among sites in large woody debris (structure coefficient = 0.96, p= 0.0001). See Appendix D for list of eigenvectors.

Stepwise multiple regression showed that only the first two principal components met the 0.05 significance level requirement for entry into the model (principal component 1: F= 33.42, df = 1, p= 0.0001; principal component 2: F= 26.31, df = 1, p= 0.0001). These two components combined accounted for 79% of the total variability in coho salmon densities (R^2 = 0.7873, df = 27). Individually, the second principal component

explained the largest proportion of the total variability in fish densities (50%), whereas the first component accounted for 28% of fish abundance. No other principal components were entered in the stepwise multiple regression model.

Juvenile coho salmon size not only differed among the different hydraulic units, but also with river section. Figure 6 shows two different trends in mean fish weight change through the watershed. In the Salmon River, coho weight was higher in both S2 and the lower reaches than in S1; whereas in Coghlan Creek coho weight increased from C2 towards the lower section where it joins the Salmon. The overall average weight and length of juvenile coho salmon were significantly lower in Coghlan Creek than in the Salmon River (weight: t (Cochran & Cox approx.) = -11.31, df = 1252, p= 0.0001; length: t = -11.61, df = 2115, p= 0.00001). Figure 6 shows that coho salmon size did not differ between streams in the S1 and C1; but the difference was larger toward S2 and C2, with Salmon River coho being significantly heavier and longer than Coghlan Creek individuals (weight: t (Cochran & Cox approx.) = -21.70, df = 585, p= 0.0001; length: t = -17.49, df = 710, p= 0.00001).

Fish weight and length also varied among different habitat types. In the Salmon River mean coho salmon weight was the highest in lateral scour pools as well as in the trench pools and glides of the lower reaches (Figure 7a). In contrast, backwater pools and middle reaches' trench pools were occupied by coho salmon with the smallest mean weights. In S1, glides also had relatively lighter fish. Taking the data section by section, in S2 both coho salmon mean weight and mean length were significantly larger in lateral scour pools than in trench pools or in glides (F= 16.77, df = 2, p= 0.0001; Tukey's test, α = 0.05, df = 502, ANOVA). In S1, variation in fish size among units increased markedly and significant differences in coho mean weight were detected among all hydraulic units (F= 133.83, df = 3, p= 0.0001; Tukey's test, α= 0.05, df = 1002, ANOVA). Essentially, coho salmon mean weight was the highest in lateral scour pools, followed in decreasing order by the weight of coho salmon in glides, then trench pools and, finally, backwater

pools. In the Salmon's lower reaches there was no difference in coho salmon mean weight between the two types of habitats that were sampled, trench pools and glides. In C2 mean coho weight did not vary among habitats (F= 0.10, df = 2, p= 0.90; Tukey's test, α= 0.05, df = 204, ANOVA) (Figure 7b). But in C1, mean coho salmon weight in lateral scour pools was significantly higher than in all other units, and mean weight in trench pools was significantly higher than in glides and backwater pools (F= 18, df = 4, p= 0.0001; Tukey's test, α= 0.05, df = 194, ANOVA). In all cases, coho salmon length was analyzed using the same techniques and the results did not show any difference with the pattern described for weight.

Table 4 shows the relationship between fish size and location within the watershed from a different angle. Fish weight for each particular type of habitat and river reach is expressed as percent deviation from the estimated mean salmon weight for the watershed (2.73 g). Thus, the mean fish weight in trench pools of the lower reaches was 44% higher than the overall mean weight, whereas it was 36% lower in backwater pools of C2.

Table 4. Size difference among juvenile coho present in different habitats of the Salmon River Watershed. Figures indicate percent deviation from overall mean weight. Fish numbers are in brackets following weight deviation estimates. (N = 2214).

| Habitat Type | Salmon River | | | Coghlan Creek | |
	S2	S1	Lower	C2	C1
Trench Pool	+20 (160)	-23 (312)	+44 (58)		-10 (129)
Lateral Scour Pool	+45 (222)	+26 (265)		-34 (77)	+15 (113)
Backwater Pool		-32 (247)		-36 (78)	-22 (17)
Glide	+22 (123)	+3 (182)	+40 (29)		-32 (120)
Riffle				-39 (62)	-20 (20)
Reach	+31	-8	+42	-36	-11
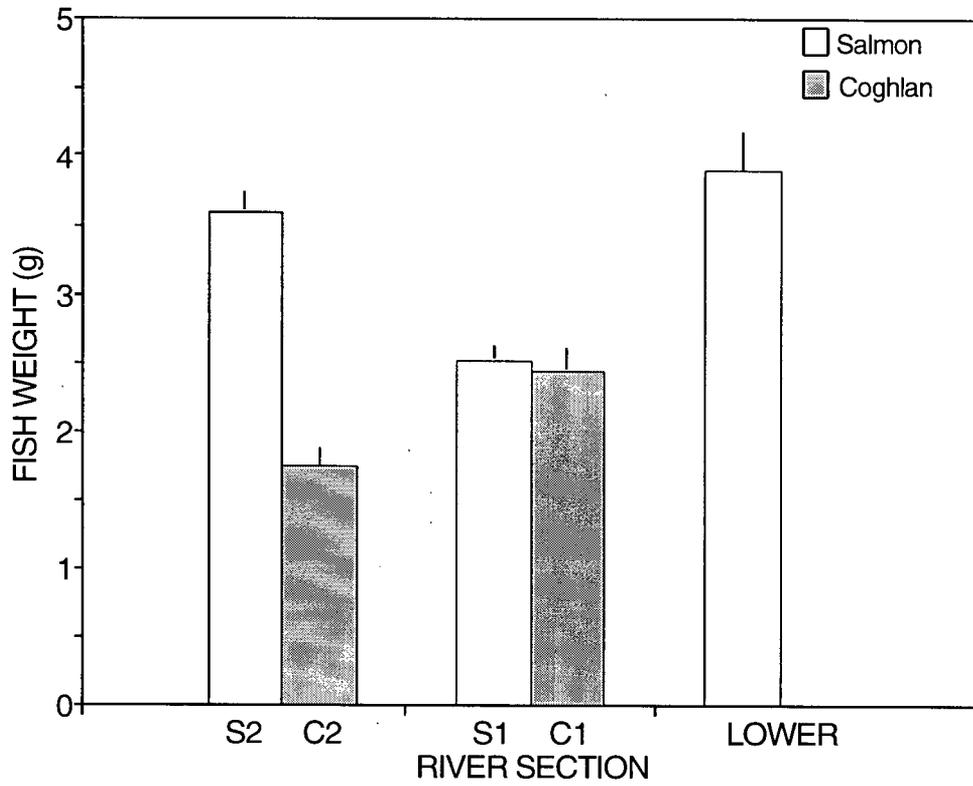
Figure 6. Juvenile coho salmon mean weight in reaches: S1, S2, C1, and C2. Vertical lines indicate two standard errors.
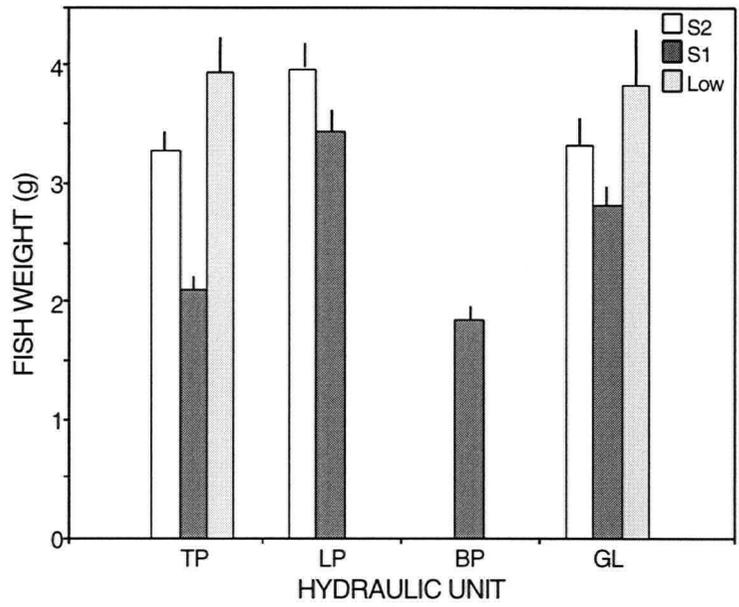
Figure 7a. Juvenile coho salmon mean weight in different habitats (TP = trench pool, LP = lateral pool, BP = backwater pool, GL = glide) and reaches (S1, S2, Low) of the Salmon River.   Vertical lines indicate two standard errors.
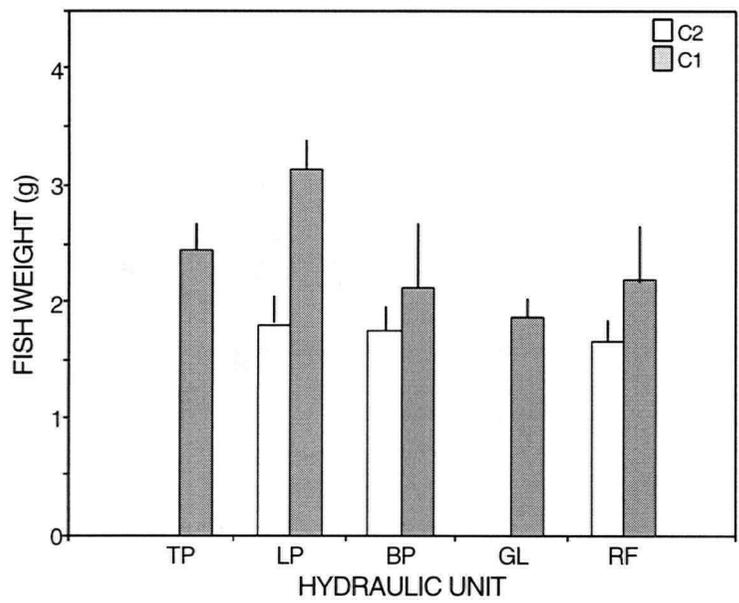
Figure 7b. Juvenile coho salmon mean weight in different habitats (TP = trench pool, LP = lateral pool, BP = backwater pool, GL = glide, RF = riffle) and reaches (C1 and C2) of Coghlan Creek.   Vertical lines indicate two standard errors.

49

No correlation was observed between fish densities and fish weights (correlation coefficient: r = -0.204, df = 25, p= 0.307). Backwater pools were the only type of hydraulic unit where relatively high fish densities (4.7 to 2.4 coho/m^2) coincided with low fish weight (1.5 to 2 g).

Mean coho salmon biomass (coho mean weight x coho density or standing crop / unit's area) in the only occupied portion of the lower mainstem (between the railway crossing and Rawlison Crescent) was much lower (glides = 0.93 g/m^2, and trench pools = 2.27 g/m^2) than in other parts of the watershed. Excluding this suboptimal reach, coho biomass was higher in the Salmon (both S1 and S2) than in Coghlan Creek. Lateral scour pools had higher coho biomass (12.52 g/m^2) than the other units, particularly in the low-middle reaches (S1 and C1). Most pools in these reaches, which are close to the confluence between Coghlan Creek and the Salmon, showed a slightly higher biomass than the upper-middle reaches (Figure 8). But, none of these differences were statistically significant, due to the large amount of variation observed among hydraulic units of the same type (log transformed data showed similar results).

3.2.4. Discussion

The distribution of summer coho salmon habitat observed in the Salmon River Watershed corresponded, in general terms, to that described in earlier studies (McMynn and Vernon 1954, Hartman 1965, DeLeeuw 1982, Watts 1992). The middle reaches of the river, roughly the section delimited between 72nd. Ave. and 256th. St., were preferred by juvenile coho salmon during the low flow period. In its lower-middle portion, corresponding to reaches S1 and C1, it sustained the highest densities of coho salmon in the entire watershed. However, strong differences were observed among different types of habitat, corroborating coho's selectivity of habitat.

The Salmon River had, on average, higher coho salmon densities than its tributary, Coghlan Creek. Based on channel morphology alone, Watts (1992) hypothesized that the

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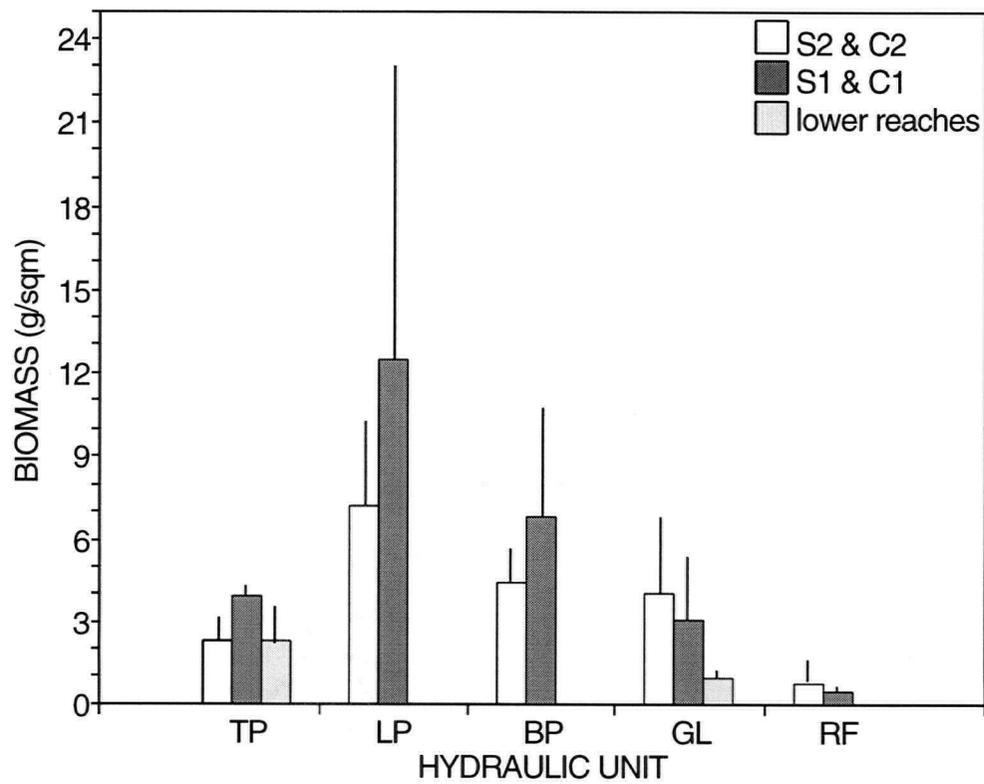
Figure 8. Juvenile coho salmon mean biomass in different habitats (TP = trench pool, LP = lateral pool, BP = backwater pool, GL = glide) and reaches (S1, S2, C1, C2 and lower section). Vertical lines indicate two standard errors.

density of coho salmon would be highest in reach C2. Instead, I estimated reach S1 had the highest densities, followed by C2, suggesting that channel morphology alone (i.e.proportion of pools) does not entirely explain coho salmon distribution in a stream. It is likely that the high coho salmon rearing capacity of reach S1 could be attributed to its abundant cover; it had the highest amount of fine wody debris among the four reaches surveyed by Watts (1992), and many of its pools had well developed undercut banks (Watts 1992). This assumption is supported by the results of my stepwise multiple regression analysis, which identified principal components mainly representing cover (fine woody debris, undercut banks and overhanging vegetation) as the most important ones in explaining variation in coho salmon densities. Although total consensus on the role of cover cannot be found in the literature, several researchers have concluded that woody debris, derived from the riparian vegetation strip, is an important component of coho salmon habitat (Bisson et al 1982, Dolloff 1986, Dolloff and Reeves 1990, Shirvell 1990, Peters et al. 1993). Additionally, undercut banks which are considered very important components of juvenile coho salmon habitat during winter (Bustard and Narver 1975), are likely to extend the importance of their role as cover beyond that season.

Among habitats, lateral scour pools and backwater pools had the highest densities of coho. They were followed, in order of decreasing density, by trench pools and glides. The very few coho salmon found in riffles were outnumbered by juvenile cutthroat and steelhead trout, the dominant species in this type of habitat. This difference in habitat selection between coho salmon and trout, with coho dominating in pools and trout (particularly steelhead) in riffles, was also observed by other investigators (Hartman1965, Bisson et al. 1982, Bugert and Bjornn 1991, Fausch 1993). The segregation in rearing habitat between these species was explained by Bisson et al. (1988) in terms of anatomical differences. Their argument was that trout (steelhead in their study), with their more elongated body and shorter fins, are better adapted for faster flowing waters, whereas

coho salmon, with relatively deeper bodies and larger fins, are better adapted to hold low-velocity positions.

Coho salmon present in backwater habitat, besides high densities, showed the lowest mean weight (as well as mean fork length) in the entire system. This negative relationship between density and mean body size, although expected (Mason 1976, Spalding et al. 1995), was not observed in main channel habitats. High densities and reduced fish body size were also observed by Bisson et al. (1982) in the backwater pools of four western Washington streams. These authors suggested that the dependence of coho salmon on terrestrial insects may, to some extent, allow them to exploit backwater pools and other off-channel habitat that other salmonids (such as trout and Dolly Varden) do not occupy. Notwithstanding, the higher densities of coho salmon in backwater pools than in trench pools and glides is not likely, for reasons already discussed, to result from competition with trout. Instead, considering the small size of individuals found in backwater pools, it is likely that they were displaced to this less profitable habitat by aggressive and territorial fish that occupied drift-rich areas. If this was the case, backwater pools may actually constitute holding habitat for subordinate fish. Because coho salmon that are unable to find and defend a territory are generally displaced downstream, and only take residency if they find unoccupied habitat (Chairman 1962), the availability of backwater pool habitat may represent an opportunity for many "nomad" fry to survive the summer. The loose aggregations of fish I observed in this type of habitat, suggests that they were mainly occupied by subordinate non-territorial individuals. If they were not retained within the middle reaches of the watershed by backwater pools, most of these fry would likely end up in the less favourable lower reaches and the Fraser River.

It is important to mention that the high holding capacity of backwater pools may be due in part to the abundant cover that is commonly present in them. All backwater pools I sampled, besides overgrown overhanging vegetation, had intermediate to high amounts of fine woody debris which was precisely one of the two variables I found

strongly associated with high coho salmon densities. This kind of cover has been considered attractive to coho salmon because it may provide protection from predation (Dolloff and Reeves 1990) and even food resources (Nielsen 1992).

Coho salmon densities in lateral scour pools were almost as high as those estimated in backwater pools. Upstream, lateral scour pools supported higher coho salmon densities in Coghlan than in the mainstem (C2 > S2), but their mean weight was higher in reach S2. Further downstream, however, the lateral pools on the Salmon River reach (S1) sustained higher densities of coho than any other unit in the watershed. This, combined with the fact that they attracted some of the largest individuals found in the central portion of the system (S1 and C1), made coho salmon biomass in these units the highest. The excellent rearing conditions, in lateral scour pools, may result from the combination of their mid-channel location with abundant cover. The extensive undercut banks, many times associated with overhanging vegetation, combined with the presence of rootwads, logs and branches derived from the eroded bank offer ample cover (somewhat equivalent to that available in backwater habitat). In addition, the location of the pool in the channel and its flow regime guarantee abundant invertebrate drift and a variety of current velocities from which the fish can choose very profitable feeding stations.

Trench pools and glides, had reduced woody debris, no undercut banks, and faster flowing waters, had lower coho salmon densities than other types of pools. Furthermore, their mean weights and lengths were intermediate between the large coho salmon found in lateral scour pools and the smallest ones observed in backwater habitat.

Difference in salmon mean weight (and fork length) between the Salmon River and Coghlan Creek was largely due to the presence of larger than average individuals in the lower reaches of the system and in the upstream reach S2. It is possible that, as Mason and Chapman (1965) suggested, this pattern was a result of larger than average individuals being displaced from some of the best nursery habitat into the suboptimal areas of both the lower reaches of the Salmon River and the upper section of reach S2. They hypothesized

that suitable habitat for these very large fish would be extremely limited and therefore a large proportion of them would be displaced, both downstream and upstream. If this displacement occurred, the important stream habitat alterations in the upstream section of S2 (such as riparian vegetation removal, and cattle trampling) that made most of this area unsuitable for spawning and therefore underseeded, could have created suboptimal vacant habitat that the displaced large individuals would occupy. There is also the possibility that larger than average coho results from the combined effect of increased invertebrate production due to stream eutrophication, and the relatively higher mean water temperatures in this section. However, more prey would also imply more fish and the relatively low rearing densities I found in S2 do not support the increased "food-base" hypothesis. Moreover, if anything, riparian overgrazing and stream bank erosion, has been associated with loss of terrestrial and aquatic insect supply, cover reduction, channel widening, lowering of the water table and water temperature increase; not with increased fish food production (Armour et al. 1991).

The upstream end of reach S2, despite the above mentioned alterations, showed a stretch with relatively high coho biomass between the 256th. St. crossing and 48th. Ave. The higher than average coho salmon weights in this section contributed to its high salmon biomass, particularly in glides (which could be considered sloughs, given the reduced flow they have in this upper section of the watershed). It is noteworthy, however, that water quality, channel structure and cover availability in this part of S2 and the upper reaches, have been clearly affected by local land use activities. For example, the elevated double culvert I mentioned earlier constitutes an impassable barrier for upstream juvenile salmon movement during the low flow period. The culvert alone, however, is not the only obstacle to coho salmon and trout utilization of the uppermost reaches. Stream conditions immediately upstream from the culvert change markedly (stations 16, 17 and 18), to the extent that the sequence of distinctive habitats observed further downstream is replaced by uniform habitat with low water velocity and high turbidity, very dense stands

of aquatic plants (such as water plantain, Alisma plantago), low levels of dissolved oxygen (1.9 mg/l at 272nd. St.), and high mean water temperatures (recorded maximum 26°C). These stream characteristics are commonly associated with animal waste loadings from intensive livestock production facilities (Kowalenko 1987, Sharpley et al. 1994), which in the particular case of the upper Salmon River are represented by a zoological centre (the ex Vancouver Game Farm, now named Greater Vancouver Zoological Centre).

In Coghlan Creek, the channel maintained its riffle-pool sequence even upstream from reach C2, and coho salmon accompanied the distribution of this habitat throughout most of the section (between stations 24 and 25).

The lower reaches of the Salmon River can be divided in an upper section of "suboptimal" summer salmon habitat, between the railway crossing (near stations 6 and 7) and Rawlison Crescent (coho salmon densities ranging from 0.25 to 0.68 fish/m^2), and a floodplain reach with unsuitable habitat (only one salmon was caught in station 5 during summer, none in stations 4, 3, 2, or 1). In this part of the river water temperatures, particularly during the low flow period, can exceed the temperature that Brett (1952) found was lethal for coho salmon. The floodplain reach fish community is dominated by minnows (redside shiners, peamouth chubs, brassy minnows) and sticklebacks; largescale suckers and juvenile northern squawfish are abundant, and sculpins quite rare. However, the lower reaches are used by juvenile coho salmon during other times of the year; namely during winter and spring. In winter these reaches offer overwintering habitat (see section 3.2.3), and in the spring a migrating corridor to the Fraser River.

The results of my study combined with the land use changes reported by Watts (1992) (particularly within a 500 m wide buffer zone) suggest that, although substantial portions of the Salmon River are still in good condition, incremental changes are occurring that will continually reduce its capacity to support salmonids. Although the most dramatic changes, both in the stream itself and its riparian forest, occurred more than four decades ago, smaller changes are still going on.

3.3. Winter distribution and habitat use

3.3.1. Methods

Information on juvenile coho salmon distribution and habitat use in the Salmon River watershed in winter was collected during January and February of 1992 and 1993. The same twenty-four sampling stations sampled in late summer (see section 3.1.1) were used during the winter surveys. Because of coho salmon redistribution during fall and early winter, sampling off-channel habitat and backwater areas was given priority over sampling units with high water velocity. Therefore, riffles were not examined, and in the lower reaches of the watershed a number of off-channel sampling sites were added near Trinity Western University (7B, 7C and 7D, Figure 3) and along the floodplain drainage-ditch network that has been developed on Davidson Creek (4B, 4C, 4D, 4E, 4F and 4G, Figure 3). The central part of the watershed was subdivided in the same four reaches (S1, S2, C1 and C2) that were described for the summer phase of this study (section 3.1.1). Their use was convenient because Watts (1992) in his thesis characterized their channel morphology and the adjacent land uses. Throughout these reaches a total of twenty-four habitat units were sampled (see Appendix B).

Minnow traps were used as described in section 3.1.1 to estimate salmon presence and relative abundance in the lower and upper reaches of the stream (Stations 1, 2, 3, 4, 5, 6, 7, 16, 17, 18, 25, 26, 27 and 28 in Figure 3), where water column depth and/or high water turbidity made electrofishing an impractical option. Bloom (1976) and Swales (1987) considered them to be very effective in capturing juvenile salmonids within the 5 to 13 cm size range. In small ponds minnow traps have been successfully employed to obtain removal estimates of fish population size (He and Lodge 1990), but their use in streams has been more limited. One of the reasons for this is that fish depletion cannot be accomplished in stream reaches unless they are closed to fish migration, which is difficult to do effectively, particularly under high winter flows, over the extended period required to remove fish by minnow traps. Nevertheless, traps can still provide useful information

on relative differences in salmonid abundance between a variety of stream habitats, as long as catch per unit of effort (CPUE) is used as a standard measure (Swales et al. 1986). In this study a unit of sampling effort corresponded to a set of nine minnow traps arranged in three evenly spaced triplets, approximately every 4 m, left overnight and for a total of 18 hours on the stream bottom. A "calibration" of the traps efficiency at catching coho salmon was done by using them in some of the same units where salmon total numbers were also estimated by other methods. The calibration was done to allow better comparisons of relative fish abundance between the lower and the middle reaches of the river. Therefore, minnow traps were used in six randomly chosen pools of the middle reaches, in which total fish numbers were subsequently estimated by the removal method.

In spite of winter's higher stream discharge, conditions in the middle reaches allowed the use of electrofishing gear and the removal method for the estimating total numbers of coho salmon in the habitats that were surveyed. After large storm events, however, the use of this equipment and census technique was not possible for several days. The removal technique was applied according to the procedure described in section 3.2.1. Total number of salmon removed in each pass was recorded, and the fork length and weight of a random subsample of 20 individuals was measured for each hydraulic unit. Fish from all three removal passes were represented in this subsample.

The same types of habitat types that were described in section 3.2.1., based on Bisson et al.'s (1982) classification system, were used in the characterization of stream winter habitat. Cover elements and other stream microhabitat components were also the same, and their abundance was again estimated on a percentage base. Although, most cover structures (logs, rootwads, etc.) that had been surveyed and measured in summer were found in the same place ,even after two winters, the proportion of area they covered was reduced during the high flow season by the increased area of each hydraulic unit. Substrate composition was not quantified in all units (due to poor underwater visibility) and, therefore, it was not used in any statistical analysis.

3.3.2. Data analysis

The analysis of winter data involved, for the most part, the same procedures applied to the study of summer coho salmon distribution and habitat use (section 3.2.2). However, only four habitat variables (large woody debris, fine woody debris, overhanging vegetation, and undercut bank) were used in the principal components analysis.

The determination of coho salmon densities in the lower reaches of the Salmon River followed a comparative procedure. Its results are suitable for a general description of the relative abundance of the fish in the floodplain section of the river and its side channels and tributaries. But they cannot be combined with data from the middle reaches of the river in any quantitative analysis. A direct relationship between number of coho salmon that entered the minnow traps and their densities was assumed. Based on it, a regression between number of coho caught per unit of effort (CPUE = dependent variable) in eight different sampling units of the middle reaches and the removal density estimates in those units (independent variable) was calculated. Within the range of the catch size obtained in the middle reaches, the regression line was used as a reference in estimating the approximate coho salmon density in the lower reaches.

3.3.3. Results

In spite of improved conditions in the upper reaches of the Salmon River due to higher water discharge and lower temperatures than during the period of low-flow, no juvenile coho salmon were found in them. Only sticklebacks and Salish suckers were trapped at stations 16 and 17, none at 18. Unit 15A, at the upstream end of reach S2, was the uppermost Salmon River pool in which juvenile coho salmon were found. In contrast, in the upper reaches of Coghlan Creek (stations 25, 26, 27 and 28) juvenile salmon were trapped in almost all areas that were surveyed (using one unit of effort, four coho salmon were trapped in station 25, two in station 26 and one in station 27).

Although, most coho salmon remained in the middle reaches of the watershed during winter, both their absolute numbers and their densities were lower than those estimated for late summer. These low density values had a double origin. On the one hand, salmon numbers in the different types of habitats were actually lower in winter than in summer. But on the other hand, higher flows augmented pool areas by approximately 50 to 70%, further decreasing fish density values. Therefore, two types of densities, raw and corrected ones, are utilized in different comparisons of fish habitat preference. The raw densities are mainly used in "within" season analyses, whereas corrected densities (based on pool area at low-flow) are used in interseasonal comparisons.

In the central section of the watershed, coho salmon preferred backwater pools and lateral scour pools to trench pools or glides (Figure 9a). This was corroborated by an ANOVA which showed that coho densities in both backwater (1.20 coho/m^2) and lateral scour pools (1.03 coho/m^2) were significantly higher than in trench pools (0.25 coho/m^2) or glides (0.32 coho/m^2) (F= 15.06, df = 3, p= 0.0001; Tukey's test, α= 0.05, df = 20). In winter the mean density of salmon in their preferred pool habitat was an average of 3.9 times higher than in trench pools and glides combined, whereas in late summer the combined mean density for lateral and backwater pools (3 coho/m^2) was only 2.4 fold higher than in glides and trench pools (1.24 coho/m^2). This increase in the proportion of coho using backwater and lateral pools is made particularly clear in Figure 9b, in which corrected densities, for smaller summer areas, make the mean density of backwater (2.19 coho/m^2) and lateral pools (2.39 coho/m^2) approximately 5.2 times higher than that estimated for glides (0.47 coho/m^2) and trench pools (0.42 coho/m^2) together.

A summary of estimated coho salmon densities in different habitats of the middle reaches, for both late summer and winter, is provided in Table 5. Besides confirming that backwater and lateral scour pools were the preferred types of habitat for coho salmon regardless of season, it shows an overall decline from late summer to winter of approximately 60% in mean fish density. It is worth noting, however, that the actual
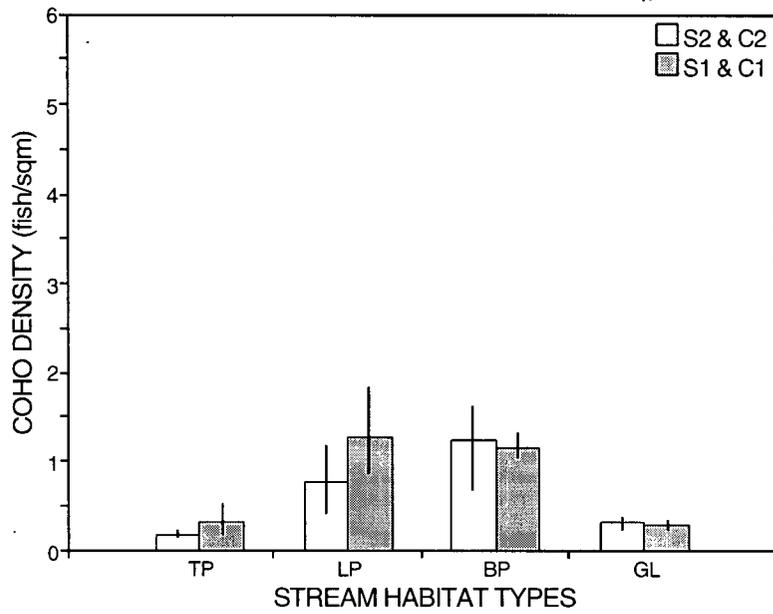
Figure 9a. Juvenile coho salmon winter densities in different habitats (TP = trench pool, LP = lateral pool, BP = backwater pool, GL = glide) and reaches (S1, S2, C1 and C2). Vertical lines indicate range.
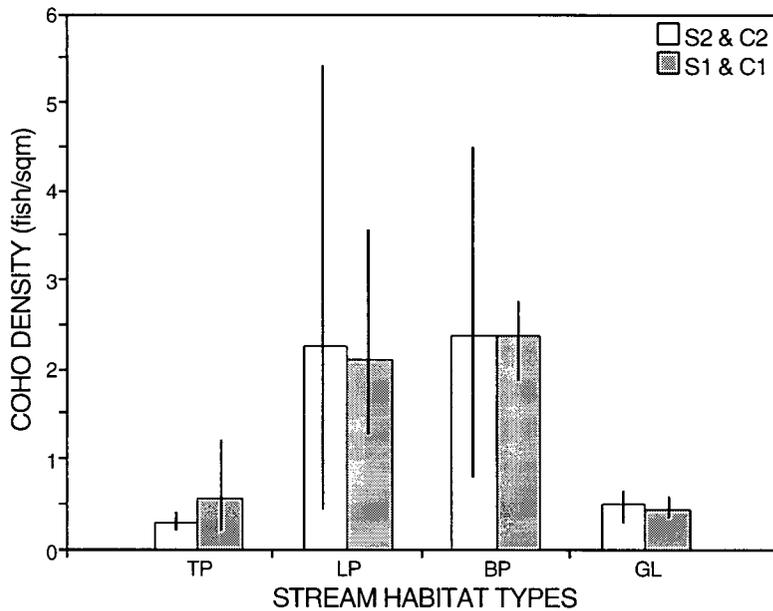
Figure 9b. Corrected juvenile coho salmon winter rearing densities in different hydraulic units (TP = trench pool, LP = lateral pool, BP = backwater pool, GL = glide) and reaches (S1, S2, C1, and C2). Vertical lines indicate range.

reduction in coho densities is smaller than that; when winter densities are estimated using summer areas, the difference between seasons becomes only 23%.

Table 5. Mean juvenile coho salmon densities in the middle reaches of the Salmon River Watershed. Corrected winter densities, based on areas at low-flow, are included in brackets following the raw winter density estimates. Fish numbers are also in brackets following density estimates.

Habitat Type	Late-Summer Density (coho/m^2)	Winter Density (coho/m^2)
Trench Pool	1.21 (441)	0.25 (0.42) (156)
Lateral Scour Pool	2.97 (378)	1.03 (2.19) (337)
Backwater Pool	3.08 (264)	1.2 (2.39) (209)
Glide	1.25 (302)	0.32 (0.47) (82)
Riffle	0.36 (20)	- -
Grand Mean	1.78	0.7 (1.37)

Coho salmon densities, pooling all different habitat types together, were not statistically different between Coghlan and Salmon ($t = -1.46$, $df = 22$, p= 0.158) mainly as a result of large variation in densities that existed among the different habitats of each reach. Analysis on log transformed data showed similar results.

Winter habitat specific utilization coefficients are summarized in Table 6. They show that backwater pools were the most utilized type of habitat within the middle reaches both in S2 and C1. In S1, coho preferred lateral scour pools to backwater pools. Lateral pools offered attractive overwintering conditions for juvenile coho salmon in all four reaches, although the most utilized pools of this kind were in reach S1, as a rate of utilization proportionately higher than the pool's abundance in the system indicates. Trench pools and glides were avoided by many of the young salmon rearing in this part of the watershed, this is shown by their very low utilization coefficients.

Table 6. Coho winter habitat specific utilization coefficients for different habitats of the Salmon River Watershed. Fish numbers are in brackets following habitat utilization coefficients. (N = 1196).

Habitat Type	Salmon River		Coghlan Creek	
	S2	S1	C2	C1
Trench Pool	-0.73 (101)	-0.49 (139)	-	-0.66 (17)
Lateral Scour Pool	+0.17 (108)	+0.91 (278)	+0.69 (73)	+0.67 (59)
Backwater Pool	+1 (36)	+0.5 (176)	+0.65 (16)	+0.94 (33)
Glide	-0.5 (73)	-0.56 (82)	-0.60 (5)	-

The first three principal components accounted for 39, 27, and 19% (eigenvalues = 1.55, 1.09 and 0.77 respectively, n = 24) respectively of habitat variability. The first principal component contrasted sites with relatively abundant overhanging vegetation (structure coefficient = 0.79, p= 0.0001) and fine woody debris (structure coefficient = 0.68, p= 0.0003) to sites with relatively low percentage area covered by large woody debris (structure coefficient = 0.66, p= 0.0005). The second component described variation among sites in undercut banks (structure coefficient = 0.91, p= 0.0001). The third component described variation among sites solely in terms of large woody debris (structure coefficient = 0.70, p= 0.0001). See Appendix D for list of eigenvectors.

Stepwise multiple regression showed that only the first two principal components met the 0.05 significance level requirement for entry into the model (principal component 1: F= 5.68, df = 1, p= 0.027; principal component 2: F= 7.03, df = 1, p= 0.015). These two components combined accounted for 40% of the total variability in coho salmon densities (R^2 = 0.403, df = 23). Individually, the second principal component explained 24% of the total variability in coho salmon densities; whereas the first component accounted for 16% of fish abundance.

The number of salmon caught per unit of trapping effort in the lower reaches of the Salmon River varied markedly among sites, ranging from 0 to 78 fish. Larger numbers of fish, however, were most often trapped in off-channel habitat than in the mainstem (Figure 10). Station 4, corresponding to several sites along Davidson Creek (see Figure 3), showed big fluctuations in numbers of salmon trapped from site to site; but catches tended to increase with distance from the main river. For example, the largest salmon catch (78 fish) was obtained on Davidson Creek, at the uppermost station (Station 4G). Upstream from Trinity Western University, larger numbers of coho were trapped in both a first order tributary (Station 7C) and a ditch (Station 7D) that connected a couple of small ponds to the river, than in either the mainstem itself or the ponds (Figure 3).

CPUE was a good estimator of coho rearing densities in the lower section of the Salmon River. The coefficient of determination of the regression between CPUE and the estimated coho densities, indicated that 87% of the total variation in coho salmon density is accounted for by the fitted regression (Figure 10a). In the lower section of the system, off-channel habitat had, on average, higher salmon densities than the main stem of the river. For example, Davidson Creek (particularly at 4B, 4D, 4F and 4G, Figure 10b) and the side ditches and small Salmon tributary near Trinity Western University (7C and 7D, Figure 10b) had coho salmon densities that were equivalent (or even high) compared to those estimated for habitat in the middle section of the system. Table 7 summarizes the approximate density values of coho salmon in the lower Salmon River and Davidson Creek based on the linear regression.

Juvenile coho salmon size varied not only among reaches of the river but also among different habitat types. The average coho weight (7.69 g, SE= 0.80, n= 196) and length (8.49 cm, SE= 0.340, n = 196) in the lower reaches were higher than those in other watershed sections (Figure 11). Out of the four study reaches in the central portion of the watershed, S2 was occupied by coho with the highest mean weight and length. However, the larger individuals were not uniformly distributed throughout it (Figure 11).

Table 7. Approximate coho densities (coho/m^2) in the lower Salmon River during winter, derived from the relationship between mean CPUE (using minnow traps) and coho removal estimates. (N= 196).

CPUE	Stations	Estimated Density
1 - 5	3A, 4A, 4C, 5A, 7A,7B	< 0.24
9	4E	0.28
12	4B	0.37
17	7D	0.51
20	7C	0.6
33	4F	0.97
39	4D	1.14
78	4G	> 1.4

Coho's mean weight in the uppermost portion of S2 (S2a in Figure 11) was significantly greater (t = -8.268, df = 157, p= 0.0001) than that found further down (S2b) in this same reach (an equivalent pattern was observed for coho's fork length). Significant differences in fish weight were detected among the study reaches in the middle and upper sections of the watershed (F= 34.24, df = 3, p= 0.0001, ANOVA). Coho in reaches S2 and C1 were significantly heavier than those in reaches S1 and C2 (Tukey's test, α= 0.05, df = 448). In all cases, coho salmon length data were analyzed using the same techniques and they showed an equivalent pattern of variation to that described for weight. These differences between reaches cancelled each other within the same stream, and resulted in no significant difference between the overall average weight (as well as length) of juvenile coho in Coghlan Creek and the Salmon River (weight: t (Cochran & Cox approx.) = -0.67, df = 252, p= 0.5036; length: t = -0.518, df = 450, p= 0.6045). Analysis of log transformed data gave similar results and, therefore, only the analysis of original untransformed data is included here.

$R^2 = 0.87$
Intercept= -0.7
Slope= 34.7

CATCH PER UNIT OF EFFORT

60

40

20

0

0.2 0.4 0.6 0.8 1 1.2 1.4 1.6

ESTIMATED COHO DENSITIES
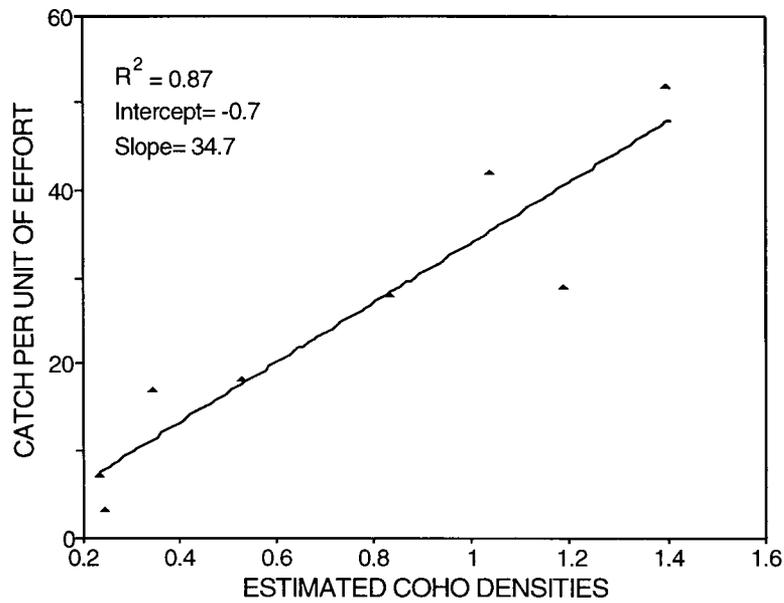
Figure 10a. Regression between estimated coho densities and CPUE in eight habitat units of the Salmon River middle reaches.

NUMBER OF FISH PER TRAP

80

60

40

20

0

Off-channel
Main Channel

Lower Reaches

Middle Reaches

SAMPLING STATIONS
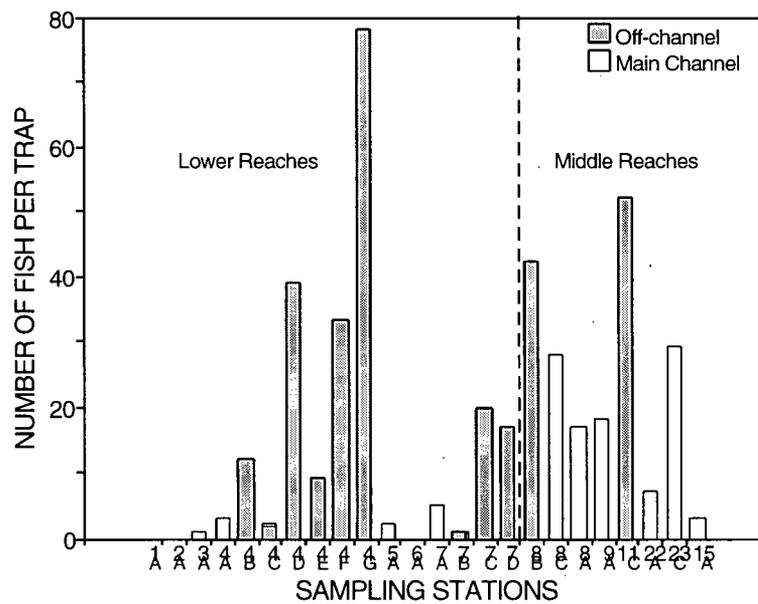
Figure 10b. Comparison between juvenile coho salmon abundance in the middle and the lower sections of the Salmon River in winter. Shaded bars = off-channel habitat
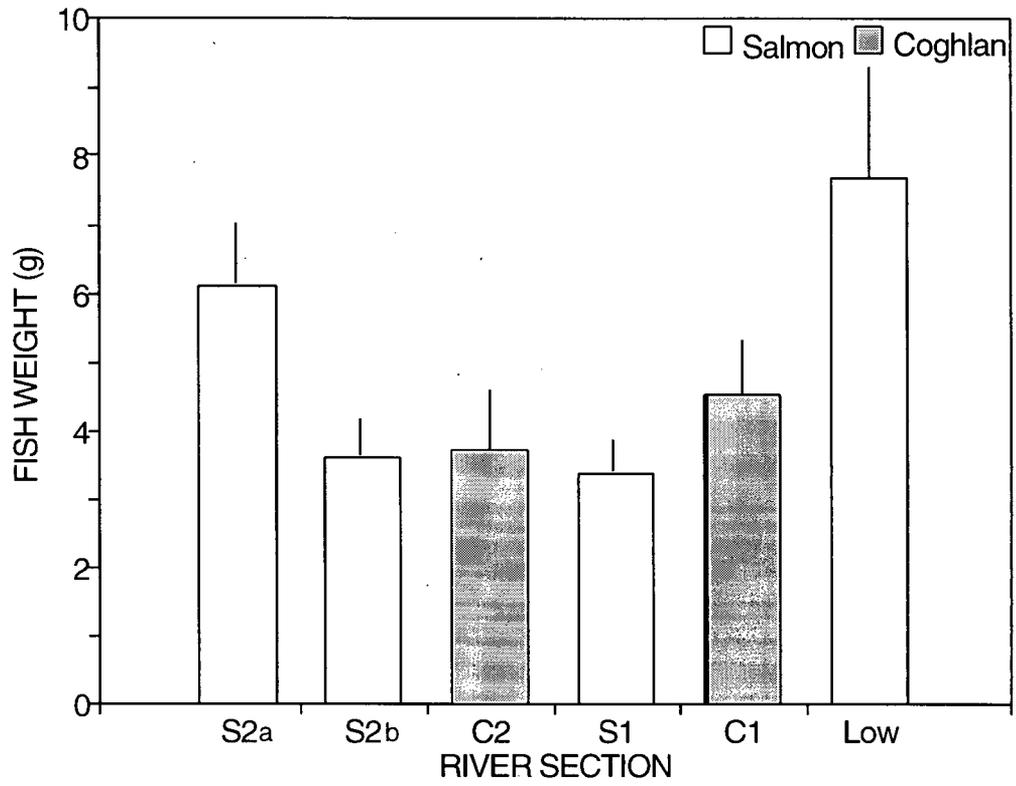
Figure 11. Juvenile coho salmon mean weight in different reaches. Vertical lines indicate two standard errors. S2a = Stations 13 and 15, S2b = Station 11.

Within reach S2 the average weight of backwater pool coho salmon was significantly lower than that of salmon found in the other three types of habitat (F=14.10, df = 3, p= 0.001; Tukey's test, α= 0.05, df = 155, ANOVA). But, in S1 the average weight of coho salmon was similar among all four types of habitats (F= 0.83, df = 3, p= 0.478, ANOVA) (Figure 12a). This homogeneity in fish mean weight among different habitats was also observed in Coghlan Creek, both in reach C1 (F= 1.18, df = 2, p= 0.314, ANOVA) and in reach C2 (F= 0.3, df = 2, p= 0.7428, ANOVA) (Figure 12b). Coho mean lengths followed the same pattern described for mean weights.

Table 8 shows percent difference between the average coho salmon weight for the entire watershed (4.84 g) and the mean weight for each type of habitat and river reach. It shows, for instance, that mean coho salmon weight in the uppermost section of reach S2 was 26% higher than the average for the rest of the watershed, whereas in reach S1 it was 30% lower. These coefficients clearly indicate that some of the largest coho salmon were found in the lower reaches, both in off-channel habitat available in the area of MacMillan Park and in the main channel. The average coho salmon weight in Davidson Creek, however, was not much higher than the mean value for the watershed, but the variability observed in that creek was very high (Figure 13). In fact, it was occupied by some of the largest and the smallest individuals found in the entire watershed. In Station 4G, for example, more than 1 km away from the Salmon mainstem, the lowest coho salmon weights and lengths were recorded (mean weight = 2.33 g, 52% lower than the average for the watershed, range= 0.6 to 7.24 g; mean length = 5.89 cm, range= 3.9 to 8.9 cm), whereas in 4D the heaviest and longest individuals were found (mean weight= 8.98 g, and range= 3.27 to 16.24 g; mean length= 9.36 cm, and range= 7 to 11.6 cm. Mean coho weight in the lower mainstem was significantly greater than in Davidson Creek (t = 1.98, df = 133, p= 0.0437) as long as 4D is not included in the comparison.

Mean coho biomass (mean coho weight x coho density) was similar in lateral and in backwater pools; but that in lateral scour pools was significantly higher than in either
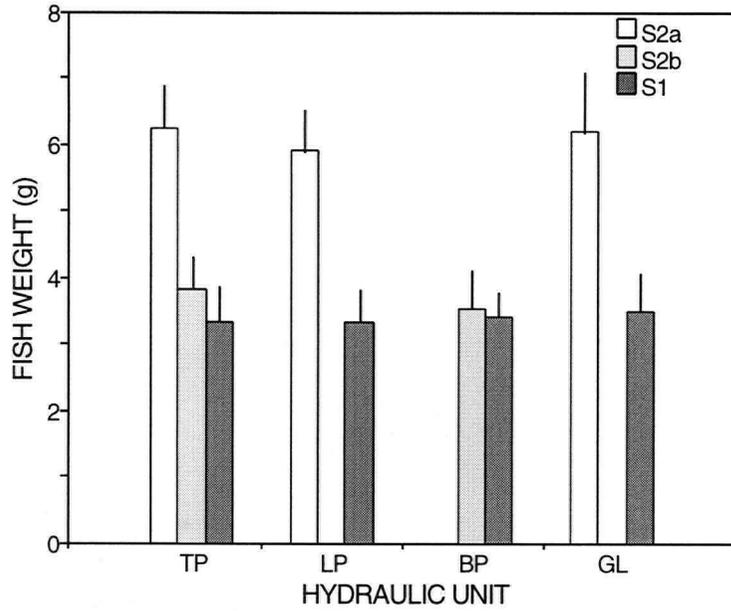
Figure 12a. Juvenile coho salmon mean weight in different habitats (TP = trench pool, LP = lateral pool, BP = backwater pool, GL = glide) and reaches of the Salmon River. S2a = Stations 13 and 15, S2b = Station 11. Vertical lines indicate 2 standard errors.
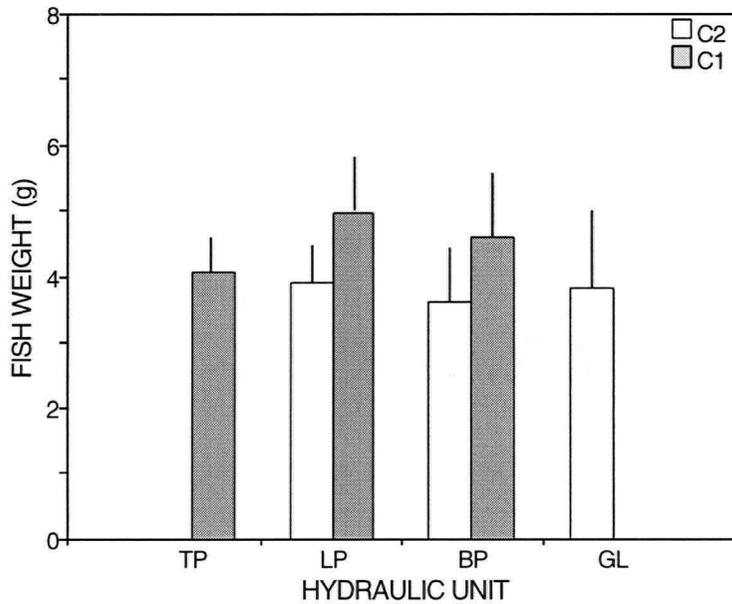

Figure 12b. Juvenile coho salmon mean weight in different habitats (TP = trench pool, LP = lateral pool, BP = backwater pool, GL = glide) and reaches of Coghlan Creek. Vertical lines indicate 2 standard errors.
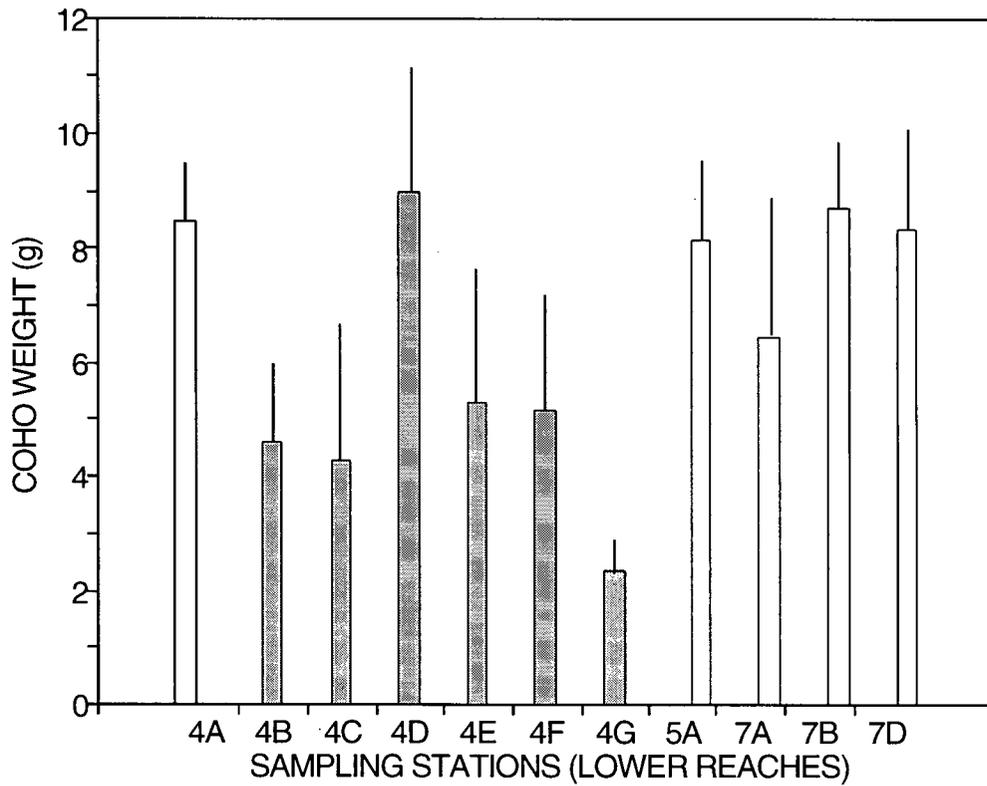
Figure 13. Juvenile coho salmon mean weight in different sampling stations of the lower section of the Salmon River. Vertical lines indicate 2 standard errors.

trench pools, glides or riffles (F= 7.88, df = 4, p= 0.0004;   Tukey's test, α= 0.05, df = 22,

ANOVA).   A comparison of coho biomass by reach (C1, C2, S1 and S2) did not show

any significant differences among them .

Table 8.   Size difference among juvenile coho salmon present in different habitats of the Salmon River Watershed during winter.   Figures indicate percent deviation from overall mean weight.   (Reach S2 divided in upper section (S2a): stations 13 and 15;   and lower section (S2b): station 11).   Fish numbers are in brackets following weight deviation estimates (N = 555).

Habitat Types	Salmon River			Coghlan Creek	
	S2a	S2b	S1	C2	C1
Trench Pool	+28 (40)	-21 (19)	-31 (60)		-16 (17)
Lateral Scour Pool	+21 (20)	-33 (40)	-32 (40)	-20 (20)	+3 (
Backwater Pool	-	-27 (20)	-29 (39)	-26 (16)	-5 (20)
Glide	+27 (40)	-	-28 (40)	-21 (5)	-
Reach	+26	-27	-30	-23	-6

	Lower Reaches .
Mainstem	+59 (8)
Off-channel (MacMillan Park)	+76 (52)
Off-channel (Davidson Creek)	+6 (59)

3.3.4. Discussion

The distribution of juvenile coho salmon in the Salmon River Watershed showed a

seasonally changing pattern, but not to the extent observed in other systems (Skeesick

1970, Peterson 1982b, Cederholm and Scarlett 1982, Scarlett and Cederholm 1984).

Lateral scour pools, backwater and off-channel units with abundant woody debris and well

developed undercut banks were selected by a large proportion of the juvenile coho salmon

during winter. However, considering that this kind of habitat was also the most utilized by them during late summer (see section 3.1.3.), it is not possible to say that a total redistribution of salmon actually took place by winter. The observed changes (consisting of proportionatelly higher numbers of coho salmon selecting off-channel, backwater and lateral scour pool habitat over the other types of habitat) could be considered an intensification, triggered by winter's conditions, of a pattern of distribution among different types of habitats that is observed throughout the year.

The higher overwintering densities estimated for reaches C1 and C2 were not necessarily reflecting the situation in the creek. Instead, they were likely the result of a bias in the proportional representation of different habitat types in the winter survey. Out of 7 habitats sampled in Coghlan Creek, 5 (71%) were lateral and backwater pools; whereas, in the Salmon River, only 7 out of the 17 (41%) units surveyed corresponded to those types of pools. Furthermore, the large range of variation in coho salmon density estimates within each reach made impossible the statistical corroboration of differences between them. This high degree of within reach variability was caused not only by the disparity in fish abundance among different types of habitat, but also within habitat type. The high representation of units offering suitable conditions for juvenile salmon among the 7 units surveyed in reaches C1 and C2 did not correspond to their actual proportion in the stream. Watts' (1992) reported that the percentage of units with low water velocities (i.e. pools, sloughs) in these two reaches corresponded to merely 29% of the channel wetted area (the rest was taken by riffles and glides), whereas in reaches S1 and S2 they represented 40%.

In the four central reaches of the watershed, backwater pools were occupied by large numbers of coho salmon, and in S2 and C1 they were the type of unit with the highest densities of coho salmon in the watershed. Previous studies of coho salmon winter ecology have considered backwater and off-channel habitat to be very attractive to the young fish because of the protection it offers from the high water velocities that

prevail in the main channel, particularly during the frequent winter freshets in coastal streams (Bustard and Narver 1975a, Bisson et al. 1982). In contrast with what was observed in summer, in reaches S1, C2 and C1, as well as the downstream half of S2, the average weight of coho salmon occupying backwater pools was not significantly different from that of coho in other type of units. This can be attributed to the redistribution of larger individuals from their summer main channel feeding territories into more sheltered winter habitat. The movement of large main channel residents into small side creeks, which were already occupied by smaller coho salmon, has been reported by Skeesick (1970) for the Wilson River in Oregon. Dense congregations of salmon of different size and status in protected habitat may occur because at low water temperatures their level of aggression is low (Hartman 1965). The uppermost half of reach S2 was not considered in this comparison, because no backwater pools were surveyed in it.

Lateral pools also represented some of the most heavily utilized wintering habitat for juvenile salmon in the middle reaches. The large amounts of fine woody debris present in these pools (rootwads, branches, etc. normally associated with the eroded bank) combined with their well developed undercut banks are thought to be responsible for high abundance of coho salmon (Hartman 1965, Bustard and Narver 1975b). Stepwise multiple regression analysis on principal components confirmed that undercut banks were strongly associated with high coho salmon densities during winter (principal component 2 vs. coho salmon density). Independent of this relationship was an association between high fish densities, and sites with relatively high amounts of overhanging vegetation, relatively abundant fine woody debris and relatively low amounts of large woody debris (principal component 1 vs. coho salmon density). Despite results of previous studies that have identified logs as an important component of coho salmon winter habitat, I found no clear independent association between large woody debris abundance and fish density.

Although coho salmon abundance in the lower reaches of the Salmon River was estimated indirectly, by comparison with density estimates from other parts of the

watershed, the results still provided important information about the winter distribution of coho and their approximate densities in the lower section of the system. In that lower section, relative coho salmon abundance varied from extremely low, in the mainstem of the river, to very high, in most of the off-channel habitats. Off-channel habitats in these reaches were not represented by the same small backwater pools and first order tributaries found in the central reaches. Instead, second order tributaries, riverine ponds (either natural or artificial), ditches and drainage channels offered coho salmon a large variety and amount of winter habitat. Large numbers of coho salmon used a small tributary to the Salmon River (Station 7C) and some side ditches (7D) that connect to a couple of ponds (7B) distributed between the grounds of Trinity Western University and the adjacent McMillan Park. The fish were mainly found in either the small tributary creek or the ditches, but for some reason the ponds were rarely used, in contrast with what has been observed in riverine ponds elsewhere (Cederholm and Scarlett 1982, Peterson 1982a & 1982b, Swales and Levings 1989).

The network of drainage ditches developed from Davidson Creek, in the floodplain area of the watershed, served as overwintering habitat to large numbers of coho salmon that either emigrated or were displaced downstream with the first freshets. This creek played a role equivalent to that of small tributaries (Scarlett and Cederholm 1984) and wall-base channels (which are formed on floodplain or terrace surfaces by the channeling of runoff through swales created by the migration of the mainstem stream) (Peterson and Reid 1984) studied in the Clearwater River Basin, Washington. CPUE figures indicated that relatively large numbers of coho salmon used the ditches during the winter. Densities varied widely among sampling stations and showed an underlying tendency to increase with distance from the mainstem. For example, some of the ditch sections closer to the mainstem had low to intermediate salmon densities, whereas closer to the headwaters of Davidson Creek (Station 4G, located about 400 m upstream from the railway crossing) relative abundance of coho salmon was similar to that observed in some of the best habitat

of the watershed's middle reaches. The factors affecting coho salmon abundance in the ditches of Davidson Creek were not examined. However, based on my results from the middle reaches and literature information on winter habitat utilization by coho salmon, it is reasonable to assume that salmon densities responded to local factors such as amount and type of cover available, water velocity, water temperature, and predation risk. The relatively dense aggregation of coho salmon found in the creek's channel at 4G could be attributed to the presence of abundant woody debris, derived from old beaver dams, relatively low water flow and riparian overhanging cover (mostly absent in any of the downstream sections of the creek). The fact that this particular reach had higher water temperature than other downstream sections closer to the Salmon River (3.5°C in Station 4G, compared to 1.5°C in 4E and 0.5°C in 4B) could have also contributed to increase the numbers of juvenile coho salmon in it.

Considering that the lower reaches of the Salmon River are unsuitable for coho salmon during the summer, I assume that most coho salmon occupying Davidson Creek in winter came from the middle reaches. This type of migratory behaviour has been observed in other systems as well. In the Clearwater River, for instance, coho salmon moved as much as 38 km downstream from summer rearing habitat before entering small tributary creeks (Scarlett and Cederholm 1984). These movements were always associated with the first fall freshets (Peterson 1982b, Peterson and Reid 1984). The finding that juvenile coho salmon in the lower reaches were, in general, larger than in the rest of the watershed suggests the differential migration of larger individuals. Scarlett and Cederholm (1984) found that small juvenile coho salmon were more prone to downstream displacement, but less successful at reestablishing themselves. Mason (1976) found that the lipid reserves of all coho salmon declined considerably during winter, but were substantially greater in fish that were less than 6 cm long. Therefore, the redistribution of salmon into distant overwintering habitat may represent, as Cederholm and Scarlett (1982) suggested, a cost that the smaller fish cannot afford. Large individuals, however, were

already found in the lower reaches by late summer. This was attributed (see section 3.1.4) to a displacement induced by a shortage of suitable habitat for very large individuals in the most utilized reaches of the system (Mason and Chapman 1965). Therefore, many of the large individuals found in the off-channel habitat of the lower reaches may have come from the adjacent mainstem reaches (particularly likely in 7B, 7C, and 7D).

The fact that individuals of two different size classes occupied Davidson Creek cannot be easily explained based on winter data alone. It is likely that coho salmon from each size class have a different origin. This bimodal distributions in the size of coho salmon present in small tributaries during winter was also observed by other researchers (Skeesick 1970, Scarlett and Cederholm 1984), who consider it evidence of two different subpopulations of coho salmon sharing winter refuges. They concluded that the large fish were immigrants from the more productive mainstem reaches, whereas the smaller fish were permanent residents of the side creeks. Therefore, at Davidson Creek larger coho salmon could have come from the mainstem in search of overwintering habitat, whereas the smaller individuals could have been permanent residents of the creek. However, they must have either entered the creek in spring or were spawned in it, because during the low-flow period both the lower section of the creek, between the railway crossing and its mouth, and the adjacent Salmon River reach were completely unsuitable for juvenile coho salmon. Spring fed reaches with abundant flow have been observed near the headwaters of Davidson Creek (Matthew Foy, pers. comm.), and resident coho must have occupied them throughout the summer. This possibility is also supported by the fact that during winter they had a broader distribution throughout the network of ditches than larger coho salmon and were found further away from its confluence with the mainstem. If they had arrived in the fall with the larger immigrants, their distribution should have been more restricted to the vicinity of the creek mouth. Larger immigrant coho salmon into small tributaries have been reported to travel longer distances from the mouth of the creek than smaller individuals, resulting in the average size of the immigrant subpopulation increasing

progressively in an upstream direction (Cederholm and Scarlett 1982, Scarlett and Cederholm 1984). In the particular case of Davidson Creek some of the smallest specimens found in 4G were small fry that measured 3.9cm and weighted 0.6 g. They seemed to have recently emerged from the gravel, although it was too early in the season (February 10). If a subpopulation of coho salmon spawn and their fry live throughout the year in Davidson Creek, the importance of this system goes beyond its capacity to shelter during winter coho salmon displaced from elsewhere in the watershed and increase its final smolt output. It provides the marginal type of environment in which a genetically different subpopulation may survive, thus contributing to the genetic diversity and even future survival of the Salmon River coho salmon stock.

CHAPTER 4

HABITAT CHOICE BY JUVENILE COHO SALMON: CAN IT BE EXPLAINED BY THE IDEAL FREE DISTRIBUTION THEORY ?

4.1. Introduction

In this chapter I examine the mechanisms behind juvenile coho salmon selection of habitat patches in summer. Mechanisms that control the distribution of the fish between the hydraulic units of a stream reach and, consequently, influence the capacity of the system to produce coho salmon smolts. My objective is to examine experimentally, under controlled conditions, how juvenile coho salmon select among patches that differ in foraging profitability, and in cover availability. After completion of my field research (Chapter 3), I identified overhead cover (undercut banks and overhanging vegetation) and instream fine woody debris as having an important role on the distribution of coho salmon.

Considering the roles that submerged and overhead cover may play in creating stream fish habitat, it is not surprising that many researchers have examined its importance for juvenile coho salmon during the summer rearing months. However, one cannot find clear consensus on whether availability of cover makes a stream reach more or less attractive to juvenile coho salmon. While the results of my empirical work (see Chapter 3) and the work of a number of investigators (Bisson et al. 1982, Dolloff 1986, Dolloff and Reeves 1990, Shirvell 1990, Peters et al. 1992) indicated positive correlation between number of coho salmon and abundance of instream and overhead cover, others reported coho salmon preference for open areas or lack of association with cover (Bugert et al. 1991, Bugert and Bjorn 1991, Fausch 1993, Spalding et al. 1995). The contradictory results may be explained by some of the many differences among these studies. First, some of them were descriptive studies (my own survey in the Salmon River Watershed, for instance, and the work of Bugert et al. 1991) whereas others involved experimental

78

manipulations (Dolloff and Reeves 1990, Shirvell 1990, Bugert and Bjorn 1991, Peters et al. 1992, Fausch 1993, Spalding et al. 1995). Second, the type of system and habitat considered varied among studies (i.e. small tributary streams less than 2 m wide and 8 cm deep in Alaska, Bugert et al. 1991; experimental streams 9 m wide with pools that were 50 cm deep, Spalding et al. 1995; artificial laboratory channels, Bugert and Bjorn 1991; the mainstem of the Clearwater River, Washington, Peters et al. 1992). Third, they were conducted at different times of the year (early summer: Bugert et al 1991, Fausch 1993, Spalding et al. 1995; and late summer: Dolloff 1986, Dolloff and Reeves 1990, Shirvell 1990, Peters et al. 1992). And fourth, they were conducted at different spatial scales (i.e. 20 to 40 m long stream sections, Dolloff 1986; 1 to 2.5 m long pools, Bugert and Bjorn 1991).

In lotic environments, resources (i.e. prey, cover) as well as other important habitat elements for fish (i.e. water depth, velocity and temperature, substrate type, etc.) and potential predators are not homogeneously distributed throughout the entire system. Instead, they associate to form patches. The morphology of stream channels, with different types of hydraulic units, accentuates this tendency further. This characteristic, combined with the continuous imput of prey transported by the current, make streams and the species of fish that inhabit them ideal systems to be studied within the context provided by ideal free distribution (IFD) theory.

I use IFD models as the practical basis for hypotheses about habitat choice in coho salmon. Previous studies have tested various IFD models, with different degrees of success, to predict fish distribution under food manipulations (Milinski 1979 & 1984, Fraser and Sise 1980, Godin and Keenleyside 1984, Gillis and Kramer 1987, Abrahams 1989, Tyler and Gilliam 1995). However, their main goal was the validation of the models, and none applied IFD theory to understand how juvenile fish select rearing habitat in response to two resources (food and cover). Additionally, this is the first time, to my

knowledge, that any dispersion models are used in the study of juvenile salmonid habitat selection.

The hypotheses I tested were:

(a) the distribution of juvenile coho salmon, between patches in a pool and between separate pools in a channel, matches input rate of prey into patches as predicted by the "classical" IFD model.

b) cover alters response of juvenile coho salmon to prey availability between adjacent patches within a pool and between separate pools.

My first hypothesis assumes that coho salmon are perfect samplers of their environment and are free to enter and leave habitat patches. However, departures from the expected pattern are likely to occur because of aggressive interactions among competitors, predator avoidance behaviour or some other violation of the assumptions of IFD. Thus, my second hypothesis supposes that patch choice of coho salmon is not solely governed by prey abundance and that habitat structural complexity may influence the distribution of fish. Both hypotheses address the issue at two different spatial scales - within individual pools and among pools - to study the effect of travelling distance in coho's patch choice. Fish can easily compare and choose between adjacent patches in a single pool, because the associated travel costs are negligible and information about the quality of each patch is readily available. The larger scale experiments were designed to reveal whether coho salmon actively sample across pools, and to what extent increased travel costs and limited access to information on patch quality alter their numerical response to food and cover.

4.1.1. Ideal Free Distribution Models

Table 9 summarizes distributions that various IFD models predict for continuous-input systems; a type of system like the one coho salmon inhabit in summer,

characterized by a continuous arrival of drifting food. Fish consume the food as soon as they detect it, and with increasing number of competitors, may interfere with each other as they attempt to obtain as large a share of the resource as possible (Parker and Sutherland 1986). This kind of interference between competitors, also known as scramble competition, reduces individual's rate of prey capture. The level of interference in a patch, which is normally high in continuous input systems, combined with its food input rate determines the profitability of that patch (Sutherland 1983). In these conditions the IFD model predicts that individuals will distribute themselves across patches in proportion to the amount of resources available in those patches (Fretwell and Lucas 1970). This distribution allows all competitors to maximize their individual intake-rate and it is known as the *numerical response* (Fretwell and Lucas 1970), *input matching rule* (Parker 1978) or *habitat matching rule* (Pulliam and Caraco 1984). This profusion of names has only complicated matters and could have resulted in some authors missapplying the theory (see Tregenza 1994). In the "classical" IFD model, maximization of individual intake-rate means that the average intake rate at equilibrium should be equal across competitors and across patches. The reason for this is that all individuals are assumed equal in this model. If their pay-offs were different, those with a lower intake would switch patches to join those with a higher intake in an attempt to increase their share, causing intake of all individuals to become more even. This is known as the "equal intake prediction" of the IFD model (Kacelnik et al. 1992).

The "classical" model does not anticipate that cover or distance between patches will alter the distribution of foragers. This is because it assumes, among other things, that competitors are "ideal" and perfect samplers, familiar with the potential intake rate in every patch, and that they are "free" to settle in any patch they choose (Fretwell and Lucas 1970, Kacelnik et al. 1992).

Table 9. Coho salmon distributions predicted by selected dispersion models under different experimental conditions. IFD= Ideal Free Distribution; IDD= Ideal Despotic Distribution; PL= Perception Limits; UC= Unequal Competitors (4 = individual competitive weights remain constant; 5 = individual competitive weights change across patches). Each cell indicates that the number of fish is either proportional to (α), or greater than expected from the model ($\uparrow$).

| MODEL | ONE POOL | | | TWO POOLS | |
| | COVER TYPE | | | COVER TYPE | |
	NONE	INSTREAM	OVERHEAD	NONE	INSTREAM
IFD[1]	α input	α input	α input	α input	α input
IDD[2]	not α input	α input	not α input	not α input	α input
PL[3]	$\uparrow$ poor patch	$\uparrow\uparrow$ poor patch	$\uparrow$ poor patch	$\uparrow\uparrow$ poor patch	$\uparrow\uparrow\uparrow$ poor patch
UC[4]	α input	α input	α input	α input	α input
UC[5]	not α input	not α input	not α input	not α input	not α input

Predictions of the models:

1. Fish distribution between patches is proportional to patch input rate (matching), and average intake is the same in all patches independently of experimental treatment

2. Without cover or with overhead cover, regardless of spatial scale, fish distribution between patches is not proportional to patch input rate (undermatching) and average intake is higher in better patch.

   With instream cover, regardless of spatial scale, fish distribution between patches is proportional to patch input rate (matching) and average intake is equal in all patches.

3. Without cover or with overhead cover, within one pool, fish distribution between patches is not proportional to patch input rate (undermatching) and average intake is higher in better patch.

With instream cover, within one pool, fish distribution between patches is not proportional to patch input rate (undermatching is more extreme than in previous treatment) and average intake is higher in better patch.

Without cover, between pools, fish distribution between patches is not proportional to patch input rate (undermatching is more extreme than in single pool experiments) and average intake is higher in better patch.

With instream cover, between pools, fish distribution between patches is not proportional to patch input rate (the most extreme undermatching is caused by this combination of treatments) and average reward is higher in better patch.

4. If individual competitive ability remains constant across patches the most likely distribution mimics the IFD.

5. If competitive ability of individuals changes across patches.

Within one pool, regardless of cover, fish distribution between patches is not proportional to patch input rate (undermatching). Distribution of phenotypes is truncated with better competitors in better patch. Their average intake is higher in better patch.

Between pools, regardless of cover, fish distribution between patches is not proportional to patch input rate (undermatching). Distribution of phenotypes is truncated with better competitors in better patch. Their average intake higher in better patch.

The Ideal Despotic Distribution (IDD) model (Fretwell and Lucas 1970) assumes aggressive monopolization of resources by dominant competitors. This behaviour will prevent individuals from switching patches at will. The violation of the assumption of "free" movement will affect the distribution of competitors; fewer fish than expected will occupy the better sites (undermatching) and more will end up in the less profitable patches (Fretwell and Lucas 1970, Fretwell 1972). The overuse of the poorer patch, however, may also result from a simple random distribution of competitors among patches (Kacelnik et al. 1992). This implies that direct behavioural observations will be needed to distinguish an IDD from a random distribution. I anticipated that visual isolation among competitors, provided by instream cover, will reduce the frequency of aggressive interactions and allow more fish to occupy a site (Dolloff 1986, Mesick 1988, Bugert et al. 1991, Fausch 1993). If competitors were "ideal", and cover diminished despotism, it

would be more likely that they would distribute in direct proportion to resource availability (Table 9, model 2).

Abrahams' (1986) Perception Limits (PL) model also predicts undermatching as a consequence of the violation of the "ideal" competitor assumption. This model assumes the existence of a perceptual limit below which competitors cannot detect input-rate differences between patches anymore. Under such conditions competitors have to choose foraging sites randomly, and deviation from an IFD will increase (Abrahams 1986). This situation can be brought about by a reduction in the overall resource rate, without changing patch profitability ratios, that sets individual intake-rates well below the limit of perception of foragers. Whereas the PL model predicts a lowered amount of total food will increase deviation from the "input matching" rule, the IFD model anticipates no change at all (Gray and Kennedy 1994). If competitors are not "ideal" I anticipate the effect of perception limits on the distribution of coho salmon to become even more accentuated in both structurally complex and coarser grain habitat (Table 9, model 3).

The last model I consider, Parker and Sutherland's (1986) Unequal Competitors (UC) model, assumes competitors are "free" to move but individuals have different foraging efficiencies or "competitive weights". It predicts that the ratio of these "competitive weights" to resources will be equal across patches. But, the actual distribution of individuals will vary depending on whether their "competitive weights" remain constant or change from patch to patch. If the competitive weight of each individual remains constant and if the sum of weights in each patch matches the local food input-rate, one may expect to observe a distribution that superficially resembles an IFD for equal competitors (Sutherland and Parker 1985, Parker and Sutherland 1986) (Table 9, model 4). Houston and McNamara (1988) estimated that this type of distribution of competitors will be the most likely to occur by chance. Regelmann (1984) maintained that it was caused by the early distribution of good competitors, that sample faster and more efficiently, and conform to their own IFD when choosing a patch. The bad

competitors adjust, after longer sampling time, to their own IFD or they may even distribute at random. Milinski (1984) provided experimental evidence for Regelmann's claim. In contrast, if the competitive weight of each individual changes between patches the result will not resemble an IFD of equal competitors, and the distribution of different phenotypes will be split up between patches (Table 9, model 5). Better competitors will occupy the most favourable patches (where they will obtain the highest average pay-offs) and worse competitors will end up in the poorer sites (Parker and Sutherland 1986). I expect to observe strongly "truncated" distributions of phenotypes in more complex habitat or in coarser grain environment, if one particular phenotype happens to have a competitive edge over others in these conditions. The better competitors will always occupy the highest quality patch.

4.2. Methods

4.2.1. Experimental apparatus and procedures:

The experiments were performed in two wooden stream channels at the Cultus Lake Research Laboratory (Department of Fisheries and Oceans), B.C. These channels were 0.9 m wide, 0.4 m deep and 17.4 m long. They received Cultus lake water pumped at a rate of approximately 120 L/min. Summer water temperature in the channels was maintained at $12\text{-}13^\circ$ C, by mixing lake hypolimnion (6° to 8°C) with lake epilimnion (13° to 19°C) water.

I conducted four groups of experiments: single pools without cover, single pools with cover, double pools without cover and double pools with cover. Those in the first group were designed to test whether age-0 coho salmon distribute between adjacent patches within a single pool in response to their profitability as predicted by the IFD model. The second group of experiments looked at, also within individual pools, whether the presence of either instream cover or overhead cover alters coho salmon response to

the foraging quality of the patch. These two types of treatments were randomly applied to the experimental pools, and the experiments were conducted from May 18 to July 28, 1992. The third group of experiments tested whether coho salmon distribute between more distant patches, represented here by separate pools, in proportion to their food availability. Finally, the fourth group looked at whether cover has any effect on coho salmon distribution between distant patches in response to pool profitability. The third and fourth sets of experiments were conducted in a random sequence from August 3 to October 2, 1992. All series of experiments tested hypotheses about coho salmon patch selection in response to either prey abundance, cover presence or a combination of both.

4.2.1.1. Single pool experiment without cover:

For the single pool experiments each channel was divided into six 2.44 m long pools, using 0.31 m high wooden partitions (Figure 14A). Water velocity was slow, varying from 3 to 7 cm/sec. at 15 cm from the bottom in different points of each pool. Fish were fed and observed from behind portable screens at the upstream and downstream ends of the pools. Pools were covered between trials with plastic screens, 25 mm mesh size, to keep predators away.

Freeze dried shrimp (Euphausia pacifica) was used as food before and during experiments. It was large enough to be easily handled and delivered as individual prey, and it stayed afloat until the fish ate it. This last attribute facilitated the creation of habitat patches of different foraging quality within a pool. Shrimp were dropped from behind the upstream screen down a pair of slides into both the right half and the left half of each pool, simulating drifting prey such as coho salmon feed upon in natural streams. Differences in patch profitability were produced by different shrimp delivery rates between right and left side of a pool, and maintained by means of a floating polyurethane rope that prevented shrimp from drifting between patches. The adjacent patches created in this way were assumed to be equally accessible to fish. Four different patch profitability ratios were

applied: 1:1, 1:2, 1:5, and 1:11. A single prey (half a shrimp) was delivered into each patch every 10 seconds to create the 1:1 profitability ratio. To obtain the 1:2, 1:5 and 1:11 desired ratios one prey was dropped into the most profitable patch every 10 seconds and into the poorer patch every 20, 50 or 110 seconds. This delivery regime simultaneously increased differences between patches and reduced total amount of available food. Pools with a 1:1 profitability ratio received 12 pieces of shrimp per minute. The ones with a 1:2 ratio received 9 pieces per minute. Those with a 1:5 ratio received 7.2 pieces per minute, and 6.5 pieces per minute were delivered in those pools under a 1:11 feeding ratio.

The distribution of coho salmon, for all treatments, was recorded every 30 seconds over a total period of 6 minutes. Feeding experiments were 6 minute long, because fish satiation (manifested as lack of interest in easily attainable prey) was observed during preliminary trials longer than seven minutes. Both the type of treatment and the poorer patch in each pool were randomly designated before each trial; this procedure reduced resource spatial predictability for the fish. Twenty replicates were obtained for each treatment.

4.2.1.2. <u>Single pool experiments with cover:</u>

In the second group of experiments, involving cover, structures were randomly assigned to one of the two patches in each pool. This resulted in seven different combinations with instream cover and another seven involving overhead cover (Table 10). In these double treatment trials, pools in each experimental pair could differ in only physical complexity (during unfed control trials or under a 1:1 feeding ratio) or in both physical complexity and foraging quality (if they received either a 1:2, a 1:5, or a 1:11 feeding ratio). The latter offered two different alternatives: a) the pool with instream cover was richer in food; or, b) the pool with cover was poorer in food.

Table 10. Combinations of feeding ratios and cover treatments used in experiments.

		FEEDING RATIOS				
SCALE	COVER	0:0	1:1	1:2	1:5	1:11
SINGLE POOL	NONE	YES	YES	YES	YES	YES
	INSTREAM	YES	YES	YES *	YES *	YES *
	OVERHEAD	YES	YES	YES *	YES *	YES *
DOUBLE POOL	NONE		YES		YES	
	INSTREAM		YES		YES *	

* Feeding ratio and cover produced two possible combinations (cover in poorer patch and cover in richer patch) that were considered as separate treatments.

When the treatment involved instream cover, twelve rectangular plywood blinds (15 cm x 40 cm) were inserted into one patch as shown in Figure 14B. These rectangular plywood sheets rested on their shorter side and were oriented parallel to the water flow; hence, reducing water deflection that could have potentially created "resting" areas for the young fish. Structures were placed in the pools at least 2 hours before the beginning of a trial. Previous observations of salmon under similar conditions showed that a minimum of 90 minutes, in the presence of new structures, were required for fish to resume their normal activities. If the treatment involved overhead cover, a rectangular plywood sheet (220 cm x 45 cm) was supported 15 cm above the water surface over one patch.

In experiments without cover, spatial distributions of fish between patches of similar foraging quality ("no feed" periods between trials and trials with a 1:1 ratio) were used as controls to the effect of the 1:2, the 1:5 and the 1:11 patch profitability ratios. In turn, fish distributions observed without cover and under these three different feeding
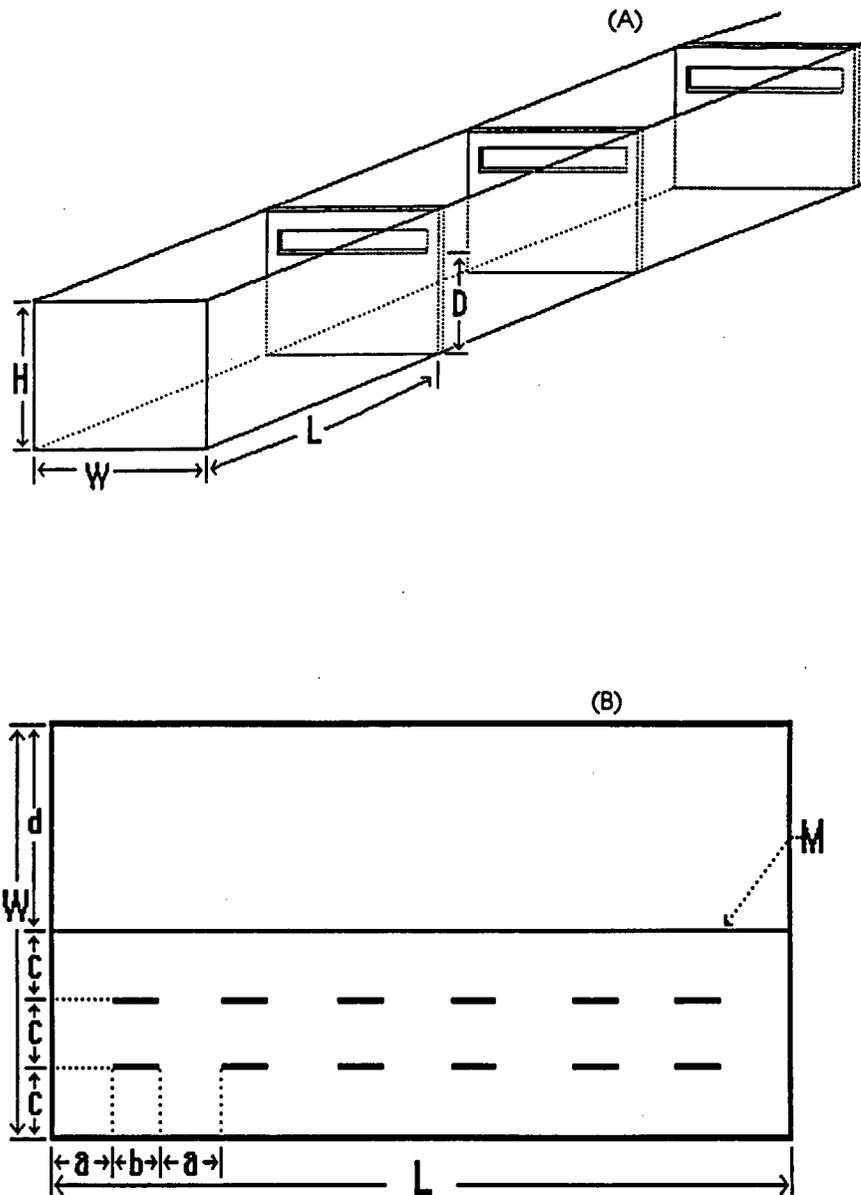
Figure 14. (A) Section of experimental channel divided into individual pools by wooden partitions. Windows in partitions were covered with fine mesh that allowed water to flow through, but prevented food and fish from moving among pools. $L = 2.44$ m; $W = 0.90$ m; $H = 0.40$ m; $D = 0.31$ m. (B) Diagram of single experimental pool, from above, with instream cover in one of its two patches. L = pool length (2.44 m); W = pool width (0.90 m); M = floating rope dividing pool in two halves; $a = 0.22$ m; $b = 0.15$ m; $c = 0.15$ m; $d = 0.45$ m.

ratios, were regarded as controls for the effect that cover had on coho salmon distribution under the respective patch profitability ratio in the second group of experiments. Observations made when cover was present, but without delivering any food, were used as controls for the effect of the interaction between different profitability ratios and cover. To distinguish the effect of visual isolation on fish behaviour from any effect that the physical presence of these structures could have had, similar size "blinds" made of clear Plexiglass were used in control trials. The combination of Plexiglass blinds in one of the patches with the different feeding ratios resulted in seven additional types of control. For each control treatment twenty replicates were obtained.

4.2.1.3. Double pool experiments:

For my third and fourth group of experiments, every second inter-pool partition was removed and replaced by a short riffle made of gravel and cobble, so that the channels were divided into three experimental units each. One experimental unit consisted of two consecutive 194 cm long pools and their interconnecting 100 cm long riffle. Because these experiments ran for seven days, automatic feeders were used to deliver shrimp at specified rates in each one of the twelve pools. Paired-pool experiments also tested fish patch choice in response to food alone or the combined effect of food and cover. Only instream cover was used this time and two feeding ratios were applied: 1:1 and 1:5. Instream cover in this group of experiments was provided by the same small plywood blinds described earlier, but this time they were distributed throughout the whole pool, not half of it. These treatments were randomly assigned to the six experimental units in both channels, and nine replicates of each combination of treatments were obtained.

To maintain the profitability ratios between pools, surface sieves (wooden framed cheese-cloth screens) were placed on the riffles to stop shrimp from washing into the downstream pool. Sieves had to be brushed twice a day to keep them in good working conditions. Wooden partitions with screened openings separated the experimental units

and kept fish and shrimp from moving between them, while allowing a regular flow of water.

4.2.2. Experimental subjects:

Age-0 coho salmon (Robertson Creek Hatchery, Vancouver Island) were used in all these experiments. One hundred and forty four coho salmon were used in "single-pool" groups of experiments; they were randomly chosen from a larger preselected group of fish (300) of relatively similar size (May mean length = 5.1 cm $\pm$ 0.05 SE, and mean weight = 1.63 g $\pm$ 0.06 SE). Homogeneous size among individuals was important in reducing initial differences in competitive abilities. The "double-pool" experiments were conducted in late summer and by that time fish were not only bigger, but also showed greater individual size variation (August mean length = 7.76 cm $\pm$ 0.15 SE and mean weight = 5.93 g $\pm$ 0.27 SE, September mean length = 7.81 cm $\pm$ 0.14 SE and weight= 6.26 g $\pm$ 0.32 SE).

At the beginning of the "single-pool" experiments 144 coho salmon were randomly assigned to the twelve pools, resulting in twelve individuals per pool. This number created a fish density within the range observed in productive coho salmon streams during the summer (Dill et al. 1981, Ptolomy 1993). The same fish were used through the whole series of "single-pool" experiments, and those that died or escaped (24) were replaced by coho salmon of similar size.

During the "double-pool" experiments 36 "naive" coho salmon were taken from the stock tanks, at the beginning of each week, and divided into six equal groups. By the time these groups of experiments had started (late summer) variation in size among fish in my stock tanks had increased notably from my earlier trials. Because bigger coho salmon have been described as dominant individuals, defending their feeding stations from other fish (Hartmann 1965), I marked them individually to detect any correlation between patch quality and fish size. Individual coho salmon weight and fork length were recorded, and

they were individually marked with small dots by injecting dye (Alcian blue) with a needleless high-pressure syringe (pan-jet) in some of their fins.

Each group was randomly assigned to and released into only one of the paired pools of each experimental unit. After seven days all individuals were removed using baitless minnow traps, placed the last evening of the trial and checked the following morning. Those coho salmon that did not enter the traps, were electroshocked and removed using a dip-net. Before electrofishing the water level in the channels was lowered, exposing the riffles to prevent fish from changing pools in response to the method of capture. The final distribution of individuals was recorded.

4.3. Data Analysis

All statistical analyses were conducted using SAS systems software (SAS Institute Inc. 1988). I performed exploratory analyses including the estimation of different descriptive for individual trials under the different treatments. I used the Shapiro and Wilk statistic (W) (Zar 1984) to test departures from normality, and it indicated that data were normally distributed. The only exception to this pattern was the distribution of the means (representing the number of fish observed in the richer patch) for each one of the thirty trials under a 1:11 profitability ratio. Their distribution departed from normality according to W (0.8647) and its associated probability value (p= 0.001).

Before analyzing the effect on coho salmon spatial distribution of the various treatments under study, it was important to investigate possible behavioural differences both among pools, and between morning and afternoon trials. The twelve groups of fish used during my first series of experiments, in spite of coho salmon initial size homogeneity, could have received different proportions of dominant and subordinate fish. Strong differences in group hierarchical composition could have produced unlike responses to the experimental treatments at the individual pool level. To investigate this,

a single factor analysis of variance was performed (one-way ANOVA) for each individual treatment (1:1, 1:2, 1:5, and 1:11 feeding ratios) as well as for the "no feed" control. Pool was the factor considered in the analysis and each individual unit represented a different level of this factor. The null hypothesis of no difference in fish spatial distribution among the 12 separate pools, is rejected only under "no feed" control conditions (F= 4.76, p= 0.0018). The associated r^2 value indicated that "pool" accounts for 74% of the variation in the observed fish spatial distribution when they are not under any particular feeding treatment. This can either be a consequence of the individual pool's position in the experimental channels, a direct result of differences in interaction between coho salmon in each one of the twelve experimental groups, or more likely, that one half of the pool was more attractive than the other in some cases (possibly due to sunlight incidence). However, differences among pools (or fish groups) were not significant when the various feeding treatments were applied (1:1 F= 1.27, p= 0.1365; 1:2 F= 0.93, p= 0.5193; 1:5 F= 1.25, p= 0.3228; and 1:11 F= 0.30, p= 0.9728) indicating that a diminishing proportion of the observed variation can be attributed to them. Other factors, such as the increasingly different food ratios, are presumed to account for the rest.

Paired t-tests between my morning and afternoon results indicated that there were no significant differences (p= 0.4351) in fish response to the treatments as a consequence of time of the trial.

4.4. Results

The distribution of salmon between patches within a pool varied in relation to the availability of food, as IFD theory predicts, but it did not match quantitatively the abundance of resources as the "classical" IFD model predicts. Figure 15 illustrates fish response (indicated as number of fish present in the best patch) to the profitability ratios over the entire 6 minutes of the trials. It shows not only that the number of fish in the
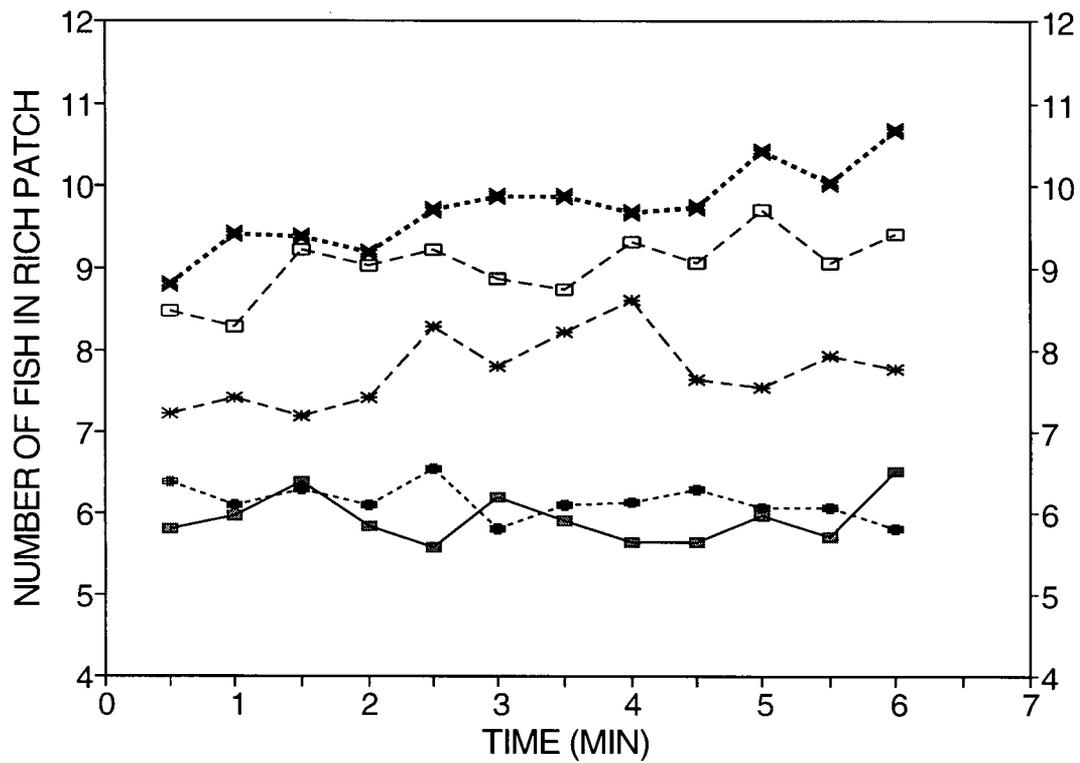
Figure 15. Mean number of fish observed in richer patch every 30 seconds during 6 minute long trials for each of the 5 different profitability ratios. Means were calculated using data from 20 replicate tests. ■ = 0:0 prof. ratio, + = 1:1 prof. ratio, * = 1:2 prof. ratio, □ = 1:5 prof. ratio, X = 1:11 prof. ratio.

richer patch increased with relative patch richness but also suggests a continuing small adjustment of fish numbers as they gather more information about the quality of the two available patches. This leads to a delay in the stabilization of the response. A consequence of this is that the first two minutes of observation, particularly under higher profitability ratios, show a smaller mean number of fish in the richer patch than observed during the remainder of the trials. Therefore, only data collected during the last four minutes of observation were used in the statistical analyses that I performed. For each replicate the results during the last four minutes were averaged to yield the estimate of fish distribution per treatment.

4.4.1. Single pool experiment without cover:

The distribution of fish was affected by food availability (one-way ANOVA, $df = 4$, F= 125.24, p= 0.0001), but not as predicted by Fretwell and Lucas' (1970) IFD model. Although, the mean number of fish occupying the most profitable patch was always higher than that in the poorer one, the observed distributions did not always match the distribution of food as predicted by the IFD model (Table 9, model 1). Fish distributed equally between the patches whenever they did not differ in profitability (one-way ANOVA with specific contrast "control vs 1:1", $df = 1$, F= 0.78, p= 0.38) (Figure 16). But their numerical response was different under each one of the four feeding treatments (one-way ANOVA with specific contrasts: "1:1 vs 1:2", $df = 1$, F= 76.35, p= 0.0001; "1:2 vs 1:5", $df = 1$, F= 21.76, p= 0.0001; and "1:5 vs 1:11", $df = 1$, F= 11.98, p= 0.0007). If one of the patches was twice as profitable as the other (1:2 ratio) the mean number of coho salmon in it was 8.12, twice the number observed in the poorer patch. Matching of proportions of fish and resources, as predicted by the IFD model, were only observed when differences in patch foraging quality were either non-existent (1:1 ratio and "no-food" control observations) or small (1:2 ratio). Under more extreme differences in

profitability between patches (1:5 and 1:11 ratios) the number of coho salmon in the richer patch increased further in response, but it undermatched patch input-rate.(Figure 16).

The fact that in my experiments the total amount of food entering a pool decreased as patch profitability ratios increased, should not have affected the final distribution of coho salmon if they were "ideal". The IFD input-matching rule predicts foragers to distribute in proportion to the distribution of food regardless of total amount. An upper limit or "ceiling" to the maximum number of fish simultaneously occupying the better patch was observed under high profitability ratios (1:5 and 1:11). This represented an additional deviation from an IFD.

4.4.2. Single pool experiments with cover:

Cover, either instream or overhead, altered coho's response to patch profitability. Fish distributions with cover present in one of the two patches were very different from distributions in pools without any cover. This effect was noticed regardless of patch profitability, provided some food was present. In general the distributions deviated further from an IFD than in the experiments without cover.

In experiments with instream cover, coho salmon distributed evenly between patches during no-food control periods (Figure 17). But as soon as food was detected they consistently over-estimated the foraging value of the clear patch and underestimated that of the patch with cover. My results suggest that coho's ability in determining habitat foraging quality is hindered by physical complexity. They underused the patch with instream wooden structures even under a 1:1 profitability ratio (Figure 17, a and b). As patch differences grew bigger more fish occupied the richer patch, but never matching the input rate. When instream cover was present in richer patch, fish numbers in it were greatly reduced compared to the prediction of the IFD model and the experiments without cover of Figure 16 (Figure 17a). Also, when instream cover was present in the poorer
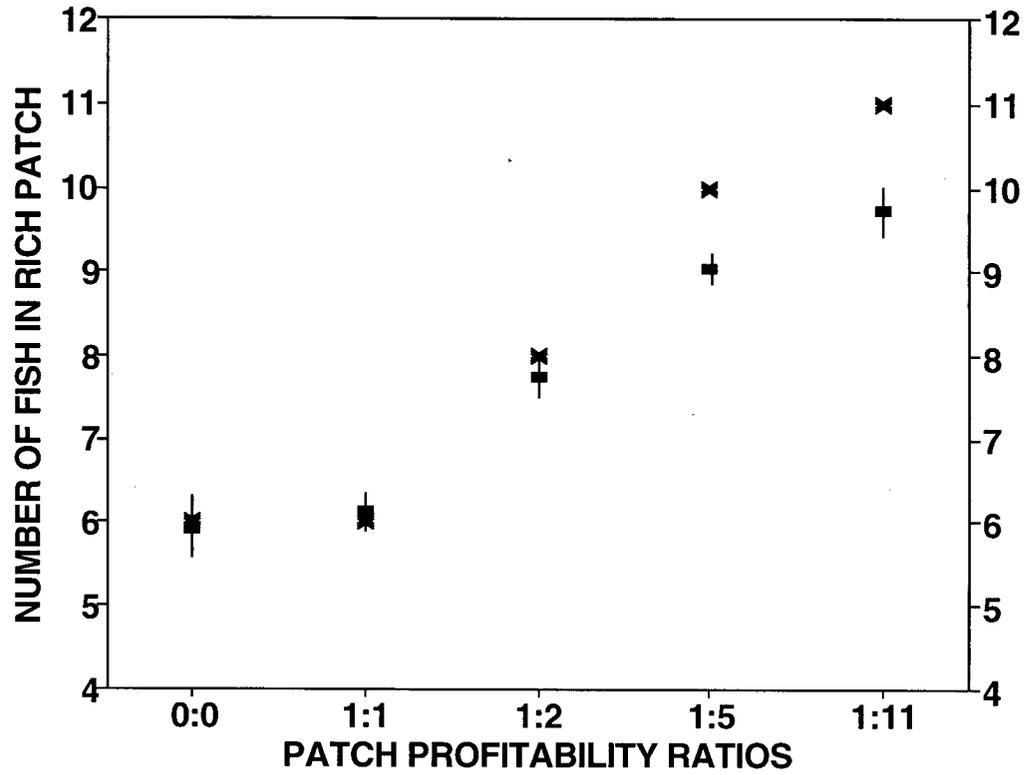
Figure 16. Mean number of fish (for total 6 minutes of trials) present in richer patch for each of the 5 different profitability ratios. The vertical bars are ± 2 standard errors. **X** = fish numbers predicted by the IFD input matching rule. ■ = mean number of fish in richer patch during this experiment.
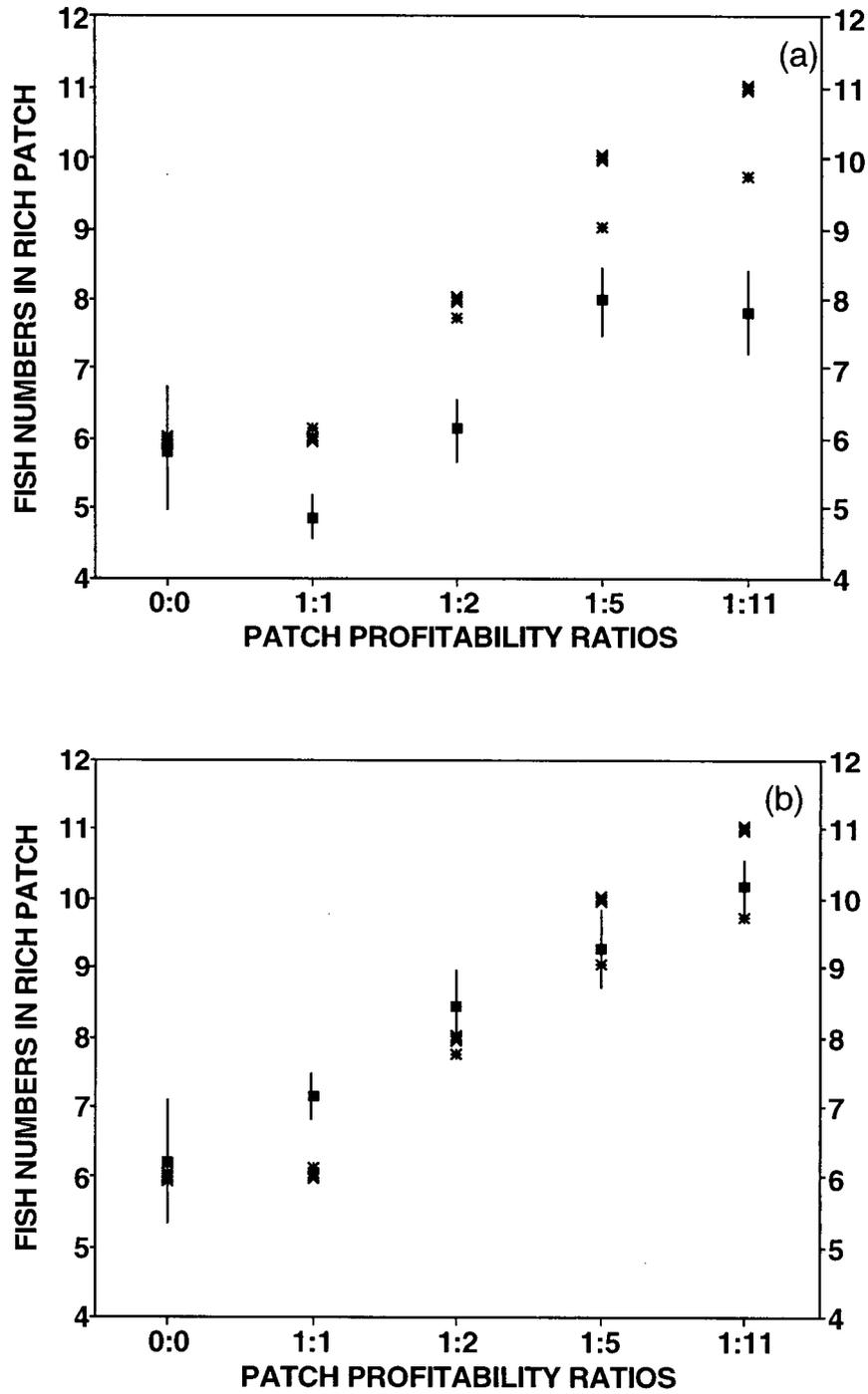
Figure 17. Mean number of fish observed in richer patch for each of the 5 profitability ratios in pools with instream cover, (**a**) instream cover present in richer patch, (**b**) instream cover present in poorer patch. The vertical bars are ± 2 standard errors. ■ = mean number of fish in richer patch during this experiment. **X** = fish numbers predicted by the IFD input matching rule. * = mean number of fish in richer patch during tests without cover.

patch, more fish occupied the richer patch than expected under feed ratios 1:1 and 1:2 (Figure 17b). Numbers of coho salmon in richer patches without instream cover were similar to results in absence of cover for feeding ratios 1:5 and 1:11. Coho salmon numbers did not increase with an almost two fold change (from 1:5 to 1:11) in patch profitability and remained below the numbers anticipated by the IFD input-matching rule (Figure 17b). Therefore, a mechanism that limits the maximum number of foragers occupying the same patch also developed when there is cover present.

A two-way ANOVA (Table 11) indicated that coho salmon numerical response in this series of experiments was affected by both treatments, patch profitability ratio and presence of instream wooden structures; also these factors interacted with each other, modifying their individual effect on the spatial distribution of fish.

Because the interaction between the main factors was significant it was appropriate to compare the means of one of the factors separately for each level of the other factor (Zar 1984). Therefore, I compared the mean number of fish in the richer patch under each of the four feeding ratios (1:1, 1:2, 1:5, 1:11) for each level of the instream wooden cover treatment (present vs absent) using Tukey's Studentized Range Test, which controls for the Type I experimentwise error rate (Zar 1984). The interaction effect changed depending on whether instream cover was associated with the poorer or the richer patch of a pool. If instream cover was in the richer patch it significantly lowered the number of fish occupying that patch (Figure 17a), but it interacted with patch profitability ratios in such a way that two significantly different subgroups were indicated by Tukey's test (Table 11). However, the effect of instream cover changed when combined with the poorer patch (Figure 17b). This is indicated by Tukey's test grouping of treatments in pairs that are not found significantly different (Table 11). Cover in the poorer patch made the richer patch more attractive to coho salmon than predicted by the IFD model for 1:1 and 1:2 ratios. At higher profitability ratios, however, the presence of cover in the poorer patch did not appear to affect the numerical distribution of fish. When feeding ratios

were 1:5 and 1:11, the distributions with cover present were not distinguishable from those where cover was not present.

Table 11. Two-way ANOVA for the effects of patch profitability ratios and instream cover.

SOURCE OF VARIATION	DF	SUM OF SQUARES	MEAN SQUARE	F	P>F
PROF. RATIO	4	316.431	79.108	33.48	0.0001
COVER	1	148.121	148.121	62.68	0.0001
PROF.RATIOxCOVER	4	31.420	7.855	3.32	0.0117
ERROR	190	449.000	2.363		

<u>Tukey's Studentized Range Tests</u>

Instream cover in richer patch: $\alpha = 0.05$, df= 95

  Group a= "control", 1:1 and 1:2   Group b= 1:5 and 1:11

Instream cover in poorer patch: $\alpha = 0.05$, df= 95

  Group a= "control" and 1:1   Group b= 1:1 and 1:2

  Group c= 1:2 and 1:5   Group d= 1:5 and 1:11

Exchanging the wooden structures for similar ones made out of clear Plexiglass confirmed that visual interference was the main effect of the opaque blinds on the fish in our experimental pools. Fish numerical response to the different patch profitability ratios was almost identical to that of the trials that lacked cover of any kind in trials with transparent structures (Figure 18 compared to Figure 16). Although Plexiglas structures did not seem to affect the ability of coho salmon to detect prey and assess differences between patches; fish often found them difficult to dodge, and in several occasions while moving across patches in the initial minutes of a trial they were delayed by these invisible obstacles. A two-way ANOVA including both feeding ratio and Plexiglas structures as

the main factors indicated that only food had a significant (df = 4, F= 86.08, p= 0.0001) effect on the distribution of coho salmon during this subset of trials, and that neither clear structures (df = 1, F= 1.33, p= 0.251) nor their interaction with the feeding treatments (df = 4, F= 0.91, p= 0.458) were significant.

The effect of overhead cover on coho salmon patch choice is qualitatively similar to that observed for opaque instream structures, but is quantitatively more extreme (Figure 19). It increased even further the proportion of fish feeding in the uncovered half of the pool. When the most profitable patch was the one beneath the cover the number of fish present in it was smaller than in the earlier no-cover experiments and far less than what the IFD model would have predicted (Figure 19a). The only exceptions were the no-feed control trials, during which the fish did not show clear preference for either patch. If the covered patch was the one receiving less food, coho salmon chose the open and richer patch in proportions very similar to those observed when instream cover was present in the poorer patch. A higher proportion of fish than expected under the IFD model input matching rule preferred the richer patch when patch profitability ratios were 1:1 and 1:2. The proportion of fish in the open and richer patch was similar to that previously observed at 1:5 and 1:11 profitability ratios, and was lower than that predicted under "ideal" and "free" conditions (Figure 19b). Again in this case a top limit to fish numbers simultaneously feeding in the same patch was observed. A two-way ANOVA, including overhead cover and patch profitability ratio as main factors, indicated that both factors as well as their interaction were highly significant (Table 12). The significant interaction among these treatments justified, once again, the use of Tukey's test for multiple comparisons among the means (Table 12).
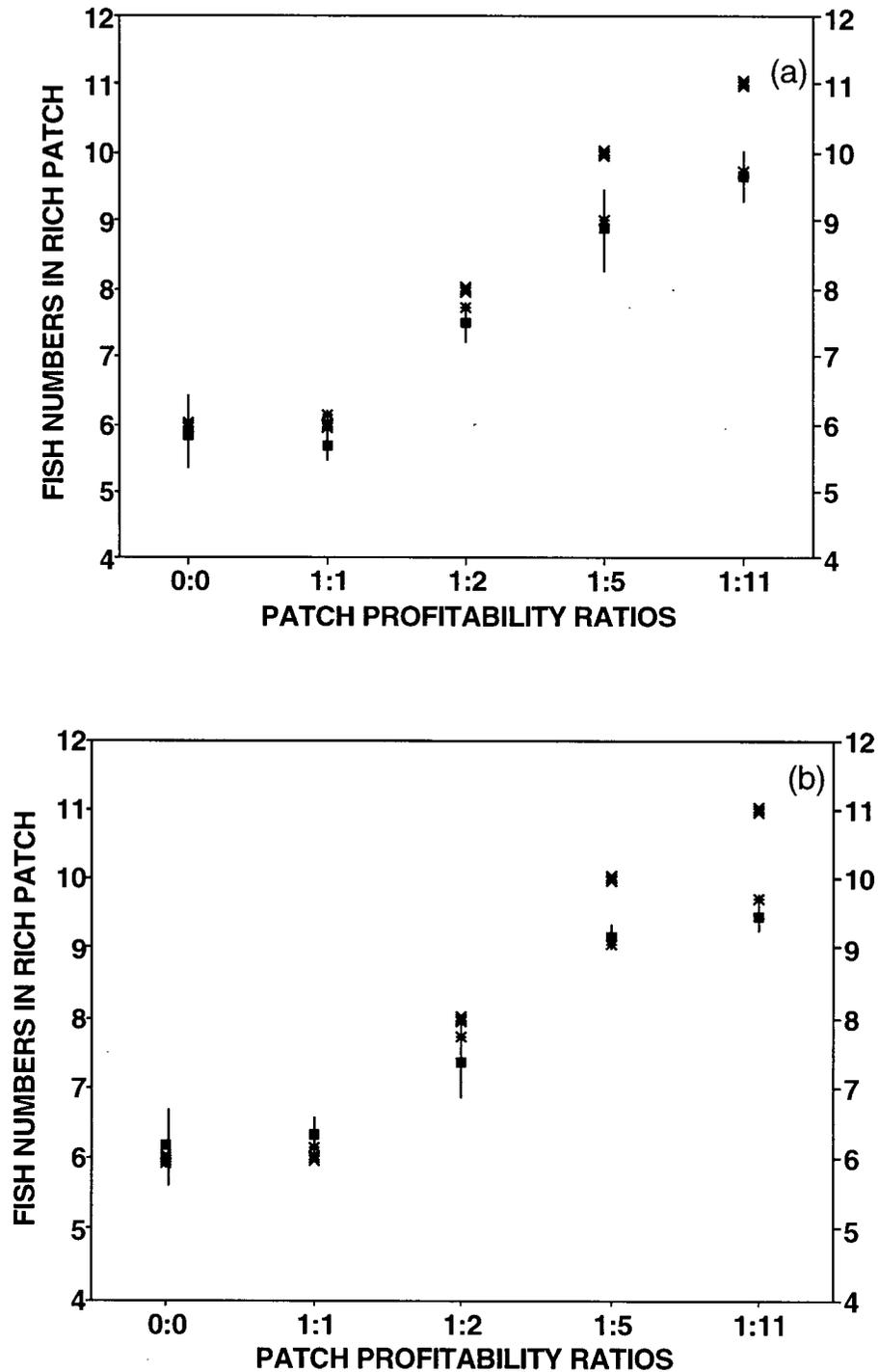
Figure 18. Mean number of fish observed in richer patch for each of the 5 profitability ratios in pools with Plexiglass structures, **(a)** structures present in richer patch, **(b)** structures present in poorer patch. The vertical bars are ±2 standard errors. ■ = mean number of fish in richer patch during this experiment. **X** = fish numbers predicted by the IFD input matching rule. * = mean number of fish in richer patch during tests without cover.
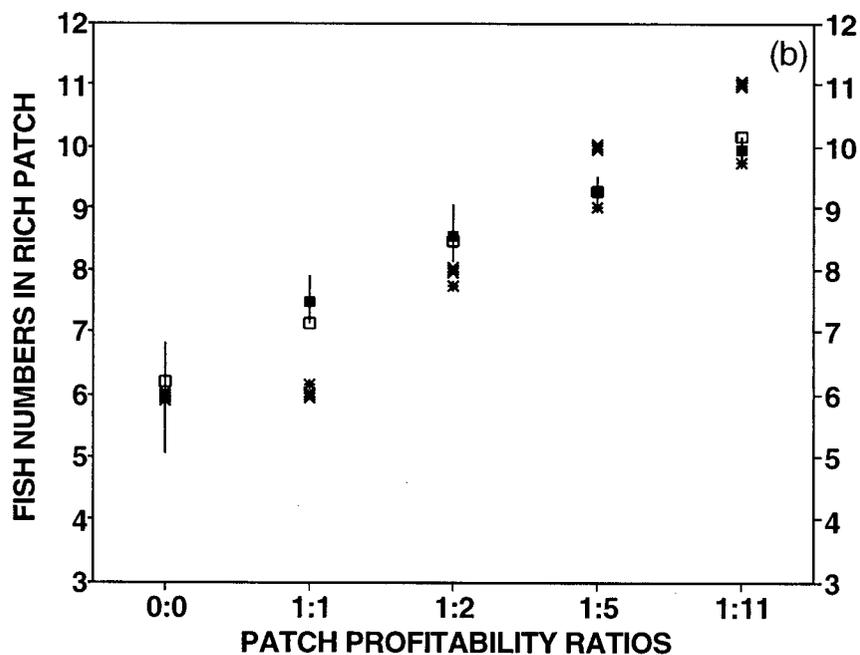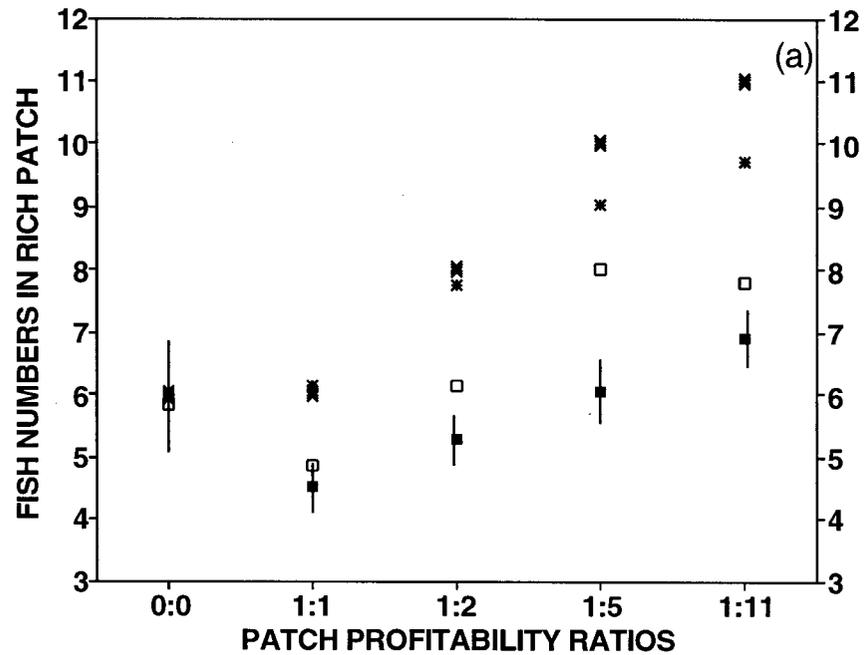
Figure 19. Mean number of fish observed in richer patch for each of the 5 profitability ratios in pools with overhead cover, (a) overhead cover present in richer patch, (b) overhead cover present in poorer patch. The vertical bars are ±2 standard errors. ■ = mean number of fish in richer patch during this experiment. **X** = fish numbers predicted by the IFD input matching rule. * = mean number of fish in richer patch during tests without cover. □ = mean number of fish in richer patch during tests with instream cover.
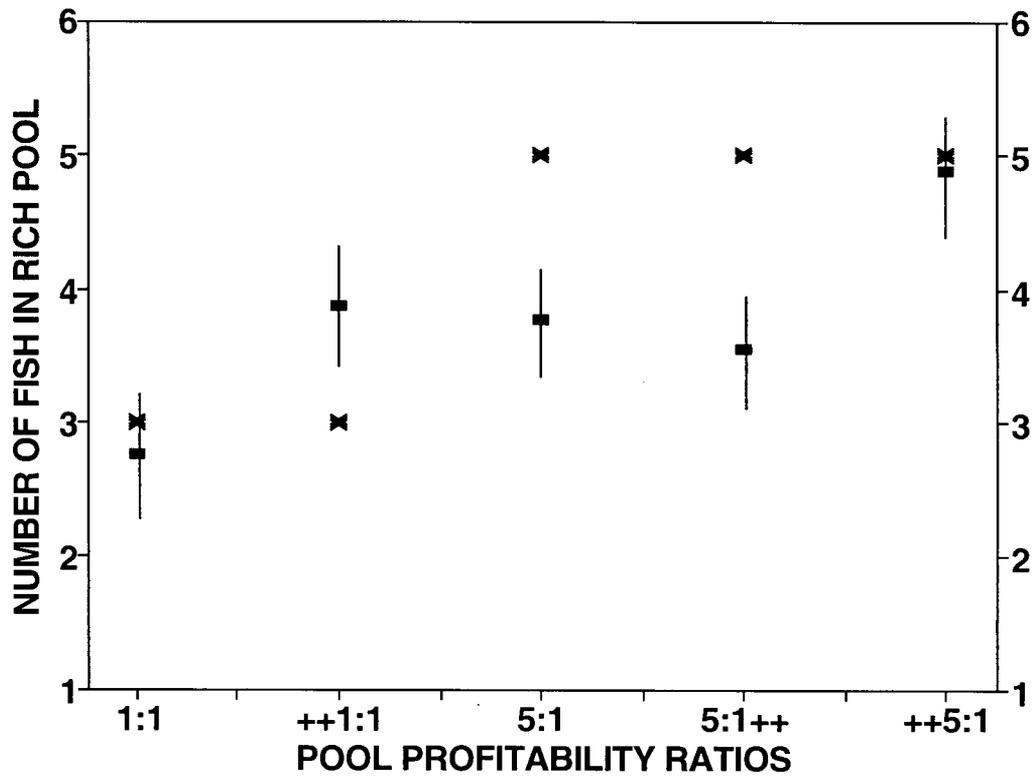
Figure 20. Distribution of coho salmon between pools in response to two different feeding ratios (1:1 and 1:5) and the presence of instream cover. ■ = mean number of fish in richer patch. **X** = fish numbers predicted by the IFD input matching rule. The vertical bars are ± 2 standard errors. ++ = indicates patch with cover.

Table 12. Two-way ANOVA for the effects of patch profitability ratios and overhead cover.

SOURCE OF VARIATION	DF	SUM OF SQUARES	MEAN SQUARE	F	P>F
PROF.RATIO	4	180.151	45.038	18.48	0.0001
COVER	1	308.554	308.554	126.60	0.0001
PROF.RATIOxCOVER	4	81.338	20.334	8.34	0.0001
ERROR	190	463.073	2.437		

Tukey's Studentized Range Tests

Overhead cover on richer patch: $\alpha = 0.05$, df= 95

   Group a= "control", 1:5 and 1:11   Group b= "control", 1:2 and 1:5

   Group c= 1:1 and 1:2

Overhead cover on poorer patch: $\alpha = 0.05$, df= 95

   Group a= 1:1 and 1:2   Group b= 1:2 and 1:5

   Group c= 1:5 and 1:11   Group d= "control"

4.4.3. Double pool experiments:

Our experiments with foraging patches in separate pools also showed that coho salmon responded to the profitability of the pools, but not always in direct proportion to the availability of food. Fish distribution between pools matched the distribution of food under the 1:1 profitability ratio. But numbers of competitors did not correspond to patch input rate when the ratio was increased to 1:5. In this case, as it happened within individual pools, the presence of cover in one of the two pools also altered coho salmon distribution. However, coho's response to patch profitability and cover differed when the habitat scale increased. In contrast to our single-pool tests, coho salmon preferred the pool with instream structures to the unobstructed one.

In double pool experiments without cover, pool foraging quality was the only factor considered. When the profitability ratio between pools was 1:1, young coho salmon distributed quite evenly between them (Figure 20). Out of a total of 6 individuals, the final distribution was not significantly different from that predicted by the "classical" IFD model (paired comparisons t-test between observed and expected number of fish, p= 0.512). Under a 1:5 profitability ratio , more coho salmon showed preference for the richer pool (x= 3.78) over the poorer one. However, the number observed was significantly lower than that predicted by the "classical" model (paired comparisons t-test, p= 0.002). The final distribution of fish did not indicate a correlation between fish size and patch quality (r = 0.02).

The presence of instream cover, in the double pool manipulations, induced further variation in the final distribution of fish. Between two pools of equal foraging quality (1:1 ratio), one with instream structures and the other one without them, significantly more coho salmon preferred the pool where cover was present (x= 3.89, paired comparisons t-test, p= 0.02) (Figure 20). If cover was added to the pool 5 times richer in food, the combined effect of higher profitability and instream cover increased the number of fish in that pool to numbers not significantly different from those predicted by the "classical" IFD model (x= 4.89 vs 5, paired comparisons t-test, p= 0.728). If cover was added to the poorer pool, the richer pool still ended up with more than half the total number of coho salmon (x= 3.56); but a number significantly smaller than predicted by the "classical" model (paired comparisons t-test, p= 0.001). In these experiments bigger individuals were not present exclusively in the richer patch with cover.

Table 13 summarizes the results of four specific contrasts between treatments performed as part of a one-way ANOVA (considering the various treatments as five different levels of a single factor). Their estimated F values and their associated probabilities indicated that fish distributions were significantly different in two cases: a) between the 1:1 (no cover) pool profitability ratio and the 1:1 ratio with cover; and, b)

between the 5:1 feeding ratio with cover in the poorer pool and the 5:1 ratio with cover in the richer pool.

Table 13. Specific contrasts of a one-way ANOVA for the effects of patch profitability ratios and instream cover in double pool experiment. Both treatments combined in 5 different ways that were considered as levels of a single factor.

CONTRAST	DF	SS	meanSS	F	P>F
1:1 vs 1:1+cover	1	5.5556	5.5556	6.71	0.013
5:1 vs 1:1+cover	1	0.0556	0.0556	0.07	0.797
5:1 vs 5:1+cover[*]	1	0.2222	0.2222	0.27	0.607
5:1+cover vs cover+5:1[**]	1	8.0000	8.0000	9.66	0.004

[*] 5:1+cover = instream cover is in poorer patch.
[**] cover+5:1 = instream cover is in richer patch.

4.5. Discussion

Juvenile coho salmon did not distribute between adjacent patches in a pool or between separate pools in a channel in proportion to patch input rate, as predicted by the IFD input-matching rule. Moreover, their choice of foraging patch was altered by the presence of cover, but its effect changed dramatically with habitat scale. Juvenile coho salmon preferred to forage in the open patch of a pool, away from structures, in larger proportions than justified by the availability of food. When offered the opportunity to move between separate pools, however, most coho salmon favour the one with cover. Therefore, my results did not support our first hypothesis, that juvenile coho salmon distribute between both adjacent and distant patches matching their food input-rate as predicted by the "classical" IFD model; but confirmed my second hypothesis, that cover affects coho's response to food availability in different habitat patches. Yet, I did not

anticipate the changing behaviour towards cover depending on whether foraging patches were adjacent to each other within the same pool or in separate pools.

The rejection of my first working hypothesis is consistent with the results of previous IFD empirical studies. Departures from Fretwell and Lucas' (1970) IFD model have been observed in most laboratory and field studies of habitat choice (for review of nineteen studies see Parker and Sutherland 1986; additional ones are Talbot and Kramer 1986, Gillis and Kramer 1987, Recer et al. 1987, Inman 1990, Grand and Grant 1994). The few studies that corroborated the IFD input matching rule did so for only some treatments (as was the case for my 1:1 and 1:2 feeding ratios in pools without cover). They had in common the fact that they were conducted in continuous-input systems using very simple and predictable conditions (Parker 1970 and 1974, Davies and Halliday 1979, Milinski 1979 and 1984, Harper 1982, Godin and Keenleyside 1984). In contrast, other studies under continuous-input conditions showed dispersion patterns that did not conform to the input matching rule using unpredictable resources (Recer et al. 1987, Grand and Grant 1994), numerous patches (Talbot and Kramer 1986), numerous competitors (Gillis and Kramer 1987) or different water velocities in each patch (Tyler and Gilliam 1995). Instead, they displayed the same type of undermatching that I observed.

Regelmann (1984) and Houston and McNamara (1987) suggest that deviation from input matching is the direct effect of competitors sampling and switching between patches. A simple random distribution, as I mentioned earlier, could also produce a lower ratio of competitors to resources in richer patches (Kacelnik et al. 1992). But the fact that fish numbers in the richer patch increased when its profitability was augmented suggests that there is more than a simple random distribution. In addition, increased habitat complexity or distance between patches had an effect on coho salmon patch choice. If coho salmon ended up in a foraging site entirely by chance, none of the distribution patterns I observed would have occurred.

I also compared my results to some of the predictions of the other three dispersion models. Initially, the IDD model (Fretwell and Lucas 1970) seemed a good alternative to the IFD model in explaining my results, due to coho's aggressive behaviour (Hartmann 1965). However, its applicability is also limited. The IDD model anticipates the undermatching that I observed, and explains it as the effect of "despotic" behaviour by dominant individuals that monopolize resources. If despotism was the cause of the numerical departures from an IFD in my experiments, visual isolation should have compensated this effect, at least in part (Table 9, model 2). Instead, instream structures caused coho salmon to forage in the open patch in numbers that were disproportionally high for the amount of food available there. Paradoxically, cover increased fish densities in the open site, thus it did not reduce but augmented the probability of aggressive interactions. Furthermore, the IDD model cannot help explain the similar effect that overhead cover had on fish distributions.

The "ceiling", or maximum number of fish occupying the same patch simultaneously, that I observed could be explained by non-despotic interference. Gillis and Kramer (1987) reported departures from an IFD only at high fish densities, when agonistic behaviour was at its lowest, ruling out despotism as the cause. They considered the "ceiling" to be an effect of population density, called it "non-despotic interference" and suggested it as an explanation to Godin and Keenleyside's (1984) experimental results. This interference would cause the largest deviations from an IFD at the highest patch profitability ratios.

The IDD model implies a clear violation of the "free" assumption. This causes unequal individual intake rates with dominant competitors occupying the best patch and receiving higher pay-offs. Although I have evidence of variation in individual intake rates, I was not successful at recording them. It was impossible to determine individual intake rates from the video recordings of my trials. Fish scrambled for food arriving into a patch. Therefore, whenever a piece of shrimp fell in the pool, dashing fish disrupted the

surface of the water for several video frames, becoming invisible in the meantime. Because I could not distinguish individual fish and I was unable to follow them continuously, it was not possible to determine individual food intake. Nonetheless my observations, combined with some information from these video taped trials, do not support the hypothesis of resource defense. In our experiments despotism, in the form of the aggressive display and nipping that Hartman (1965) described for this species, was mainly observed during the no-food control trials (before prey was made available to coho salmon). During these control periods few fish seemed to defend territories and most of them swam around individually (sometimes in groups) in many cases over the entire pool. Aggression disappeared almost entirely as soon as feeding began. Coho salmon did not appear to defend the resource from competitors. Any fish that dashed toward a piece of shrimp was seldom intercepted or chased away. Individual success seemed to depend more on the early detection and fast seizure of prey than on its active defence. Aggressive behaviour to defend a feeding station has been reported for coho salmon in stream reaches with fast flowing waters that cause an almost unidirectional prey drift. But, in pools with very slow current (where food items appear from any direction), fish show a tendency to form loose and slowly cruising groups and to scramble for food (Mundie 1969, Fausch and White 1986). The slow current in my units could explain the lack of territoriality. Furthermore, aggressive defence of a drifting piece of food by an individual against a large number of competitors exploiting the same patch is unlikely to be economical. The briefest time that an aggressive fish invests in chasing others can be easily used by any of the other competitors to capture the prey. This situation is likely to be intensified in a continuous-input system like mine, where prey arrive sequentially and are consumed almost as soon as they enter the patch (Parker and Sutherland 1986). Spatial predictability of resources has been reported to encourage despotic behaviour in fish when resources can be defended (Grand and Grant 1994) but not if protection is uneconomical (Milinski 1979 and 1984, Godin and Keenleyside 1984, Abrahams 1989,

Milinski and Parker 1991). This second alternative is more likely in my experimental pools.

The IFD equal intake rate prediction has been violated in most resource partitioning studies (Parker 1970 and 1974, Davies and Halliday 1979, Milinski 1979 and 1984, Whitham 1980, Harper 1982, Godin and Keenleyside 1984, Courtney and Parker 1985, Grand and Grant 1994), and authors attribute these deviations either to despotism or to different competitive abilities among individuals. The evidence I have about unequal individual intake rates is indirect. It is represented by the large variation in size among individuals that I observed by the end of my experiments in individual pools (which started in May and ended in July, and used the same fish) in spite of the initial relative size homogeneity among the coho fry I chose. This disparity in size among individuals, if not caused by resource monopolization, implies either different metabolic efficiency at assimilating food or unequal competitive skills among experimental subjects. The supposition that competitors may differ, apart from territorial or despotic behaviour, in their ability to exploit resources is reasonable. The mechanisms that give rise to those dissimilarities may be numerous, and they may interact in many ways to produce the behavioural responses that I observed. Initial behavioural and/or metabolic differences may initiate size variance among members of a cohort. For example, fish that become slightly larger or longer than the rest have a competitive edge over their counterparts in swimming speed (Webb 1978) which improves their chances at capturing prey. Thus, a small initial advantage may further increase fish differences in size and, in this case, in access to resources.

Having discarded both the IFD and the IDD models, I was left with the PL and the UC models to account for my results. Abrahams' (1986) PL model also anticipates the overuse of the poorer patch and the underuse of the richer patch that I observed. But his model considers that this distribution results from the random choice animals make when they cannot perceive differences between patches, because they are not "ideal" samplers as

the IFD model assumes. His model may explain the difference in size that developed among my fish, because it predicts unequal individual intake rates. As a consequence of their biased distribution, fish in the better patch receive a higher reward than those in the poorer one. This pay-off difference increases concurrently with the deviation from an IFD. The situation continues as long as the difference in individual pay-offs do not exceed the perception limit of individual competitors, otherwise those who detect a difference would switch patches and reduce the deviation from the IFD (Abrahams 1986). The PL model does not formally anticipate which competitors will exploit the richer patch.

The relatively even distribution of coho salmon between patches of similar quality (no-food and 1:1 ratio) that I observed in the single-pool-no-cover experiments, does not constitute an example of fish accurately assessing patch profitability; but it can be explained by competitors choosing patches at random. If I apply the perception limit model to explain the 1:2 profitability ratio results, I can speculate that this difference in food input may have been too small to be detected by most of my fish (roughly 2/3 of them) which had to choose a feeding patch at random. Only a reduced number of them may have perceived a difference, and distributed accordingly. The presence of fewer individuals than expected in the richer patch, although it is not a statistically significant deviation, weakly follows the distribution that Abrahams' PL model predicted.

At bigger patch differences (1:5 and 1:11), however, the PL model forecasts a distribution that deviates less and less from the IFD numerical prediction as the difference between patches increases and, consequently, the proportion of competitors able to detect it grows. The larger the proportion of foragers that can track the difference, the smaller the number that will have to choose a foraging patch randomly. Nevertheless, I lowered the total amount of food as feeding ratios became more extreme. Thus, two conflicting forces may have influenced the distribution of coho salmon. One of them created by the larger differences in profitability that reduced the number of fish having to guess which one was the better patch. The other force was represented by the reduced amount of

112

total food that lowered the average intake rate per individual. This could have caused the difference in patch profitability to fall below the perception limit of a larger proportion of fish and, hence, increase the ratio of them having to guess which patch was better (Abrahams 1986, Gray and Kennedy 1994). The fact that fish numbers in the more profitable patch increased when patch differences augmented without ever matching food distribution, could have been produced, in part, by these opposing pressures.

The increased deviation from the IFD numerical prediction that I observed in more complex habitat or with increased distance between patches is predicted by the PL model (Abrahams 1986) (Table 9, model 3). This model suggests that deviations from an IFD grow as complexity increases, because animals must make a larger number of decisions with less accurate information about a more complex habitat. My results indicated that coho salmon did not avoid cover per se. This is shown by their even distribution in the pool during no-food control periods. However, as soon as prey were detected coho salmon consistently over-estimated the foraging value of the clear patch and underestimated that of the patch with either instream wooden structures or overhead cover. Since coho salmon are visual predators, it is likely that the reduced field of vision in the complex patch, or the reduced light under the overhead cover, hindered their ability to detect prey and assess patch quality. When instream cover was present in the richer patch, coho salmon consistently underestimated its value, even when the feeding ratio was 1:1. As patch differences grew bigger more fish occupied the richer patch, but never in the proportions anticipated by the "classical" IFD model. Instream cover in the poorer patch induced fish to regard the richer open patch as being far richer than it actually was. This became particularly evident when dissimilarities in food availability between patches were reduced or did not exist (i.e. 1:1 and 1:2 profitability ratios) and more coho salmon than anticipated under an IFD, or observed earlier in the no-cover experiments, were in the clear patch. A "ceiling" to the maximum number of fish in the richer patch was observed again. Coho salmon numbers did not increase at all with an almost two fold

change (from a 1:5 ratio to a 1:11 ratio) in patch profitability. It is possible, as I suggested for the experiments without cover, that the limit to how many fish could forage in a patch was caused by the combination of perceptual constraints with another factor, such as non-despotic interference.

The PL model did not predict the extreme deviations from input matching produced by overhanging cover. This type of cover should not have impaired coho salmon vision more than submerged structures did. The model did not anticipate either the fish distribution that I observed between separate pools with cover in one of them. Under a 1:1 profitability ratio the pool with instream structures attracted more fish than expected. And when instream cover was in the richer patch (1:5 ratio), fish proportions in it increased to the point of matching food availability. It is clear that coho salmon reached this distribution in response to the combined effect of both higher food input rates and cover availability.

The UC model (Parker and Sutherland 1986) anticipates, if individual competitive weights remain constant across patches, a distribution that superficially imitates an IFD (Table 9, model 4). Several other different ideal free equilibrium distributions are also possible, but the one resembling an IFD has the highest probability to occur (Sutherland and Parker 1985, Houston and McNamara 1988). The model predicts in this case some degree of undermatching too, originated by worse competitors choosing sites more slowly or at random (Regelmann 1984, Milinski 1984). This type of distribution matches my experimental results in single-pool experiments in the absence of cover. But it does not correspond to the results of any other of my experiments.

If the foraging efficiency of individuals changes with patch, however, the UC predicts a segregation of phenotypes by patch type (a "truncated" distribution sensu Parker and Sutherland 1986) (Table 9, model 5). Each individual will occupy the kind of patch in which it can compete better. This split distribution of phenotypes is not obvious in my experimental results. I do not have any evidence from my single-pool

114

manipulations, but I recorded the distribution of marked individuals in my double-pool tests. No relationship between fish size and patch profitability was observed. For example, larger fish were not exclusively found in the better patch. Coho salmon of different lengths were equally represented in both patches. I chose coho salmon size as a surrogate measure for dominance and foraging success, given that larger coho salmon are always dominant over smaller ones. Small individuals tend to become proportionately smaller with time because their limited access to resources makes them grow more slowly than bigger coho salmon (Chapman 1962, Sandercock 1991).

It is important to bear in mind that the explanations for dispersion that these models present do not need to be mutually exclusive. A disproportionally high exploitation of the poorer patch is predicted by three of the models, and the assumptions about animal behaviour on which they are based do not need to rule each other out. Competitors may be unequal in their abilities to exploit resources and also have limitations to detect them. Despotism may also exist and it may manifest only under certain circumstances. For example in his research on birds, Inman (1990) observed dominant starlings (*Sturnus vulgaris*) monopolizing the resources of a patch only when they competed with four or less subordinate individuals.

In my experiments, coho salmon responded to patch profitability but not exactly as predicted by the IFD model. There was a limit to the maximum number of individuals that could simultaneously occupy a foraging site, possibly caused by non-despotic interference. Fish numerical response to increased patch profitability and the large variation in body size observed by the end of the single-pool experiments suggested that competitors were unequal, thus violating one of the main assumptions of the "classical" IFD model.

Habitat complexity or greater distance between patches increased deviations from the IFD prediction, suggesting that a finite perception limit was affecting fish patch choice. Neither instream nor overhead cover were avoided when there was no food, but easier

115

food detection in the clear patch always attracted more fish, thus causing the described overmatching. From their perspective coho salmon may have been acting as "ideal" foragers, but the complexity of their environment and their individual differences prevented them from attaining an ideal and free distribution.

It is also possible that juvenile coho salmon prefer to stay away from cover when feeding, because cover may either harbour predators or delay detection of an approaching predator. Nonetheless, if predators are present and display certain type of behaviour coho salmon swiftly hide away under submerged or overhead cover (Bugert and Bjorn 1991, Uli Reinhardt, pers. comm.). I observed this on the few occasions that external disturbance interrupted my experiments (i.e. a dog drinking from the pool or a cap falling in the water) and fish either remained motionless close to the substrate or moved rapidly into the covered patch. Because risk of predation was extremely low in my experimental channels coho salmon may have fed in the open patch in higher proportions than they would in a natural stream.

The greater avoidance for overhead cover that I observed corresponds to other research. Dolloff and Reeves (1990), Bugert et al. (1991) and Fausch (1993) reported that coho salmon were, in general, less responsive to overhanging cover and wandered to forage further away from it than other juvenile salmonids. However, this seems to change as the fish grow older (Hoar 1958). Coho's association with cover has also been reported to change with seasons, since both instream and overhead cover are important to create suitable rearing conditions in winter (Tschaplinski and Hartman 1983, Dolloff 1987, McMahon and Hartman 1989, Nickelson et al. 1992a and 1992b).

Environment grain affected coho salmon patch choice. The cost of sampling increases by increasing the distance between patches. Fish are predicted to switch patches less often and, therefore, to gather less precise information on patch quality, which leads to undermatching (Regelmann 1984, Bernstein et al. 1991a, Milinski 1994). The final distribution may represent the equilibrium point between this tendency towards

increased undermatching and the lower amount of undermatching caused by less switching per se (Milinski 1994). In my experiments with separate pools, coho salmon responded positively - although not proportionately - to pool profitability. They preferred richer pools over poorer ones, pools with cover over those that were clear of structures. But, whenever it was possible, coho salmon chose pools that combined the largest proportion of food with the presence of instream cover.

My seemingly contradictory results (coho salmon favouring pools with woody instream structures, yet avoiding the patch with cover within a pool) explain, to some extent, the inconsistency I detected among studies of coho salmon behaviour and habitat use. The month during which the research was done and environment grain that was used may largely be responsible for the contradictory observations of past studies. Early summer coho salmon fry and late summer coho parr respond to cover in different ways (see section 5.3). Most studies that find coho salmon avoiding or indifferent to cover were conducted between early May and early July (Bugert et al. 1991, Fausch 1993, Spalding et al. 1995) and all those reporting strong positive correlations between coho salmon abundance and cover availability were done between July and September (Dolloff 1986, Dolloff and Reeves 1990, Shirvell 1990, Peters et al. 1993).

Coho salmon preference for pools with cover and, within those pools, for cover free patches indicate the need for a combination of accessible refuge and open foraging sites, where prey and perhaps also predators are easy to detect. This can be a behavioural adaptation to a relatively brief freshwater rearing period before smolting. In the southern part of their distribution, including southern British Columbia, most coho salmon migrate after a single summer of rearing in freshwater. Both their winter survival and smolting rate are positively correlated with fish size (Sandercock 1991). Thus, any behaviour that maximizes food intake and growth during their first summer of life is very likely to evolve in these populations. Feeding in the open may increase predation risk. However, coho salmon have been reported to be less sensitive to risk of predation and, therefore, to make

longer feeding excursions when fish densities are increased than when they are tested in isolation (Dill and Fraser 1984). The very large numbers of coho salmon present in productive coastal streams may indeed decrease the individual risk of predation in patches without cover.

Our results indicate that the predictive abilities of IFD models could be improved by combining elements that have been considered in separate models until now. Specifically, forager's perception limits (Abrahams 1986) and unequal competitive abilities among individuals (Parker and Sutherland 1986) should both be incorporated in a single model of dispersion. Furthermore, the observed change in the response of juvenile coho salmon to the distribution of resources with the cost of sampling, which depended on the grain of the environment, suggests that any realistic extension of IFD models should incorporate the cost for competitors of acquiring information.

CHAPTER 5

HABITAT CHOICE BY JUVENILE COHO SALMON IN RESPONSE TO THE MANIPULATION OF COVER AND FOOD AMONG STREAM POOLS

5.1. Introduction

In the previous chapter I investigated the mechanisms controlling summer habitat choice by juvenile coho salmon in relation to the distribution of food abundance and cover using artificial channels. In those experiments I tested the effect that different levels of patch profitability had on the number of fish that simultaneously occupied a patch, and the effect that the presence of cover had on patch choice at habitat scales that involved different levels of sampling and information processing by the fish. Juvenile coho salmon responded to the distribution of both food and cover among habitat patches within a single pool, aggregating when foraging was most profitable but also strongly preferring to forage away from cover. When patches were represented by separate pools, however, most coho salmon preferred the pool that was both richer in food and contained cover. Although I tried both instream and overhead cover, I did not manipulate cover abundance to test coho's response to different densities of woody debris.

In this chapter I investigate the influence that cover and food abundance, may have on the distribution of juvenile coho salmon, but this time using natural stream reaches. These experiments were planned bearing in mind my previous results (Chapter 4) and the conflicting information found in the literature. Because the age of coho fry differed among many of those studies, I repeated some experiments at different times of the summer to measure changes in coho's response to cover with age. To address the effects of cover and food, I manipulated the amount of both in the natural stream reaches.

I conducted my experiments in two different natural systems: a section of Spring Creek, that does not have a natural population of coho salmon; and, three different stream sections in Coghlan Creek, a coho salmon bearing stream.

My working hypotheses were:

a)   Juvenile coho salmon select patches with medium to low amounts of woody debris if food is abundant. This combination of factors provides some predation protection and minimum interference in prey detection, and it was the most desirable combination of food and cover in artificial channels.

b)   The response of coho salmon to cover and food changes with age. Most spring and early summer work on coho salmon has yielded no correlation between cover and coho salmon abundance (Bugert et al. 1991, Bugert and Bjorn 1991, Fausch 1993, Spalding et al.. 1995), whereas late summer studies concluded that high coho salmon densities were always associated with the presence of woody debris (Bisson et al. 1982, Dolloff 1986, Dolloff and Reeves 1990, Shirvell 1990, Peters et al. 1993). An ontogenetic change in response to cover seems a likely explanation for the conflicting results in the literature.

c)   Density of coho salmon reflects an interaction between cover and food abundance. In artificial channels, I observed that coho salmon numbers increased with the foraging quality of a patch, but that the response to food was strongly mediated by the presence of cover.

d)   The response of coho salmon is affected by the type of woody debris, not only by its abundance. Large woody debris constitutes an effective velocity refuge in fast flowing waters (Bilby and Ward 1989); but results from my summer survey in the Salmon River indicate that coho salmon prefer fine woody debris, which has been suggested to provide protection from predators and to increase visual isolation among competitors (Dolloff 1986, Mesick 1988, Bugert et al. 1991, Fausch 1993).

Most other studies have looked at the effect of a single type of woody debris and did not test coho's choice between the two main types of woody debris used in salmon habitat restoration programs.

5.2. Methods

My experiments were conducted in four short reaches of two different streams in Southwestern British Columbia. One reach was a long pool between small waterfalls in the lower section of Spring Creek, an inlet of Cultus Lake. The other three were long shallow glides in the upper reaches of Coghlan Creek, the main tributary of the Salmon River, Langley. Both creeks are small, with a consistent flow in summer. None of the reaches had instream debris or overhanging vegetation prior to my manipulation of cover.

5.2.1. Spring Creek

Spring Creek originates at the base of Isar Mountain, on the International Ridge of the Skagit Mountains. From its origin it runs through an artificial pond, a golf course and a small residential development before reaching the southern shore of Cultus Lake, near Lindell Beach. With the exception of chum salmon (Oncorhynchus keta) and the odd cutthroat trout (O. clarki), no other fish are found in this creek. Chum spawn in early winter, and their fry leave the system shortly after emergence in April or May. The creek had a coho salmon run which disappeared several years ago. The Department of Fisheries and Oceans (DFO) presently stocks hatchery coho salmon fry in the lower reach of the creek (downstream from the golf course) each spring. No adult coho salmon have yet returned from these stocked fry.

The upper half of Spring Creek, from its origin to the end of the golf course, does not offer good coho salmon rearing habitat. In contrast the lower half of the stream offers good summer rearing habitat. It is well shaded by the surrounding vegetation and

has abundant overhanging cover and has a substrate of gravel and sand. This stream section has a stairway like aspect due to a series of low wooden dams placed 2 to 50 m apart. The dams create a series of waterfalls (20 to 40 cm high) that are separated by long pool/glides. I used the first pool in the lower section of Spring Creek to build my experimental arena. The location of this unit allowed me to conduct my work upstream from where DFO had already released coho salmon fry. The pool was 20 m long and 4.5 m wide. Its upper end was delimited by a small waterfall (29 cm) created by a wooden dam. A 40 cm high waterfall and a fish-trap at the downstream end of the pool prevented coho salmon from moving upstream into the experimental unit.

Water temperature in this creek varies considerably during the summer. The temperature at the head spring is constantly 9°C but increases downstream. Daily fluctuations in temperature also grow with distance from the source (particularly during warm days). Average daily water temperatures entering my experimental reach fluctuated between 12.3°C (morning) and 15.6°C (evening) in May, between 13.1°C (morning) and 19.5°C (evening) in June, between 14°C (morning) and 23.2°C in July, and between 14.2°C (morning) and 22.9°C (evening) in August. During a few unusually hot (35°C) days in August, water arriving at the experimental reach was 26°C. Heating, within the reach, was ameliorated by cool groundwater input along its length which created complex temperature conditions. During the hottest days of the summer I observed some mortality (2 to 7 coho salmon were found dead in the riffles at the end of three of my experimental trials). Some fish could have been eaten by birds or raccoons, therefore, I cannot rule out higher losses.

I built three riffles within the experimental unit with large gravel and cobble which divided the unit into 4 smaller pools. The whole unit was further divided longitudinally with a 2mm mesh barrier to create 2 parallel channels with 4 pools and 3 riffles each (Figure 21). All possible crevasses were sealed to prevent fish from moving between the 2 adjacent channels. The resulting pools were all very similar, with a mean length of 4.13

m and a mean width of 2.0 m (mean area = 8.26 m^2). Their maximum depth was 0.5 m and their mean depth was 0.32 m.

I placed a net across the upstream waterfall to prevent any of the fish used in the experiments from leaving the unit. However, this net clogged with leaves in two occasions and overflowed allowing some fish to escape. The downstream waterfall entered a fish-trap box. All fish that fell in the trap were retained there until the end of an experimental trail.

In this unit, I conducted four different types of cover and food manipulations to test my various hypotheses about coho salmon stream habitat choice. Cover was represented by bundles of tree branches simulating the type of fine woody debris or rootwads that are common in many streams. Each bundle was made of 8 red alder (<u>Alnus rubra</u>) twigs (0.5 to 1.5 cm thick and 1.2 to 1.5 m long) combined with a branch of douglas fir (<u>Pseudotsuga menziesii</u>), and one of red cedar (<u>Thuja plicata</u>), 1 to 1.2 m long with foliage intact. All branches were tied together and anchored with rocks so they would not drift away. The sunken twigs provided salmon with instream cover, and the fan shaped coniferous branches that spread on the water surface served as overhead cover.

I used freeze dried shrimp (<u>Euphasia pacifica</u>) as food. It was delivered into the pools by belt conveyor type automatic feeders. In experiments involving different amounts of food delivered to consecutive pools, I placed small mesh screens on the riffles to prevent shrimp from drifting into the downstream pools. This mechanism was not entirely effective as the screens sometimes clogged with leaves and other debris, and they were displaced by the water on several occasions.

I used age-0 coho salmon from the Chilliwack River Hatchery, British Columbia, in all these experiments, the same as the stock used by DFO to re-establish a run in Spring Creek. At the beginning of each trial, equal numbers of fish were released into the pools and allowed 72 hours to explore and redistribute themselves before I began to retrieve them. I placed nets on each riffle and at both ends of the unit to confine fish to the pool
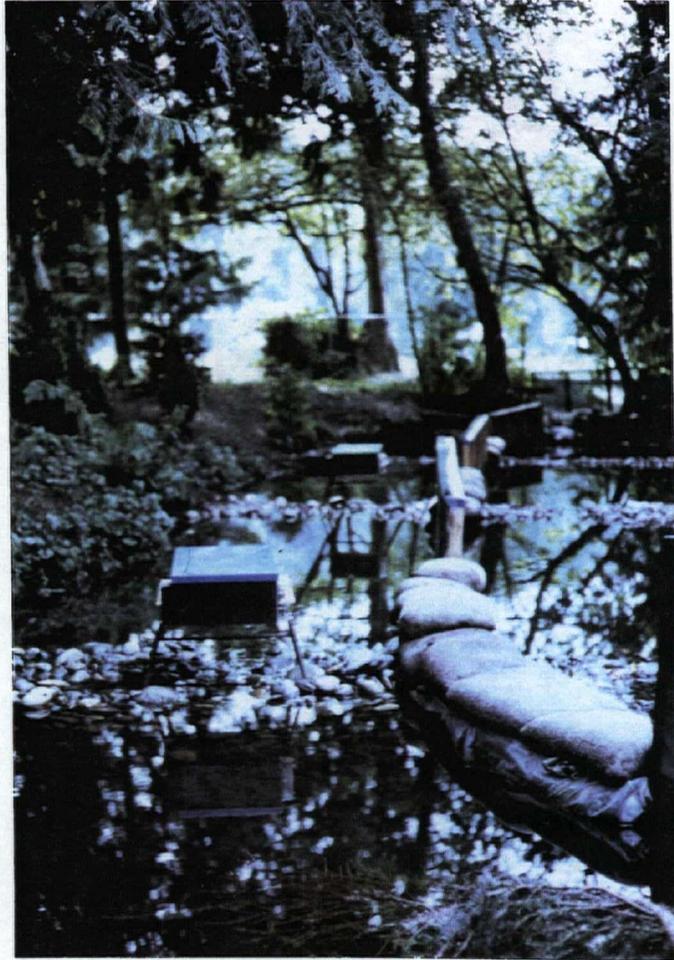
Figure 21. Partial view of Spring Creek divided longitudinally into 2 channels. Feeders were placed over riffles, with openings above head of pools. A debris bundle can be seen in the lower right corner.

they had chosen most recently. I removed the fish using a pole seine until no coho salmon were caught in 2 consecutive passes. Thereafter, any coho salmon remaining in the pools were captured by electrofishing.

In experiment 1, I examined whether juvenile coho salmon preferred pools with sparse cover when food is abundant (food vs. no-food channels), and whether the fish's response to cover changed over the summer (May vs. August trials). It addressed my first two hypotheses. Pools in each channel randomly received one of three different amounts of cover: none, sparse and fine cover (1 bundle of twigs) or abundant and fine cover (3 bundles). The sparse cover treatment introduced a low density of woody debris that could offer predation refuge and visual isolation from competitors but, at the same time, left a large proportion of the pool unobstructed. In contrast, fine cover occupied almost the entire pool, leaving almost no open feeding areas available to the fish. Pools receiving food were supplemented, using feeders, the same amount. Each pool in the supplemented channel received 7.5 g of food per day. The supplemental daily ration in the pools receiving food was approximately 15% of the biomass of fish released per pool. I obtained 10 replicates for each food treatment. The experimental factor "cover" was nested within the factor "food".

The effect of food addition was expected to be significant because invertebrate production in the creek was very low, making it an ideal system to study the effect of hunger on coho's response to cover. During the summer I took four midwater drift samples (June 21, July 12, July 26 and August 11) inmediately upstream from my site. Each drift net (200 μm mesh) was 1 m long and its mouth opening was 3 cm by 15 cm. The nets were left in the stream for 24 hours. No aquatic invertebrates were captured and only a few terrestrial insects (mean = 2.25 insects per sample, from orders Coleoptera, Diptera, and Hemiptera). I took four benthic samples (2 on July 12 and 2 on July 26), in the pool inmediately upstream from my experimental channels, using a 929 cm^2 Surber sampler with a 200 μm mesh net. These samples contained only few caddisfly

(Trichoptera) larvae (mean = 1.62 larvae per sample) and a total of 2 worms (Annelida). The caddisfly larvae were too large for coho salmon to feed on. Most of the invertebrates that coho salmon could eat were insects that fell in the creek from the surrounding vegetation.

During my early summer trials (May 24 to June 27), I released 50 coho salmon (mean length = 4.3 cm ± 0.06 SE, and mean weight = 1.0 g ± 0.09 SE) in each experimental pool (a total of 200 fish in each one of the adjacent experimental channels). The number of fry released in each pool was sufficient to create a very high initial density (6 fish/m^2), similar to early summer densities reported for some highly productive coho salmon streams in this part of the province (from B.C. Ministry of Environment data set used by Ptolomy, 1993). Under these conditions, I expected a large fraction of coho salmon fry to move downstream and be captured in the fish-trap (Chapman, 1962). For the late summer experiments (August 18 to September 9) I reduced the number of coho salmon released into the channels to 25. Because the fry were larger (mean length= 5.7 cm ± 0.09 SE, and mean weight= 2.06 g ± 0.11 SE), this number gave a similar biomass per pool to the earlier experiments (about 6.15 g/m^2).

Experiment 2 (conducted between July 22 and August 11) addressed my hypotheses about coho's density reflecting the interaction between cover and food abundance. In this case, however, the experimental design was crossed. Both treatments had 2 levels: food vs. no-food, and abundant fine cover vs. no-cover. Each one of the four possible combinations (food and abundant cover, food and no-cover, no-food and abundant cover, and no-food and no-cover) was tested in the same channel and was randomly assigned to 1 of the channel's 4 pools. In this experiment, 25 coho salmon were released in each pool at the beginning of every trial and 11 replicates were obtained.

I conducted a third type of experiment which was not intended to specifically address any of the hypotheses listed in the introduction to this chapter. Instead, I wanted to determine whether pool selection by coho salmon in a stream channel without cover

was dependent upon food abundance. I created three different profitability levels among the pools of a channel by delivering different amounts of food . Cover was not considered in this test. The first pool in each experimental channel did not receive any type of treatment and for practical purposes was considered to function as an upstream fish-trap. Food was randomly assigned to any of the other three pools in each channel, which received either no food at all or a daily ration of either 7.5 g or 15 g of shrimp. Experiment 3 was replicated 10 times, each with 25 coho salmon per pool. Six replicates were conducted between July 15 and July 22 and the other four between September 9 and September 15.

Experiment 4 was a "control" test to measure pool effects alone. No treatments were applied to any of the pools, and coho salmon distribution among them was recorded. Ten replicates were also obtained for this test. In the first six, conducted between July 1 and July 11, I released 50 coho salmon per pool. In the last four, conducted between August 12 and August 18, I released 25 fish per pool.

All fish used in my experiments were cold branded (Bryant et al. 1990) by touching the fish with brands cooled in a mix of acetone and dry ice. Fish assigned to different pools received distinct markings, allowing me to determine the "pool of origin" among recaptured fish as well as to detect immigration of coho salmon from downstream units where DFO had released fry in early spring. Very few (15) of these fish managed to get into my channels at different times during the summer. I did not include them in my experimental results.

5.2.2. Coghlan Creek

Additional field experiments were conducted at 3 sites on Coghlan Creek, an upper tributary to the Salmon River, Langley. The sites were near the headwaters of the creek (see "experimental area" in Figure 3) in an agricultural area. In the summer of 1994, the creek had a mean flow of 0.06 m^3/sec and its temperature ranged from 12.9 to 16.6°C

(mean = 14.8°C).   Two of the experimental sites (B and C) were 40 m apart in a shallow treeless ravine and lacked cover.   The downstream site (C) was 19.46 m long, and averaged 0.24 m deep and 3.44 m wide.   The upstream site (B) was 18.56 m long, and averaged 0.19 m deep and 1.98 m wide.   The third site (A) was about 1 km further upstream.   This site was 24.4 m long, and averaged 0.35 m deep and 1.96 m wide.   It was partially shaded by surrounding trees, but it did not have any type of cover in it.   All three sites were glides with well defined riffles at both ends.   I constructed three riffles of gravel and rocks about 1 m long and 0.03 m deep within each glide, thus creating four "experimental" pools of approximately equal size.

Coghlan Creek, as well as the rest of the Salmon River watershed, is highly productive.   Therefore, it was not a good system to study coho's distribution in response to experimental food manipulations.   Absence of cover and uniformity, however, made the 3 sites suitable for testing the effects of woody debris on the distribution of coho salmon in a natural stream.   Three out of the 4 pools built in each glide received different cover (large woody debris, sparse fine woody debris or abundant fine woody debris), while the other one was kept clear of all debris.   The large woody debris treatment consisted of 2 logs (diameter at least 20 cm) forming a "λ" in the pool.   They were tied to large adjacent objects to keep them from floating away, and big rocks were used to sink them.   Pools receiving sparse fine cover got 3 bundles of branches.   Each bundle was anchored to rocks sitting on the stream banks.   The bundles were made of 8 red alder twigs tied by the middle and 1 fan shaped red cedar branch (their dimensions were similar to those used in the Spring Creek experimental channels).   Pools receiving abundant fine cover got a total of 9 of these bundles, which was sufficient to cover the entire pool.   All treatments were randomly assigned to the 4 pools at each site (Figure 22).

By early June the preparation of all experimental pools had been completed and experiments were begun.   Each pool was closed with nets (5 mm mesh size) and all fish

Figure 22. View of one of the experimental sites in Coghlan Creek. Channel was divided into 4 consecutive pools with different cover treatments.

were removed using a pole seine. Fish were counted, and sorted by species into separate holding buckets. Each pool was seined until no fish were caught in 2 consecutive passes. Finally, after allowing each pool to rest for at least 1 hr. the remaining fish were electro-fished.

Besides coho salmon, 3 other species of fish were captured: steelhead trout (Oncorhynchus mykiss), cutthroat trout (O. clarki), and three-spine sticklebacks (Gasterosteus aculeatus). All fish but coho salmon were returned to the pools in which they had been caught. At the start of the experiments, coho salmon were divided into 4 equal groups, measured, marked with a distinctive group cold-brand, and then randomly assigned to 1 of the 4 pools at the site where I had caught them. Experimental cover treatments were applied to each pool before the fish were released (from 75 to 120 fish per pool, depending on experimental site).

Because of the time required to capture the fish, prepare the pools and initiate an experiment, trials were begun at each site on different dates in June. Each site was sampled three more times, and each time fish were removed, counted, measured, marked and released. During each of these sampling times, cover treatments were randomly re-distributed among pools before coho salmon were released back into the pool in which they were found. Thus, although the type of cover coho salmon found in their pools could have changed, each individual found itself in the same pool it had occupied just before sampling began. Fish response to this manipulation should show whether individuals moved among pools looking for specific cover conditions, or were faithful to the same pool regardless of its complexity. Marking allowed me to distinguish original pool residents from newcomers and the unit of origin of some of the immigrants. However, large numbers of unmarked coho salmon were also caught in every survey, because these units were totally open to fish movement from up and downstream.

Since I worked with Chilliwack River hatchery coho salmon in Spring Creek and wild coho salmon in Coghlan Creek, I compared habitat selection between these two

different coho salmon stocks in a laboratory channel. I used an artificial channel at Cultus Lake Research Laboratory (DFO), British Columbia, for this experiment because it was not permitted (DFO regulations) to conduct fish transplants between different watersheds. The channel I used had a long riffle (10 m long, 0.9 m wide, and 0.05 m deep) and 2 side pools (3 m long, 0.9 m wide, and 0.5 m deep) connected to it. The channel received Cultus lake water and its temperature was maintained around 13° C by mixing deep lake water (6° to $8^{\circ}C$) with surface lake water (13° to $19^{\circ}C$) which reached the lab by independent pipelines. Pool water velocity was 1 cm/sec, and riffle water velocity was 20 cm/sec.

Distributions of coho salmon from both stocks were compared in this test. Groups of 24 fish, either all hatchery or all wild, were released in the pools (12 in each one), and their final position was recorded 72 hrs. later. A dense woody debris bundle, providing both instream and overhead cover, was randomly assigned to 1 of the 2 pools at the beginning of each trial. Every evening 5 g of shrimp were delivered into each pool. Ten replicates were obtained, 5 with each salmon type, from August 9 to September 15.

5.3. Data Analysis

I used the number of fish found in each pool to express the results of Experiments 2 and 3. However, fish proportions (number of fish present in individual pool/total number of fish present in the channel) were used to make the results of early and late summer trials of Experiment 1 comparable, because I reduced the number of coho salmon that were released in each pool. The large variation in coho salmon total numbers among my different experimental sites on Coghlan Creek, was also compensated by using fish proportions in the data analysis. Considering that proportions tend to form binomial distributions, I transformed my data (using the arcsine of the square-root of each proportion) to obtain an underlying distribution that was nearly normal (Zar, 1984).

To assess whether the different cover treatments and the different food treatments altered the mean number of fish occupying each individual pool, I used analysis of covariance (ANCOVA). Pool order in the channel was used as covariate to adjust for any effect of pool position on the distribution of juvenile coho salmon. I used Tukey's Studentized Range Test, which controls for the Type I experimentwise error rate (Zar 1984), for all univariate pairwise comparison to determine which means differed significantly (P<0.05). A nested design was used in the ANCOVA for Experiment 1, with "cover" treatment nested within "food". Differences in the proportion of each type of coho salmon (wild and hatchery) found in each one of two pools with different cover (no cover or abundant fine cover) were tested for significance with Student's t-test. All statistical analyses were conducted using SAS systems software (SAS Institute Inc. 1988).

5.4. Results

5.4.1. Spring Creek

Results from the early summer trials of Experiment 1 revealed that the covariate (pool position) was the only factor that had a significant effect on the final number of coho salmon present in each pool (F= 47.21, df = 2, p= 0.0001). The first pool (which received the inlet waterfall) in each channel attracted a large fraction of coho salmon, regardless of its experimental treatment. None of the cover treatments had a detectable effect regardless of feeding treatment (Figure 23a). In the late summer repetition of this experiment, fish distribution among pools was not affected by the food treatment (F= 0.55, df = 1, p= 0.4691), but was affected by cover abundance (F= 4.68, df = 4, p= 0.0034). The covariate, pool position, also had an effect on the number of salmon in each pool (F= 11.72, df = 2, p= 0.0001) (Figure 23b). This analysis suggests a difference in coho's response to cover between early and the late summer trials. Given the nested design of the treatments it was not possible to test for interactions between them.
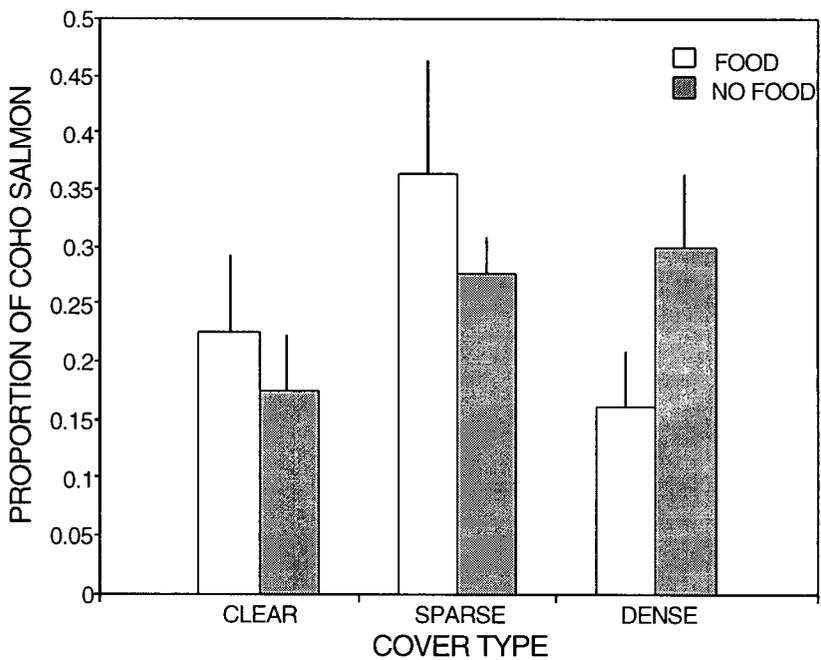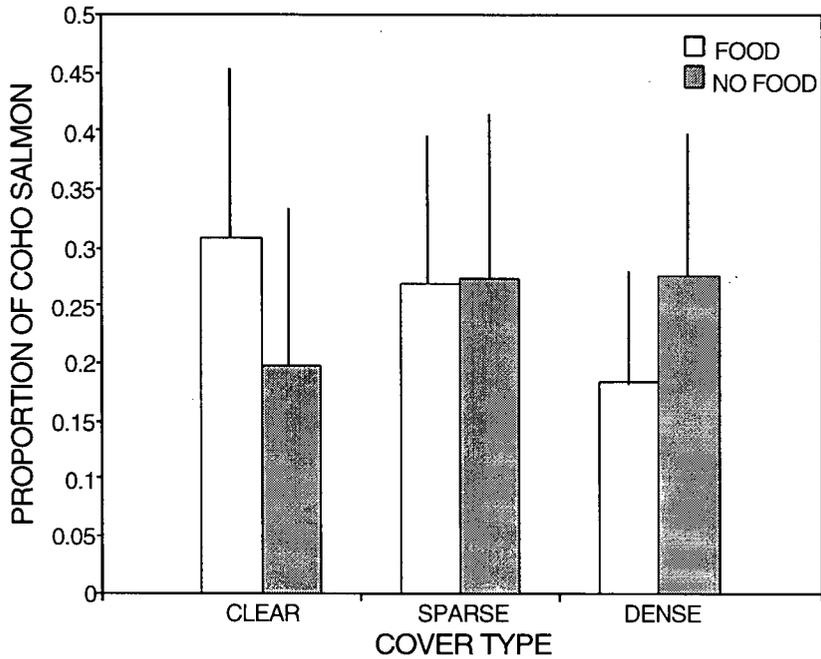
Figure 23. Proportional distribution of coho salmon among pools that received one of the following cover treatments: dense cover, sparse cover, or no cover. Entire channel food treatment was: food or no food supplement. **(a)** = early summer trials, and **(b)** = late summer trials in Spring Creek. Bars represent mean values, and vertical lines indicate 2 standard errors.

The number of coho salmon that moved out of both experimental channels and fell in the outlet fish-trap decreased with time. Both the mean number of fish emigrating (May/June x = 121.83 fish/trial ± 20.81 SE, vs. August/September x = 9 ± 2.87 SE) and the proportion of fish emigrating (May/June x = 0.30 ± 0.05 SE, vs. August/September x = 0.05 ± 0.01 SE) was higher in early summer than later in the season. A proportion of fish released in the channels (x = 0.36 ± 0.02 SE in May/June and x = 0.17 ± 0.014 in August/September) were not retrieved at the end of each trial. I assume bird predation was responsible for this. Green-backed herons (Butorides striatus) and belted kingfishers (Ceryle alcion) were common in the area. One heron was observed on several occasions standing on the lid of the fish-trap box. It is unlikely that it could reach the fish that were already inside the box, but it could easily catch each fish that came close to the head of the waterfall. A few dead fish in the channel were likely affected by high water temperatures in the stream.

In Experiment 2, food had a significant effect on the distribution of coho salmon among pools (F= 8.88, df = 1, p= 0.001) and there was a significant interaction between food and cover treatments (F= 2.44, df = 1, p= 0.028) which confirmed my third hypothesis. Cover alone did not affect coho's pool choice (F= 1.08, df = 1, p= 0.568). The highest proportion of coho salmon were attracted by pools offering both food and dense cover, and the smallest proportion chose pools without food and dense cover (Figure 24). Pool position in the channel (covariate) also had a significant effect on the number of coho salmon occupying a pool (F= 31.92, df = 1, p= 0.0001). The first pool in each channel attracted proportionally more coho salmon than any of the other pools. A pre-planned orthogonal contrast showed that pools with food attracted a significantly larger number of coho salmon (F= 8.88, df = 1, p= 0.005) than those without food. Tukey's Studentized Range Tests confirmed this difference between the two levels of food by classifying them separately.
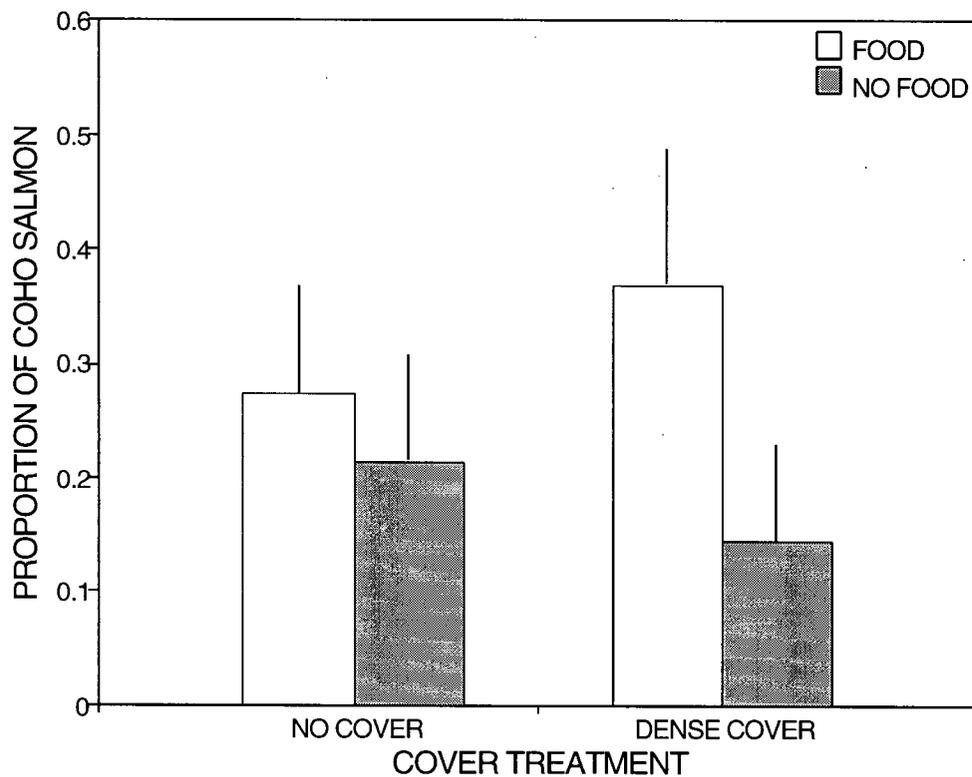
Figure 24. Proportional distribution of coho salmon among Spring Creek pools that received one of the following treatments: cover and food, no cover and food, cover and no food , no cover and no food.   Bars represent mean values, and vertical lines indicate 2 standard errors.

The results of Experiment 3 showed that the amount of food in a pool affected the number of coho salmon found in it (F= 18.14, df = 2, p= 0.0001). In the absence of cover, fish numbers increased with food abundance, but not proportionately. Pool position (covariate) had a significant effect (F= 6.48, df = 1, p= 0.017) on the number of fish observed in each pool, despite the fact that the very top pools of the channels were not used in this experiment. Coho salmon found in these top pools were considered emigrants and were not included as part of the total number of fish present in the channel. Pre-planned individual orthogonal contrasts among the 3 levels of food, showed a significant differences between the effects of full vs. half ration of food (F= 16.38, df = 1, p= 0.0004), and the effects of full food ration vs. no-food (F= 34.23, df = 1, p= 0.0001) on the distribution of coho salmon (Figure 25).

5.4.2. Coghlan Creek

Juvenile coho salmon in Coghlan Creek responded to cover manipulations (F= 7.23, df = 3, p= 0.0014) but the response, changed throughout the summer. This was confirmed by the significant interaction term between cover and month in the ANCOVA I performed using data from June, July and August pooled together (F= 3.59, df = 6, p= 0.0117). Pool was used as covariate. Figure 26 reveals that coho salmon showed an increasing preference for pools with either large woody debris or sparse fine cover as the summer progressed. Tukey's Studentized Range Test grouped the means (indicating no significant difference) of the various treatments in the following manner: sparse fine cover in one set with the highest proportion of fish, and dense fine cover, large woody debris and clear pools in a separate set, with lower proportion of fish. A series of orthogonal contrasts confirmed that sparse fine cover attracted a larger proportion of coho salmon than any of the other cover treatments.

An ANCOVA on July and August data detected the significant effect of cover on fish abundance (F= 17.3, df = 3, p= 0.0001), while neither month nor the interaction
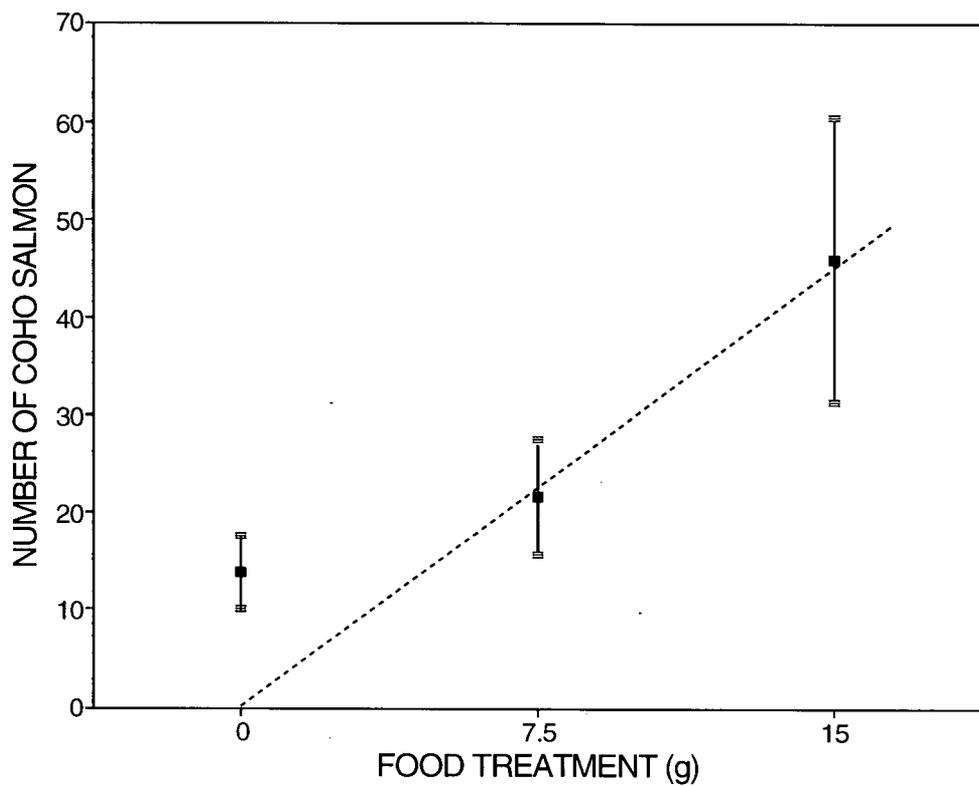
Figure 25. Mean proportion of coho salmon in Spring Creek pools that received one of the following three treatments: no food, 7.5 g of food, or 15 g of food. Vertical lines indicate 2 standard errors. Dotted line represents Ideal Free Distribution

between month and cover were significant. Tukey's Studentized Range Test grouped the means of the treatments in the following manner: sparse fine cover alone in one set with the highest proportion of fish; large woody debris and dense fine cover in a separate set; and, dense fine cover and clear in the third set.

Separate analyses of my experimental results by month showed changes in the effects of the treatments. In June, for example, no differences were detected among the different treatments. In July, fine sparse cover had a significant effect as indicated by Tukey's Studentized Range Test, which grouped all similar treatments together and left fine sparse cover apart. The results of the August data analyses showed that the effect of large woody debris changed and resembled more that of fine sparse debris, rejecting my fourth working hypothesis. Tukey's Studentized Range Test formed two groups, one with sparse fine debris and large wood, and the other one with large woody debris, fine dense debris and clear pools.

Although the covariate, pool, was not significant in any of the ANCOVAs I performed, including it in the different analyses altered the level of significance of the "cover" treatment. Thus, even when a clear preference for the different experimental pools could not be detected, fish densities seemed to have been affected to some extent by the pools. Many of the coho salmon I marked were repeatedly found in the same pool, even when cover conditions had changed, suggesting some site fidelity or even some territoriality.

Comparison between wild and hatchery coho salmon.

I compared the proportions (arcsin square-root transformed) of wild and hatchery coho salmon that chose the pool with cover over the clear pool or the riffle in the laboratory channel. No significant difference ($df = 8$, $t = 1.64$, $p = 0.1386$) in habitat preference was detected between fish of these two groups.
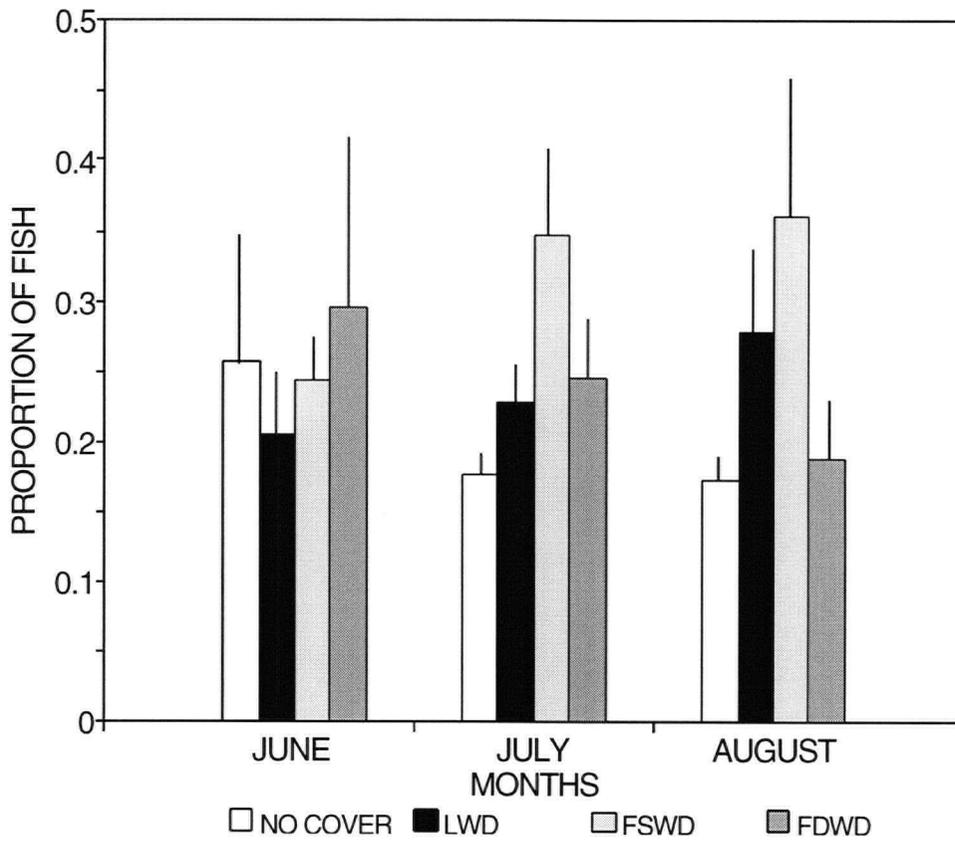
Figure 26. Proportional distribution of coho salmon among Coghlan Creek pools that received one of the following cover treatments: no cover, sparse fine debris (FSWD), dense fine debris (FDWD), or large woody debris (LWD). Bars represent mean values for 3 different experimental sites. Vertical lines indicate 2 standard errors.

139

5.5. Discussion

My results support the hypothesis that juvenile coho salmon prefer pools with medium to low density cover whenever food is abundant. This behaviour became more evident by August-September, both during the repetition of Experiment 1 and my final sampling in Coghlan Creek. During the early summer trials of Experiment 1, coho salmon did not prefer any particular cover treatment in the channels. But in the late summer trials with abundant food in the channel, the proportion of coho salmon decreased in clear pools and increased in pools with sparse fine debris. Under food-rich conditions, pools with a dense cover of fine woody debris were the least attractive to fish (Figure 23b). Instead of occupying pools with the highest cover density available in the channel when food abundance was high, taking advantage of high intake rates to minimize the total risk of predation, most coho salmon chose pools with sparse or no cover. An equivalent behaviour was observed by Gilliam and Fraser (1987) in creek chubs (<u>Semotilus</u> <u>atromaculatus</u>). They reported that the fish spent less time in a refuge area (without food) as the food level increased in the unprotected environment. They argued that the fish did not behave in accordance with a goal of obtaining a fix ration of food. Otherwise the fish would have moved into the refuge area as soon as that ration was acquired. Besides, it is likely that, for visual drift feeders like coho salmon, the negative impact that physical complexity may have on their foraging efficiency is strong enough to justify what appears to be risk-prone behaviour. Ware (1973) demonstrated that habitat complexity reduces the foraging efficiency of rainbow trout, probably by impairing the detection of prey.

When there was no supplemental food in the channel, however, the number of coho salmon occupying densely covered pools was similar to that in pools with sparse cover, and this distribution remained unchanged throughout the whole summer; only the use of clear pools decreased slightly towards the end of the season (Figures 23b). This suggests that when there is no food available in the channel, a very unusual situation in a

natural stream, most coho salmon select pools that offer any amount of cover (from sparse to very dense). But, with high levels of food in the channel, a larger proportion of individuals moves into pools with sparse cover at the expense of pools with dense woody debris. This behaviour can be compared to the tendency to choose the clear pool patch that coho salmon displayed whenever food was delivered in my artificial channel pools, regardless of the relative profitability of the two patches (see Chapter 4).

The results of Experiment 1, which showed that juvenile coho salmon change their summer habitat preferences as they grow older, also support my second hypothesis. During the early summer trials of Experiment 1, coho salmon's pool choice was not affected by any of the different experimental treatments. But in the late summer trials, at least in channels with abundant food, the effect of cover on the distribution of fish became evident.

Conflicting evidence for coho's preference for cover in the literature (Bisson et al. 1982, Dolloff 1986, Dolloff and Reeves 1990, Shirvell 1990, Bugert et al. 1991, Bugert and Bjorn 1991, Peters et al. 1993, Fausch 1993, Spalding et al. 1995) may be partially explained by my results. Studies conducted in spring and early summer (Bugert et al. 1991, Bugert and Bjorn 1991, Fausch 1993, Spalding et al. 1995) did not find a preference for cover whereas those conducted later in the summer did (Bisson et al. 1982, Dolloff 1986, Dolloff and Reeves 1990, Shirvell 1990, Peters et al. 1993). This is exactly the pattern of change in preference that I found.

It is important to mention, however, that by late summer most coho salmon used in the second run of Experiment I had already been released once during the first run of that experiment and were likely "survivors" of predation. Therefore, the increase in cover use that coho salmon developed over the summer, could have resulted from a behavioural change caused by previous exposure to predation (Milinski and Heller 1978, Krebs 1980, Dill and Fraser 1984). It is also possible that my results, as well as those of other researchers, reflected a change in the proportional representation (due to differential

survival) of "risk averse" and "risk prone" individuals in my stock, or in the population, rather than a behavioural change at the individual level. This differential survival among dissimilar phenotypes (cautious vs daring) may also explain the higher proportion of Coghlan Creek coho salmon found in pools with either sparse fine cover or large logs during late summer (Figure 26). Notwithstanding, an ontogenetic change in both habitat preference and risk aversion cannot be ruled out entirely as the cause of this shift. The results of my experiments in artificial channels (Chapter 4) showed that coho salmon had a strong preference for patches with instream cover in the late summer, even when the fish had never been exposed to any predation that could have altered their behaviour or the phenotypic composition of the group.

During the early summer trials, a large proportion of the fish disappeared from the experimental channels (60%). Many of these "missing" fish tried to emigrate, a behaviour that is common among coho salmon fry in spring and early summer (Chapman 1962). They were found at the end of the trials inside the fish-trap box (24% of released fry). A small number may also have moved into the upstream creek section as the upstream fall was not an absolute barrier to emigration. Most of the fish that were neither in the experimental pools nor in the trap-box, however, were likely taken by predators (approximately 36% of total fish released). In contrast, 78% of fish released in late summer remained in the experimental pools. Of the small fraction (22%) missing from the pools, 5% had entered the fish-trap box, and the rest (17% of total) remained unaccounted for.

This reduction, over time, in the proportion of fry emigrating from the channels could be explained in two ways: Emigrants may have been more vulnerable to predation and more likely to be eliminated during early trials (Dill and Fraser 1984). Thus, a larger proportion of the fish used in late summer trials were sedentary by nature. Alternatively, a larger proportion of the fry released into the channels were able to find territories and became residents during the late trials because I released smaller numbers of fish. The

142

decline (from 36% to 17%) in the proportion of fish that remained unaccounted for could be attributed to a lower rate of predation in mid-late summer. For example, the preference of the fry for pools with cover in late summer could have reduced their vulnerability to predation. Although, some authors (Spalding et al. 1995) doubt that fine woody debris such as I used could effectively protect fish from the surprise attacks of most avian predators, I consider it likely to have deterred belted kingfishers (Ceryle alcion) from diving in the pools with this kind of cover. Stalking green-backed herons (Butorides striatus) may have been less affected by the presence of instream brush than kingfishers, but it is reasonable to assume that coho salmon occupying the central area of my debris piles may have faced a lower risk of predation than those elsewhere. However, instream fine woody debris may work more effectively against swimming predators such as fish (Angradi 1992), common mergansers (Mergus serrator) and river otters (Lutra canadensis) (Dolloff 1993), which I did not observe in my experimental site.

Coho's preference for pools with sparse cover when food was abundant was a very consistent response. I observed it in three very different systems: artificial channels (see previous chapter), Spring Creek channels and Coghlan Creek; and, with different fish stocks (hatchery coho salmon from 2 different river systems and wild coho salmon). In the artificial channels I observed more coho salmon in pools that combined the highest abundance of food with the presence of instream woody debris. Within those pools, however, most fish were foraging in the available open patches (instream cover was evenly distributed throughout the pools and was low in density) where prey, and perhaps also predators, were easier to detect. Yet, by choosing those pools, coho salmon always were only a short distance from the protection of cover. In Spring Creek, sparsely covered pools attracted the highest proportion of coho salmon, followed by clear pools. In Coghlan Creek, coho salmon numbers were higher in pools with sparse cover than in either pools with dense cover or pools without cover. Larger woody debris also attracted more fish than clear pools in late summer. Both cover treatments had a low density of

debris, sparsely distributed logs or fine debris that provided refuge next to open foraging patches. When fish were undisturbed, I observed them feeding in those unprotected patches.

Experiment 2, with crossed food and cover treatments, presented different choices to coho salmon. The fish were not choosing among pools that had a uniform abundance of food, but only differed in the availability and type of cover. Rather, both cover and food abundance changed from pool to pool, and cover was reduced to only two types: dense fine cover, and no-cover. Under these conditions, the largest proportion of fish chose the pool that combined food and dense cover, and the smallest proportion occupied the pool with dense cover and no food (Figure 24). Clear pools attracted intermediate numbers of coho salmon regardless of food. These results suggest a rather flexible response to a variety of reward and risk situations, and an interaction between food abundance and cover availability in the determination of coho salmon rearing densities. This supports my third hypothesis. It is possible that somewhat contrasting fish distributions under different combinations of the experimental treatments (cover and food) resulted from a ranking of priorities by coho salmon. For example, food acquisition may have priority, followed by use of cover, and other factors such as rearing density, influencing the final distribution. The predominance of food over cover has already been observed in other salmonids. For example, Wilzbach (1985) concluded that food abundance was more important than cover in determining the abundance and microhabitat distribution of adult cutthroat in laboratory channels. This could explain why almost 70% of coho salmon chose pools with food treatment. Among them, a slight majority preferred pools which also offered cover (Figure 24). The possibility that sparse cover would have been preferred, as it was observed in previous experiments, exists. But that option was not available in this experiment. The fish had to choose between either dense cover or no cover at all. The reasons why the remaining 30% of the fish occupied pools without food (i.e. habitat sampling, displacement from more favourable sites, avoidance of

competition, etc.) could not be determined from my experimental results. Direct behavioural observations of individual fish would have been required to accomplish this. However, the fact that two thirds of these fish were in pools without cover suggests that prey detection received priority over predation-risk reduction. As Dill and Fraser (1984) observed, hungry coho salmon are prepared to take more risk and to continue foraging even when predators are sighted.

The response of coho to different food densities among pools (Experiment 3) varied greatly among trials. Although, fish distribution was affected by food abundance (see Figure 25), fish numbers were not proportional to the amount of food available in each pool. The pools that did not receive food made evident that coho salmon did not follow an ideal free distribution in these channels. In theory, no fish should have occupied foodless pools when the adjacent ones were receiving ground shrimp. This distribution, although under different experimental conditions, resembles the overuse of poor habitat patches that is reported and discussed in the previous chapter. Despite this deviation, a larger proportion of coho salmon selected pools with food, and fish numbers were almost double in pools with full rations than in pools receiving half rations of food.

My Coghlan Creek experimental results showed that coho salmon fry initially did not distribute among pools in response to cover abundance or type. By July, however, coho salmon began to showed preference for units with cover, in particular for those that had low-mid density fine woody debris. This changed towards August, because in late summer coho salmon parr showed affinity for both sparse fine woody debris and large debris (logs). Therefore, my hypothesis that coho's response depended upon the type of woody debris present was only valid in mid summer as coho salmon began to use cover. Later in the season the fish did not discriminate between pools based on the size of their debris (fine vs. large). It is very likely that large woody debris plays a very different role in faster flowing streams, particularly in fall and winter. But in small valley streams with low summer flows the density of the debris may be more important for coho salmon than

the diameter of its pieces. In small reaches like the ones I selected in Coghlan Creek, with slow water velocity, these two types of debris mainly offered limited cover from predation. However, in faster flowing waters they would differ in their habitat forming capacities. Logs can effectively contribute to pool creation and channel complexity (Bisson et al. 1987, Bilby and Ward 1989, Fausch and Northcote 1992, Naiman et al. 1992, Ralph et al. 1993) while providing velocity refuges for fish. Fine branches do not play a very important role in pool formation.

In summary, juvenile coho salmon distribution in a stream reach during summer depends primarily on the distribution and abundance of food. Food abundance in stream pools affects not only the number of fish rearing in them, but also alters their response to cover. In a food-rich environment, the association between coho salmon and woody debris increases as the summer progresses, and the trend continues throughout winter according to Bustard and Narver (1975) and Nickelson et al. (1992). In mid-late summer sparse fine woody debris increases the coho salmon rearing capacity of pools. This tendency was observed under a variety of experimental conditions (i.e. different spatial scales, levels of predation risk, water column depth, water temperature, etc.) and with either hatchery or wild origin coho salmon. Low cover density may create favourable summer rearing habitat for the young fish, because it leaves large unobstructed patches, where prey and possibly also predators can be easily detected, next to patches with cover protection from predation and, perhaps, some visual isolation from competitors. The fact that excessive amounts of woody debris in a stream reach can have the same kind of undesired effects on juvenile coho salmon rearing densities as total lack of cover has to be considered by fisheries managers when planning coho salmon habitat protection or restoration programs.

CHAPTER 6

INFLUENCE OF WATER FLOW AND FOOD AVAILABILITY ON JUVENILE COHO SALMON DOWNSTREAM MOVEMENT IN WINTER

6.1. Introduction

Water discharge rate has always been considered to play an important role for juvenile coho salmon rearing in streams (Sandercock 1991). Early studies suggested that low summer flows reduced habitat to the point that coho salmon production was limited (Neave 1949, McKernan et al. 1950, Wickett 1951, Smoker 1953). This hypothesis was further supported by records of relatively constant annual smolt production in many streams (Salo and Bayliff 1958, Hunter 1959, Chapman 1962), and by the discovery that juvenile coho salmon were territorial during summer, which caused many subordinate fish to be displaced downstream and presumably lost to the population (Chapman 1962, Chapman 1966, Hartman 1965).

When Mason (1976) increased the summer carrying capacity for juvenile coho salmon in a stream by supplemental feeding, the existence of a another "bottle-neck" to smolt production became evident. His results suggested that any gains made by releasing the summer control mechanisms were cancelled by a shortage of winter habitat that gave protection against freshets, regardless of fish size or condition. Freshets have been considered by several researchers to be one of the leading causes of the high mortality that coho salmon populations experience in coastal streams during winter (Tschaplinski and Hartman 1983, Brown and Hartman 1988). The magnitude, as well as the frequency, of high winter flows and the availability of velocity refuges may restrict the number of coho salmon smolts that a stream produces.

Contrary to Mason's (1976) conclusions, there is now considerable evidence that the size juvenile coho salmon have when they enter winter affects their chances of survival

(Cederholm and Scarlett 1982, Swales et al. 1988, Holtby 1988). Holtby (1988) observed that an extension in the length of the growing season, caused by increased water temperatures after logging in Carnation Creek, allowed fingerlings to enter winter at a larger size and, thus, survive it better. It is possible that larger fish or fish with more reserves can better afford the cost of relocation after a winter freshet.

If this is the case, coho salmon may improve their chances of survival by augmenting or, at least, maintaining their condition during the coldest months. Juveniles of other salmonid species, indeed, continue feeding during the winter and thus increase their chances of surviving until spring. For example, brook (Salvelinus fontinalis) and brown trout (Salmo trutta) were observed feeding during the winter months, even at temperatures below 4°C (Cunjak and Power 1987). Dominant individuals of juvenile Atlantic salmon (Salmo salar) enter winter at a larger size than subordinate fish, continue feeding in spite of low temperatures and even manage to grow moderately (Metcalfe 1994). The strategy adopted by juvenile coho salmon has not been well determined. Some authors consider that coho salmon virtually stop feeding and growing during the winter (Sandercock 1991), whereas others report that the young fish continue feeding and may even grow while they overwinter in riverine ponds (Peterson 1982a).

Water flow plays a key role in eliciting the emigration or displacement response in coho salmon (McMahon and Hartman 1989). However, it is not clear how the availability of food in a channel and the body condition of the fish affect their response to flow increase. My objective was to examine experimentally whether or not water flow level, food availability, and individual fish size or condition affect the downstream movement of juvenile coho salmon during winter.

6.2. Methods

I conducted the experiments in six aluminum rearing troughs at the Capilano Salmon Hatchery, North Vancouver, British Columbia, from January 23 to March 3, 1994. The experimental troughs were 6.38 m long, 0.6 m deep and had a "U" shaped cross-section with a maximum inner width of 0.8 m at the top. They were located in an underground chamber, which had an artificial light period that was automatically set to match the length of the natural light regime.

Water (from the Capilano River reservoir) entered the troughs at one end through a variable number of PVC pipes, and went out the opposite end through a single drain pipe. Each trough had an aluminum screen in front of the outlet pipe to prevent fish from escaping. A 0.4 m high wooden partition was placed 0.35 m upstream from this aluminum screen, creating a downstream compartment that worked as a fish-trap and set the trough water level at approximately 0.4 m. Water spilled over the wooden partition and formed a 0.20 m waterfall into the trap. Any fish that entered this compartment was not able to return to the main section of the trough.

Flow, was controlled by varying the number of water lines that simultaneously entered a trough. The troughs received water at two different rates: 100 l/min (low flow) and 500 l/min (high flow). These flows created mean surface water velocities of approximately 0.64 cm/sec and 3.2 cm/sec respectively. To test for the effects of food some troughs were fed ad libitum while others received no feed. I used ground freeze dried shrimp (Euphasia pacifica), which was delivered into the troughs by belt conveyor type automatic feeders.

I combined both experimental factors creating four different treatments: low flow without food, low flow with food, high flow without food, and high flow with food. Instream and overhead cover were available in all troughs and this factor was constant throughout all trials. Six sand bags placed approximately 1 m apart along the bottom of

each trough provided fish with flow shelter. Cover over each sand-bag was supplied by a PVC sheet (1 m x 0.80 m) that rested on the edges of the through.

Treatments were randomly assigned to the six troughs, and 14 replicate trials were completed for each treatment. Most replicates of the same treatment were sequentially performed, and only a small proportion of them (usually no more than two at a time) were run simultaneously. One factor that changed with time and, therefore, varied among replicate trials was water temperature. It was recorded daily, and it gradually decreased from a maximum of 4.9°C (on January 27) to a minimum of 3°C (on February 23).

I used Capilano Hatchery age-0 coho salmon (mean length = 10.67 ± 0.06 SE, and mean weight = 13.78 ± 0.26 SE) in these experiments. The fish were individually cold branded (Bryant et al. 1990) by touching them with brands cooled in a mix of acetone and dry ice. Individual fish identification was important to determine whether some fish were more prone to enter the trap than others. Thirty coho salmon were placed in each trough, creating a high winter rearing density that could make the available refuge space insufficient for the number of fish present.

Each experimental trial lasted 70 hrs. and fish-traps were checked every 24 hrs, because during a few pilot tests fish left in traps with high flow longer than 36 hrs. died. The length of these tests (70 hrs) was considered adequate based on the results of my preliminary tests and both Taylor's (1988) and McMahon and Hartman's (1989) experience. They found that the patterns of fish residency, emigration and habitat use in experimental channels under winter conditions became stable after the first 24 hrs of observation.

Fish that entered the traps were removed, measured, weighed, their marking recorded and temporarily moved to a holding tank. To reduce fish handling to a minimum, fish that remained in the main section of each trough were left in it for the next trial, and the fish that fell into the trap were replaced by fish from the holding tank. Once the total number of 30 fish was complete, they were left to rest in the trough for 24 hrs.

(with minimum flow and no food) before starting a new trial. Fish seemed to recover from this stress within 2 hrs of release. Tight schooling and rapid swimming behaviours disappeared, while feeding and aggressive interactions were observed. I used the same group of fish in the different trials because I only had access to a limited number of hatchery fish (220). The small number of fish meant that almost all of them were released in the troughs at the start of each trial, and every fish had virtually the same chance to be used in this experiment and drift downstream. It was not possible, for sanitary reasons, to bring either wild coho salmon or coho salmon from another hatchery into this facility. At the end of all experimental trials all fish stomachs were examined and all of them, except 5 of the smallest ones, had shrimp inside.

6.3. Data Analysis:

All statistical analyses were done using SAS systems software (SAS Institute Inc. 1988). I performed exploratory analyses including the estimation of different descriptive statistics for individual trials under the various treatments. The Shapiro and Wilk statistic (W) (Zar 1984) indicated that data were normally distributed.

I used fish proportions (number of fish found in trap / 30, total number of fish released in trough) to express my results. To normalize the distribution of proportions, that otherwise tend to form a binomial distribution, each proportion was transformed using the arcsine of its square-root (Zar 1984). Analysis of covariance (ANCOVA) was used to assess the effect of the different treatments on the proportion of fish entering the traps. Temperature was used as covariate in these analyses, to adjust for its possible effect on coho's movement. A t-test was used to compare the proportion of "emigrants" observed in the six replicates obtained during the pilot tests to the results of the main experimental trials without food.

Size and Fulton's Condition Factor, K (Ricker 1975), of fish that entered the traps were compared to the mean size and K of the entire stock to detect differences between the "average" experimental fish and those that moved downstream. Because I tried to minimize fish handling, the entire group of fish was measured and weighed only at the beginning and at the end of all experimental trials. Fish length increased slightly, from an initial mean of 10.67 cm to a final mean of 10.80 cm, during the six weeks that this experiments lasted. Their mean weight, however, decreased from 13.78 g to 13.32g and, consequently, their condition factor (K) was smaller in early March than in January. The mean length and weight for the entire group of fish were estimated at three day intervals using linear interpolation. The mean length and K of fish that emigrated in each trial were compared to that date's estimated mean length and K for all fish in the six troughs and assigned a score of 1, if greater than the population mean, or 0, if less than the population mean. The number of means in each category were analyzed with Fisher's Exact Test (the number of counts per cell, in the contingency tables, was too small to apply χ^2 test) (Zar 1984).

6.4. Results

Water flow affected the proportion of fish that moved downstream (Figure 27). High flow caused more fish to leave the main sections of the troughs and enter the downstream traps than low flow (F= 85.47, df = 1, p= 0.0001). Food supply neither affected the proportion of fish moving downstream (F=1.85, df = 1, p= 0.1792), nor interacted in any significant way with flow (F= 1.03, df = 1, p= 0.3148) (Figure 27). Temperature, the covariate, had an effect on fish movement (F= 21.22, df = 1, p= 0.0001). As water temperature decreased, from 4.9°C to 3.3°C, so did the proportion of fish moving downstream (Figures 28 a, b).
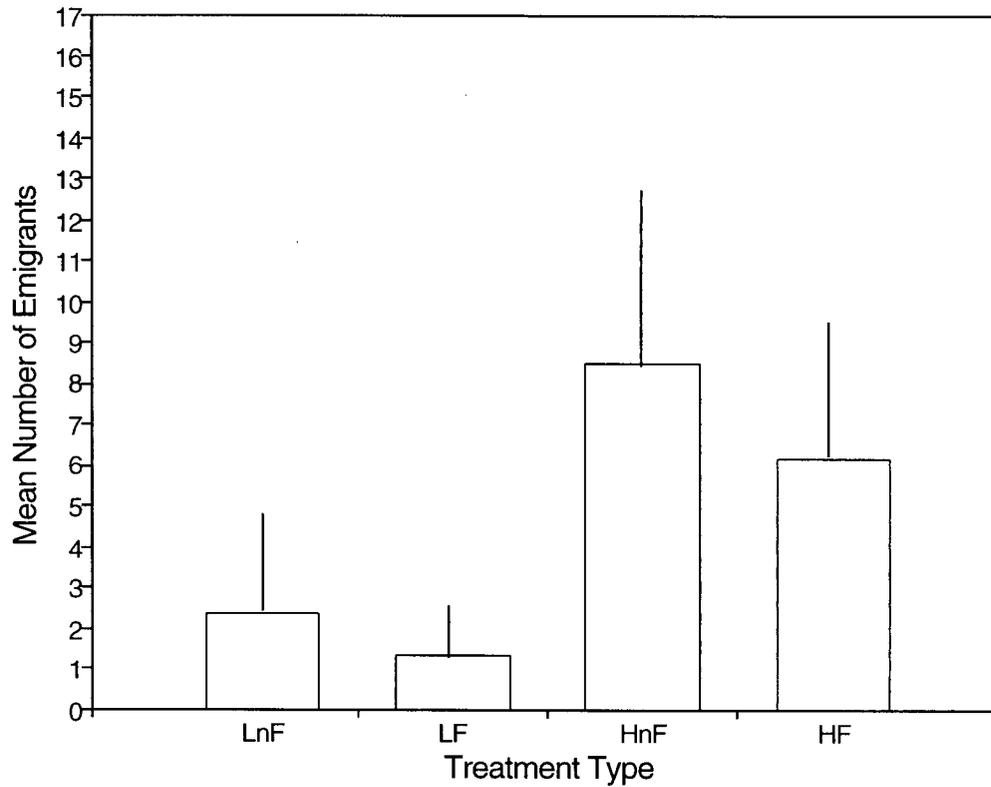
Figure 27. Mean number of coho salmon moving downstream in experimental troughs under 4 different treatments: LnF = low flow and no food; LF = low flow and food; HNF = high flow and no food; and, HF = high flow and food. Bars represent mean values, and vertical bars are 2 standard errors.
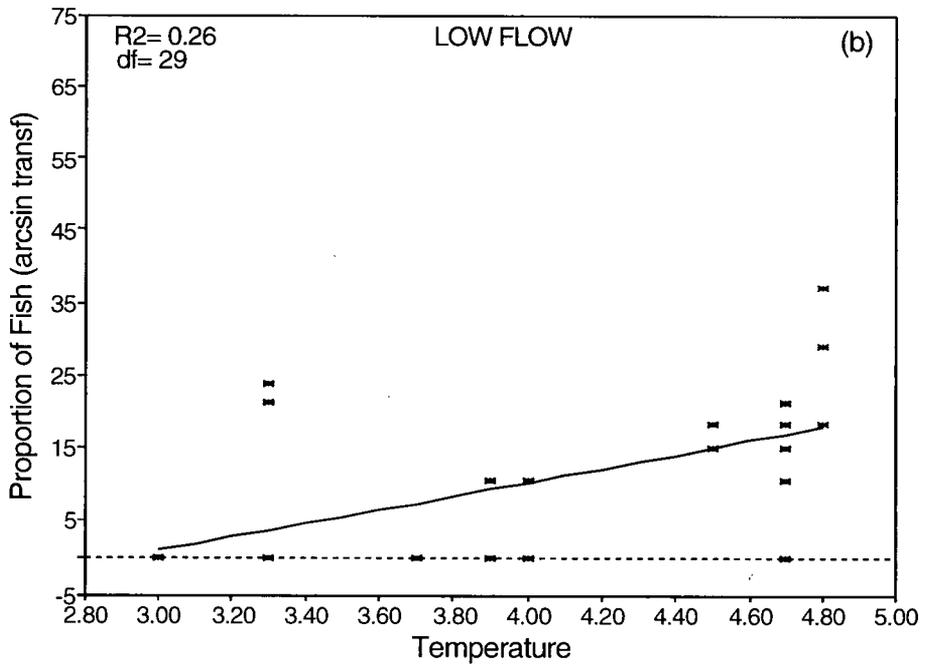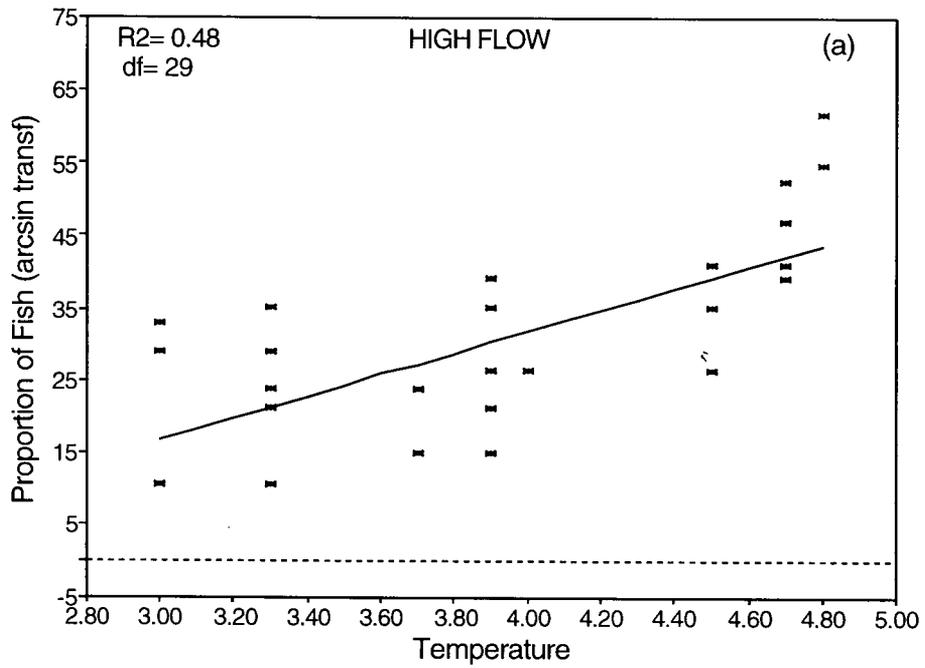
Figure 28. Relationship between proportion of juvenile coho salmon moving downstream under high flow and water temperature. **(a)** = troughs with high flow; and **(b)** = troughs with low flow.

Since the fish were individually marked I was able to determine that no individuals entered the downstream traps more frequently than others. Moreover, the length and condition (K) of the fish that moved downstream did not differ significantly from the total group of fish (p= 0.531 for length, and p= 0.082 for K, 2-tail Fisher's Exact Test).

6.5. Discussion

The results of this experiment indicate that increased water flows trigger the downstream movement of overwintering coho salmon and, therefore, support previous studies on the effect of floods on juvenile coho salmon (Peterson 1982a, Tschaplinski and Hartman 1983, McMahon and Hartman 1989, Nickelson et al. 1992a).

Tschaplinski and Hartman (1983) reported that during winter coho salmon were found in habitats with water velocities well below 30 cm/sec., and McMahon and Hartman (1989) did not observe any coho salmon in artificial riffles with water velocities as low as 2 to 7 cm/sec. In my troughs water velocities varied from 0.64 cm/sec. under low flows to 3.2 cm/sec. under high flows. Despite these very low velocities flow increases still affected the number of coho salmon that began moving downstream. This fact suggests that it may be the increase in flow itself, regardless of actual water velocity, that induces the fish response. In my experiment, coho salmon actually experienced the flow changes between the recovery period, with very little flow, and the beginning of the actual trials, with either low or high water discharge rates. It is possible that the small difference in flow between recovery period and low experimental flow failed to effect coho's movement. But the five fold difference in flow between the resting periods and the high flow treatment trials was sufficient to stimulate many fish to move somewhere else. An early response of this kind, in anticipation of potentially worse future conditions, has more adaptive value than a response that occurs once it is too late to avoid a negative effect. This is not just a winter phenomenon, downstream movement in response to changes in

streamflows were also reported for summer rearing coho salmon by Shirvell (1994). In a stream with an average water velocity of 18 cm/sec, he observed that coho salmon moved downstream with increasing flows independently of the magnitude of the flow change (below or above 60% of the previous flow). Considering that coho's swimming abilities are substantially reduced at low temperatures (Glova and McInerney 1977), it is reasonable to assume that the flow increase that coho salmon experienced in my experiment could have been enough to provoke the fish to move downstream, even with low absolute water velocities.

During low flow trials I observed that few coho salmon positioned themselves behind the cover (sandbags imitating boulders) that was available in the troughs. Many of them formed an aggregation holding position at the upper end of the trough. The distribution of fish, however, was very different with high flow treatments. None of them held position in an open area near the inlet, and the majority had moved to positions behind the few available sandbags.

The contradictory reports over the importance and the functions that cover plays in the ecology of juvenile coho salmon during summer (see Chapters 4 and 5) are replaced by a strong consensus on the critical role it has during winter. Instream cover not only shelters overwintering coho salmon from high water velocities during winter freshets (McMahon and Hartman 1989, Nickelson et al. 1992b); it is likely to protect the fish from predation during a period characterized by reduced fish activity (Bustard and Narver 1975b, Peterson 1982a, Dolloff 1993). It may even increase visual isolation among individuals, thus reducing the frequency of agonistic behaviour that, although diminished, continues during winter (McMahon and Hartman 1989) .

Falling water temperature induces hiding behaviour in stream dwelling salmonids (Chapman and Bjornn 1969). It is possible that the combined effect of decreasing temperature and increasing streamflows initiate coho's overwintering shift into secluded habitat. Once temperatures fall below 5 or 4.5°C the level of activity of coho salmon, as

well as that of other juvenile salmonids, decreases markedly (Reimers 1963, Bustard and Narver 1975a). In my experiment water temperature had an effect on the proportion of fish that were moving downstream. As water temperature fell (from 4.8°C to 3.0°C) so did the number of fish that entered the traps, presumably as a consequence of a decline in fish activity (Figure 28).

Food did not alter the pattern of coho salmon movement in my experiment. Coho salmon were observed feeding under the low flow treatment, and the analysis of their stomach contents, at the end of the experiment, confirmed that all fish, with the exception of five individuals, were feeding despite the low temperatures. However, they barely grew and the mean condition factor (K) for the entire stock decreased from January to March. Stream-resident brook and brown trout, have also been reported to loose weight in winter despite the fact that they continue feeding. This weight reduction is attributed to the reduced assimilation of ingested food, which moves throughout the digestive tract faster than it can be digested at low temperatures (Cunjak and Power 1987).

My study shows that coho salmon are sensitive to small changes in streamflow during the winter. Their tolerance for any increase in water velocity is limited, and they seem ready to move to secluded sites and to use velocity refuges as soon as a flow increase is perceived. This type of behavioural adaptation contributes to a more efficient use of limited body reserves, that coho salmon are not always able to replenish during a season marked by low temperatures and food scarcity. The evolution of this strategy suggest that any costs associated with shifting habitats (i.e. energy costs, predation risk, etc.) must be compensated by its benefits (i.e. energy savings, protection from displacement and predation, etc.).

CHAPTER 7

COHO SALMON HABITAT: CONTROLLING FACTORS, THREATENING ACTIVITIES, AND PROTECTIVE ACTIONS

7.1. Natural factors controlling coho salmon habitat availability

Approaching the lotic system at different hierarchical levels, as Frissell et al.
(1986) proposed, propitiates a more clear view of its different components and their
connectivity. These components are: basin geomorphology, hydrologic regime, water
quality, riparian vegetation, and habitat features; and they integrate, at different spatial
scales, a number of factors (i.e. discharge, water chemistry, sediment load, temperature,
woody debris abundance, flow pattern, food abundance, trophic pathways, etc.) that affect
species-specific processes (i.e. population dynamics) (Naiman et al. 1992). This approach
allows the effects of factors that are not observed at one spatial scale to become
potentially more visible at a different scale. One simple way to illustrate this is as a multi-
layered universe, where watershed scale components, such as basin geomorphology and
hydrologic pattern (ranking high in the functional hierarchy), interact to control reach level
components, such as channel morphology or riparian community composition (with an
intermediate ranking), which in combination affect smaller scale components, such as fish
habitat characteristics which rank low in the hierarchical classification (Naiman et al.,
1992). This ranking system is a tool that helps to identify the main spatial scale at which
each ecosystem component influences the characteristics of the stream, but it does not
imply that components at lower hierarchical levels are less important than those ranked
higher. As a matter of fact, the connectivity of the lotic environment involves feedback
mechanisms by which a variety of factors of the smaller scale components may influence
larger scale ones (DeAngelis et al. 1986, Naiman 1988).

Watershed connectivity allows disturbance introduced at one particular spatial scale (i.e. removal of the riparian vegetation of an entire stream section) to reflect on other components of the system that are either at the same or a different scale (i.e. channel morphology in that section, water quality in one of its reaches, fish habitat characteristics, etc.). For this reason, an effective management plan has to consider factors controlling fish abundance and distribution at different scales. The alternative approach, focusing exclusively on maintaining local fish habitat by protecting or enhancing selected reaches is very ineffective in the long term, because its effects are constantly neutralized by changes in the stream system that occur at a larger scale.

Based on the results of my empirical and experimental work and information derived from the literature I present a summary of habitat factors affecting coho salmon distribution at different spatial scales. The identification of controlling factors at these scales will serve as an introduction to my management recommendations, which consider both watershed and reach scale actions.

7.1.1. Factors controlling coho salmon distribution at the watershed level

At the watershed level, the distribution of young coho salmon reflects the strong physical (and biological) differences that exist among the three main river sections. Although, the middle section of the system is the only one that appears to be of any importance for coho salmon production, a closer examination reveals that that is not necessarily the case. Coho utilize habitats throughout the entire drainage network at different stages of their life cycle, emphasizing the connectivity between different habitats.

The upper reaches of the mainstem do not offer suitable spawning or rearing conditions to coho salmon but they are very important in the initial collection, filtration, and channelling of water, nutrients and sediments as well as in their downstream delivery (Naiman et al. 1992). In this way, they contribute to create the favourable habitat that coho salmon occupy further downstream. In a broad sense, the same applies to the upper

159

reaches of Coghlan Creek; but conditions there are somehow less extreme than in the mainstem, and small numbers of coho salmon are found within a relatively short distance of the creek's headwaters (Chapter 2).

In contrast, the middle reaches, with their pool-riffle sequence, abundant cover, higher benthic productivity, heterogeneous substrate and permanent flow, offer the best juvenile coho salmon summer habitat in the entire watershed. The large numbers of coho salmon that occupy this section of the basin are evidence of this.

Juvenile coho salmon prefer pools over stream habitat with faster water velocity. Both lateral scour pools and backwater pools support some of the highest densities of coho salmon in the entire watershed. Lateral scour pools have a combination of abundant cover against one of the banks with adjacent clear drift-rich patches in mid-channel location which attract relatively large size juvenile salmon. In contrast, backwater pools are selected by coho salmon that are, on average, smaller than those elsewhere. Thus, this type of habitat is used by fish that, otherwise, would be displaced from the watershed's middle reaches and, likely, lost to the poor quality summer habitat of the lower reaches (Chapter 2).

The lower reaches of the watershed are almost not used by juvenile coho salmon during summer. The high water temperatures there, fluctuating dissolved oxygen levels, poor benthic insect production, and scarce cover do not provide what young coho salmon require. Only the "transitional" zone between the stream reach by Trinity Western University and Rawlison Crescent, offers marginal habitat which is occupied by a few individuals during the low-flow period. The importance of this section, however, changes with seasons. Coho salmon that move downstream with the first high flows find overwintering refuge in the off-channel habitat of the lower reaches. The mainstem of the river is used by comparatively few individuals, but coho relative abundance in some off-channel areas is estimated to be high (Chapter 3).

Among the many differences between watershed sections, water quality seems to be a dominant component affecting the distribution of coho salmon in summer. The watershed scale pattern of coho parr distribution suggests that marginal habitat can be used by, at least, a small proportion of individuals provided water temperatures and oxygen concentrations are not beyond limiting values. This is likely due to the fact that other factors - such as food, cover and water velocity - either do not reach limiting levels in the entire watershed or where they do, they coincide with extreme water quality conditions and are masked by them. The utilization of the upper reaches of Davidson Creek by coho salmon during the summer months illustrates this point. The suitable conditions maintained by cold spring waters seem to be enough for a small coho salmon subpopulation to rear in the headwaters of the creek throughout the summer, although conditions for growth do not seem good.

As water temperatures begin to decline, coho salmon leave their main channel feeding grounds and move into protective habitat with abundant cover (Peterson 1982a, Tschaplinski and Hartman 1983, McMahon and Hartman 1989, Nickelson et al. 1992a). Initial habitat relocations likely take place within the same pool or, at least, the same reach that the individuals were occupying during summer (Chapter 3). But with the first fall freshets large numbers of coho salmon redistribute into available off-channel habitat (Scarlett and Cederholm 1984). This strategy protects them from being swept out of the system by fast flowing waters, specially when cold temperatures reduce their metabolism to the point of affecting their swimming ability (Hartman 1965). Under these conditions, even small increases in water velocity are sufficient to trigger coho's downstream movement (Chapter 6). Water velocity controls their selection of habitat, and their distribution both within and between reaches reflects the pattern of distribution and abundance of areas sheltered from velocity. Therefore, the large number of coho salmon that utilize the off-channel habitat in the lower section of the system in winter suggests a

shortage of suitable habitat elsewhere (Chapter 3). Many of the reaches in the middle

section run through narrow ravines that do not allow any side channel development.

Because only a fraction of the fish that move downstream during freshets are able

to relocate (Peterson and Reid 1984) and the larger than average individuals are more

successful at relocating in overwintering habitat (Scarlett and Cederholm 1984), large

coho parr are abundant in the off-channel habitat of the Salmon River floodplain. It is

likely that many of the fish that initially choose suboptimal winter habitat, which does not

shelter them effectively from the current, move and relocate for a second time when water

velocities increase. Many fish may go through this displacement process more than once

during the fall-winter period, which may result in the loss of the individuals that either do

not have enough energy reserves to relocate several times (Cederholm and Scarlett 1982)

or reach the mouth of the stream before finding a new holding location.

7.1.2. Factors controlling coho salmon distribution at the reach level

The results of my summer survey indicated that water velocity is one of the main

factors influencing the distribution of juvenile coho salmon among different types of

habitat in a stream reach. Although, they are found in all habitats, most coho salmon

prefer those that are characterized by reduced water velocity, such as pools or glides, and

very few individuals occupy riffles. In addition, I confirmed a positive relationship

between coho salmon numbers and abundance of cover (both woody debris and undercut

banks) (Chapters 2 and 3). This was consistent with what other researchers have

observed both in stream and in artificial channels, but it did not elucidate the contradictory

information published about coho's use of cover. The results of my experimental

manipulations helped to explain the cause of some of this contradiction (Chapters 4 and

5). They showed that coho salmon foraging behaviour changes with age (Chapter 5) and

suggest that individuals respond differently depending on a number of environmental (i.e.

resources, temperature, number of competitors, predation risk, etc.) and physiological

conditions (such as energy reserves, see Croy and Hughes, 1991). Not all fish can afford the costs associated with sampling all habitat patches, and a trade-off is made between feeding in a relatively poor patch and continuing the search for the best possible patch in the area.

My results indicate that coho salmon distribution, among habitats of comparable flow, responds most strongly to food. When cover is absent, juvenile coho salmon distribute among separate pools in relation, although not in proportion, to their foraging quality. The separation of pools in a stream reach by unfavourable areas (riffles) does not deter coho from moving among them and, as a consequence, finding the units that offer the best foraging opportunities. But their distribution is not "ideal", because as habitat complexity increases so does the proportion of individuals that fail to choose the most profitable patch. The fish must make a larger number of decisions on foraging, having less accurate information about patch profitability as a result of increased habitat complexity (Chapter 4).

Woody debris, by increasing the cost of sampling, also affects coho's response to prey abundance between pools. But its effect on fish distribution is complex, because it represent a resource in itself and not a mere barrier to coho's acquisition of information. The changing use of this resource reflects ontogenetic changes that are likely associated with the development of learning mechanisms and rules (Kacelnik and Krebs 1985). Young fry do not show preference for units with woody debris over clear ones, but this changes with time and in late summer coho parr always prefer pools that offer some type of cover. As young coho salmon mature and move away from the stream margins into the mid-channel waters (Bisson et al. 1987) cover becomes an important habitat component, one that represents refugia from both predation and water velocity (Dolloff 1986, Mesick 1988, Bugert et al. 1991, Fausch 1993). If they have the option, coho parr always pick pools with low-intermediate densities of woody debris over units that have a very high density of it. In mid-summer coho salmon prefer fine woody debris to large

logs, but later in the season (August-September) they do not make this distinction (Chapter 5). The importance of woody debris reaches a peak in winter, when coho use it as water velocity refuge.

The influence that woody debris has on the distribution of coho salmon among the pools in a stream reach is evidence of the important role that riparian forests have at the reach scale in the upper and middle sections of a watershed. Large woody debris plays an important role as a structural element in the creation of salmonid habitat in low gradient and intermediate order reaches (like S1, S2, C1, and C2 in this study) (Bisson et al. 1987, Bilby and Ward 1989, Naiman et al. 1992, Ralph et al. 1993). Large fallen logs deflect the flow of water and, depending on their position, create different types of pools that coho use in summer (Bisson et al. 1982). Although the impact of large woody debris on channel structure decreases towards the mouth of the river, it still remains an important element of the bank structure that can influence the pattern of meanders (Naiman et al. 1992). This changes in winter, because any riparian forest left on the banks of lower mainstem, as well as along the lateral channels in the river floodplain, directly or indirectly creates coho salmon winter habitat (Naiman et al. 1992).

In addition to supplying cover and altering the structure of the stream channel, riparian forests also influence the distribution of coho salmon among reaches through other indirect processes. The density of the forest canopy controls the amount and quality of light that reaches the water, thus affecting its temperature, the level of primary productivity in the reach, and even the behaviour of organisms (Naiman et al. 1992). During my experimental work in Spring Creek, I was able to record in a small creek the dramatic increase in water temperature that results from riparian cover removal. The 200 to 300 m long stream reach without riparian cover was enough to increase more than two fold the temperature of water, compared to its temperature at the source, during summer.

Riparian forests also regulates the productivity of streams through the contribution of allochthonous (terrestrial) organic matter. Leaves, wood, and nutrients dissolved in

subsurface waters, all represent an important source of energy for benthic invertebrates (Anderson and Sedell 1979, Richardson 1991) which are eventually consumed by fish. Terrestrial insects that fall from the riparian vegetation are another important contribution of fish food. This resource is particularly important for juvenile coho, because it has been reported to constitute between 21 and 40% (dry weight) of their daily prey consumption (Chapman 1965).

Winter use of habitat at the reach scale follows the same general pattern described in the previous section. During this period feeding virtually stops. But largely due to the scarcity of prey. If juvenile coho salmon find themselves in food rich habitat (i.e. some types of riverine ponds) they continue feeding at temperatures below 5°C (as I observed in my troughs, Chapter 6) and can even grow (Peterson 1982a).

7.1.3. Factors controlling coho salmon distribution at the pool level

At the level of pools or glides, as for entire reaches, coho salmon respond to patch profitability. Patches with higher prey densities attract more fish but their distribution is not proportional to prey abundance, especially if the pool has either instream woody debris or overhead cover. However, the effect that cover has on coho parr distribution at this scale differs markedly from that reported for entire reaches. The young fish prefer pools that have woody debris at a low to intermediate density, but their distribution within each pool tends to be biased in favour of clear patches. My experimental results suggest that fish overestimation of the foraging quality of unobstructed patches cause this bias (Chapter 4). Yet nearby patches with woody debris are beneficial, because they offer accessible refugia from predation, dominant individuals and water velocity changes.

My experiments showed that the spatial distribution of the invertebrate drift is another important factor controlling coho's patch choice within pools (Chapter 4). Therefore, the pattern of flow that sweeps benthic invertebrates into pools influences the distribution of coho salmon within pools, and may account for the tendency of dominant

individuals to position themselves at the pool's head (Hartman 1965, Jenkins 1969, Fausch 1984, Fausch and White 1986). The pattern of flow is controlled by the morphology of the stream channel and the presence of logs and large boulders that deflect the water.

Backwater pools and off-channel units offer coho salmon excellent overwintering habitat. But within the main channel, lateral scour pools are the most utilized type of unit, because of their abundant debris and undercut banks with abundant riparian rootwads (Chapter 3).

The above mentioned factors represent a subset of some of the most important forces regulating coho salmon smolt production, and reflect the state of different components of a healthy watershed (i.e. water quality, riparian forests characteristics, and aquatic habitat features). In the following section I reflect on the connectivity of the watershed ecosystem to evaluate the potential impacts that the prevalent land uses in the Salmon River Basin can have on factors controlling juvenile coho salmon distribution and abundance.

7.2. The effects of land use on coho salmon habitat

Human activities, through the modification of watershed components, such as hydrologic regime, stream channel morphology, and riparian communities, can have a strong impact on the availability and quality of fish habitat and, therefore, in an indirect way limit fish production. The impacts of forestry on salmonid bearing systems have been the subject of many investigations since the early 1970's (see Hartman 1982, for a review on ten years of research in Carnation Creek; Hicks et al. 1991, and Bisson et al. 1992, summarize more recent developments in this field). The study of the effects of agriculture on streams has attracted less attention and most of it has been focussed on one specific activity, livestock grazing (Johnson 1992). In contrast, the role of urbanization as an agent of stream alteration has been overlooked (MacKenzie 1987, Booth 1991) and very

few investigators have studied its impact on salmonid habitat (Perkins et al. 1980, Steward 1983, Lucchetti and Fuerstenberg 1993).

As I mentioned in Chapter 2, agriculture is the predominant human activity in the Salmon River watershed (approximately 50% of its catchment area is classified as farmland). But residential land use has increased steadily. Watts (1992) estimated that between 1979 and 1989 the percentage area of the basin under urbanization increased 3% in the entire watershed, to a total of 7% (the actual urban area is closer to 14% after some areas were revised and reclassified based on aerial photographs and two previously unmapped zones of the watershed were completed, Sandra Brown and Alice Kenney, pers. comm.). Development is not uniform throughout the watershed and in some areas the rate of urbanization was higher than in others. For example, within a 500 m wide riparian corridor located in the middle reaches of the watershed, urban development increased approximately 16% during that decade (Watts 1992). Although, both agricultural and urban land uses can have a detrimental impact on fish habitat, it is urbanization with its profound and irreversible changes in the stream's flow regime that poses a more serious threat to the production of coho salmon in a watershed like the Salmon River.

Although, coastal watersheds of the Pacific Northwest are adapted to natural disturbances, they do not recover in a similar manner from anthropogenic alterations. The reason behind this is that the types of disturbances differ in fundamental aspects (Franklin 1992). Natural catastrophic events (i.e. landslides, floods, fires, etc.) tend to be restricted in area and in time, thus increasing the complexity and patchiness of the system and contributing to perpetuate high species diversity. They also leave behind a very large number of surviving organisms (biological legacy) that contribute to the relatively fast redevelopment of the system's complexity (Franklin 1990 & 1992). In contrast, man-made disturbances, even temporary ones (i.e. clearcutting), reduce the biological legacy so drastically that the total recovery of the system is much slower (Franklin 1992). If the

disturbance is permanent (i.e. agricultural use of land, and urbanization) the ecosystem never recovers its original complexity and biodiversity.

7.2.1. Agriculture and urbanization

At the watershed scale, the main effect of agriculture (including livestock production) and urban development on stream systems is the overall change in hydrologic regime they cause. Hydrological changes associated with both types of land uses are similar in nature. But those created by urbanization are much more extreme in magnitude than those brought about by forestry or agriculture. The combined effects of vegetation removal, soil compaction and, in the case of urban development, construction of buildings and roads, modify the type and the amount of storm runoff (water which enters a stream channel within approximately a day after landing as rainfall) (Booth 1991).

Water can reach a channel directly as surface runoff (also known as overland flow) or indirectly as subsurface flow. The latter predominates in the coastal region of the Pacific Northwest, due to the combined effects of soil characteristics, vegetation abundance, and rainfall frequency (Booth 1991). In forested areas most of the subsurface flow is lost to evaporation and plant transpiration, only a small fraction of the precipitation is stored in the soil and may reach the water table. Despite this, the frequent winter storms in the coastal region contribute enough subsurface flow to rise the water table, expanding the area of saturated ground around the channel and increasing the amount of overland flow that enters the stream channel (Hewlett and Hibbert 1967, Booth 1991). These processes are all altered by the increase in impervious surfaces (i.e. compacted soils pavement, roofs) associated with agricultural and urban development, and result in a larger proportion of rainfall reaching the channels as surface runoff instead of subsurface flow (Lucchetti and Fuerstenberg 1993).

Under agricultural land use, flow alterations derive from two common practices: vegetation cover removal and large scale water withdrawal for irrigation. The elimination

of the vegetation cover decreases the rate of water percolation in the soil, magnifying peak water discharges during heavy rainfalls and reducing baseflows during the dry season (McMynn and Vernon 1954, Hamilton and Buell 1976). The use of large amounts of either surface or underground water for irrigation can affect stream flow during the dry season. In the Salmon River, the already low summer flows are, in theory, further affected by farmer's large scale water withdrawal from the stream. According to Paish (1980), the large number of water license holders in this system may reduce the stream summer flow by 25% in the mainstem, and by 50% in Coghlan Creek. Lower summer flows not only reduce the amount but also the quality of fish habitat, by augmenting water temperatures, and reducing dissolved oxygen levels and benthic prey abundance (Hamilton and Buell 1976).

Perhaps the most obvious impact of urbanization is the dramatic increase of the maximum water discharge associated with flood events. Booth (1991) argues that urban development not only magnifies peak discharges, but also creates entirely new ones. Depending on their magnitude, high flows can have important disrupting effects on stream habitat (causing channel erosion and expansion, woody debris displacement, pool filling, gravel bar scouring, etc.). This type of disturbance, however, increases habitat heterogeneity and can, theoretically, benefit the lotic system as long as its frequency of occurrence is relatively low (approximately one major channel alteration every ten years, Naiman et al. 1992). But urbanization not only increases the magnitude but also the frequency of peak water discharges, thus altering in a permanent way the physical characteristics of the stream. Its substrate becomes uniform, its channel looses it complexity with the elimination of distinctive hydraulic units, and its banks are eroded and cut almost vertically. Woody debris is eliminated over time and the severely altered riparian vegetation cannot replace it (Booth 1991). All this results in the loss of habitat and a decline in species diversity (both invertebrates and vertebrates), because while some species are favoured by this process, most are not. In the particular case of salmonids,

coho salmon numbers decline markedly whereas cutthroat abundance increases, to the point that cutthroat is often the only salmonid species left in many urban creeks (Muto and Shefler 1983, Lucchetti and Fuerstenberg 1993). Coho salmon are particularly sensitive to the reduction in abundance of relatively large pools, off-channel habitat, and woody debris caused by urban development. The species, given its reliance on small coastal streams, has been exposed to urbanization in many areas along the coast of the Pacific Northwest. The largest declines in Washington State coho salmon populations, for example, have been observed in the most urbanized areas of King County, where more than half of the "urban" streams are used exclusively by small resident cutthroat trout (Lucchetti and Fuerstenberg 1993).

Although in the Salmon River watershed only a small percentage (14%) of the total catchment area has been developed as residential land. A slow but steady rate of urban development in the watershed represents a serious threat to the integrity of the stream system and to the size of its coho salmon population. Particularly so, if the pattern observed in the 1980's is allowed to continue. During that decade, the fastest rates of residential development in the entire watershed occurred within 250 m from the stream, both on the mainstem (reach S1) and on Coghlan Creek (reach C1) (Watts 1992). This developed area integrates a larger urban zone of approximately 680 ha, known as the Salmon River Uplands, that in combination with Fort Langley (by the river mouth) is occupied by about 55% of the population in the watershed (Corporation of the Township of Langley 1994).

Additional urbanization in the Aldergrove area and the neighbouring District of Matsqui threatens to alter the headwaters of the river. An area that plays, as I mentioned before, a very important role in water collection and routing into the surface and underground subsystems of the middle section of the basin. The connectivity of the system will make the urban development in this area to affect the hydrologic pattern of the entire watershed, and impact negatively on coho salmon rearing downstream.

Besides the alterations to the hydrograph I discussed above, agricultural practices such as land tillage and livestock grazing promote soil erosion and compaction. Their impacts on the aquatic environment vary largely in scale - from entire watershed sections to short reaches - depending on the intensity, the extension and the location of these activities in the basin. Soil exposed before seeding or after harvesting can be easily washed into the stream. This erosion not only reduces the fertility of the soil, but contributes to soil compaction. Compacted soils have reduced water holding capacity (SOE Report 1992). From the stream perspective, erosion increases the load of fine sediments in water. Sediments threaten salmonid egg and alevin survival by clogging spawning gravels, thus causing anoxia and physical entrapment (Björn and Reiser 1991). Depending on the amounts, sediments may also fill in pools and smother or displace benthic invertebrates, causing a reduction of fish habitat and food production (Armour et al. 1991, Harr and Nichols 1993). Concurrently, the systems productivity may be affected because suspended sediments increase the turbidity of the water, which reduces the amount of light reaching the primary producers in the benthos (Moore 1989).

Livestock grazing may affect the aquatic habitat. Cattle are attracted to the riparian zone because of the quality and variety of forage, availability of water, and shade (Ames 1988). The animals can reduce the riparian vegetation, and cause bank degradation, channel widening and off-site soil erosion (Platts 1989, Armour et al. 1991, Johnson 1992). In the upper-middle (S2) and upper reaches of the Salmon River and Coghlan Creek, cattle stream wading and trampling is a common occurrence, and entire reaches have had their riparian vegetation reduced or entirely eliminated as a result. In contrast, the negative impact of livestock grazing in the riparian of the river's floodplain, is largely restricted to the small tributaries. This is so because farmers, for the most part, restrict the access of livestock to the mainstem of the river.

Intensive farming, which normally increases with growing urbanization, results in a greater risk of severe soil erosion. Its excessive dependence on agrochemicals (i.e.

pesticides, insecticides and fertilizers), and the accumulation of large amounts of manure (which is also used as fertilizer) derived from high density livestock production, presents another serious threat to water quality in many Fraser Valley streams (Moore 1990, Schreier et al. 1991). In the Salmon River Watershed, intensive agricultural operations occupy 11% of the total catchment area. But these operations, as in the case of urban development, concentrate in the central part of the basin, surrounding the Salmon River Uplands. They are located above the Hopington Aquifer, where - along with the numerous septic systems from the residential areas - contaminate ground-water with NO_3-N (Cook 1994). Nitrogen and phosphorus concentrations in stream water, however, are not high enough at any time of the year to be of concern as causes of eutrophication (with the exception of a few "trouble" sites in small tributaries and inmediately downstream from the Greater Vancouver Zoological Centre) (Cook 1994).

Septic systems are the predominant wastewater disposal and treatment method that residents of the Salmon River Watershed use. Only a small area in the northwest side of the basin is serviced with sewers (Cook 1994). No wastewater disposal system is totally problem free. Nitrate pollution by sewage overflow and leaching into groundwater and then to streams is a common problem associated with deteriorated septic systems (Hall and Wiens 1976). Municipal rezoning that allows increasing residential densities, particularly in environmental sensitive areas (ESAs) (i.e. above aquifers, next to watercourses, etc.) only make matters worse.

With regards to agricultural and urban stream systems, stormwater runoff is probably a more significant, and a more direct, source of contaminants than septic systems. Because it represents a nonpoint source of pollution, its control poses the most difficult problem in water quality management (Hall and Wiens 1976, MacKenzie 1987). Agricultural runoff carries pesticides, fertilizers, and animal manure. The list of pollutants in urban runoff according to several studies reviewed by MacKenzie (1887) include: high levels of suspended solids (i.e. rubber particles, asbestos fibres, general litter), nitrogen,

phosphates, hydrocarbons, phenols, chlorides, lead (and other trace metals), and coliform bacteria. In the Salmon River levels of copper and zinc which exceeded the "threshold of harm" (10 µg/l) recommended for salmonid fishes were recorded by Hall and Wiens (1976) in eight of fourteen sampling stations. The fact that higher trace metals concentrations were measured during high flow periods suggest that this pollution was associated with diffuse sources. Hall and Wiens (1976) indicate that high trace metal levels in some of the samples they collected, in the Salmon lower reaches and Coghlan upper reaches, for example, could derive from soils of marine sediment origin; whereas this type of pollution in middle reaches' samples may be caused by runoff from the Salmon River Uplands residential zone.

Additional impacts on stream systems are caused by channelization, dredging and dyking, which are designed to eliminate the natural instability of rivers (i.e. channel migration, seasonal floods, etc.) in agricultural and residential areas. The problem, however, is that they disconnect fluvial systems from their floodplains. Consequently, seasonal wetlands, secondary channels, beaver ponds, sloughs, small tributaries and riverine ponds are eliminated with the ensuing reduction in productivity, filtering capacity, biodiversity, and critical habitat for wildlife - including fish - in the basin (Pinay et al. 1990, Henderson 1991). In the particular case of the Salmon River, channel dyking and dredging affects the lower section of the system. Dyking of the river mouth to prevent the Fraser's spring freshet from flooding the lowlands, has an important impact on salmonid resources. Spring migrating salmon and trout smolts are held up by the system's flood gates, and the dyke's water pump represents their only way into the Fraser River. This "migration route" has a relatively high mortality risk associated with it. Dredging of the lower mainstem and its floodplain tributaries to increase their land draining capacity, may seriously alter critical coho parr off-channel winter habitat in that section of the basin (Henderson 1991).

Channelization and stream bank stabilization, designed to constrain the flow to a single channel, eliminate complex edge habitat along stream margins. The most developed edge habitat (i.e. backwater areas, eddy pools, etc.) is used extensively by juvenile coho (and other species) throughout the year. Newly emerged coho fry remain closely associated with the stream edge until their swimming skills allow them to venture into the middle of the channel (Bisson et al. 1987); and migrating coho smolts may use the edge habitat along the lower river section as resting and feeding areas (Bisson et al. 1992).

Considering that the restoration of the watershed to its pre-colonial times is not a viable alternative, I decided to elaborate a management strategy that could maximize the capacity of the system to sustain coho salmon within the bounds of present land use patterns. Approaches to habitat rehabilitation are well documented in the literature and some of them could be applied to the Salmon River. Information, however, about the mechanisms through which some habitat components, such as physical complexity or food, influence coho salmon distribution is derived from my experimental results. In my management recommendations I consider the different spatial scales of the watershed components affecting coho salmon distribution and abundance, and emphasize the importance of maintaining the connectivity of the system.

7.3. Coho salmon habitat protection within an integrated management plan

The close links and mutual interactions between a stream and its valley require that we consider rivers in a landscape context (Hynes 1975, Vannote et al. 1980, Pinay et al. 1990, Stanford and Ward 1992). Managers have to be particularly aware of this, because any stream protection or rehabilitation plan will be effective only if the entire watershed is adequately managed and protected (Reeves et al. 1991).

Simplistic habitat rehabilitation methodologies that are described in the literature have varying degree of success in achieving their goal, and they cannot be used to compensate for poor watershed management practices. The problem is that if the structural and functional nature of the entire watershed is ignored, all localized management practices will likely produce results very different from the expected ones. This is because habitat enhancement projects that are not planned in the context of the entire ecosystem tend to interfere at some point with the processes that maintain the connectivity among watershed components. For example, high rates of damage and failure of artificial stream structures were reported in southwest Oregon and Washington streams following high peak flows (Frissell and Nawa 1992). Artificial stream structures which caused flow alterations and changes in channel morphology and stability were the ones subject to the highest rates of damage and displacement. In contrast, anchored naturally occurring woody debris accumulations, which minimally altered pre-existing channel characteristics, showed lower rates of failure or impairment. In all cases, the highest failure rates of these habitat enhancement projects were observed within watersheds with eroding roads, logged slopes, and deteriorated riparian areas (Frissell and Nawa 1992). This indicates that watershed-driven processes controlling channel dynamics need to be considered when stream habitat restoration projects are planned. The use of a stream hierarchical classification system (see Frissell et al. 1986) in the early planning stages of this type of projects would greatly increase their success rate.

Unfortunately, agencies responsible for fish habitat management have a tendency to apply "handbook" methodologies, which rely either on little empirical and experimental information or were developed for ecosystems that differ from the ones managers end up implementing them in (i.e. coastal instead of interior streams , valley instead of upland wetlands, etc.). Programs of stream rehabilitation that consist of a variety of isolated and target oriented management techniques (the target being a particular habitat type associated with a specific stage of the fish life-cycle) are not uncommon. It is likely that

these practices are further encouraged both by studies reporting increased salmonid abundance as a result of local manipulations of stream habitat (Shetter et al. 1946, Saunders and Smith 1962, Hunt 1969 & 1971, Ward and Slaney 1981, House 1991, Nickelson et al. 1992b), and by the fact that studies showing no effect or even negative effects on fish abundance have been published less frequently than those with favourable results (Hamilton 1989).

An additional problem associated with small scale habitat rehabilitation projects is that the vast majority of them, after completion, are never monitored over extended periods of time to assess whether the initial long term goals are actually met (Stanford and Ward 1992). The risk of this practice is that, potentially valuable management techniques and initiatives may loose public support over time, as people realize that of the many habitat rehabilitation projects that were publicly funded over the last decade very few were ever evaluated and produced documented evidence of an actual increase in salmonid numbers (Reeves et al. 1991).

Despite their limitations, properly planned local habitat enhancement projects may benefit salmonids, and may be better than no action at all. My experiments and field observations show that juvenile coho salmon move among pools in stream reaches (both downstream and upstream) and they respond to local conditions by settling into the most suitable habitat patch they find (Chapters 4 and 5). Evidence of high rates of fish movement in streams is also provided by Riley and Fausch (1995) and Fausch et al. (1995), who reported that localized increase in trout densities in response to the installation of individual log structures was largely caused by fish immigration from untreated stream sections. As a result of this, small scale habitat enhancement projects may potentially boost streamwide fish production by making available to "subordinate" individuals habitat left vacant elsewhere.

However, a watershed management perspective is fundamental to ensure that the increase in fish production achieved through local habitat enhancement projects is

176

maintained in the long term. An integrated (or cooperative) management plan represents a more rational approach to watershed management. A single agency, much less an individual manager, cannot possibly deal with the actual complexity of an entire catchment area. Cooperation among a large number of "managers" from different government agencies and interest groups is necessary for the evaluation of the best management practices (BMPs) (state-of-the-art environmental protection measures, as defined in Bisson et al. 1992) that are based on long term data and research and that do not interfere with the natural connectivity of the watershed.

Approximately twelve years passed between completion of the first reports recommending cooperative watershed management in the Salmon River (see Paish 1980 & 1981) and the first clear step towards implementing such a management plan. This step was the creation of the Salmon River Watershed Management Partnership (SRWMP) in 1992. The SRWMP represents a concerted effort by a variety of government agencies, public organizations and educational institutions to overcome the difficulties associated with fragmented jurisdictions among agencies and to eliminate traditional insular approaches to resource management. Its list of current members, in addition to the Township of Langley, includes federal agencies: DFO, Environment Canada, Fraser Basin Management Program, and the Fraser River Action Plan; provincial agencies: Ministry of Environment, Lands and Parks (MOELP), and the Ministry of Agriculture, Fisheries and Food (MOAFF); educational institutions: the University of British Columbia, and Kwantlen College; and non-government organizations: Langley Environmental Partners Society, Langley Environmental Organization, Langley Field Naturalist, Fort Langley Farmers, and the Matsqui/Langley Soil Conservation Group.

Of the several phases in the development of a watershed management plan, the SRWMP has completed the first and fundamental one; a preliminary scientific survey of habitat sensitivity or vulnerability (see Cook et al. 1993). This type of analysis indicates the sensitivity that habitats, communities, and species have to environmental change. It

177

also identifies very fragile components that are difficult to restore. The next phase would involve the development of the management component of the plan in relation to social needs and desires. At this point, options for protecting, rehabilitating, or modifying the systems hydrologic pattern and the stream channel characteristics have to be chosen. For example, if the integrity of the stream and the conservation of salmonid resources are important, it will be necessary to consider a minimum guaranteed summer flow, and plan on an acceptable winter flood regime that enhances the connectivity of the stream with its valley and increases the availability of fish habitat. The next option involves making management decisions regarding biological components of the watershed, which can be manipulated to attain predetermined objectives (i.e. riparian community, beaver populations, fish species, etc.). Land use management decisions follow, and they must be consistent with the selected flow and biological options chosen earlier. They involve controls on man-induced damage to the physical and biological components of the system (i.e. rezoning of sensitive areas, cattle fencing, manure management, etc.). The last option to be included in the plan is the compensation scheme and the non-development alternative. Compensation may be necessary if development is allowed in areas of high or intermediate sensitivity (ESA 1 and ESA 2 in Cook et al. 1993). For example, developers using land either in or adjacent to ESAs should be required either to dedicate or set a conservation covenant of an environmentally sensitive area (for a detailed explanation on different local governments tools to encourage non-development in ESAs see DFO 1993). The high level of "sensitivity" of an area (i.e. presence of endangered species) may justify its designation as a conservation zone.

7.3.1. Management recommendations

Valuable information for the development of the Salmon River cooperative management plan is already available from the evaluation of ESAs in the Township of Langley by Cook et al. (1993), and from several general manuals on fish habitat

enhancement by DFO and MOELP (Adams and Whyte 1990, Chilibeck et al. 1992, DFO 1993), and agriculture waste management guidelines (MOAFF 1992a & 1992b). The implementation, through different incentives, of many of the management practices presented in the above mentioned publications will help attenuating human impact on stream habitat. However, the redefinition of terms of cooperation among agencies, the design of effective regulatory instruments (see Bowen 1987, Feitelson 1987, Hocker 1987, and Pearce et al. 1989 for information on taxation, trusts and other regulatory instruments), and the arrangement of an active public consultation system, represent important "political" obstacles that still have to be overcome for the management plan to actually achieve the desired effects.

Technical problems, although very important in many circumstances, tend to be less of an obstacle. It is important to remember that a management plan will be most effective if it is flexible enough to respond to new scientific knowledge and the development of new techniques. In addition, the plan efficacy will be enhanced by the consideration of the three following principles: a) watershed integrity should be protected through the conservation and enhancement of connectivity among its components; b) long-term monitoring and study programs should be conducted to evaluate the effectiveness of best management practices, and determine whether environmental changes are naturally caused or man-induced; and c) management decisions should be made within the context of the entire watershed, and contingency plans should be developed in case monitoring reveals that the implemented management actions interfere with processes that maintain the connectivity of the system (Stanford and Ward 1992).

Because of this connectivity, the long term protection of salmon habitat can only be accomplished within the context of integrated watershed management. Given the hierarchical organization that a stream system has, and for practical purposes, a

management project should consider the different spatial scales of the watershed components and linking processes. Therefore, a possible strategy would be to devise two "spatially nested" plans.

1 - A large scale plan should encompass the entire watershed and focus on ecosystem components that are higher in the functional hierarchy. Components that can only be effectively managed for the entire basin (i.e. hydrologic regime, water quality, etc.). For example, the preservation of a hydrologic regime that ensures a regular flow of low temperature waters in the river during summer and maintains the natural frequency and magnitude of floods in winter, is crucial for the conservation of salmon habitat. This can only be achieved if actions are taken at the watershed scale to control, among other things, underground water extraction and urban sprawling. Excessive extraction of water from aquifers and the expansion of urbanized areas close to the headwaters (Aldergrove) and in the middle reaches (Salmon River Uplands) of the stream will negatively affect water quality and flow regime. Unusually frequent and large winter peak flows, induced by vegetation removal and urbanization, will displace and damage small scale habitat enhancement projects.

A first step to deal with these problems has already been taken with the creation of the Agricultural Land Reserve (ALR). Because changes to the system's hydrology caused by agricultural lands are smaller than those created by urbanized areas, the protection of the agricultural character of a large proportion of the watershed facilitates the conservation of a regular flow regime. But, although land zoning is a useful management tool, it cannot successfully protect the stream from human disturbances if additional control mechanisms are not implemented. This is illustrated in part by the fact that despite the ALR, a progressive withdrawal of land from agriculture is occurring in the watershed (Watts 1992). A small fraction of it has been urbanized, while the largest proportion remains undeveloped, possibly awaiting the opportunity for subdivision. Further interference with the watershed's hydrology and the quality of its water will likely

be increased by the implementation of intensive farming practices, suggesting that the impact of the individual farms on the lotic system will perhaps increase. More emphasis on conservation of natural areas (i.e. dense woods, wetlands, etc.) is recommended, but as an isolated strategy will not be enough to counter balance the effects of increasingly intensive agricultural practices and slow, but ongoing, residential development. Therefore, the large scale management plan must include mechanisms that complement land zoning legislation. Farm water use optimization should be promoted (evidence suggests that less than half the water used in irrigation actually benefits the crops, see Postel 1990), water needs of water license holders should be reviewed, and underground water extraction should be regulated. An education campaign should be carried out to increase the awareness of the watershed's residents about the negative impacts, the routes (point vs non-point sources), and sources (i.e. household chemicals, fertilizers, manure, etc.) of pollution that affect both stream and underground water quality. Finally, mitigation strategies to reduce the impact of urbanized lands on the hydrology of the system should be considered a "must" if the preservation of the stream normal hydrograph is actually expected (for a review of techniques see DFO 1993, and for engineering flaws associated with some of those techniques see Booth 1991).

2 - The smaller scale management plan, should seek to protect watershed components of a lower hierarchical level, managing them at the scale of reaches and stream sections (i.e. riparian communities, input of woody debris, channel morphology, bank erosion, etc.). Because the stream characteristics change from the headwaters to the mouth, the plan should consider the application of different management strategies to the three main sections of the Salmon River. As my winter surveys revealed, the lower reaches of the watershed are important in the winter phase of coho's life cycle by providing refugia. In summer, however, they only offer - along with some of the upper reaches - suboptimal summer habitat for juvenile coho salmon.

Protecting and increasing the amount of available winter habitat in the lower reaches, should have a positive effect on a system like the Salmon River, which seems to have an overall shortage of overwintering refugia in its middle reaches (see Chapter 3). A first step would involve a thorough field survey of potential winter habitat in the watershed to estimate whether it actually represents the bottle-neck of coho salmon production in the Salmon River. If its scarcity is confirmed, the next action should be directed to improve the existing off-channel habitat (tributaries like Davidson Creek, riverine ponds at MacMillan Park, side ditches, sloughs, etc.). Winter habitat enhancement plans should include several kinds of actions: a) to increase the availability of woody debris in many of the already existing habitats (i.e. the riverine ponds I surveyed had very little woody debris); b) to improve connection between these off-channel units and the mainstem of the river (fish should be able to have access to off-channel habitat, and move out of them when their water level declines); c) to deepen some of the ditches, and place natural flow deflectors in case storm's run-off increases the velocity of the water in them (overwintering coho salmon are extremely sensitive to changes in water velocity); d) to redesign those ditches that have been dredged to drain faster into the mainstem so they retain water for longer periods of time, fish use them if water velocity in them is slow (this measure may not be welcomed by many farmers, but not all ditches are draining farm fields); and d) livestock should be fenced off all channels and ponds, to protect the physical integrity of all these units. Some units may respond very quickly to the slightest improvement and attract increasing numbers of fish, while others may remain unused for a variety of reasons. It is important to ensure that any enhancement work conducted in the stream is adequately supervised and its effects are monitored over an extended period of time. Lack of post-treatment data is a common problem in many habitat enhancement programs, and this information is necessary to assess the actual effectiveness of the selected rehabilitation technique. In many instances choosing enhancement methodologies out of a "manual" is relatively simple. But it is recommended that small

scale experimental manipulations be conducted in the field, to identify the most effective enhancement technique for a particular habitat type.

Only if after enhancing the currently available winter habitat (both in the lower and the middle reaches) its abundance was confirmed to set a limit to the production of juvenile coho in the Salmon River, should construction of artificial overwintering areas be considered (see Adams and Whyte, 1990, for information).

Davidson Creek deserves special attention given its unique characteristics. As my empirical data suggest it sustains throughout the year what is likely to be a subpopulation of Salmon River coho, and it offers extensive off-channel habitat for overwintering fish from other parts of the watershed (see Chapter 3). The same management principles to increase winter habitat I discussed earlier could be applied to the lower reaches (between the railway and its confluence with the Salmon River) of this creek. But the middle-upper reaches of Davidson Creek should receive more protection than they currently do, considering their salmon spawning and rearing potential (i.e. beaver ponds have been repeatedly blown up according to some neighbours of the area, and instream garbage blocking fish passage is not uncommon).

Management in the lower reaches offers a unique opportunity for testing the *in situ* effectiveness of a number of habitat enhancement methodologies. A flexible strategy combining best management practices, with research and long-term monitoring will increase the chances of successfully increasing not only winter but perhaps also summer habitat in this part of the river. The management plan to be implemented in the lower reaches should emphasize off-channel habitat physical protection. It is likely that impact mitigation techniques (i.e., riparian tree planting, fencing, bank stabilization, etc.) will have to be utilized frequently, particularly where agricultural activities reach the watercourse. However, the cooperative nature of the management plan should allow fisheries managers to work more effectively with the farmers, instead of against them.

In the central part of the watershed, considering it offers coho very good spawning and summer rearing habitat, the management plan should emphasize protection from man-made disturbances. The maintenance of a well developed riparian forest is very important because it works as a buffering agent that diminishes the impact of land use in the vicinity of the stream channel. It is important to underline that riparian buffer strips can reduce but not eliminate all problems created by different land uses. In Alaska, their minimum effective width has been estimated to be approximately 30 m on either side of the stream. Apparently, any significant supply of either woody debris, aquatic food or shading for the stream decreases markedly beyond this distance (Murphy et al. 1986, Budd et al 1987). Many municipalities in Washington State have also adopted a 30 m wide buffer corridor. But, the optimal buffer strip width has to be re-considered regionally based on the local topography, hydrology, soil composition and the adjacent development. A width of 30 m may not be enough to protect the stream habitat from the impacts of high density urban development or extraction activities (Booth 1991).

Riparian forests not only protect stream banks from erosion, but increase the hydraulic diversity by incorporating elements of "roughness" (i.e. logs, etc.) that deflect or slow down the current. Large fallen logs (especially red cedar, *Thuja plicata*) create different types of pools that offer a variety of habitat conditions for juvenile salmonids. Pools constitute the type of habitat that coho salmon prefer. My experimental work also indicates that they favour pools with intermediate to low densities of woody debris which offer open foraging grounds close to covered areas (see Chapters 4 and 5). I found that pools with high density of fine woody debris have a lower density of coho in them than pools with intermediate-low debris abundance. High densities of woody debris cause shortage of the type of open areas that coho prefer to forage in. These results caution against indiscriminate artificial placement of woody debris, because there is a risk of having too much of a supposedly "good" thing. They also suggest that short riparian clearings (the length of a few pools) may not have a negative impact on the capacity of the

system to produce coho salmon. Small open areas may even increase the local production of benthic invertebrates that coho salmon feed upon, therefore, their entire obliteration by excessive treeplanting may not be the best management strategy. Besides, tree planting projects should put the emphasis on recreating the diversity of the original riparian community, not just on planting the largest possible number of trees. Trees like the ones that dominate the second growth riparian forest in the middle reaches of the watershed (red alder and vine maple) contribute mainly fine woody debris to the stream. Compared to old conifer logs, red alder logs are too small to have any important effect on the morphology of the channel and do not last long (a red cedar log may last over 100 years in the stream). For this reasons, projects involving large woody debris stabilization, addition of large coniferous stumps and rootwads in reaches that lack hydraulic complexity, and riparian coniferous planting should bee given priority in this section of the watershed.

Management in the upper section of the watershed should have a similar approach to that already described for the lower section. It should also emphasize the implementation of mitigation and protection actions. The effectiveness of any of the mitigation methodologies should be monitored and, as in the lower reaches, there is the possibility of conducting small scale experimental manipulations to developed habitat enhancement and mitigation techniques that better adapt to the specific characteristics of this system. The fact that these reaches are occupied by Salish suckers should help to further promote the protection of the systems headwaters in any management strategy. The upper reaches have a very important role in the collection and transference of water and sediments to the downstream reaches. Therefore, their management should stress control of soil erosion (i.e., riparian planting, cattle fencing, adequate land tillage, etc.) and improvement of water retention capacity in the land they drain (i.e., development of holding ponds and wetlands to offset the impact of urban zones, restriction of further urbanization near the system's headwaters).

The protection of structural complexity and habitat heterogeneity is a fundamental tenet in any watershed management plan designed to maintain, or increase, the production of coho salmon smolts. Management should protect habitat heterogeneity by controlling the causes of its reduction (i.e. frequent peak flows, lack of instream structures) and preventing further degradation, instead of fighting their consequences with small scale enhancement methodologies alone. Management of natural resources has often been reactive in its approach, a more proactive view is long overdue. This implies that the prevention of habitat degradation and loss must start now, instead of considering that current mismanagement can continue, because effective rehabilitation techniques may be available in the future. Habitat protection is by far the most effective stream rehabilitation and enhancement technique. The intention of the SRWMP of creating a long term cooperative management plan for the watershed is an important step in the right direction.

Effective salmon habitat protection plans will require that land use within watersheds change to reflect the needs of the aquatic organisms. The endorsement of such a stream habitat protection plan by farmers, among other watershed residents, will be necessary to ensure its viability. Their support will not be obtained unless the costs to their economy originated by new stream protection regulations are fully covered. Therefore, society will have to be prepare to pay the costs associated with sustainable management plans. It is possible that the benefits to both the local and the regional economy derived from the protection of stream resources are enough to offset those costs. Healthy coho salmon stocks will maintain a lucrative sport fishing industry and will also contribute to the economy of the commercial industry. Taxes generated from these sectors could contribute to pay for the rehabilitation of stream habitat. At a municipal scale, it is likely that the long term preservation of the rural nature of the watershed gave origin to economic activities (i.e., organic farming, recreation, short-term tourism, etc.) that could also contribute to counterbalance some of the costs derived from environmentally sound farming practices and extremely restricted residential development.

CHAPTER 8

SUMMARY AND CONCLUSIONS

8.1. Juvenile coho salmon distribution and habitat use during summer

In the Salmon River Watershed the middle reaches, between 72nd. Ave. and 256th. St., offer coho salmon the best summer rearing habitat. Among them, reach S1 (which is comparatively larger and more complex than the other study reaches) holds the largest proportion of the population of coho salmon and shows the highest average rearing density. C2 is second to S1 in coho salmon density and is followed in order of decreasing fish density by the other two reaches, S2 and C1. No coho salmon are found in the upper reaches of the Salmon River, upstream from S2. But in Coghlan Creek their distribution extends beyond C2 into the creek's headwaters.

In the lower reaches of the watershed two sections can be identified, and upper one with suboptimal habitat (which extends between 72nd Ave. and Rawlison Crescent), where coho salmon rear at very low densities, and a downstream section (that runs through the floodplain from Rawlison Crescent to the mouth of the river), that is unsuitable for juvenile coho salmon during the summer. In contrast, the headwaters of a spring fed floodplain tributary of the Salmon, Davidson Creek, offer suitable conditions to sustain a small coho salmon subpopulation throughout the year.

Mean coho salmon size varied among reaches. The lowermost reaches and S2 were occupied by coho salmon that, in average, were larger than in other parts of the watershed. Reaches S1 and C1 had coho salmon of intermediate size, whereas C2 was the reach that reared the smallest size coho salmon in the system (with the exception of Davidson Creek).

At a reach level the distribution of coho salmon is not uniform, and their rearing densities vary greatly among the different types of hydraulic units. Pools are preferred by

coho salmon over units with faster water velocity, and among them two types: lateral scour and backwater pools, stand out as offering the best combination of habitat factors to a large proportion of coho salmon in the watershed. Trench pools and glides sustain much lower rearing densities. Riffles are almost unused by juvenile coho, but play a very important role as spawning grounds and benthic invertebrate producing habitat.

Large size coho salmon predominate in lateral scour pools, as well as in other main-channel units such as trench pools, where the unidirectional arrival of food induces them to establish feeding territories. Lateral pools offer some of the best rearing conditions, because they combine abundant cover against one of the banks, with adjacent clear drift-rich patches in mid-channel location. Backwater pools, as well as any available off-channel habitat, are utilized by coho salmon that are, on average, smaller than those in other types of habitats and, apparently, of lower hierarchy. Units removed from the main-channel flow, do not offer benthic invertebrate drift and most prey that coho salmon can find come from terrestrial sources. These units, with their lower foraging quality, do not attract coho salmon that can successfully defend a territory in main-channel habitat. Instead, backwater pools and off-channel units are utilized by large numbers of coho salmon that forage by cruising along the entire unit and do not establish territories. This type of hydraulic units provide rearing habitat to fish that, otherwise, would be displaced and lost to the poor quality habitat of the watershed's lower reaches.

8.2. Juvenile coho salmon distribution and habitat use during winter

At a watershed scale, distribution of coho salmon changes among reaches of the Salmon River Watershed with seasons. Specifically, the lower reaches of the system and its network of off-channel habitat become an important overwintering area for coho salmon that emigrated from the middle reaches.

Within the middle reaches, however, changes are not that obvious. Lateral scour pools, backwater and off-channel units are selected during winter by a large proportion of juvenile coho. But, because this kind of habitat is also the most utilized by them during late summer, it is not possible to speak about a complete seasonal redistribution of coho. Backwater pools show the highest rearing densities, particularly in reach S2 and reach C1. In contrast with what is observed in summer, the average weight of coho salmon occupying backwater pools is not significantly smaller than that of coho salmon in other type of units. These units are not longer exclusively used by small subordinate coho. This is likely to derive from a habitat shift by many of the individuals that occupied the main channel during summer and moved into these backwater pools with the first fall freshets.

Coho salmon prefer units with abundant cover and, in general, remain closely associated with it. Most of them do not use open patches at all. Instream cover not only shelters overwintering coho salmon from high water velocities, it is also likely to protect them from predation during a period characterized by reduced fish activity, and it may even increase visual isolation among individuals.

As winter approaches the importance of the lower reaches in the life cycle of Salmon River coho salmon increases markedly. Coho salmon that move downstream with the first high flows find overwintering refuge in the off-channel habitat of the lower reaches. The mainstem of the river is used by comparatively few individuals, but coho salmon relative abundance in some off-channel areas is estimated to be high. Small tributaries, ditches and drainage channels were preferred to off channel ponds, in which almost no coho salmon were found.

Davidson Creek, in the watershed's floodplain, provides good overwintering habitat. Its rearing densities vary broadly from one site to the next, but tend to increase with distance from the mouth of the creek. Although large coho salmon predominate throughout the lower reaches, individuals in Davidson Creek belong to two different size

classes. The larger coho salmon are likely Salmon River emigrants entering the creek in search of overwintering habitat, whereas the smaller fish may be permanent "residents" of the creek. There are signs that these "resident" coho salmon are spawned near the headwaters of this creek, and survive the summer in spring waters. If the existence of this coho salmon subpopulation in the Salmon River Watershed is confirmed, the importance of this creek goes beyond its capacity to shelter overwintering coho. Its marginal subpopulation may contribute to maintain the genetic diversity of the Salmon River coho salmon stock.

8.3. Downstream movement of juvenile coho salmon during winter

My experimental results showed that coho salmon are sensitive to small changes in streamflow during the winter. Their tolerance for any increase in water velocity is limited, and they seem ready to move to secluded sites and to use velocity refuges as soon as a flow increase is perceived. Water temperature affected the proportion of fish that moved downstream. As it decreased, less fish try to leave the channel. Instead, the availability of food did not alter the pattern of coho salmon movement in my experiment. Coho salmon fed, but they barely grew and the mean condition factor (K) for the entire stock decreased from January to March.

8.4. Juvenile coho salmon choice of habitat in response to food and cover

The results of my experiments show that coho salmon numbers increase with patch foraging quality. But they are not directly proportional to patch profitability as predicted by the ideal free distribution model. The addition of physical complexity, such as instream or overhead cover, further deviated the distribution from an ideal and free pattern. When choosing a foraging patch within a pool, coho salmon preferred open patches away from cover. But favoured pools with cover when selecting between

separate pools. None of the alternative dispersion models that I considered (ideal despotic distribution, ideal free distribution of unequal competitors, and ideal free distribution with perception limits) fully explains the observed dispersion patterns.

Coho's ability to maximize food intake rate was not only affected by the physical complexity of their habitat, but also by intraspecific competition and interference. The complex stream habitat that coho salmon favour (that provides still water patches next to drift-rich currents and open pool areas close to heavily covered ones), hinders their ability to assess relative patch quality. This consistently results in underestimation of the value of food-rich patches and overestimation of food-poor patches.

It is likely, that non-despotic and despotic interference further complicate the process of resource detection and consumption for individual coho, regardless of their social status. The unequal size of coho salmon by the end of my series of individual pool experiments, in the absence of evidence of despotism, implies that they differed in their abilities to exploit food resources.

The importance of instream structures for coho salmon changes over time. Earlier in the summer, fry are indifferent towards cover, but as they become older their association with instream woody debris increases. If food is abundant in the system, they prefer pools with low-medium cover density which offers accessible refuge and leaves unobstructed foraging patches where prey and perhaps also predators are easy to detect. Feeding in the open patches during summer is a strategy that maximizes food intake and growth, therefore, influencing winter survival and smolting rate. However, it also increases predation risk. But coho salmon have been reported to be less sensitive to risk of predation when fish densities are high (Dill and Fraser 1984). The very large numbers of coho salmon present in productive coastal streams may indeed decrease the individual risk of predation in clear patches.

Results from my experiments (coho salmon favouring pools with woody instream structures, yet avoiding the patch with cover within a pool; different response to cover

by spring coho salmon fry and late summer coho salmon parr) help explain the contradictory information found in the literature on the role of cover in coho salmon habitat. A rather flexible response to a variety of reward and risk situations, and an interaction between food abundance and cover availability in the determination of coho salmon rearing densities was observed when both cover and food abundance changed from pool to pool in a channel. It is possible that the final selection of habitat patches results from a ranking of priorities by coho. Food acquisition may have top priority, followed by cover utilization. Ultimately other factors, such as density of competitors, may also influence the distribution of the fish.

Coho salmon preferred fine woody structures in mid-summer (July). But by late summer (August-September) they showed similar affinity for both large woody debris (logs) and sparse fine debris., indicating that at least during the low-flow period debris size is not an important factor. It is very likely, however, that large logs play a very different role in faster flowing streams, particularly in fall and winter. But in small valley streams with low summer flows the density of the debris may be more meaningful for coho salmon than the diameter of its pieces. In my experiments in Coghlan Creek, both sparse fine debris and large logs offered some cover from predation in the middle of open pool patches.

8.5. Habitat degradation and habitat protection

In many streams of the Lower Fraser Valley, adequate juvenile coho salmon habitat is being eliminated by a large number of development associated activities. In the Salmon River in particular agriculture and residential development represent the two land uses with potentially greater impacts on coho salmon habitat. Although the effects of urbanization are potentially more dramatic, they both increase size and frequency of winter peakflows and reduce baseflows in the stream. Fish that survive the increased restrictions

in summer flow, enter a season of frequent and magnified freshets without adequate flow refuges. This is because marshes, sidechannels, beaver ponds, off-channel ponds, sloughs and small tributaries are reduced or entirely eliminated a result of land uses associated with agriculture and urbanization. Additional detrimental changes to coho salmon habitat derive from: a) increased soil erosion that translates into higher water sediment transport; b) riparian forest alteration that reduces the imput of woody debris to the stream (whilst woody debris from the channel is removed by increased peakflows); c) water quality degradation by increased temperatures (resulting from riparian removal), and pollution (farming activities, septic systems, urban runoff); and d) reduction of channel complexity (by loss of structures, pool filling, channel widening).

A watershed management plan that has the protection of salmonid resources among its priorities would benefit from considering the different scales that watershed components have and the connective functions that maintain its vitality and resilience. If the plan only considers management strategies that deal with habitat issues at one single scale (most commonly that of a stream reach or section) the results may be satisfactory in the short term. For the positive effects of local projects to be felt in the long term they must be coordinated as part of a plan at the watershed level. Thus, strategies that protect watershed scale components (hydrologic pattern, channel morphology, water quality and quantity) must be implemented as the top layer of the plan. Under it, a set of strategies aimed at managing and protecting fish habitat in different stream sections is recommended.

In the particular case of the Salmon River Watershed it is possible to distinguish a lower, a middle and an upper section. management strategies for these three sections should be decided taking into account their different physical and biological characteristics. The middle section is important to ensure the survival of the local salmon population, and habitat conservation should have special emphasis in it. In the headwaters, management strategies should be directed towards maintaining a regular supply of good quality water to the middle section of the basin (and the underground

reservoirs). The protection of the water "collecting and filtering" role of the upper reaches is essential to maintain salmonids rearing downstream. In the lower section of the river strategies that increase the availability of coho salmon winter habitat are recommended. This relatively simple objective, may translate in an important increase in coho salmon smolt production in the system. Naturally, the reduction of smolt mortality at the river mouth's pump (i.e. pump replacement, permanent trap system in the floodplain reach of the river) should be included among the strategies directed towards increasing coho salmon production.

The final layer of the plan includes protection, enhancement and mitigation methodologies tailored to address the particular conditions of different reaches within the differen river sections. These methodologies will vary from reach to reach, but in most cases will involve restoration and protection of riparian forests. Riparian vegetation contributes in many different ways to the quality of coho salmon habitat, and this must be recognized as central to any management plan.

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Appendix A: List of habitat units sampled during the summer of 1991.

ID (Location)	Type of unit	Length (m)	Mean Width (m)	Mean Depth (m) (mid-channel)	Area (m²)
6A (low)	TP	8.00	7.00	0.73	56.00
6B (low	GL	13.70	4.67	0.55	63.98
6C (low)	GL	15.50	4.52	0.44	70.00
7A (low)	TP	12.00	6.86	0.63	82.35
8A (S1)	GL	10.90	4.25	0.37	46.32
8B (S1)	BP	17.60	3.53	0.39	62.13
9C (S1)	GL	25.00	4.90	0.26	122.50
9D (S1)	LP	10.10	5.25	0.61	53.02
10A (S1)	TP	26.00	9.33	0.50	242.58
11A (S2)	LP	21.70	7.23	0.59	156.89
13A (S2)	LP	20.50	5.06	0.34	103.88
13B (S2)	TP	16.00	6.75	0.82	108.00
13C (S2)	GL	16.00	5.83	0.77	93.32
15A (S2)	TP	32.15	5.30	0.70	170.47
15B (S2)	GL	24.50	2.74	0.25	67.25
20A (C1)	GL	9.60	5.88	0.19	56.52
20B (C1)	LP	11.30	4.71	0.55	53.25
20C (C1)	BP	6.90	2.55	0.33	17.59
20D (C1)	RF	15.00	7.83	0.10	117.56
22A (C1)	TP	14.40	5.51	0.50	79.38
22B (C1)	GL	22.10	4.15	0.19	91.72
22C (C1)	RF	15.50	4.00	0.14	62.00
23A (C2)	RF	19.50	4.70	0.22	91.65
23B (C2)	BP	6.65	2.52	0.34	16.73
24A (C2)	BP	4.70	4.40	0.22	20.68
24B (C2)	LP	10.00	2.64	0.31	26.37
25B (C2)	RF	17.70	3.65	0.08	64.60

Note: ID number indicates sampling station (for locations see Figure 3), ID letter identifies the individual habitat unit.

RF = Riffle
LP = Lateral scour pool
BP = Backwater pool
TP = Trench pool
GL = Glide

Appendix B: List of habitat units sampled during the winters of 1992 and 1993.

ID (Location) (year)	Type of unit	Length (m)	Mean Width (m)	Mean Depth (m) (mid-channel)	Area (m^2)
8A (S1)('93)	GL	12.50	6.26	0.71	78.25
8B (S1)('93)	BP	44.30	3.77	0.76	166.86
8C (S1)('93)	LP	16.40	7.43	1.07	121.90
9A (S1)('93)	TP	18.60	8.00	0.82	148.80
9C (S1)('92)	GL	31.00	5.66	0.65	175.60
9C (S1)('93)	GL	25.00	5.57	0.52	139.20
9D (S1)('92)	LP	15.10	6.80	1.15	102.68
10A (S1)('93)	TP	26.70	10.48	0.90	279.90
10B (S1)('93)	BP	8.40	2.70	0.54	22.68
11A (S2)('92)	LP	23.00	7.32	1.13	168.47
11B (S2)('93)	TP	26.00	7.71	0.90	200.50
11C (S2)('93)	BP	7.70	4.10	0.57	31.60
13A (S2)('92)	LP	20.60	6.12	0.71	126.00
13B (S2)('92)	TP	16.00	9.09	1.31	145.55
13C (S2)('93)	GL	16.00	8.09	1.27	129.50
15A (S2)('92)	TP	34.00	7.47	1.35	253.86
15B (S2)('92)	GL	27.00	5.25	0.57	141.75
20B (C1)('93)	LP	14.00	4.90	0.99	68.60
20C (C1)('93)	BP	8.25	3.95	0.60	32.59
22A (C1)('93)	TP	14.50	5.65	0.63	82.02
23B (C2)('92)	BP	10.70	4.30	0.78	46.01
23C (C2)('92)	LP	11.50	6.67	0.84	76.70
24A (C2)('92)	BP	4.80	5.00	0.46	24.00
24C (C2)('92)	GL	10.10	2.97	0.48	30.00

Note: ID number indicates sampling station (for location see Figure 3), ID letter identifies the individual habitat unit.

RF = Riffle
LP = Lateral scour pool
BP = Backwater pool
TP = Trench pool
GL = Glide

Appendix C: Sample size, estimated coho salmon numbers, densities, mean weight and mean length at each sampling station in summer.

ID	n	Leslie's Pop. Est.	SE	Density (fish/m²)	Max.Lik. Pop. Est.	SE	Mean Weight	Mean Length
6A	34	38.52	7.96	0.69	35	1.88	4.20	6.96
6B	12	16.59	0.57	0.26	17	0.26	3.24	6.42
6C	17	17.58	0.14	0.25	18	0.97	4.21	7.05
7A	34	36.97	4.19	0.45	34	1.08	3.74	6.69
8A	104	105.90	1.41	2.28	105	1.26	2.69	6.00
8B	247	294.74	36.14	4.74	263	6.37	1.85	5.25
9B	312	437.16	45.34	1.80	435	7.40	2.10	5.50
9C	78	82.90	9.92	0.68	81	2.78	2.99	6.24
9D	265	274.20	12.91	5.16	266	1.39	3.44	6.50
11A	153	301.50	43.59	1.92	292	12.10	3.08	6.39
13A	169	252.50	37.21	2.43	263	37.18	4.24	6.89
13B	59	85.00	0.48	0.79	85	1.97	3.54	6.28
13C	27	57.30	3.81	0.61	51	3.59	4.35	6.83
15A	101	102.70	3.08	0.60	101	1.07	3.10	5.83
15B	96	120.27	12.36	1.79	111	3.57	3.03	5.87
20A	14	15.38	0.05	0.27	15	0.59	2.15	5.54
20B	113	123.43	8.35	2.32	124	5.99	3.14	6.20
20C	38	42.04	5.07	2.39	39	1.82	2.01	5.30
20D	12	14.94	4.13	0.13	12	1.17	2.62	5.95
22A	129	132.15	1.45	1.66	132	2.55	2.45	5.66
22B	106	171.38	19.57	1.87	136	10.46	1.83	5.17
22C	19	20.28	1.08	0.33	19	0.77	1.77	5.16
23A	20	21.75	1.40	0.24	20	0.88	1.75	5.22
23B	44	44.53	1.55	2.66	45	1.48	1.91	5.27
24A	46	52.71	9.32	2.55	49	8.04	1.51	4.96
24B	77	80.15	1.16	3.04	78	1.61	1.81	5.16
25B	42	47.38	9.31	0.73	43	1.78	1.62	5.04

Leslie's Pop. Est.= coho salmon numbers were estimated using Leslie and Davies' CPUE formula.

Max.Lik. Pop. Est.= coho salmon numbers were estimated using maximum likelihood method.

Density of coho salmon in each unit was obtained dividing Leslie's Pop. Est. by that unit's area.

Appendix D: Eigenvector loadings of habitat variables on first three principal components.

Summer:

	Princ. Comp. 1	Princ. Comp. 2	Princ. Comp. 3
LWD	-0.086	0.013	0.934
FWD	0.357	0.605	0.092
IVG	0.493	-0.375	-0.151
OHC	0.564	-0.199	0.018
UCB	0.324	0.619	-0.068
FINES	0.446	-0.265	0.301

Winter:

	Princ. Comp. 1	Princ. Comp. 2	Princ. Comp. 3
LWD	-0.526	0.422	0.554
FWD	0.545	-0.112	0.800
OHC	0.631	0.219	-0.199
UCB	0.166	0.872	-0.115

Abbreviations for variable names:

LWD = Large woody debris;   FWD = Fine woody debris;   IVG = Instream vegetation;
OHC = Overhanging vegetation;   UCB = Undercut banks;   Fines = Fine sediments.

Appendix E: Sample size, estimated coho salmon numbers, densities, mean weight and mean length at each sampling station in winter.

ID	n	Leslie's Pop.Est.	SE	Density (A) (fish/m^2)	Density (B) (fish/m^2)	Max.Lik. Pop.Est.	SE	Mean Weight	Mean Length
8A	25	27.67	3.14	0.35	0.60	26	1.97	3.40	6.41
8B	157	172.80	8.90	1.04	2.78	171	6.75	3.59	6.72
8C	87	102.22	12.04	0.84	1.28	100	7.83	3.01	6.41
9A	67	78.49	7.33	0.53	1.21	75	5.81	3.04	6.26
9C*	44	46.79	3.99	0.24	0.34	45	1.71	3.86	6.53
9C	38	41.90	3.81	0.34	0.38	40	2.54	3.17	6.47
9D*	181	189.94	15.71	1.85	3.58	192	1.47	3.61	6.71
10A	47	51.00	4.39	0.18	0.21	48	1.56	3.61	6.53
10B	17	24.80	5.00	1.09	1.86	20	4.46	3.26	6.52
11A*	45	69.35	19.90	0.41	0.44	62	14.66	3.25	6.61
11B	19	27.00	0.22	0.14	0.23	23	5.56	3.81	6.43
11C	36	44.18	9.38	1.40	1.89	40	4.09	3.81	6.65
13A*	63	93.40	19.87	0.74	0.90	86	16.63	5.87	7.51
13B*	26	28.29	3.41	0.19	0.26	27	1.90	6.99	7.88
13C	36	49.42	5.61	0.38	0.53	44	7.63	6.05	7.81
15A*	56	62.93	5.32	0.25	0.37	59	2.87	5.42	7.47
15B*	37	44.04	4.85	0.31	0.65	41	4.16	6.28	8.04
20B	59	80.17	6.55	1.17	1.51	70	8.04	4.98	7.18
20C	33	44.37	11.01	1.36	2.52	40	7.06	4.58	7.27
22A	17	19.34	3.99	0.24	0.24	17	1.02	4.06	6.63
23B*	68	75.00	8.36	1.63	4.49	73	4.02	3.88	6.72
23C*	73	91.00	12.04	1.19	5.44	86	8.49	3.89	6.69
24A*	16	16.50	3.31	0.69	0.80	16	0.72	3.32	6.51
24C*	6	8.28	1.71	0.28	0.31	6	1.00	3.82	6.45

Leslie's Pop. Est.= coho salmon numbers were estimated using Leslie and Davies' CPUE formula.

Max.Lik. Pop. Est.= coho salmon numbers were estimated using maximum likelihood method.

Densities of coho salmon in each unit was obtained dividing Leslie's Pop. Est. by that unit's area.
Density (A) was calculated using the area of each unit at winter high-flow.
Density (B) was corrected to facilitate comparison with summer densities; it calculated using the area of each unit at summer low-flow
ID*: indicates that unit was sampled in 1992, all other units were sampled in 1993.

Appendix F: Fish numbers caught with minnow traps in the lower section of the Salmon River during winter. Mean coho salmon weight and length at different sampling stations.

Sampling station	CPUE (# coho)	CPUE (# coho)	CPUE (# coho)	Mean CPUE	Mean Weight (g)	Mean Length (cm)
1A	0	0	0	0	--	--
2A	0	0	0	0	--	--
3A	1	1	1	1	8.17	8.90
4A	1	3	5	3	8.49	9.08
4B	9	15	12	12	4.62	7.62
4C	1	3	2	2	4.28	7.45
4D	82	12	23	39	8.98	9.36
4E	11	4	12	9	5.30	7.90
4F	52	29	18	33	5.17	7.69
4G	72	111	51	78	2.33	5.90
5A	0	5	1	2	8.14	8.89
6A	0	0	0	0	--	--
7A	6	1	8	5	6.46	7.35
7B	1	0	2	1	8.71	9.12
7C	19	6	35	20	8.53	8.95
7D	9	23	19	17	8.30	8.76