Coho Salmon (*Oncorhynchus kisutch*) Life History Patterns in the Pacific Northwest and California

Final Report

March 2007

Prepared for
U.S. Bureau of Reclamation
Klamath Area Office

Prepared by
Lawrence C. Lestelle

Biostream
environmental

17791 Fjord Drive NE Suite AA
Poulsbo, WA 98370
360-697-6702

ACKNOWLDGEMENTS

Table of Contents

List of Figures

List of Tables

Executive Summary

In 1997 coho salmon (*Oncorhynchus kisutch*) in the Klamath River basin, as part of the Southern Oregon Northern California Coasts evolutionary significant unit (SONCC Coho ESU), were listed as threatened under the Endangered Species Act (ESA). The National Marine Fisheries Service (NMFS) cited water management, water quality, loss of habitat, overfishing, and other factors as causing a serious decline of the species within this ESU.

In the Klamath basin, the roles of different habitats to the performance of coho salmon have been a subject of much debate and controversy. Of particular concern is the use and importance of the mainstem Klamath River relative to the tributaries. This issue has a significant bearing on how flows are to be regulated in the mainstem river for the protection and restoration of the species. It also bears on how managers perceive the relative importance of different habitats in formulating an overall recovery plan for coho salmon in this basin.

The purpose of this report is to review coho life history patterns and associated life stage specific survivals. The report is a stand-alone document that synthesizes a large body of scientific information on life histories of the species over most of their range in North America. Emphasis is given to the Pacific Northwest (Southeast Alaska, British Columbia, Washington, and Oregon) and California. The report describes patterns of life history evident across this range and variations from common patterns. It describes how coho salmon utilize different types of habitat, including various sizes of streams and rivers, as part of their repertoire of life history tactics.

This report also serves as a background reference for an analysis of coho performance in the Klamath River basin being prepared by Cramer Fish Sciences (CFS). Their analysis summarizes and synthesizes extensive data collected in the Klamath basin and includes the formulation of a life cycle model designed to help assess coho performance in the basin.

This report aims to describe the central themes of coho salmon life histories as well as the types and extent of variation documented in the Pacific Northwest and California. Two underlying questions are considered throughout the report. How similar are coho life history patterns across the species' range? And what kinds and extent of variation occur with respect to these patterns, particularly as variation might relate to the SONCC Coho ESU and Klamath River coho?

Life History Overview

Distribution Patterns

Coho salmon inhabit very small coastal streams as well as the largest rivers in western North America. Within larger river systems, coho salmon spawning is typically distributed in tributaries to mainstem rivers. This pattern for spawning principally in smaller streams has given coho salmon a reputation of being primarily associated with small rivers and streams.

In the ocean, coho salmon generally do not migrate as far as the other species of Pacific salmon and steelhead trout . Coho originating in rivers of California, Oregon, and Washington tend to feed along the Continental Shelf associated with the region of origin.

Life Cycle Overview and Unique Characteristics

Most coho salmon across the species' geographic range have a three year life cycle, divided about equally between time spent in fresh and salt water. The basic life history begins in natal streams when spawners mate and deposit eggs into nests dug in the stream substrate. Spawning typically occurs between mid autumn and early winter in small tributaries to larger rivers, though timing can occur much later for some populations.

Returning adults in populations at the southern end of the range (both California and southern Oregon) are sometimes stalled in their river entry due to a lack of rainfall and sufficient stream flow for upstream migration, delaying spawning, sometimes even pushing it into March. This suggests that southern coho populations may have greater flexibility in adjusting their maturation timing than more northern populations; maturation would appear to be controlled partially by entry into fresh water. Factors controlling variability in maturation timing of coho salmon are not well known.

After spawning, the adults die. Following egg incubation, surviving fry emerge from the substrate in late winter and spring and begin their free swimming life.

The emergent fry move quickly to slow velocity, quiescent waters, usually along the stream's margins or into backwaters where velocities are minimal, a consistent behavior across the species range This affinity for slow velocity areas remains characteristic of juvenile coho throughout their freshwater life, unlike most other salmonid species.

Juvenile coho typically spend one year rearing in fresh water, during which time they may remain close to their natal sites or they may move considerable distances to find suitable summer and/or overwintering habitat. Dispersal by some fry to areas downstream shortly following fry emergence is a pattern seen throughout the geographic range of the species. In fall another movement pattern often occurs with juveniles in some areas of the river system redistributing to habitats more favorable for overwinter survival, particularly to off-channel habitats.

At approximately 18 months of age, coho juveniles undergo smoltification during spring and enter the marine environment, where they experience very rapid growth. Their smolt to adult survival rate can be strongly affected by exposure to large estuarine complexes like Puget Sound or the Strait of Georgia. In contrast, wild smolts entering the Pacific Ocean from the rivers along the outer coasts of Washington, Oregon, and California typically survive at 1/4 to 1/3 of rates for fish moving through large estuarine complexes.. This difference gives populations originating inside the Strait of Juan de Fuca a tremendous boost in productivity compared to those along the outer coasts and makes them naturally more resilient to habitat perturbations.

Adult coho begin arriving at the entrances to their home rivers in late summer, but more typically in early autumn. Fish arrive earliest back to their home river in northern most rivers and latest in populations further south. This pattern is related to the timing of fall and winter rains and increases in stream flow—flows typically rise later moving from north to south.

Within the basic life history, variations exist in age structure, generally following patterns associated with latitude. One variation occurs because some juveniles spend an additional year rearing in fresh water and emigrate seaward at approximately 30 months of age; these return and spawn at four years of age. This life history pattern primarily occurs in more northern populations, particularly in Alaska One notable occurrence of age 2 smolts has been found in Prairie Creek, tributary to Redwood Creek, in Northern California.

A central theme in the freshwater life history of juvenile coho is their close association with slow velocity habitats. Body morphology and fin sizes of juvenile coho salmon are particularly adapted to slow velocity habitats. Most coho juveniles have a laterally compressed body with long dorsal and anal fins, thought to be adaptations for life in slow water. In contrast, steelhead fry have cylindrical bodies in cross section with short dorsal and anal fins, adapted to higher velocity habitats than used by juvenile coho. Juvenile Chinook have a body form and fin sizes intermediate between coho and steelhead.

These differences in body shape and fin sizes are consistent with water velocity and depth preferences reported for these three species. Coho prefer much slower velocities than either steelhead or Chinook; Chinook preferences are intermediate between coho and steelhead. It is logical to expect that selection of habitat types by these species would reflect their adaptation to water velocity and depth.

Variation has been found to exist between regions both with respect to body morphology and swimming performance. Two morphological forms have been identified based on differences in body shape and fin size: a "coastal" form, characterized by large dorsal and anal fins and a deep robust body, and an "interior" form with smaller fins and a more streamlined body shape. These two forms have been found to have different swimming performance characteristics. The interior form has a body form and swimming performance that would generally favor long distance in-river migrations, such as occurs in the Fraser River. It is not known whether both morphological forms exist in the Klamath River, where both interior and coastal ecoregions exist. Differences have also been found in the body morphology between juveniles that inhabit lakes and those in streams.

Another aspect of life history that may differ between regions is foraging behavior. Foraging behaviors can vary between individuals of the same population or even of the same family. Four foraging behaviors have been identified in Northern California as distinct phenotypes, referred to as *thalweg* (the stereotypical coho foraging type), *margin-backwater*, *estuarine*, and *early emerging*. Juveniles typically do not switch to other foraging phenotypes once they begin to display a certain type. Three of the phenotypes are known to exist in other regions. One type (early emerging) may be unique to the southern portion of the species' range (i.e., California). These phenotypes utilize habitats differently. The early emerging type has been characterized as being more trout-like than is common among juvenile coho. During summer this type forages only at dawn and dusk on drifting invertebrates. During the day, they seek refuge in undercut banks, often associated with cold-seeps along terrace cutbanks. It has been suggested that this phenotype represents a pattern of adaptation significant to coho salmon in the southern portion of their range.

Freshwater Habitat Utilization

Spawning Migration

Adult coho salmon use the main channel of mainstem rivers and tributaries for migrating to spawning sites. They utilize all habitat types within the main stream and can generally be found holding to rest during the migration in deep water areas, particularly pools.

Survival during the freshwater migration is assumed to be high in streams of the Pacific Northwest. In short rivers where natural predators are not abundant, survival exclusive of any harvest impact is likely very high – it may approach 100% in many cases.

Spawning

Coho salmon tend to spawn in small streams or in side channels to larger rivers. They also sometimes spawn along the river margins of larger streams, but normally not in large numbers.

Coho salmon spawn heavily in groundwater channels where these habitats exist along the floodplains of rivers, often in relatively high densities.

Egg and Alevin Incubation

Survival from egg deposition to fry emergence can vary significantly between streams depending on stream characteristics and local conditions. Changes in stream conditions due to land use can severely reduce survival to emergence.

Average survival to emergence for coho in streams that might be considered typical in the Pacific Northwest is much less than occurs under optimal conditions in nature. In streams with no or relatively moderate and recent land use, survival to emergence averages approximately 30%, as seen in studies in Oregon, Washington, and British Columbia.

Two factors are most often cited as affecting the survival to emergence of coho salmon: fine sediment loading and bed scour. Following extensive and prolonged land use practices in a watershed, survival to emergence can be reduced by half or more. Survival in spring fed streams with upwelling groundwater is often much higher than in runoff streams.

Fry Colonization

Upon emergence coho fry move quickly to slow velocity habitats, typically along the channel margin, or they continue to move downstream. They have a strong affinity for very slow velocity water and generally move there as rapidly as possible. Fish that emerge during high flows can be swept downstream, moving them to less suitable habitats, increasing bioenergetic costs, and increasing predation exposure. Large rivers typically provide little suitable habitat for young coho fry.

Young coho fry that move to larger rivers can subsequently move into off-channel habitats as a result of their need for calm, slow velocity water.

Survival during the fry colonization stage is mostly density-independent because of the short time period involved. Estimated survival rates for Deer Creek in the Alsea watershed study (Oregon Coast) show a modest density-dependent effect. An estimate of the density-independent component of survival for Deer Creek is 81% during a period prior to logging and recently completed logging.

Subyearling Summer Rearing

Juvenile coho are found residing in a wide variety of stream types and sizes during summer. They are typically found in highest densities within their natal streams since the majority of fry usually do not migrate large distances from spawning sites.

The need for slow velocity water by juvenile coho remains strong during this life stage. Juvenile Chinook and steelhead will often be found feeding near velocity shears within main channels, while coho remain more closely associated with the shoreline or dense cover of woody debris. This pattern indicates a much stronger affinity for slow velocity by coho salmon than the other species during this life stage.

Juvenile coho are most often found in pools. The highest densities of juvenile coho during this life stage are usually found in the smallest streams. The large differences seen between densities of small and large streams likely occurs because a smaller proportion of the total cross-section in large streams provides depths and velocities preferred by juvenile coho salmon.

The influence of wood on rearing densities during summer is not the same across all stream types and sizes. Evidence exists that the affinity of juvenile coho salmon for wood accumulations increases through the summer with growth. In mainstem rivers during summer the presence of large wood is much more important than in small streams for juvenile coho salmon

In large rivers, secondary channels (i.e., side channels and off-channel habitats) provides important rearing areas for juvenile coho. Groundwater channels are usually utilized almost exclusively by coho salmon and can be very productive for the species.

High water temperatures during summer can be an important factor affecting the distribution, growth, and survival of juvenile coho salmon. High water temperatures can trigger movement of juvenile coho salmon during summer, when little movement typically occurs. Movement occurs as fish seek refuge from high temperatures. One foraging behavior that has only been described in Northern California streams may be particularly adapted to use of thermal refugia.

Survival of juvenile coho salmon during summer can be strongly density-dependent in smaller streams. Competition for shrinking space—due to declining flows in late summer—and limited food results in reduced survival at higher juvenile abundance.

An estimate of the density-independent component of survival for Deer Creek (Alsea watershed, Oregon) is 86% during a period prior to logging and recently completed logging.

Fall Redistribution and Overwintering

In many streams, some juvenile coho salmon move from their summer rearing locations in fall, triggered by increased flows associated with autumn rainfall. This movement is another demonstration of the affinity that these fish have for slow velocity water. Water velocities increase in main stream habitats with rising flow, either dislodging juveniles from summer rearing sites or stimulating them to move to find more favorable habitats prior to the coming of larger, more frequent winter storms.

During this period of redistribution, some juvenile coho salmon immigrate into off-channel habitats. These habitats provide refuge from high flow velocities. This movement of juvenile coho salmon from mainstem streams during fall and winter appears to be due to fish leaving unfavorable areas in search of improved survival conditions. Within mainstem streams, they evacuate sites with high exposure to high velocities. Large wood accumulations are especially important as velocity refuge sites during winter, particularly in large streams. Juvenile coho have been found to rarely use cobble substrate as overwinter cover.

Overwinter survival of juvenile coho is approximately 2-6 times greater in off-channel habitats than within main channel habitats. This difference in survival rates between in-channel and off-channel habitats is especially important in watersheds that have undergone significant changes due to land use. Coho populations subject to high overwinter mortality—as experienced within main channel habitats—have much reduced life cycle productivity compared to populations with good overwinter habitat.

Smolt Migration

Smoltification and the corresponding smolt migration begins earlier in the southerly part of the species' geographic range, being somewhat later in northern streams. The timing pattern is very similar in California, Oregon, Washington, and southern British Columbia.

A wide range of smolt outmigration patterns can exist within the overall critical time window in a single watershed. Both migration timing and rate of migration can be affected by smolt size, location in the watershed at the start of the migration, migration distance, and stream flow. This overview is focused primarily on free-flowing rivers.

Larger salmonid smolts, for several species including coho salmon, generally begin their migration earlier than smaller ones, presumably because smaller ones require additional time to gain size necessary for smoltification and for improved marine survival.

In streams on the Washington Coast, the coho smolt migration typically begins first for fish emigrating from off channel sites, followed by fish from runoff tributaries. Smolts emigrating from off channel sites are consistently larger than those coming from runoff tributaries.

Early migrants tend to migrate downstream more slowly than late timed fish, a pattern that occurs for salmonid species in general.

Smolts that begin their migration far from the estuary generally travel downstream much faster than those that begin closer.

Flow can affect migration timing and migration rate, which has been well described in the Columbia River system. The effects of flow on migration rate is most evident through the extensive reservoir system of the Columbia and Snake rivers.

Factors that can affect the survival rates of migrant smolts in fresh water have been extensively studied in the Columbia and Snake rivers—and intensely debated. Much of the debate has focused on the relationship between mainstem flow and outmigrant survival. It is well known that predation can be high on juvenile salmonids as they outmigrate through impounded systems such as the Columbia River. The Columbia system has large populations of northern pikeminnow and exotic predatory fishes. It has often been assumed in these cases that the travel rate of smolts, affected by flow, determines predation rates by regulating the amount of time that juvenile migrants are exposed to the predators. More recent research, however, indicates that while migration rate is affected by flow, survival of yearling and older smolts appears to be largely a function of migration distance and not travel rate.

Within the mainstem Columbia River hydrosystem, another factor shown to be important to the survival of outmigrant yearling smolts is water temperature. It is thought the effect of temperature on yearling smolt survival operates mainly by affecting the activity of predatory fishes (pikeminnow and exotics)—as water temperatures increase, their feeding rate increases.

The effect of migration distance on yearling smolt survival has also been demonstrated for free-flowing streams upstream of Lower Granite Dam on the Snake River. A strong inverse relationship exists between survival and migration distance for hatchery spring Chinook smolts released at various hatchery sites in the Snake River system. In this case, it appears that water temperature during the period of migration does not help explain mortality within the free-flowing tributaries to the Snake River, suggesting that temperature has a stronger role in the prey-predator dynamics within the extensive reservoir system downstream.

Studies conducted in free-flowing rivers without pikeminnow and abundant exotics present suggest that smolt survival during their outmigration is typically very high.

Studies of wild coho smolts show that their migration is not continuous but interspersed by periods of holding. In many cases, it is not rapid once it has been initiated, apparently progressing as if in stages. Smolts generally use slow velocity habitats during periods of holding and resting.

Discussion and Conclusions

Two underlying questions are considered throughout this report as they relate to how coho salmon utilize physical habitats within a watershed. How similar are coho life history patterns

across the species' range? And what kinds and extent of variation occur with respect to these patterns, particularly as variation might relate to the SONCC Coho ESU and Klamath River coho?

These questions relate to Moyle's statements about coho salmon in his book "Inland Fishes of California":

> "…evolutionary forces keep coho salmon (and other salmon) surprisingly uniform in morphology and life history throughout their range, while producing runs that show strong, genetically based adaptations to local or regional environments. In California coho populations are the southernmost for the species, and they have adapted to the extreme conditions (for the species) of many coastal streams."

On its surface, Moyle's statement may seem contradictory. He concludes that coho salmon show a high degree of uniformity (or similarity) in life history patterns across their range, yet he asserts there is also significant variation and local adaptation. In context, Moyle is saying that coho salmon—like other salmonid species—exhibit significant variation in life histories, but the range of variation remains within what he sees as unifying life history themes for the species. The central themes of life history similarity are morphology, age structure, spatial distribution within a watershed, general timing patterns of migrations and other movements, development and growth patterns, foraging patterns, effects of environmental stressors, and habitat use patterns—among others. But significant variations exists within these unifying themes, enabling considerable adaptation to local conditions.

One unifying theme in the freshwater life history of juvenile coho is their affinity for slow velocity habitats in all life stages. Body morphology and fin sizes appear to be generally adapted to life in these habitats—notwithstanding variations that exist between coastal and interior forms (discussed further below). Their affinity for slow water is evident across the species' range—in both northern and southern regions and coastal and interior regions. Juveniles in all life stages—though to a lesser extent during the smolt stage—primarily rear and seek refuge in slow velocities associated with pools, channel margins, backwaters, and off-channel sites (alcoves, ponds, and groundwater channels). Their affinity for low velocity water is strongest during the fry (very young fry) and overwintering life stages.

This association with low velocity habitats tends to result in several patterns of distribution within a watershed. Juvenile rearing—particularly in summer—occurs to a large extent within the natal streams. Emergent fry generally remain relatively close to their natal areas, though some dispersal downstream typically occurs. The maximum extent that dispersal occurs downstream is not known. Spawning which occurs in higher gradient streams appears to result in a greater downstream dispersal of fry. In that case, the young move—or are displaced by high velocity flows—to low velocity habitats in reaches of lower gradient.

Another related distribution pattern is the association that juvenile coho have for physical cover. Cover types within the water column or overhead are preferred (wood, rooted macrophytes, roots, overhead structure), as opposed to substrate cover provided by cobbles or turbulence cover associated with velocity shears. In smaller streams, cover is not a strong determinant of habitat

selection in summer, though association with it grows by summer's end. Physical cover appears to be a much greater determinant of habitat selection in large rivers, probably due to the likelihood for higher water velocities and more predators.

The affinity for low velocity habitats is particularly strong during winter. This season often brings rapidly changing, adverse conditions within a stream—both in coastal and interior regions—whether due to flow fluctuations or extreme cold and icing. Survival appears to be strongly related to how successful juvenile coho are in locating suitable refuge from harsh conditions. Movement seems to be volitional, or when flows are high, due to displacement. In dynamic rivers, redistribution to overwintering sites can be quite dramatic in terms of distances traveled and numbers of fish that move.

Off channel sites (alcoves, ponds, groundwater channels) are particularly desirable overwintering habitats throughout the Pacific Northwest and California. These provide the highest survival rates compared to other habitats. Low velocity locations within main stream channels having undercut banks with exposed root masses or sites of large wood accumulations also provide refuge habitat. Side channels with low velocities and some form of cover are also used. Juvenile coho rarely use cobble substrate for overwintering cover, as commonly occurs for juvenile steelhead.

Variations on the central themes of coho life history exist and several types could affect habitat utilization patterns. Juvenile coho in the southern part of the range can exhibit a summer movement pattern different from what is seen further north. This movement pattern appears to be a redistribution to find thermal refugia. There is no evidence that fish in the southern region have a higher thermal tolerance than fish further north, though some greater tolerance may exist. While the fate of fish that move in search of thermal refugia has not been determined, some do successfully arrive at cooler water sites. It is unknown what level of mortality or loss in other performance measures might occur while moving to refugia or the distance that fish can travel. The early emerging foraging phenotype, having some adaptation to warm conditions, may be suited for movement during early to mid summer to seek out refugia. Their larger size than other foraging phenotypes would be advantageous for such movement. Habitat utilization in warm water streams will reflect overlapping areas of tolerable temperatures and water velocities.

Another life history variation is seen in differences in body morphology and fin sizes between coastal and interior populations and associated swimming performances. It is not known how far south such a coastal-interior distinction might extend. Do both forms exist within the Klamath River basin? There is no evidence that these morphological forms have different habitat requirements, i.e., does the interior form, which has greater swimming stamina, have less of an affinity for slow water habitats than the coastal form? Or do cover type preferences differ between the forms? Evidence shows that both forms exhibit the same selection for slow water habitat types and cover types. Researchers have suggested that the adaptive benefit of these variations to interior coho (more streamlined body, smaller fins, greater swimming stamina) is in their ability to negotiate long in-river migrations, both as smolts and adults. An interior-type body form would presumably aid upper Klamath River coho in their movements (including summer and fall redistribution movements) within the mainstem Klamath River, if this body form occurs there.

Perhaps the most obvious variation in life history patterns seen in southern coho populations is their ability to delay river entry timing during periods of drought or late arriving rainfall. In the extreme, river entry can apparently be stalled several months. This would thereby delay spawning and would presumably have cascading effects on emergence timing and subsequent growth and habitat use patterns.

Coho salmon exhibit a wide variety of life history patterns in large, diverse watersheds. These patterns are phenotypic expressions of the interaction of genotype and environmental factors. Among others, these factors include flow characteristics, gradient, water temperature, and habitat structure. Diverse phenotypic expressions enable the species to utilize a wide variety of physical habitats across a range of gradients, habitat sizes, and qualities—but within limits set by the species' genetic blueprint. To understand the performance of a species in any watershed requires a life history perspective, seen across the full cycle.

Coho Salmon (*Oncorhynchus kisutch*) Life History Patterns in the Pacific Northwest and California

1.0 Introduction

In 1997 coho salmon (*Oncorhynchus kisutch*) in the Klamath River basin, as part of the Southern Oregon Northern California Coasts evolutionary significant unit (SONCC Coho ESU), were listed as threatened under the Endangered Species Act (ESA). The National Marine Fisheries Service (NMFS) cited water management, water quality, loss of habitat, overfishing, and other factors as causing a serious decline of the species within this ESU. The SONCC Coho ESU is composed of populations produced between Cape Blanco in Southern Oregon (just north of the Rogue River) to Punta Gorda in Northern California (includes the Mattole River). The geographic setting of the SONCC Coho ESU includes three large basins, which include Klamath basin, and numerous smaller basins across diverse landscapes (Williams et al. 2006). The large basins encompass both interior and coastal type landscapes.

In the Klamath basin, the roles of different habitats to the performance of coho salmon have been a subject of much debate and controversy (Hardy and Addley 2001; Vogel 2003; NRC 2004). Of particular concern is the use and importance of the mainstem Klamath River relative to the tributaries. This issue has a significant bearing on how flows are to be regulated in the mainstem river for the protection and restoration of the species. It also bears on how managers perceive the relative importance of different habitats in formulating an overall recovery plan for coho salmon in this basin. Complicating this issue is the fact that habitats, including associated flow patterns, have been altered in both the mainstem and tributaries due to land use, flow regulation, and irrigation withdrawals.

The purpose of this report is to review coho life history patterns and associated life stage specific survivals. The report is a stand-alone document that synthesizes a large body of scientific information on life histories of the species over most of their range in North America. Emphasis is given to the Pacific Northwest (Southeast Alaska, British Columbia, Washington, and Oregon) and California. The report describes patterns of life history evident across this range and variations from common patterns. It describes how coho salmon utilize different types of habitat, including various sizes of streams and rivers, as part of their repertoire of life history tactics. Uncertainties are identified where evident.

This report is intended to serve as a background reference for an analysis of coho performance in the Klamath River basin being prepared by Cramer Fish Sciences (CFS). Their analysis summarizes and synthesizes extensive data collected in the Klamath basin and includes the formulation of a life cycle model designed to help assess coho performance in the basin. The CFS analysis is intended to assess the effects of flow regulation within the Klamath river relative to other survival factors in the basin. That analysis focuses on characteristics of habitat and populations within the Klamath basin. Therefore, the report presented here makes no attempt to synthesize various data sets from the Klamath watershed, nor to draw conclusions about specific

factors affecting coho population performance in that basin. The focus here is broader, though information from the Klamath basin is incorporated as part of the coastwide perspective. Some commentary is given to address specific situations in the Klamath basin to aid the reader in considering how Klamath population characteristics might differ or align with those in other basins.

This report is not redundant of the many other documents that summarize life history patterns of coho salmon (e.g., Shapovalov and Taft 1954; Laufle et al. 1986; Hassler 1987; Sandercock 1991; Pearcy 1992; Behnke 2002; CDFG 2002; Moyle 2002; Quinn 2005). Those documents are used as the basis for some of the material presented here. A more in-depth presentation is provided here of habitat utilization patterns exhibited by the species and some of the factors believed to shape those patterns. To the extent that information is available, variations from common patterns are described. Survival rates associated with particular life history strategies are described where possible.

Life histories lie at the heart of the biology of a species (Stearns 1992). Life history traits are directly related to survival and reproduction—they are phenotypic expressions of the interaction of genotype and environment. Individuals of a population that express different life history traits vary in fitness within a set of environmental conditions. This drives natural selection. Habitats are the templates that organize life history traits (Southwood 1977). The range of life history diversity within a species is the result of evolutionary trade-offs of costs versus benefits in the process of adaptation to habitats.

Each salmon species has a characteristic general life history pattern with unique attributes that separate it from the other species (Lichatowich 1999). Among these attributes are age structure, length of freshwater residence, and their spawning and rearing distributions within a watershed. These generalized life histories are central themes around which populations express life history variation in response to local habitat conditions (Lichatowich 1999). Moyle's (2002) description of this dynamic is useful here:

> "Coho salmon have thousands of semi-isolated populations in coastal streams over a wide range. At the same time, fish from different regions mix at sea, and individuals may 'stray' into nonnatal streams for spawning. These two opposing and dynamic evolutionary forces keep coho salmon (and other salmon) surprisingly uniform in morphology and life history throughout their range, while producing runs that show strong, genetically based adaptations to local or regional environments. In California coho populations are the southernmost for the species, and they have adapted to the extreme conditions (for the species) of many coastal streams."

This report aims to describe the central themes of coho salmon life histories as related to habitat use as well as the types and extent of variation documented in the Pacific Northwest and California. Two underlying questions are considered throughout the report. How similar are coho life history patterns across the species' range? And what kinds and extent of variation occur with respect to these patterns, particularly as variation might relate to the SONCC Coho ESU and Klamath River coho?

The report is organized into four sections:
1. Introduction
2. Life history overview
3. Freshwater habitat utilization
4. Discussion and conclusions

Section 2 provides an overview of the distribution and major life history characteristics of coho salmon. These topics are well covered elsewhere (e.g., Sandercock 1991) and the intention here is not to duplicate this material. Coverage here highlights recurring patterns and issues seen to be particularly applicable to the life history and performance of Klamath coho salmon as related to habitat utilization and survival.

Section 3 describes patterns and rates of utilization of different freshwater habitats by coho salmon as seen in various areas of western North America. Variations from and within these patterns are identified together with causal factors. Life stage specific survival rates are summarized.

Section 4 provides discussion and conclusions regarding the two central questions being examined: 1) How similar are life history patterns across the species' range that relate to habitat utilization; and 2) what kinds of variations are expressed by the species as they might relate to Klamath River coho?

2.0 Life History Overview

This section provides an overview of the major patterns and characteristics of coho life history in Western North America. Variations to life history themes are described, particularly as they might provide insight about variations in California coho life histories. Life history characteristics that can affect habitat utilization patterns are emphasized here.

2.1 Distribution Patterns

Populations of spawning coho salmon are distributed along the coasts of both the Asian and North American coasts of the North Pacific Ocean. In North America, they currently populate streams from Monterey Bay (Waddell and Scott creeks) in Central California (south of San Francisco Bay) to Point Hope on the northwest corner of Alaska (Sandercock 1991; Brown et al. 1994). They are much less common in both the northern and southern fringes of their distribution and most abundant across the mid section of their ranges (Sandercock 1991). Naturally produced coho in California, both in the SONCC ESU and Central California Coast Coho ESU (CCC Coho ESU), are believed to be in a general state of decline; the number of streams supporting the species is substantially reduced from historic distribution (Brown and Moyle 1991; CDFG 2002). This is particularly true on the extreme southern fringe of their distribution—within the CCC ESU.

Coho salmon inhabit very small coastal streams as well as the largest rivers in Western North America—including connected lakes within these stream systems. Within the largest rivers, their upstream migrations are longest in more northerly rivers, being approximately 1,400 miles on the

Yukon River, 425 miles in the Fraser system, and currently about 300 miles in the Columbia system (Sandercock 1991). Historically, they inhabited streams in the Columbia River Basin 500 miles from the ocean (Mullan 1984). In the Klamath River, they are believed to have historically ascended to the vicinity of Spencer Creek, approximately 230 miles from the river mouth (Hamilton et al. 2005). In the Sacramento River, Behnke (2002) states that coho salmon were always extremely rare and says it is unclear why conditions are so ill-fitted for this species. Brown et al. (1994), however, suggests that coho may not have been entirely rare in the system historically. Moyle (2002), citing Leidy (1984), states that coho were never common in the Sacramento basin but small numbers probably once spawned in the McCloud and upper Sacramento rivers, in excess of 300 miles from the marine environment.

Within larger river systems, coho salmon spawning is typically distributed in tributaries to mainstem rivers. In smaller streams that empty directly to the marine environment, they will spawn over the stream's length, from just above tide water to headwater reaches. This pattern of spawning principally in smaller streams has given coho salmon a reputation of being primarily associated with small rivers and streams (Behnke 2002). In contrast, Chinook (*O. tshawytscha*), chum (*O. keta*), and pink (*O. gorbuscha*) salmon often spawn in large mainstem rivers, although each of these also spawn in small streams. Coho also spawn on beaches of some Alaskan lakes (Ruggerone and Rogers 1992). Sandercock (1991) described the typical spawning distribution of coho salmon as follows:

> "Their success as a species may be partly attributed to their utilization of a myriad of small coastal streams and to their aggressiveness and apparent determination to reach the small headwater creeks and tributaries of larger rivers to spawn. In many cases, they overcome difficult obstructions to reach areas inaccessible to other salmon and then share these locations with only migrant steelhead or perhaps resident cutthroat trout. These small headwater streams generally provide cool, clear, well-oxygenated water, with stable flows that are ideal for incubation and subsequent rearing."

Lichatowich (1999) illustrated differences in typical patterns of spawning distribution for salmon species in a hypothetical watershed (Figure 1), showing that coho salmon normally spawn higher in river systems relative to other species. In large rivers (e.g., Columbia, Snake, and Fraser rivers), Chinook salmon ascend the mainstem river further than coho.

A representative example of this pattern is seen in the Clearwater River on the Olympic Peninsula (Washington Coast). Edie (1975) delineated three zones within the river system as utilized by anadromous salmonids (Figure 2): Chinook zone, coho zone, and cutthroat (*O. clarki*) zone. These distributions are related to the physical and hydrological characteristics of the stream system, not to differences in water quality variables such as temperature. Water temperature remains within safe limits for these species in this river. Flow in the mainstem river during spawning months is typically in the range of 800-3,000 cfs. Edie (1975) described the Chinook zone as being the main river and the lower reaches of larger tributaries (see Figure 43 top for a picture of the Clearwater River). This zone is mostly used by Chinook salmon and steelhead (*O. mykiss*) trout and to a much lesser degree by coho salmon. Stream gradient is mostly less than about 1%. The coho zone, immediately upstream of the Chinook zone, encompasses the middle reaches of larger tributaries, the downstream portion of smaller tributaries, and the very upper

portion of the mainstem river. Gradients in this zone are moderate, mostly 1-2% but can be as high as 4%. This zone is primarily used by coho salmon and steelhead trout but significant cutthroat utilization can also occur. The upper zone, the cutthroat zone, is the domain of cutthroat trout. Streams are steep (2-6% but can be higher) and small (1-10 ft in width). This zone can be used by sea run cutthroat trout as well as small resident fish. While spawning by different salmonid species overlaps across zones, the pattern is instructive regarding general species usage.[1]
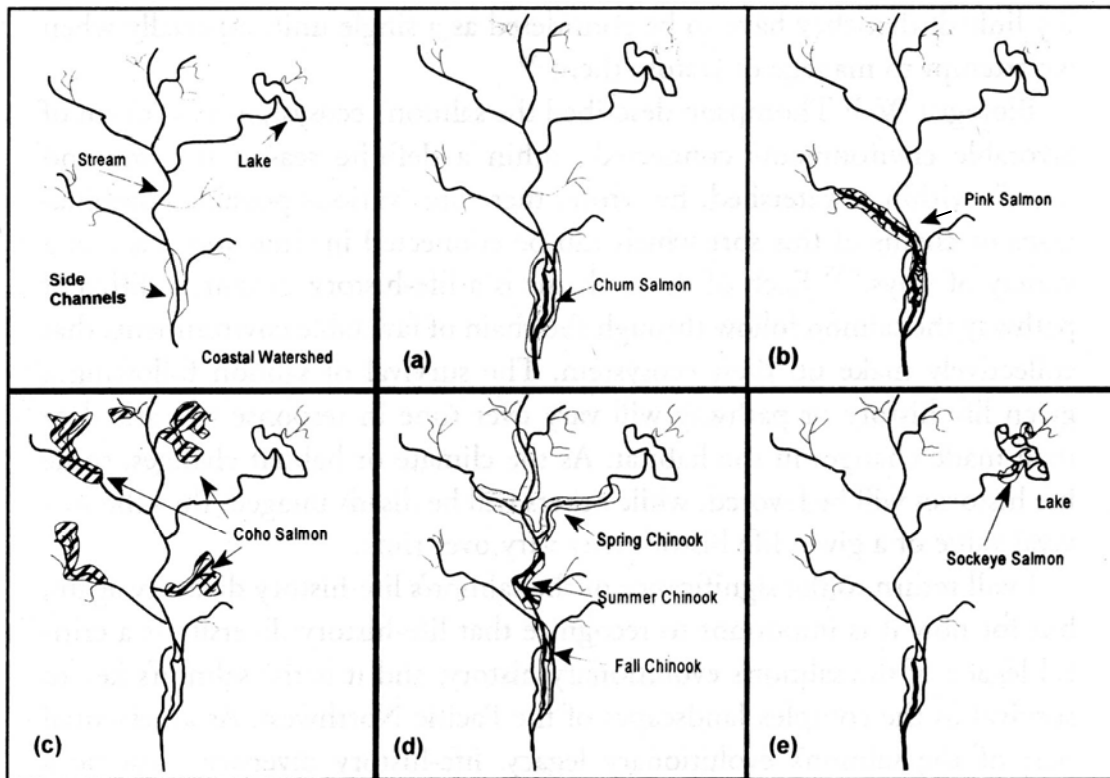
Figure 1. The spawning distribution of Pacific salmon in a hypothetical watershed. Typical distribution of chum (a), pink (b), coho (c), Chinook (d), and sockeye (e). From Lichatowich (1999).

In the ocean, coho salmon generally do not migrate as far as the other species of Pacific salmon and steelhead trout (Behnke 2002). Coho originating in rivers of California, Oregon, and Washington tend to feed along the Continental Shelf associated with the region of origin (Sandercock 1991; Pearcy 1992; Moyle 2002)(Figure 3). However, coho stocks originating farther north are found farther offshore (Quinn and Myers 2005).

---

[1] / One reviewer of this report raused a question regarding how habitat alterations due to land use might have influenced the pattern observed by Edie (1975). In the view of this author, whose research on the Clearwater began in 1971, when major areas of the watershed were still unroaded and unlogged, the pattern depicted by Edie is representative of the pristine state.
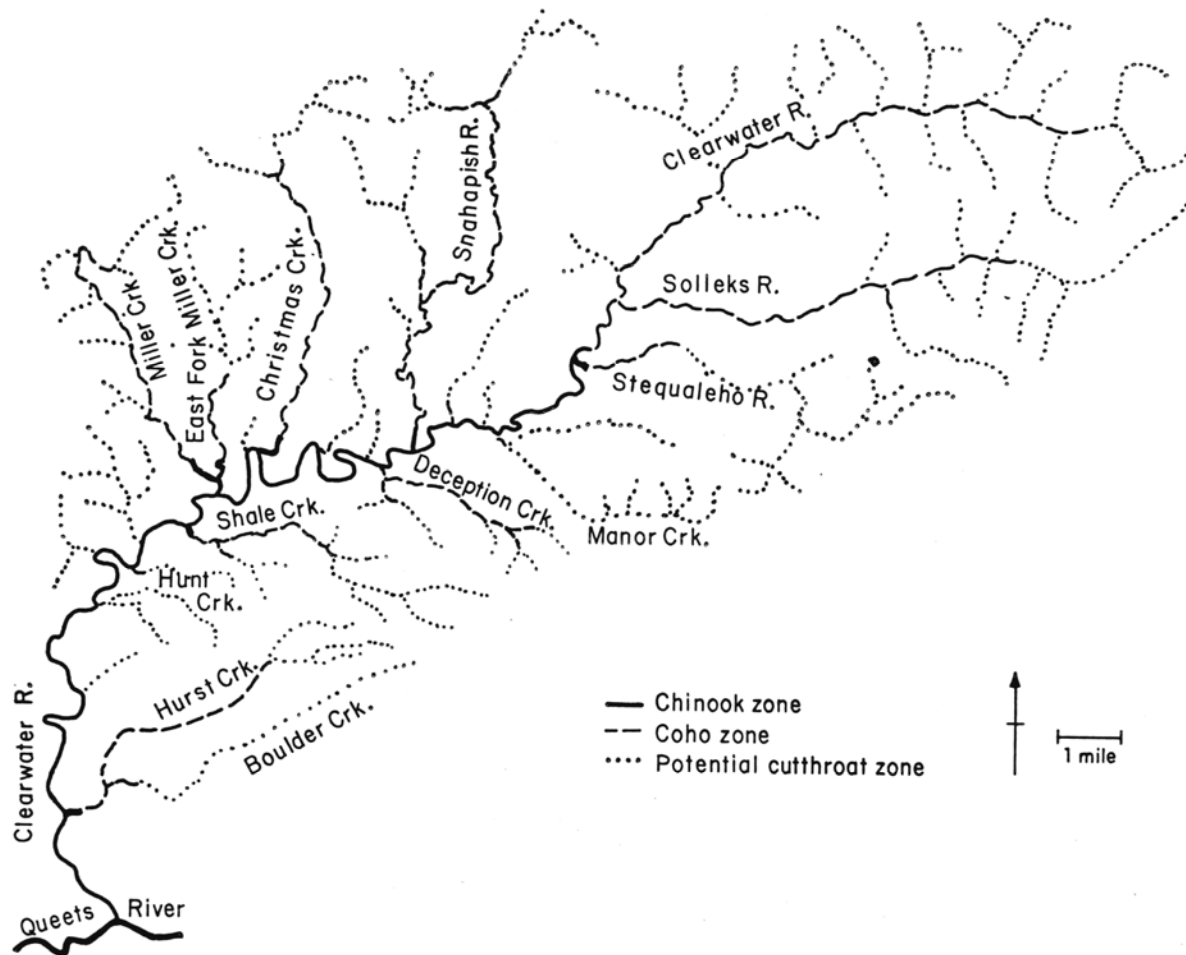
Figure 2. Salmonid usage zones in the Clearwater River (Olympic Peninsula, Washington) delineated by predominate species. From Edie (1975). Distribution patterns in this river reflect those that commonly occur for these species in the Pacific Northwest and California.
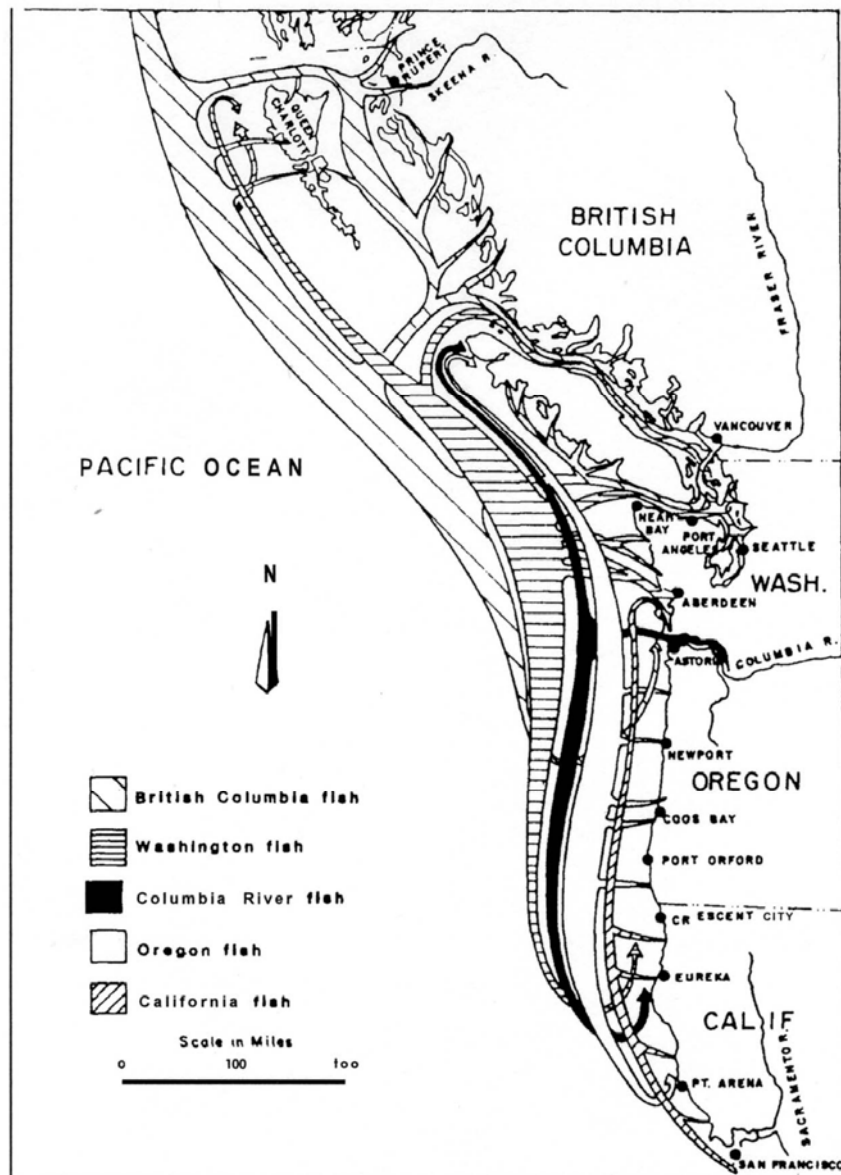
Figure 3. Oceanic distribution patterns of coho salmon originating in California, Oregon, Washington, and British Columbia. From Wright (1968).

2.2 Life Cycle Overview and Unique Characteristics

Most coho salmon across the species' geographic range have a three year life cycle, divided about equally between time spent in fresh and salt water (Sandercock 1991). The basic life history begins in natal streams when spawners mate and deposit eggs into nests dug in the stream substrate. Spawning typically occurs between mid autumn and early winter in small tributaries to larger rivers, though timing can occur much later for some populations.

Returning adults in populations at the southern end of the range (both California and southern Oregon) are sometimes stalled in their river entry due to a lack of rainfall and sufficient stream flow for upstream migration, delaying spawning, sometimes even pushing it into March (Shapovalov and Taft 1954; Moyle 2002). This suggests that southern coho populations may have greater flexibility in adjusting their maturation timing than more northern populations; maturation would appear to be controlled partially by entry into fresh water.[2] Factors controlling variability in maturation timing of coho salmon are not well known.

After spawning, the adults die. Following egg incubation, surviving fry emerge from the substrate in late winter and spring and begin their free swimming life.

The emergent fry move quickly to slow velocity, quiescent waters, usually along the stream's margins or into backwaters where velocities are minimal, a consistent behavior across the species range (Sandercock 1991; Nickelson et al. 1992; Hampton 1988; Nielsen 1994; CDFG 2002). An affinity for slow velocity areas remains characteristic of juvenile coho throughout their freshwater life, unlike most other salmonid species.

Juvenile coho typically spend one year rearing in fresh water, during which time they may remain close to their natal sites or they may move considerable distances to find suitable summer and/or overwintering habitat. Their movements can disperse them to streams of all sizes—from tiny rivulets to large rivers and all sorts of connected water bodies, including lakes, ponds, springbrooks, flooded wetlands, and estuarine areas.

Figure 4, based on extensive studies in the Clearwater River (Olympic Peninsula, Washington), illustrates a variety of life history patterns within the same river system (Lestelle et al. 1993a). Most spawning in this river occurs in tributaries, in both low (<1.5%) and high (>1.5%) gradient streams, and in the upper portion of the mainstem where it narrows and steepens. The low gradient tributaries typify streams considered by many biologists to be highly productive for coho salmon—small low velocity streams with abundant pool habitat interspersed with woody debris. While the steeper streams support good numbers of spawners, emergent fry appear to largely disperse downstream from them into more suitable summer habitat.

Dispersal by some fry from natal reaches to areas downstream shortly following fry emergence is a pattern seen throughout the geographic range of the species (Figure 5)(Lister and Genoe 1970; Au 1972; Hartman et al. 1982; Murphy et al. 1984; Nielsen 1994). Downstream movement by young fry can result from intraspecific competition with other fry (Chapman 1962), displacement during high flows (Hartman et al. 1982), or not finding suitable colonization habitat (Au 1972). Some fry emigrants arrive at the stream mouth estuary (not shown in Figure 4) where they rear successfully in brackish water conditions. They apparently utilize the freshwater surface water

---

[2] / Pink and chum salmon can reach sexual maturation while still in saltwater (Groot and Margolis 1991), while some species like sockeye salmon seem to need to mature in freshwater (Hodgson and Quinn 2002). This author has found that fall Chinook salmon returning to rivers on the Olympic Peninsula (Washington Coast) appear to have very little flexibility in adjusting maturation based on their river entry timing. These populations enter the rivers from the ocean mostly during freshet conditions. In years of severe drought, they delay entry until just before or the time of full maturation, when they swim in large numbers over shallow riffles in the lower river. They tend to spawn in the lower reaches of the river during such years. Their maturation timing appears to be little different, even unchanged, from years during normal river entry patterns.

lens to some extent, a rearing strategy observed in California (Nielsen 1994), Oregon (Miller and Sadro 2003), Washington (Beamer et al. 2004), British Columbia (Tschaplinski 1988), and Alaska (Murphy et al. 1984).
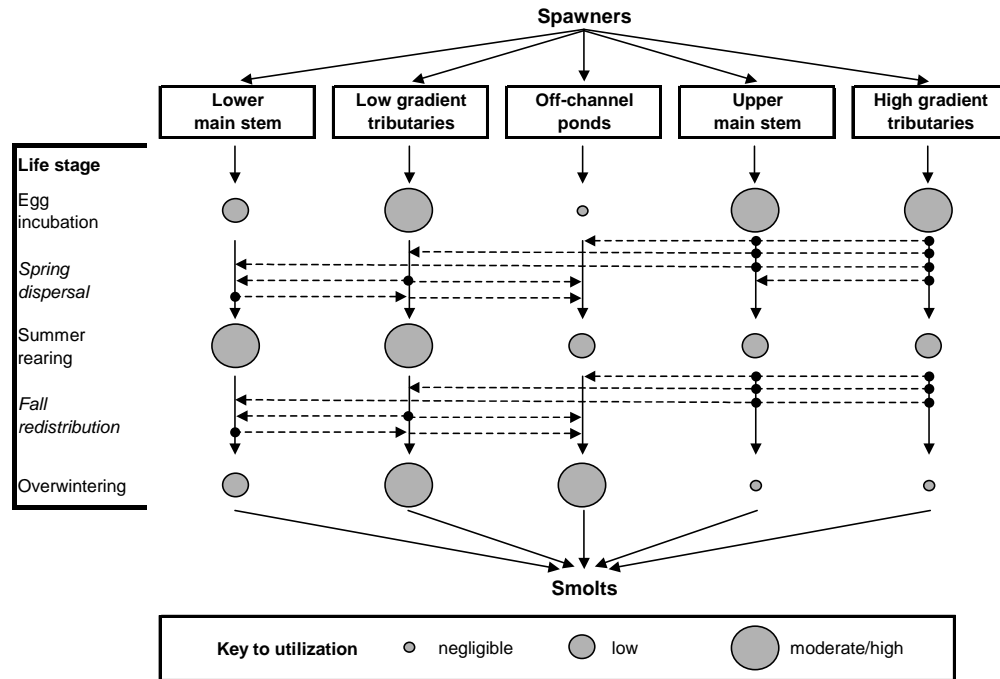
Figure 4. Utilization pattern by coho salmon of different areas of the Clearwater River (Olympic Peninsula, Washington) by life stage. Circle size reflects the relative amounts of production attributed to each area. Dashed lines show movements of fish from one area (dot) to another area (arrow). From Lestelle et al. (1993a). The chart illustrates the extent that coho juveniles can move during freshwater life to locate suitable habitats.

Freshwater rearing during summer typically occurs without extensive movement where flow and temperature conditions do not reach extreme conditions for survival (Figure 5)(Au 1972; Lindsay 1974; Kahler et al. 2001). However, more limited movement appears to be the norm in at least some streams. Kahler et al. (2001) observed that small-scale movement (i.e., several habitat units) and especially upstream movement was common for juvenile coho in three study streams in Western Washington. The researchers concluded that habitat quality rather than social dominance was the primary factor affecting movement.

More extensive summer movement, perhaps over relatively long distances, can be triggered by excessively high water temperatures or severely diminished flows, as documented in some Northern California and coastal Oregon streams (Figure 6)(Kruzic 1998; Chesney and Yokel 2003). Direction of movement in these cases has been observed to be downstream as seen in screw trap catches, though it should be noted that the sampling gear could only detect downstream movement. Juvenile coho have been found to move out of mainstem rivers during periods of high water temperature and into cool water tributaries. This behavior has been

described in the Klamath River, where juvenile coho have been found moving upstream in excess of 3,000 ft from the mainstem in cool water tributaries (Toz Soto, Karuk Department of Natural Resources *personal communications*).[3]
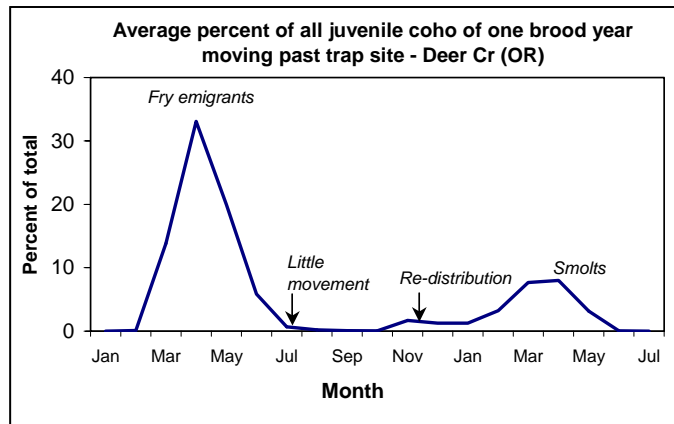
Figure 5. Representative pattern of movement and migration of juvenile coho salmon seen in many streams across the species' geographic range. Created from data in Au (1972) for Deer Creek, Alsea River system (Oregon Coast).
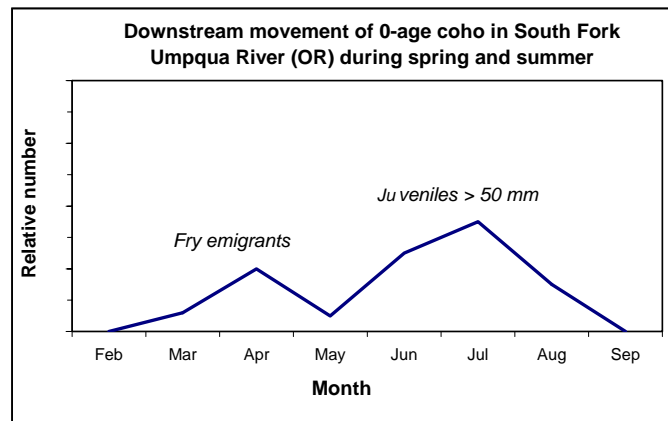
Figure 6. Movement of juvenile coho salmon past trap site in the South Fork Umpqua River (Oregon Coast) during spring and summer. Pattern is stylized from data in Kruzic (1998). Movement of juveniles during summer is believed due to high water temperatures.

In fall another movement pattern often occurs with some juveniles redistributing from oversummering sites to habitats more favorable for overwinter survival (Figure 4)(Skeesick 1970; Bustard and Narver 1975; Peterson 1982a; Cederholm and Scarlett 1982; Swales et al. 1986; Brown 2002). Harsh winter conditions for survival exist in many streams of the Pacific

---

[3] / Stream-type juvenile Chinook exhibit the same behavior to escape high water temperatures in mainstem rivers. Lindsay et al. (1986) reported juvenile Chinook to move up to 7.5 miles upstream in some cool water tributaries from the mainstem John Day River (Central Oregon) during periods of high water temperature.

Northwest and Northern California, due either to frequent high flows in western regions or prolonged cold temperatures in eastern regions (Brown 2002). Limited winter habitat is believed to be a major constraint on coho populations in many Pacific Northwest watersheds (Mason 1976a; Hartman et al. 1998; Solazzi et al. 2000; Brown 2002). Moyle (2002), in referring to the importance of overwintering habitat for juvenile coho in California, concluded:

> "Availability of overwintering habitat is one of the most important and least appreciated factors influencing the survival of juvenile coho in streams."

A redistribution in fall at the onset of high flows or cold temperatures is an adaptation that many salmonids exhibit, particularly coho salmon. The question arises as to how far juvenile coho will move during this fall redistribution. In the Clearwater River, juvenile coho have been found to move up to 20 miles downstream from summer rearing sites to overwintering habitat (Peterson 1982a; Cederholm and Scarlett 1982). This distance was nearly the maximum that could possibly have been observed in that river due to its size and how the study was designed. In the Vedder-Chilliwack River (tributary to the lower Fraser River), Fedorenko and Cook (1982) found some juvenile coho to redistribute downstream from summer rearing sites nearly 40 miles to overwintering sites. In this case, juveniles had been captured and tagged in Chilliwack Lake in fall, then were recaptured the following spring emigrating from tributaries to the lower river—downstream of the lake up to 40 miles. These lower tributaries are only a short distance from the mainstem Fraser River, thus it is possible that some fall migrants had gone even further downstream to overwinter. But how far will juvenile coho travel to find suitable overwintering sites in large river systems, such as the Klamath River?

Inquiry was made of Richard Bailey[4] of Fisheries and Oceans Canada on what is known about redistributions of juvenile coho in the Fraser River system. Bailey reported that his agency is currently pursuing the answer to this very question. It has been hypothesized that juvenile coho move downstream from the upper Thompson River (upstream of the city of Kamloops) in fall to the Fraser River, and continue to move until they arrive in the lower Fraser River valley where abundant overwintering habitat exists, a distance of over 250 miles. In summer of 2006, Bailey's agency initiated a study to investigate this matter. The Thompson River is in the interior region of the Fraser Basin.

The Fraser River study highlights the level of importance that biologists in that region associate with the potential role of overwintering habitats to coho salmon. Such a view is consistent with Moyle's perspective of an equally important role to California coho, quoted above.

Figure 4 illustrates the effect of how movements during the freshwater life history can result in a significant rearrangement of where smolts are produced compared to where spawning takes place. Movements, though mostly directed downstream, can also occur in upstream directions. The pattern seen in Figure 4 is considered representative of many coho populations in the Pacific Northwest (Fedorenko and Cook 1982; Hartman et al. 1998; Brown 2002). It is reasonable to conclude that multiple life history patterns that incorporate some form of redistribution within a

---

[4] / Richard Bailey, based in Kamloops, British Columbia, is assigned to assess the performance of Thompson River coho, a population that has experienced significant decline in recent years. It is a stock of concern in planning fisheries off the coasts of the Pacific Northewest by the Pacific Fishery Management Council.

watershed are common to the species. It is believed that coho home to their natal sites, regardless of redistributions that occur during freshwater residence (Lestelle et al. 1993a).

Moyle (2002) described the importance of redistributions of juvenile coho to California populations as follows:

> "Juveniles show pronounced shifts in habitat with season, especially in California streams. In spring, when stream flows are moderate and fish are small, they are widely distributed in riffles, runs, and pools. As stream flows diminish in summer, they increasingly concentrate in pools or deeper runs. During winter, before emigration, they seek refuges from high velocity flows generated by winter storms. Especially important are large off-channel pools with complex cover or small spring-fed tributary streams."

The utilization pattern illustrated in Figure 4 can be viewed as being representative of a river system with one or more connected lakes having access to coho. Lakes provide a significant component of coho production in some watersheds in coastal Oregon (Zhou 2000), Western Washington (Baranski 1989; Lestelle et al. 1993b), British Columbia (Holtby et al. 1993), and Alaska (Ruggerone and Rogers 1992; Ruggerone and Harvey 1994). Lakes can be important rearing areas during summer (Swain and Holtby 1989) and/or winter (Quinn and Peterson 1996). Lakes would tend to function in the same way as off-channel ponds.

At approximately 18-19 months of age (from egg fertilization), coho juveniles undergo smoltification during spring and enter the marine environment, where they experience very rapid growth. Their smolt to adult survival rate can be strongly affected by exposure to large estuarine complexes like Puget Sound or the Strait of Georgia (Spence 1995; Coronado and Hilborn 1998; Pinnix 1999; Beamish et al. 2000). For example, wild coho smolts that enter Puget Sound survive at rates that average nearly 20% (survival to recruitment to fisheries) during favorable regimes of the Pacific Decadal Oscillation (PDO)(Lestelle et al. 1993b). In contrast, wild smolts entering the Pacific Ocean from the rivers along the Washington north coast, which have no or limited extended estuarine habitat, typically survive at 1/6 to 1/3 that rate (Figure 7)(Sharma et al. 2006; Volkhardt et al. 2007; Quinault Department of Natural Resources *unpublished*). This difference gives populations originating inside the Strait of Juan de Fuca a tremendous boost in productivity compared to those along the outer coasts and makes them naturally more resilient to habitat perturbations. Spence (1995) suggested that coho smolts originating in rivers on the outer coast of Washington, Oregon, and California are affected by ocean upwelling conditions, which influences prey abundance, more immediately and directly than smolts passing through extensive estuarine areas. Hence, marine survival of smolts produced on the outer coasts are more strongly affected by interannual variability in intensity and timing of ocean upwelling events.

Survival to Age 3 Recruits
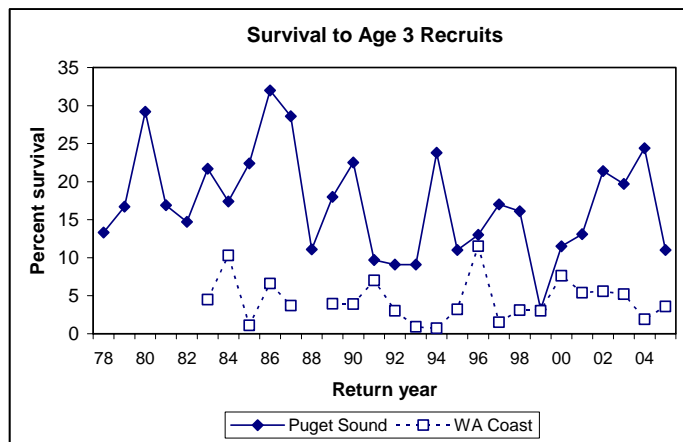
Figure 7. Marine survival from smolt to 3-year old ocean recruitment for wild coho originating in rivers of the Puget Sound and Washington outer coastal regions. Populations representing the two regions are Big Beef Creek and Bingham Creek for Puget Sound and WA coast, respectively. Data from Volkhardt et al. (2007).

Marine survival for populations along the south to central coast of California typically are the lowest of North American coho (Coronado and Hilborn 1998). Those in Northern California (e.g., Klamath) are higher but still below average when compared to other states and provinces (Coronado and Hilborn 1998). Survival rates for Oregon coho are higher yet but tend to also be less than in regions farther north. This latitudinal pattern in survival is correlated with certain factors as reported by Pearcy (1992). He indicated that protected bays, inlets, and shallow littoral areas that favor survival of juveniles are rarer to the south, especially off California and Oregon. In addition, oceanographic variability, resulting from interannual fluctuations in the intensity of upwelling or El Niño events, appears to be greater in the southern part of the species' range.

Recently reported marine survivals for wild fish (brood years 1996-2001) in the West Fork Smith River (Umpqua Basin, Oregon Coast)(Miller 2005) range between 1.3 to 21.7% (mean of 10.2% over 6 yrs) and illustrate the tremendous variation that has occurred over the past decade.[5] A regime shift in ocean conditions is believed to have occurred in 1998-1999, positively affecting many salmon populations in the southern half of their range (Beamish et al. 2004). However, marine survival for some populations within this part of their range was extremely poor in return year 2006 and is forecasted to again be low for 2007 (Volkhardt et al. 2007).

The ocean migration of coho salmon occurs mainly along the coastal waters of the continental shelf in the southern part of the species' range (Quinn and Myers 2004). Northern populations migrate farther off-shore (averaging four times as far from tag recovery work). In the southern region, waters are warmer farther off-shore, less productive, and dominated by other fishes (Pearcy 1992).

---

[5] / The mean for these years reported for West Fork Smith River is much higher than would be expected over a much longer period because it is skewed high by exceptionally high survivals in several years since the regime shift of 1998. Such high survivals also occurred in areas farther north, as seen for some populations on the Washington Coast. This apparently was not the case for Bingham Creek coho shown in Figure xx.

After roughly 16-17 months in the sea, adult coho return to their home rivers. They begin arriving at the entrances to their home rivers in late summer, but more typically in early autumn. Sandercock (1991) noted that fish arrive earliest back to their home river in northern most rivers and latest to rivers farther south. This pattern is generally correlated with the timing of fall and winter rains and increases in stream flow—flows typically rise later moving from north to south. Many smaller streams in Oregon and California are blocked to upstream migration until elevated flows open sand bars formed across their mouths during summer. In larger rivers whose mouths remain open to the ocean, low flows that extend into early or mid fall keep riffles shallow and can slow upstream migration of adult salmon.[6] Major runs within British Columbia and Washington enter their home rivers primarily during September through November (Sandercock 1991). Moyle (2002) described river entry timing for Klamath River coho as between September and late December, peaking in October and November. He noted that river entry in the Eel River, located farther south, is approximately 4-6 weeks later. Shapovalov and Taft (1954) reported entry timing for several Central California streams as being primarily between mid October and end of January. A similar latitudinal pattern of river entry timing also exists for fall-run Chinook in many short coastal rivers (Nicholas and Hankin 1988; Healey 1991), presumably due to effects of flow timing and in-river thermal patterns regulating spawning timing.

To this author's knowledge, an effect of stream temperature on the upstream migration timing of adult coho has not been described in the scientific literature. Water temperatures are typically cooling when adult coho begin their freshwater migration.[7] Quinn (2005) concluded that variation in river entry and migration timing seems to be fundamentally controlled by accessibility to spawning grounds and spawning date. As shown earlier in this section, however, coho in the southern extent of their range appear to be able to postpone spawning if access is significantly delayed. Much remains unknown about factors affecting both migration and spawning timing, including the connection between flow and thermal regimes (Quinn 2005).

River entry across an entire run of fish often occurs in pulses—coinciding with storm events— over a period of three months or more (Shapovalov and Taft 1954; Sandercock 1991), though it can be shorter in small coastal systems. River entry can be continuous when flows are sustained by frequent storms (Holtby et al. 1984). Shapovalov and Taft (1954) reported that run entry in Waddell Creek at the southern end of the geographic range extended over about three months.

Typically moving during high flows, coho salmon return to their natal streams—usually with a high degree of fidelity—to complete their life cycle at spawning. Time of spawning is typically later than that of other species and more protracted such that instantaneous spawner density is often low.

---

[6] / Prolonged low flows in fall can slow the upstream migration rate of adult coho even when the river mouth remains open to the ocean, as seen by the author in major rivers on the Olympic Peninsula in Washington when rains are significantly delayed. This same effect has been noted in the early part of the run on the Klamath River when flows are exceptionally low (CDFG 2004).

[7] / Water temperatures in the lower reaches of rivers in the southern part of the range are often still elevated in September when the earliest run component of coho can begin entering freshwater. Elevated temperatures at this time can contribute to mortality rate on migrating coho, as documented in at least one case on the Klamath River (CDFG 2004).

Within the basic life history, variations exist in age structure, generally following patterns associated with latitude. While the majority of coho are age 3 at spawning, some males mature precociously at age 2 as "jacks", after spending approximately six months at sea (Sandercock 1991). Drucker (1972) suggested that the percentage of jacks in the population decreases from south to north. This life history is virtually absent in the northern end of the range. Precocity, while having some genetic basis, is related to freshwater growth rate and smolt size, both of which decrease with latitude. In the southern half of the range, percentage of jacks in a population is related to quality and productivity of habitat (Young 1999). High quality habitats produce faster growth and larger smolts, resulting in greater precocity—though the percentage of jacks in a population can vary significantly between years (Shapovalov and Taft 1954; Young 1999). Young (1999) suggested that jacks could be critically important in maintaining genetic structure of coho populations because they provide the only gene flow between otherwise isolated brood years for the species.

Another deviation from a three year life cycle occurs because some juveniles spend an additional year rearing in fresh water and emigrate seaward at approximately 30 months of age; these return and spawn at four years of age. This pattern occurs primarily in more northern populations, particularly in Alaska (Sandercock 1991), and is due to growth rates being slower in colder streams, requiring an additional year for fish to attain a size necessary for smoltification. South of British Columbia, very few juveniles typically smolt at 30 months of age (Sandercock 1991), though exceptions exist.

One notable occurrence of age 2 smolts has been found in Prairie Creek, tributary to Redwood Creek, in Northern California by Bell (2001). Twenty eight percent of the smolt yield was reported to be age 2 (approximately 30 months old) in a single year of study. Bell noted that age 2 coho smolts had not been previously documented in California and that they are a small component of smolt yield on the Oregon Coast (citing Moring and Lantz 1975). Walt Duffy (Humboldt State University, *personal communications*) indicates that such a high percentage of age 2 smolts does not occur every year in Prairie Creek, but small numbers likely do, as well as in other Northern California streams. Bell attributed the occurrence of age 2 smolts in Prairie Creek to poor winter and spring growth rates. Duffy (*personal communications*) believes that high rearing densities associated with cool summer temperatures in this stream may be responsible. Nielsen (1992a) observed that one foraging phenotype in some Northern California streams produced exceptionally small yearling migrants (< 70 mm) without smolt like characteristics. Nielsen's observations may provide insights into the occurrence of age 2 smolts in Prairie Creek and other California streams; this is discussed further later in this section.

A central theme in the freshwater life history of juvenile coho is their close association with slow velocity habitats. Body morphology and fin sizes of juvenile coho salmon are particularly adapted to slow velocity habitats. Most coho juveniles have a laterally compressed body with long dorsal and anal fins, thought to be adaptations for life in slow water (Bisson et al. 1988b)(Figures 8-10). Figures 9-10 are from Stein et al. (1972) from observations made on coho and Chinook salmon in the Sixes River (Oregon Coast).[8] Note the significant differences in fin sizes between Chinook and coho juveniles at around 60 mm body length in Figure 9. In contrast

---

[8] / The Sixes River in Southern Oregon is the first river immediately north of the northern boundary of the Southern Oregon Northern California Coasts Coho ESU.

to coho fry, steelhead fry have cylindrical bodies in cross section with short dorsal and anal fins, adapted to higher velocity habitats than used by juvenile coho (Bisson et al. 1988b). Juvenile Chinook have a body form and fin sizes intermediate between coho and steelhead (Figures 8 and 9). These morphological differences between juvenile coho and other salmonid species appear to favor coho in interspecific interactions in habitats most favored by coho (Stein et al. 1972; Hartman 1965; Glova 1986; Young 2001). Coho generally dominate in competitive interactions within slow water habitats with Chinook, steelhead, and cutthroat. Fin morphology is believed to be important in social interactions of salmonids (Keenleyside and Yamamoto 1962; Stein et al. 1972).

These differences in body shape and fin sizes between species are also consistent with water velocity and depth preferences reported for these species (Figure 11). Data in Figure 11 come from a study in the Trinity River in the Klamath River basin (Northern California)(Hampton 1988). Almost identical depth and velocity preferences are reported for juvenile coho salmon in rivers of Western Washington (Figure 12)(Beecher et al. 2002). Coho prefer much slower velocities than either steelhead or Chinook; Chinook preferences are intermediate between coho and steelhead. It is noteworthy that preferred water velocities of juvenile coho salmon change little between fry (<50 mm) and parr (>50 mm), whereas a significant change occurs for juvenile Chinook salmon. Juvenile coho are typically 60-70 mm in size by the end of their first summer of life. It is logical to expect that selection of habitat types by these species would reflect their adaptation to water velocity and depth.

Figure 8. Juvenile coho salmon (top), Chinook salmon (middle), and steelhead trout (bottom) illustrating differences in fin size and body morphology. Photos courtesy of Roger Tabor, U.S. Fish and Wildlife Service, Lacey, Washington. Note that the dorsal and anal fins of the coho are easily recognized by their white leading edges.
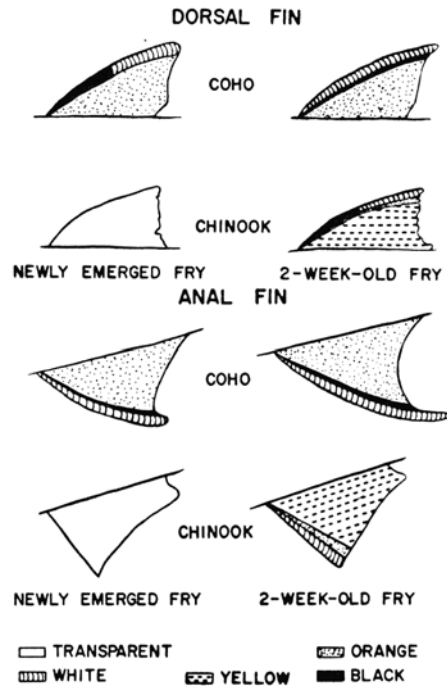
Figure 9. Diagrammatic sketches of the dorsal and anal fins of recently emerged and 2-week old coho and fall Chinook salmon in Sixes River (Oregon Coast). From Stein et al. (1972). Note that differences in size of fins between species increase as fish grow (see Figure 10) and appear to be greatest at lengths of about 60 mm, which for coho would typically occur between mid to late summer.

Juvenile coho can adjust their velocity preferences to a limited extent depending on food availability. Based on controlled experiments, Rosenfeld et al. (2005) reported that increased food abundance resulted in greater growth of both dominant and subdominant juvenile coho and a shift to higher average focal velocities. Increased food permits juvenile coho to exploit higher velocity microhabitats that might otherwise be bioenergetically unsuitable with less available food. The authors observed that average focal velocities shifted from 6.5 cm/s to 8.4 cm/s, with maximum growth occurring in the range of 10-12 cm/s. Still, the shift reported by these authors was small, with velocities remaining within the strongly preferred range shown in Figure 12.
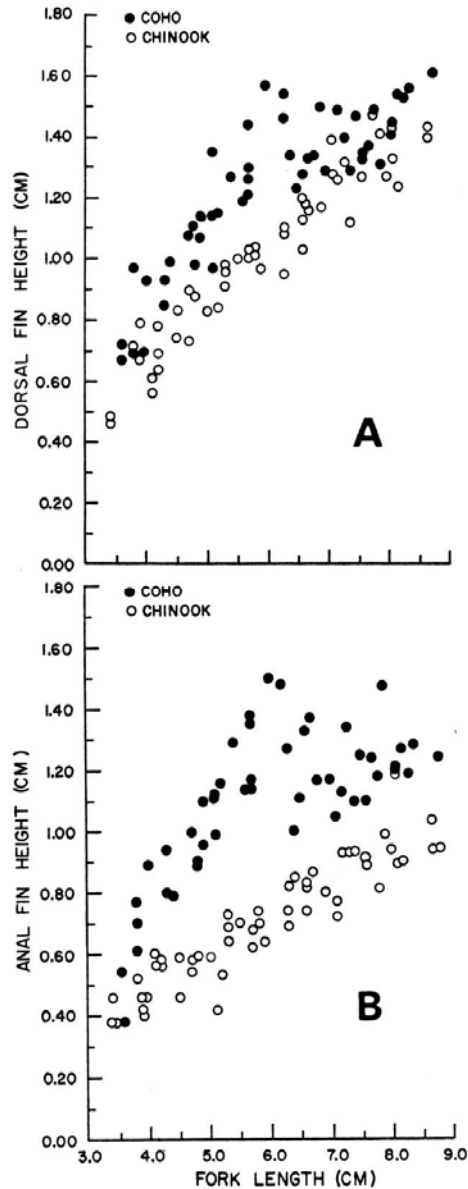
Figure 10. Differences in dorsal and anal fin sizes between juvenile coho and Chinook salmon. From Stein et al. (1972).

Variation has been found to exist between regions both with respect to body morphology and swimming performance. Taylor and McPhail (1985a) identified two morphological forms based on differences in body shape and fin size: a "coastal" form, characterized by large dorsal and anal fins and a deep robust body, and an "interior" form with smaller fins and a more streamlined body shape. Figures 8-10 illustrate characteristics of what those authors called the coastal form. The study was based on a comparison of samples collected in the Thompson River subbasin (interior Fraser basin), lower Fraser River tributaries, and Vancouver Island streams. In addition, the authors performed breeding experiments to determine if these morphological differences are inherited. Further, to see if morphological differences between interior and coastal populations

found in these areas exist in other regions, they sampled preserved juvenile coho (from fish museums) from the upper Columbia system and from creeks in north coastal British Columbia and Alaska. They concluded that the coastal-interior stock differences in morphology is part of a coastwide pattern and that the differences are at least partially inherited. The authors also reported that adult coho sampled in the same areas showed some of the same morphological differences displayed by the juveniles.
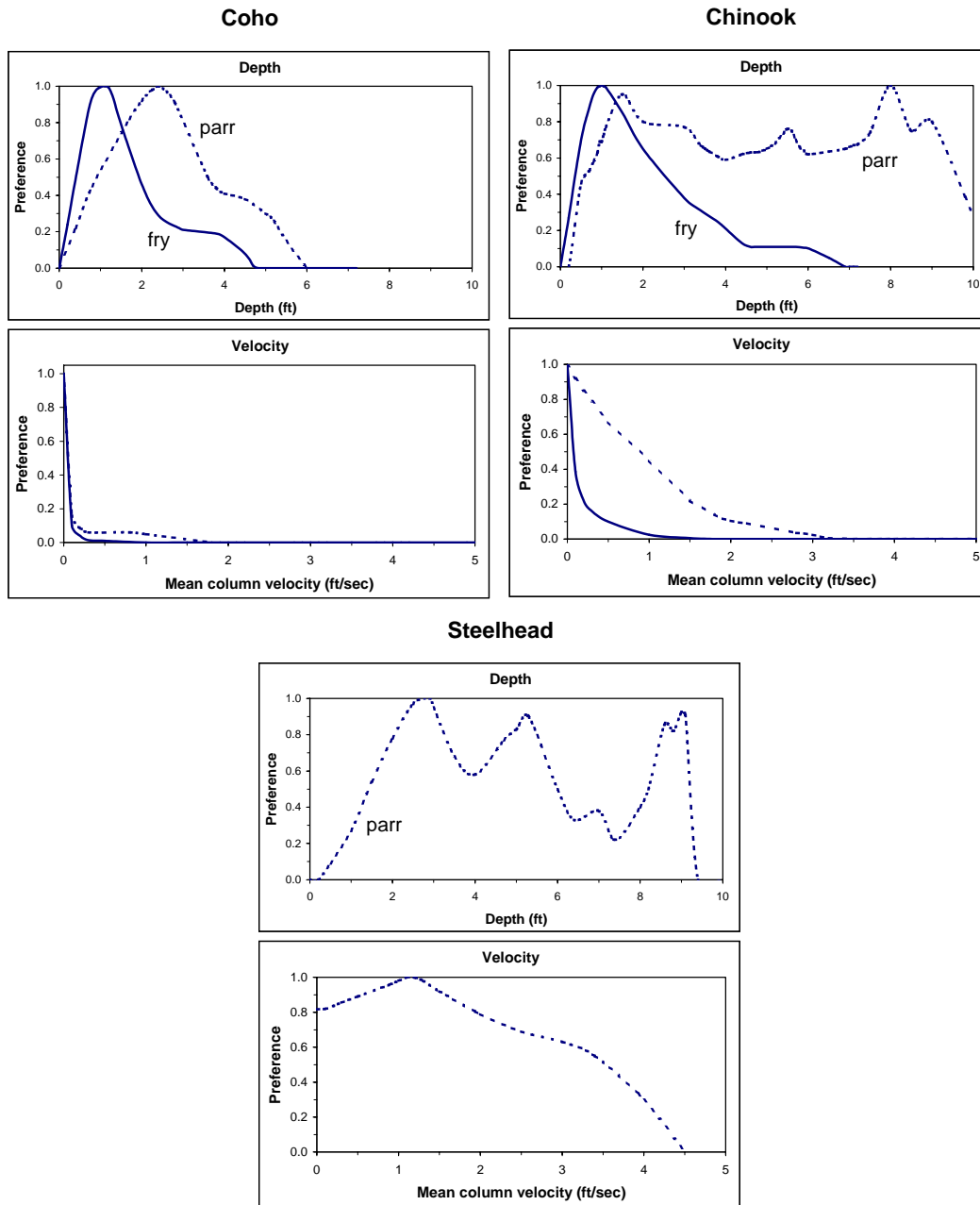
Figure 11. Water depth and velocity preferences of coho salmon, Chinook salmon, and steelhead trout fry (<50 mm) and parr (>50 mm), as observed in the Trinity River in the Klamath River basin (Northern California). Water velocities are mean column values. Adapted from Hampton (1988).

Coho
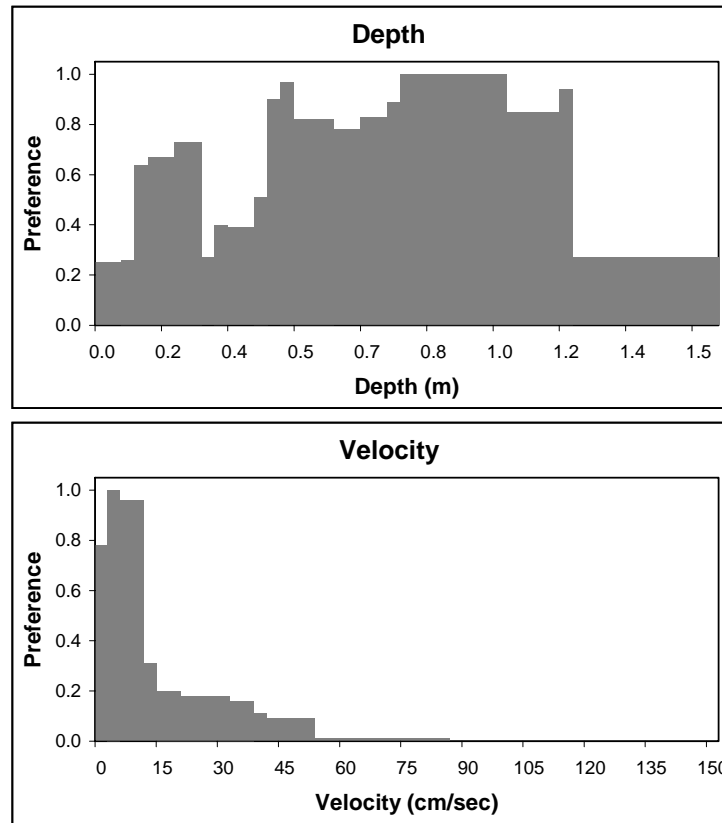
Figure 12. Water depth and velocity preferences of subyearling coho salmon found in rivers of Western Washington. From Beecher et al. (2002). Water velocities are measured at 0.6 depth (approximately equal to mean water column values). Note: 30.5 cm = 1 ft.

These two morphological phenotypes differ in swimming performance (Taylor and McPhail 1985b). Coastal juveniles were found to have greater burst velocities (fast start) than the more streamlined interior form. In contrast, the interior form was found to have significantly greater swimming stamina, on average four to five times the prolonged swimming performance of coastal juveniles. Taylor and McPhail (1985b) concluded that differences in swimming performance were related to body and fin morphology. They noted that variations in swimming performance are probably adaptive and related to differences in the energetic demands of their freshwater migrations (smolt and adult) and perhaps to levels of predation experienced by coastal and interior forms. Burst speed would favor fish exposed to abundant predators under conditions where swimming stamina is not as important. In contrast, swimming stamina would favor smolts and returning adults that migrate long distances in swift, turbulent rivers, such as the Fraser and Thompson rivers.[9]

---

[9] / Swimming stamina would also favor long distance movements of pre-smolts, as has been hypothesized for a fall redistribution of Thompson River coho described earlier.

The findings of Taylor and McPhail (1985a and b) raise a question about whether both morphological forms exist in the Klamath River where interior and coastal ecoregions occur. Within the interior portion of this basin, some coho are currently produced in excess of 200 miles from the ocean. Their migrations in the mainstem Klamath River traverse many turbulent, swift reaches, not unlike the Fraser River but on a smaller scale. Implications of this question are discussed later in this document.

Variation in morphological forms—similar to that described above—has also been found at a much smaller scale than that of ecoregions. Swain and Holtby (1989) reported distinct differences in body morphology between life history forms associated with different habitat use patterns in a single river system. Certain morphological characteristics of juvenile coho rearing in a small lake within the Cowichan River system (Vancouver Island) were significantly different than those of stream-rearing coho in the lake's inlet stream. Lake rearing fish had more posteriorly placed pectoral fins, shallower bodies and smaller, less brightly colored dorsal and anal fins than did stream rearing fish. The dorsal and anal fins of stream fish were larger and more falcate than lake fish. Lake rearing fish were schooling and non-territorial, unlike the highly territorial stream fish, which displayed frequent aggressive behavior. These characteristics, both morphological and behavioral, were maintained when both forms were placed within a common laboratory environment for two months.

The researchers concluded that differences between forms may be genetically based, or environmentally induced and fixed early in life. They inferred that the differences between forms are adaptive, with fin size, body shape, coloration, and behavior of each form more suited to survival within their respective rearing environments. While they proposed a plausible mechanism for genetic differentiation, phenotypic plasticity seemed just as likely. Their findings showed that either through genetic divergence or phenotypic plasticity, coho within a relatively small—yet diverse—river system can adapt to exploit contrasting habitats, thereby reducing intraspecific competition and increasing overall utilization of the system. More recent research suggests that the findings of Swain and Holtby (1989) were due to phenotypic plasticity—not genetic differentiation—as fin size and body morphology of juvenile salmonids has been found to be shaped by water velocity (Pakkasmaa and Piironen 2001). It should be noted that species-specific responses to water velocity differs between species, likely due to different energetics and cost reduction strategies.

Another aspect of life history that may differs between regions is foraging behavior. Foraging behaviors can vary between individuals of the same population or even of the same family. Nielsen (1992a; 1992b; 1994) identified four foraging behaviors of juvenile coho—she considered them distinct phenotypes. She suggested that one of the four types may be unique to the southern portion of the species' range (i.e., California); see also Moyle (2002). Nielsen's findings were based on studies conducted in one Puget Sound stream over two years of study (Nielsen 1992b) and in ten Northern California streams over four years (Nielsen 1992a and 1994). In the California work, Nielsen (1992a and 1994) monitored foraging behaviors of individual fish from fry emergence until outmigration as yearlings. Fry were trapped and marked as they emerged from distinct redd sites, their subsequent movements and feeding patterns were observed, they were remarked at larger sizes (still knowing their origin) so they could continue to be followed and observed through summer and winter. Drought conditions in California during

the years of study allowed observations to continue throughout winter. Each foraging phenotype was found to utilize habitat features differently (Table 1). All four phenotypes were consistently found in the Northern California streams. Fish rarely changed their foraging behavior once they had been associated with a phenotype. Nielsen concluded (Nielsen 1994; Jennifer Nielsen, U.S. Geological Survey, *personal communications*) that the phenotypes are not genetically distinct but are the result of population responses to different environmental conditions.[10]

In her earlier work, Nielsen identified two of the four foraging phenotypes in a Puget Sound stream (Nielsen 1992b), the *thalweg hierarchy* and *margin-backwater* types. The *thalweg hierarchy* type is the most common foraging behavior of juvenile coho found in the Pacific Northwest and California during summer. It is the stereotypical coho foraging pattern, used by the largest proportion of a population (Table 1). The primary habitat used by this type is main channel pool, i.e., pools associated with the channel thalweg. Fish that employ this foraging pattern are grouped in partial dominance hierarchies, with dominant and subdominant individuals. They feed predominantly on invertebrate drift and grow throughout the summer, attaining sizes of 60-85 mm by winter (Figure 13), when growth typically slows. A surge in growth occurs in spring, when they reach sizes of 90-105 mm in California streams. They smolt and emigrate to sea between March to June. This foraging pattern occurs in other regions.

The second phenotype found both in Washington and California is the *margin-backwater* type, called "floaters" in Nielsen (1992a)(see also Puckett and Dill 1985). This type is composed of fish that move to slack water habitats at or near the channel margin immediately following emergence and do not subsequently move to deeper water as they grow. They do not form dominance hierarchies but instead roam relatively large forage arenas feeding opportunistically on food of terrestrial and aquatic origin. Forage arenas are characterized by extremely low velocity flow along the channel margin or in backwater pools. Growth rates of these fish are low compared to other foraging phenotypes (Figure 13). Margin-backwater fish remain small throughout summer, fall, and winter (Nielsen 1992a and b).

---

[10] Nielsen (1994) gives details on the numbers of families and individuals that were monitored by marking wild fish for brood years 1990 and 1991. Newly emerged fry were captured by trapping 16 distinct redds in five of the study streams. Fry were marked using a broadcast spray of fluorescent pigment, with different colors used on fish from adjacent redds. Fish were released at the redd sites following marking and allowed to disperse naturally. After several weeks, marked fish were recaptured (at approximately 45 mm in size), then re-marked as individuals using a Pan Jet innoculator with acrylic paint. Surviving marked individuals were observed over the course of the study. A total of 105 individuals were observed at the time of smolt migration and an additional 40 fish were sacrificed for analysis at 6-16 months following marking with the Pan Jet. Nielsen did not identify how many other marked fish were observed at various times during the study.

Table 1. Characteristics used to depict wild coho phenotypes in 10 streams in Mendocino County, Northern California 1989-1992. Recreated from Nielsen (1994). Sample sizes were not reported for each phenotype in the original papers—see footnote in text regarding overall numbers of marked fish observed in some years of the study.

Coho characteristic	Coho foraging phenotype			
	Thalweg	**Margin**	**Estuarine**	**Early emerging**
Primary habitat	thalweg flows	margin/backwater	estuary tidal prism	cutbank/rootwad
Social system	large groups (17-38) operating in partial dominance hierarchy	isolated roving individuals	individuals found in widely dispersed large groups (14-23)	small integrated groups of 2-4 fish, no obvious hierarchy
Emergence timing	February – April	February – April	February – March	January – February
Foraging behavior	forage stations	forage stations	opportunistic	forage stations
Forage timing	diurnal	diurnal	diurnal	crepuscular
Primary diet source	aquatic invertebrates	terrestrial invertebrates	aquatic invertebrates	terrestrial invertebrates
Mean diet caloric content (season)	low (all year)	empty to high (seasonally mixed)	highly variable (all year)	high (all year)
Intraspecific agonistic behavior	highly competitive	little interaction	highly competitive	little interaction
General growth pattern – spring	dominant = fast subdominant = average	slow	slow	fast
General growth pattern – summer	dominant = average subdominant = slow	slow	average	slow
General growth pattern – fall/winter	dominant = fast subdominant = fast	slow	slow	fast
Size-at-age	dominant = large subdominant = average	small	average	large
% emerging population	67%	17%	13%	3%

Coastal Coho Phenotypes
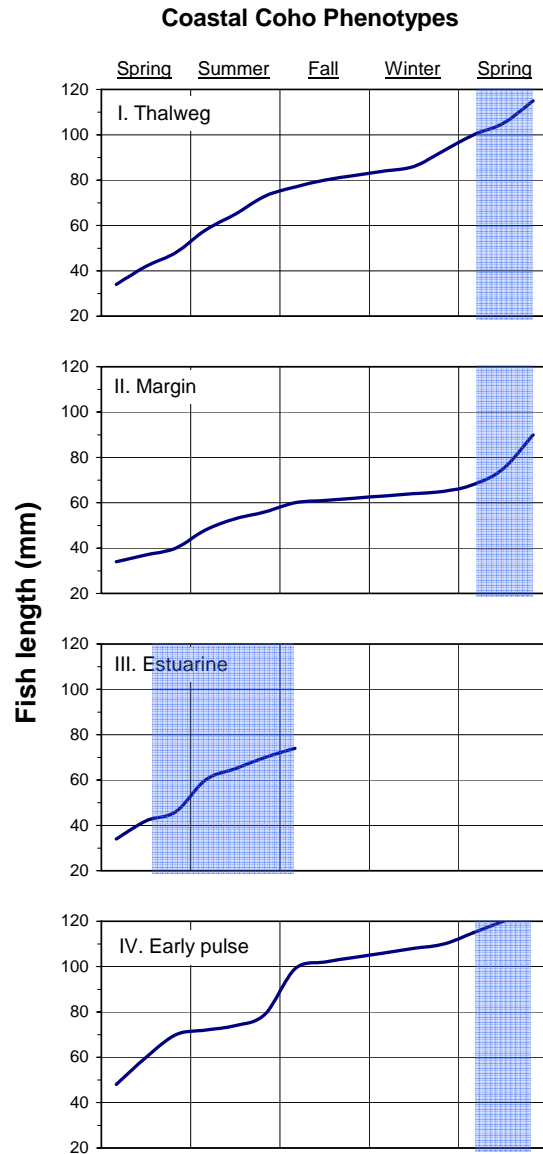
Figure 13. Coastal coho foraging phenotypes, showing unique growth rate cycles and movement from fresh water to the stream mouth estuary, as documented in Northern California streams. Presence within the stream mouth estuary is shown as shaded. Adapted from Nielsen (1992a).

In Northern California streams, Nielsen (1992a) reported that margin-backwater juveniles moved to the estuary in spring as small yearlings (<70 mm) without smolt characteristics, their fate being uncertain. Fish of this size should tend to remain in fresh water for another year and smolt as two year olds. This would explain Bell's finding of a large number of age 2 smolts in Prairie Creek in one year. Nielsen (1994), however, noted that no evidence was ever found for age 2 smolts in the ten populations studied in Northern California (from scale analysis). Perhaps all of the conditions that would cause fish of this phenotype to remain in fresh water for an added year occurs infrequently in this region. The question arises as to the adaptive benefit of a foraging strategy that produces such small yearling migrants, whose survival appears questionable. They may experience rapid growth in the stream mouth estuary and move into the open ocean at a

much larger size (Figure 13). Alternatively, if fry exhibiting this phenotype move from natal tributaries following emergence into larger mainstem rivers, when present (see Figure 4), and find greater food supplies there, growth could be much faster during summer. Growth rates during summer in mainstem rivers, where water temperatures are suitable[11], normally exceed those in small natal streams (Cederholm and Scarlett 1982). Fish displaying this foraging behavior may also be those found to move into riverine ponds or alcoves soon after emergence, residing there through summer and winter (discussed later in this document). Fish that do so would be expected to attain a size necessary for smoltification, assuming suitable water temperatures exist in summer. Thus, the contribution of this foraging type to population sustainability may depend on availability of certain habitat types and adequate food resources.

The third phenotype is the *estuarine* type (Table 1; Figure 13). Although not observed by Nielsen in Washington (due to the location of the study), this foraging behavior occurs across the species' range, as described earlier in this document. In California, Nielsen (1994) described fish exhibiting this phenotype as moving up and down the stream mouth estuary[12] during spring and summer within the freshwater surface layer. The juvenile coho foraged opportunistically on whatever was found in the water column, as well as picking up food items along the substrate. They fed on items of both freshwater and marine origin. In an Alaskan stream, Murphy et al. (1984) found young of the year coho to grow more quickly in the stream mouth estuary than in freshwater reaches upstream. Similarly, Tschaplinski (1988) found juvenile coho within a stream mouth estuary in British Columbia to significantly outgrow those rearing upstream; by fall the estuarine fish were longer by 16-18 mm.

Nielsen was unable to follow the estuarine fish through winter—she noted that their distributions during winter and the following spring remained unknown (Nielsen 1992a). Murphy et al. (1984) found in an Alaskan stream that most juvenile coho evacuated the stream mouth estuary prior to winter; the authors presumed—but could not confirm—that fish moved upstream to more favorable freshwater sites. In British Columbia, Tschaplinski (1988) reported that juvenile coho left the stream mouth estuary between late September and November—no overwintering occurred in the estuary. Moreover, Tschaplinski found only a small number of juveniles to move back upstream into fresh water to overwinter. He inferred that the majority of estuarine juveniles moved into Barkley Sound. Based on lab studies, he concluded that juveniles that reared in the stream mouth estuary during summer, gradually being acclimated to brackish water, were able to physiologically tolerate brackish to moderately high salinity of the nearshore, surface waters of Barkley Sound. However, the lab studies showed that the estuarine reared juveniles could not fully osmoregulate in 30 ‰ sea water at the time of their departure despite their size being comparable to yearling smolts. Miller and Sadro (2003) conducted extensive marking and ultrasonic tag tracking studies to investigate seasonal movements of juvenile coho within portions of the relatively large Coos Bay estuary in Southern Oregon. They found no evidence that juveniles moved beyond the upper estuary into the strongly marine environment during fall. They concluded that similarities in life history patterns between southern and northern regions of

---

[11] / Suitability of various temperatures to growth and survival is discussed later in this report.

[12] / The estuarine zone immediately associated with its principal freshwater source is referred to in this document as a stream mouth estuary. Estuaries can be very large and can include a continuum of conditions from areas having no salinity (at the upper end of tidal influence) to those with near fully marine characteristics. Puget Sound is technically considered an estuary.

the species' range include downstream movement to the stream mouth estuary at age 0 during both spring and fall, use of the upper estuarine zone for months, and upstream movements during fall to overwinter in fresh water. They stated that regional differences likely exist in how estuaries are used by juvenile coho given the profound differences in nearshore oceanographic conditions between regions.

Nielsen (1992a; 1994) called the fourth foraging phenotype the *early emerging* or *early pulse* type (Table 1). This phenotype has only been described in Northern California. It is comprised mainly of early emerging fry from individual redds. Nielsen found that a small proportion of the fry in a redd emerged much earlier than the majority of fry; approximately 3% emerged during January and February. These fish demonstrated an unusually fast growth pulse immediately after emergence.[13] They attained lengths of 65 to 78 mm by late May or early June (Figure 13). Growth then shut down during summer, followed by another growth pulse in early fall. By late September they could be 105 mm in size and by spring they tended to resemble two year olds.

The foraging behavior of early emerging fish was found to be distinctly different than the behaviors of the other phenotypes. Upon emerging, the fry fed initially in groups of 3 to 5 fish on drifting aquatic invertebrates at the margins of pools. Few agonistic interactions occurred within the small groups. As they grew, these fish occasionally left their positions at the margins and fed briefly on drift aquatic invertebrates in deeper water (March to April). By summer their foraging behavior was characterized as being more trout-like than is common among juvenile coho. They foraged only at dawn and dusk on drifting invertebrates in the water column. During the day, they sought refuge in undercut banks, often associated with cold-seeps along terrace cutbanks.

Nielsen (1992a) stated that only this fourth phenotype was found to be in close proximity to cold-seeps along terrace cutbanks. She reported that this phenotypic expression was dominant in streams subject to drying during the drought that was then underway at the time of the study. She concluded that this behavior is "the one most likely to survive to smoltification in freshwater stream habitats" subject to extreme drought conditions. Thus, she suggested that the phenotype represents a pattern of adaptation significant to coho salmon in the southern portion of their range.[14]

Limitations of Nielsen's descriptions of foraging phenotypes should be recognized. The descriptions did not identify how fish moved longitudinally within a stream system upstream of the estuary, as depicted in Figure 4. It is not known whether one or more type is more likely to move longitudinally along the stream system during spring, summer, or fall. A further limitation is that the observations were made during drought conditions. It is uncertain how the types might

---

[13] / It is noteworthy that Koski (1966) found that the earliest emerging coho fry from individual redds in Oregon coastal streams were consistently the largest of all fry produced from the redd. Fry length typically would steadily diminish for later emerging fish. The size differential between the early and late emerging fry was nearly 3 mm on average (38 mm vs 35 mm). The average number of days over which fry emerged from a individual redd was about 35 days.

[14] / It is uncertain to this author whether or to what extent juvenile coho might switch from the thalweg phenotype to an early pulse type phenotype under severe drought or high water temperature conditions. Nielsen's work suggests that switching would generally not occur, that is, fry that emerge during the peak of emergence would not display the foraging behavior of the early emerging fry.

differ during wet cycle years with regard to phenotype composition, foraging and growth patterns, and migrant sizes. It is also unknown how the patterns might differ with stream size.

3.0 Freshwater Habitat Utilization

This section describes the relative utilization—or importance—of various physical habitats to coho salmon and associated survivals within the freshwater environment. It is necessary for clarity to begin with a short description of the various riverine habitats utilized by salmonids. In fresh water, coho primarily utilize stream habitats, though they also rear in lakes where present within the accessible stream network of a watershed (Sandercock 1991). Emphasis is given in this report to describing use of stream habitats with some limited coverage on lake utilization.

3.1 Description of Channel and Habitat Types

Riverine habitat types refer to physical features of the aquatic system defined by channel and valley morphology and flow characteristics—they can be defined at multiple scales (Frissell et al. 1986; Burnett 2002). In this document they are defined either by geomorphic (channel) unit type, edge unit type, or channel type (Figure 14).[15]

Geomorphic units (or channel units) are distinct physical features of the channel that have relatively homogenous characteristics of depth, velocity, and substrate (Bisson et al. 1982; Montgomery and Buffington 1998). There are many classification schemes in use to distinguish geomorphic units (e.g., Hawkins et al. 1993)—the units shown here capture the main ones referred to often in salmonid ecology studies. In studies of coho salmon, pools are often further delineated as being either scour pools or dammed pools (such as beaver ponds)(Level II from Hawkins et al. 1993) or even further into other pool types as often done on the Oregon Coast (e.g., Nickelson et al. 1992).[16] It suffices here to keep the delineation fairly broad but reference to Nickelson's classification is also used in this document.

Delineation of channel edge habitats is based on Murphy et al. (1989), Beechie et al. (2005), and Schwartz and Herricks (2005). Three types of edge units are recognized, consistent with Beechie et al. (2005): backwater pools, bank edges, and bar edges (Figure 15). These habitats can be particularly important as velocity refugia to small fish as flows increase. Backwater units (or backwaters) are partially enclosed, low velocity areas separated from the main river channel (Figures 16). They often form at the mouths of remnant channels or small tributaries. Expansion eddy units, as defined by Schwartz and Herricks (2005), are considered backwater units here. Bank and bar edges are localized hydraulic dead zones formed at the channel margins associated either with vegetated banks or gravel bars. As flows increase above baseflow, vegetation along bank edges can be wetted and inundated (Figure 17).Another aspect of the channel form sometimes used to distinguish habitat types is channel type, such as main channel, side channel,

---

[15] / Habitat type delineation in this document is drawn from Lestelle et al. (2005).

[16] / The classification scheme applied to pool types in Oregon coastal streams refers to one type as an <u>alcove</u>, which is actually an off-channel habitat type. Along mainstem rivers, this habitat type is often called an off-channel pond, as commonly done in Washington State and British Columbia. Hence, in this report alcoves and off-channel ponds are synonymous. Elsewhere in Oregon State, such as along the Willamette River, the term "alcove" is sometimes used to refer to backwater pool units (Landers et al. 2002—discussed in Lestelle et al. 2005).

or wall-base channel (Peterson and Reid 1984; Stanford et al. 2002). Identification of channel type is particularly important in addressing habitat issues in large mainstem rivers where geomorphic channel units do not adequately describe all of the features utilized by salmonids. In this document, channel types are grouped according to Lestelle et al. (2005).

All channels other than the primary (or largest) channel of the main river—including off-channels—are called secondary channels. Numerous terms have been applied to the continuum of secondary channels that exist in various river types—often without clear definitions of distinguishing characteristics. Types are grouped here to facilitate recognition of various habitats referred to in the scientific literature and as a way to simplify a wide variety of terms that have been used. (It is recognized that classifying channel types presents difficulties, however, because there is actually a continuum of channel conditions that change with flow level. Some channels are mixtures of different types and some are transitional between types.)
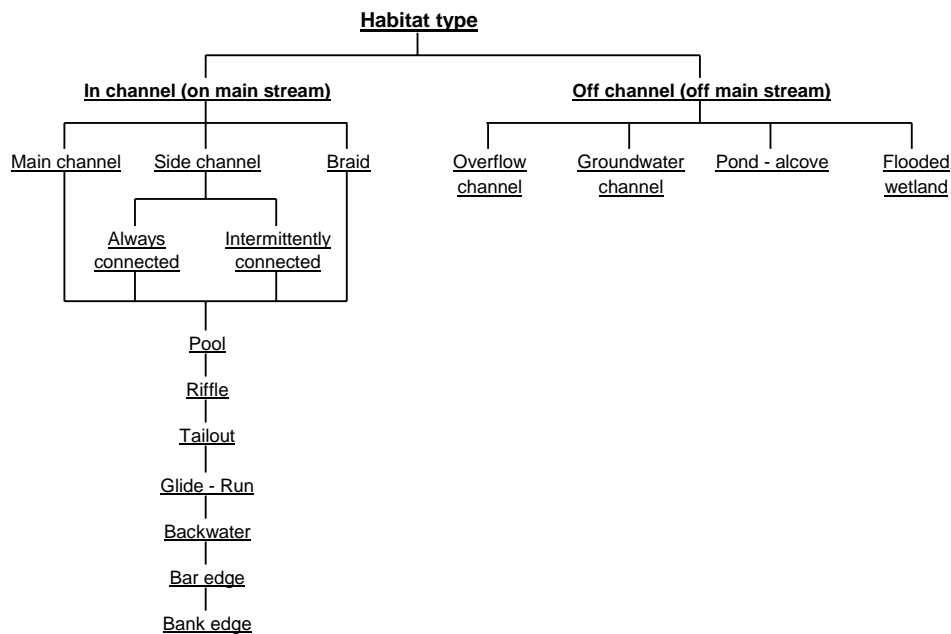
Figure 14. Riverine habitat types utilized by salmonid species. From Lestelle et al. (2005) with revision to use of the term "alcove" – see text. In channel mesohabitats occur in the main channel, side channels, and braids.

Riverine habitat types can be grouped according to their location with respect to the main stream channel as being either in-channel or off-channel. The distinction here is made consistent with Peterson and Reid's (1984) classification (Figure 18), which closely resembled the more recent classification of riverine channels by Tockner et al. (1998), Ward et al. (1999), and Zah et al. (2000).[17] The relative importance of main river versus off-channel habitats can vary widely

---

[17] / Tockner et al. (1998) and Ward et al. (1999) identified six channels based on surface hydrological connectivity with the main channel and source of water: (1) main channel, (2) side channels, (3) intermittently-connected side channels, (4) mixed channels, (5) groundwater channels, and (6) tributaries. They also provided a subdivision of groundwater channels. They did not address braids. Mixed channels were those that had a mixture of flow sources. Zah et al. (2000) subdivided ground water channels into (a) alluvial groundwater channel and (b) lateral groundwater channel, comparable to Peterson and Reid's percolation and wall-base channels.

between salmonid species and life stages. The need to recognize off-channel habitats is particularly relevant to coho salmon.
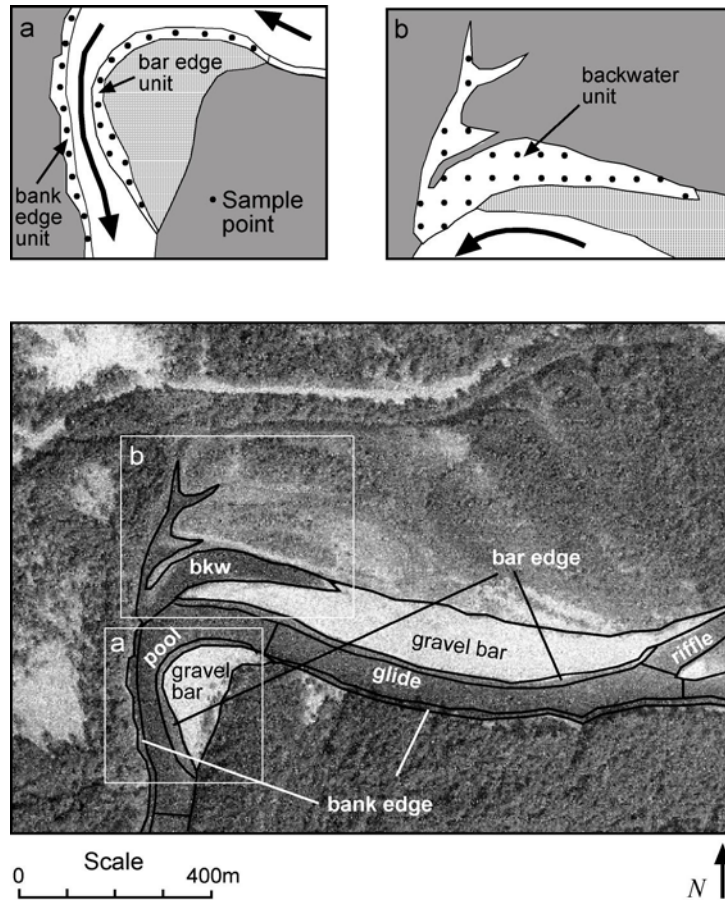
Figure 15. Illustration from Beechie et al. (2005) showing example of locations of habitat units delineated on the Skagit River (Washington). Note the very large backwater unit. Backwater units were most commonly located where off-channels or side channels joined the main river. See Figure 16 for photograph of the backwater shown in this figure.

Figure 16. Backwater habitat unit on the Skagit River illustrated in Figure 15. Photograph provided by Eric Beamer of the Skagit River System Cooperative.

Figure 17. Bank edge habitat unit along the Klamath River during spring runoff.

Although Peterson and Reid's (1984) classification of channels is often cited in the scientific literature, some of these references are inconsistent with Peterson and Reid in that they classify side channels as being off-channel habitats (e.g., Sedell et al. 1984; Landers et al. 2002; Saldi-Caromile et al. 2004). The term "off-channel" as applied here is reserved to those habitats without direct openings at their upstream end to the main river, except when flows overtop the

floodplain, consistent with Peterson and Reid (1984). Flow source and fish behavior, such as how fish move into a habitat, differ markedly between off-channel habitats as defined here and those located in main river channels.
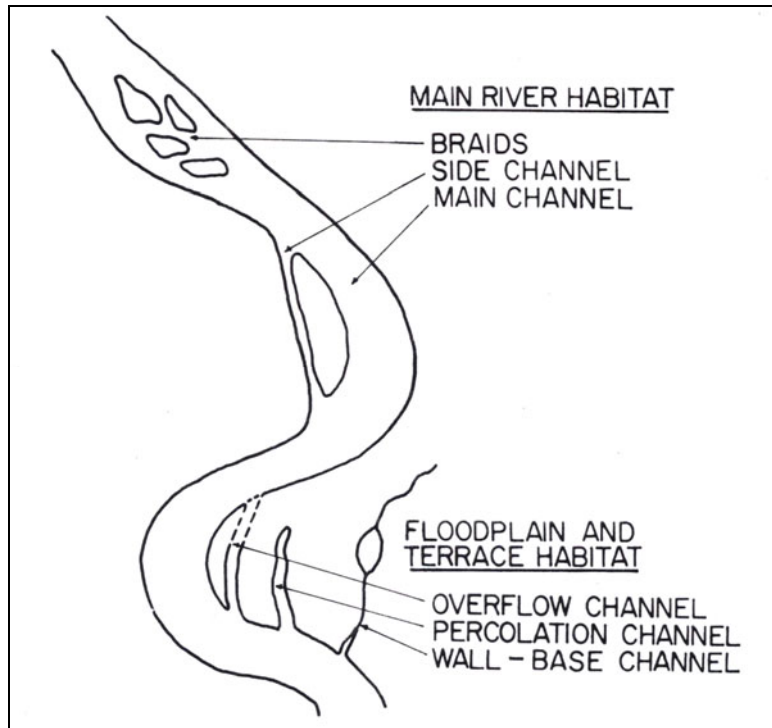
Figure 18. Main river and off-channel channel types from Peterson and Reid (1984).

Within the category of main river habitat, the distinction between braids and side channels is important. A braided channel reach is one that typically has numerous branches, separated by exposed alluvial bars. The bars tend to be transient, unvegetated and submerged at bankfull flow (Knighton 1988). Braided channels generally have high bed load, erodible banks, and relatively high stream power—hence they are unstable and prone to shift. Braided reaches occur naturally, particularly in glacial valleys, but they can also result from riparian destabilization caused by vegetation removal (Buffington et al. 2003). From an ecological perspective, they are hostile environments because of their dynamic nature (Tockner et al. *in press*). A side channel is an active channel separated from the main river by a vegetated or otherwise stable island (Knighton 1988) and carries surface flow at flows less than bankfull. Islands tend to be large relative to the size of the channels. While side channels can occur in almost any type of river, they frequently occur in anastomosing rivers—those characterized by having extensive multiple channels with relatively stable islands. This river type is normally associated with unconfined channels with relatively wide floodplains. Historically such rivers in the Pacific Northwest often carried high wood loads, which acted to create and stabilize islands and frequency of channel avulsions (i.e., shifts). These features served to "meter" flow into many small side channels, providing very stable conditions for small fish year-round (Sedell and Frogatt 1984; Collins et al. 2003).

Off-channel habitat types are those not fed by surface water from the main river when flows are less than bankfull.[18] They are fed by floodwaters, groundwater (or hyporheic flow)[19], and in some cases, by water sources from higher terraces. They occur on a stream's floodplain, sometimes on the higher elevations of the extremities of the floodplain (Figure 19). Peterson and Reid (1984) identified three types of off-channel habitats: overflow channels, percolation channels, and wall-base channels. Tockner et al. (1999) combined percolation channels and some forms of wall-base channels and called them groundwater channels, which is done here. Saldi-Caromile et al. (2004) separated floodplain ponds from wall-base channels, also done here. None of these authors included seasonally flooded wetlands as a distinct channel type but they are increasingly recognized as being an important habitat feature in some rivers (Sommer et al. 2001; Lestelle et al. 2005).

For some salmonid species, groundwater channels, ponds/alcoves, and seasonally flooded wetlands can be especially important in their life history. Groundwater channels are usually relict river or overflow channels fed largely by subsurface flow, though surface flow from higher terraces can also contribute. They can be small features with little base flow (Sedell et al. 1984) or much more extensive where former river channels receive substantial subsurface flow (Figure 20). They usually have little flow velocity, clear water, and temperatures colder in summer and warmer in winter than in the main river. Stanford and Ward (1993) referred to them as "hotspots" of production for some aquatic species.[20] Groundwater channels often can be recognized by the presence of abundant aquatic vegetation, indicating stable flow and substrate (Figure 21).

Floodplain ponds and alcoves are water filled depressions, partially or entirely filled with water year-round (Dykaar 2000). Floodplain ponds are often cut-off oxbows with small egress channels to the main river (Figure 19). Ponds in meandering valley segments are vulnerable to high water temperatures and low dissolved oxygen during summer, depending on their water source, but these often provide high quality habitat during winter. Where present along tributaries to larger rivers, floodplain ponds are often small features and called alcoves within some classification schemes (as commonly done on Oregon coastal and Northern California streams). Alcoves along small streams can be very small features (Figure 20). In Prairie Creek in Northern California, some alcoves are as small as 3 ft across or smaller (Walt Duffy, Humboldt State University, *personal communications*).

Seasonally flooded wetlands occur on the floodplains of large rivers and are the remnants of ancient ponds and relict channels (Dykaar 2000). These areas are typically flooded during fall-winter or spring, depending on a river's runoff pattern (Figure 21). They can be relatively small

---

[18] / It is recognized that the lower ends of some off-channel types can be supplied from surface water backed up from the main channel.

[19] / Technically hyporheic water and true groundwater are not the same. Hyporheic water is a type of shallow subsurface water beneath and beside streams—it is the interface between true groundwater and surface water (Edwards 1998). True groundwater is typically deeper and older in its origin than hyporheic flow. In this document, they are treated as the same as is often done in the fish ecology literature.

[20] / Groundwater channels as defined here are referred to by different terms in the scientific literature: springbrooks, spring channels, percolation channels, hyporheic channels, groundwater side channels, wall-base channels, and terrace tributaries—all tend to have similar features.

in size or very expansive, as occurred historically along many large rivers in the Pacific Northwest and California (Sommer et al. 2001; Lestelle et al. 2005).
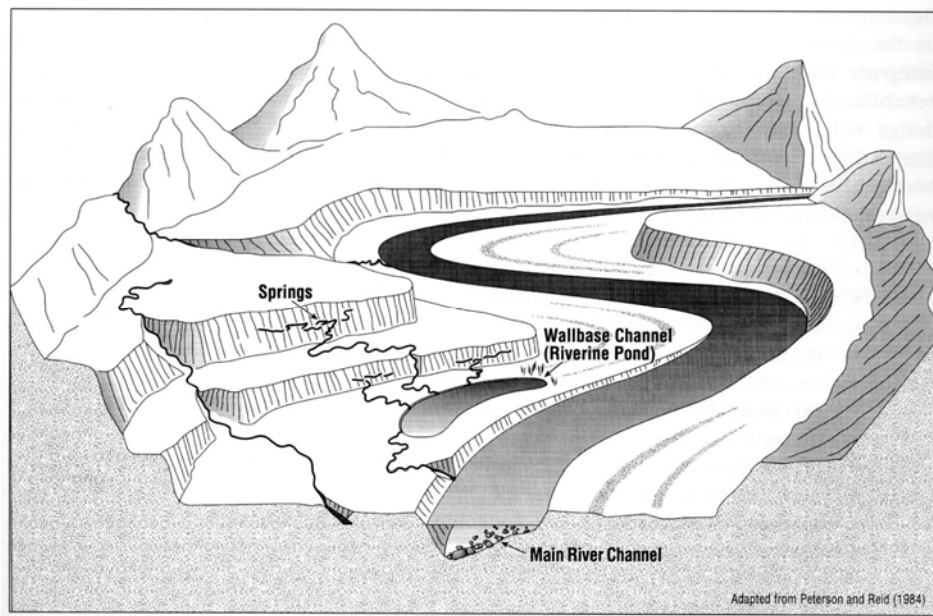
Figure 19. Up-valley oblique view of meandering river and associated floodplain, showing examples of wall-base channels—a subtype of groundwater channel—and a riverine (floodplain) pond. From Peterson and Reid (1984) and Cederholm et al. (1997a).
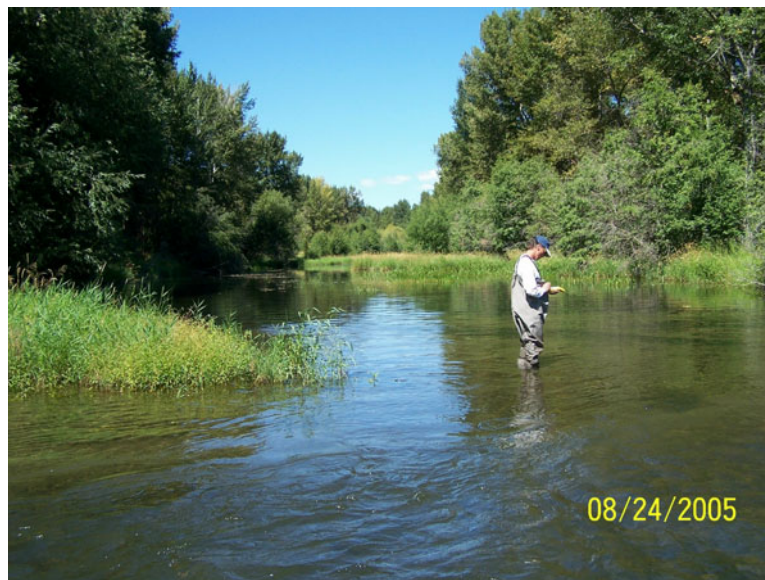
Figure 20. Groundwater channel contained within a relict channel of the Yakima River (Eastern Washington) supplied by hyporheic water. The mouth of the groundwater channel is shown (where individual is standing). The flowing river channel is shown in the immediate foreground.

Figure 21. Groundwater channels often contain abundant aquatic vegetation, indicating stable, low velocity flows and stable substrate conditions, seen here in a groundwater channel along the Queets River within Olympic National Park (Olympic Peninsula, Washington). Abundant newly emerged coho fry were actively feeding amongst the vegetation when this picture was taken.

Figure 22. Four acre floodplain pond formed within an ancient channel of the Chehalis River (Western Washington). Pond drains to the main river through a small egress channel seen on left side of pond.
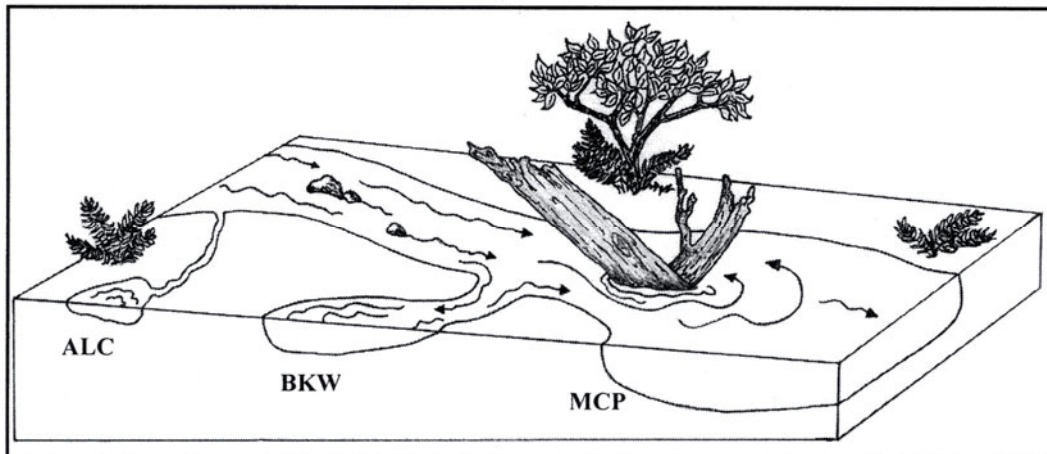
Figure 23. Diagrammatic view of three habitat types within small to medium sized streams. ALC = alcove, BKW = backwater pool, MCP = main channel pool. Diagram is based on features found in Prairie Creek (Redwood Creek basin), Northern California. From Bell (2001).

All of these off-channel types can provide critical habitats in some life stages to salmonids – particularly for coho salmon. These habitats provide refuge from high velocity flow, as well as thermal refugia during some times of the year.

3.2   Life Stage-Specific Habitat Utilization and Survival

Utilization patterns by coho salmon of different habitat types in each life stage are described below, together with reported survival rates. Variations from common patterns are described where they have been found. Only freshwater life stages are covered.

3.2.1 Spawning Migration

Adult coho salmon use the main channel of mainstem rivers and tributaries for migrating to spawning sites. They utilize all habitat types within the main stream and can generally be found holding to rest during the migration in deep water areas, particularly pools.

As described earlier, river entry of adult coho is primarily keyed to storm events in autumn. Their migration into tributary natal streams often occurs during high flows (Koski 1966).

Because arrival time to rivers generally coincides with the onset of fall rains, water temperature usually poses no problems for migration success. Fish that enter the river at the beginning of a run may encounter elevated water temperatures, as reported in some years in the Klamath River—in which case, mortality can result (CDFG 2004).

Survival during the freshwater migration is assumed to be generally high in streams of the Pacific Northwest. In short rivers where natural predators are not abundant, survival exclusive of any harvest impact is likely very high, perhaps approaching 100% in many cases. Predation by sea lions and seals can occur in the lower reaches of rivers and estuaries, potentially preventing

recovery of listed coho populations under some circumstances (Moyle 2002). Hillemeier (1999) determined that pinnipeds preyed primarily on Chinook salmon in the lower Klamath River, consuming over 8% of the returning run in 1997. The predation rate on returning coho salmon was much less, roughly estimated at 2% of the run. Williamson and Hillemeier (2001) found a similar pattern of relative impacts on Chinook and coho salmon in that river in 1999 with estimated losses of 2.3% and 1.3% of the returning run sizes.

Figure 24. (Top) Oxbow-wetland within the floodplain of the Chehalis River (Western Washington) during a flood event in March 2003. The site is flooded from its lower end where it drains to the main river, located at the far end of the photo. No river water enters at the top end of the ponded area. (Bottom) Water levels receding at the same site in April 2003. Water is draining toward the main river, located in the far end of photo. Water drains through a swale in a natural levee. Structure in picture is the fyke net and a migrant trap located in the distance. Both Chinook and coho juveniles were captured by fyke net and migrant trap. The site was dry by late spring. From Henning (2004).

In drought years in Southern Oregon and California when sand bars blocking stream mouths persist, it is reasonable to assume that some adults may be prevented from spawning. Walt Duffy (Humboldt State University, *personal communications*) has observed late timed adult coho

struggling to swim over barely inundated sand bars blocking Stone Lagoon, a lagoon about 2 miles south of Redwood Creek (Northern California).

Coho production from some streams is correlated with streamflow during the migration and spawning life stages (Lestelle et al. 1993b; Volkhardt et al. 2007). In years of high flow during these life stages, penetration by migrating adults into a river system is believed to be increased, thereby increasing the total miles of habitat able to be used by the population, resulting in increased production (Bradford et al. 1997). Scarnecchia (1981) found that the annual catch of coho off the Oregon Coast from 1942 to 1962 was correlated with total streamflow during the corresponding years of freshwater life. He suggested that one likely explanation was that years of high flow would have allowed greater access by spawners to streams in the upper areas of river systems.

3.2.2 Spawning

Coho salmon spawn mainly in small streams or in side channels to larger rivers, a pattern seen across the species range (Burner 1951; Sandercock 1991; Moyle 2002). They sometimes spawn along the river margins of larger streams, but normally not in large numbers (author's personal observations). Under unusually dry weather conditions when access into smaller spawning tributaries may be blocked, they will spawn in larger numbers in mainstem rivers. Such behavior has been observed in the Thompson River in the Fraser River interior region; survival of eggs and fry is thought to be reduced in such case due to relatively poor quality of habitat for incubation (Richard Bailey, Fisheries and Oceans Canada, *personal communications*). Coho have also been observed to spawn in significant numbers in mainstem rivers where hatcheries are located in close proximity to the river downstream of a dam. This has been observed in the mainstem Rogue River (Southern Oregon)(McPherson and Cramer 1981) and the Klamath River (Brown and Moyle 1994; NRC 2004) and in rivers farther north.

Coho salmon spawn on pool tailouts and along the margins of riffles in main channel habitats, often close to or under cover. They generally spawn in small gravels (Burner 1951).

They spawn heavily in groundwater channels where these habitats exist along the floodplains of rivers, often in relatively high densities (author's personal observations). These channels often have fine substrates with high amounts of fine or sand sized particles. These areas, despite their high sediment load, produce high egg survival because of upwelling that occurs there (Bjornn and Reiser 1991; Waters 1995).

They also spawn within the littoral areas of some lakes in Alaska, such as Chignik Lake (Ruggerone and Rogers 1992).

High water temperature is generally not an issue to spawning success of coho salmon in the Pacific Northwest and California. Spawning begins in late fall after streams have had significant cooling.

Survival from the onset of nest digging to the completion of spawning in rivers of the Pacific Northwest is assumed to very high under normal conditions.

3.2.3 Egg and Alevin Incubation

Egg and alevin incubation habitat is the same as that described above for spawning. Nest sites are selected by spawners, eggs are deposited, and except for some relatively small amount of lateral movement by pre-emergent fry, eggs and fry remain within or very near the original nest sites.

Survival from egg deposition to fry emergence can vary significantly between streams depending on stream characteristics and local conditions. Changes in stream conditions due to land use can severely reduce survival to emergence.

Under the most optimal conditions occurring in nature survival to emergence can reach approximately 80%. Quinn (2005), referring to salmon species in general, states that "if scour does not occur and the size of gravel is ideal, up to 80% of the eggs may survive to produce free-swimming fry. This typically only takes place in artificial spawning channels where presorted gravel and regulated flows provide nearly ideal conditions." Moring and Lantz (1975) reported that the maximum observed survival to emergence in a study of three streams in the Alsea watershed (Oregon Coast) for coho salmon was 82% (of 94 redds trapped). The eight year study included years prior to and following logging. Tagart (1984) reported a maximum observed survival to emergence of 77% for coho salmon in tributaries to the Clearwater River (Olympic Peninsula, Washington)(of 19 redds trapped over two years). The EDT model[21] applies a 60% survival from egg deposition to emergence to represent the average survival expected over some period of years (e.g., 10 years) in stream reaches that contain the best conditions that occur in nature (Lestelle et al. 2004). The single highest observed survivals in studies like those conducted by Koski and Tagart would not be expected to occur for groups of redds in an optimal stream reach averaged over a period of years. The average survival in this case is lower than maximum observed values.

Average survival to emergence for coho in streams that might be considered typical in the Pacific Northwest and California is much less than occurs under optimal conditions in nature. Moring and Lantz (1975) summarized survival to emergence in three small Oregon coastal streams over eight years (Table 2). In redds where some fry emergence occurred, the average survival across all years and streams was 32.7%. Including redds with no successful emergence, average survival was 28%. Zero emergence occurred in 14.5% of the redds. Koski (1966), who reported on the first year of study, included redds with zero emergence to compute an average survival to emergence. He discounted the possibility of false redds because of the intensive observations he made on spawners and redds. Koski concluded that redds with zero emergence resulted from gravel scour. Logging occurred in the Deer Creek and Needle Branch watersheds approximately half way through the eight year study. Flynn Creek remained unlogged. There was no significant shift in survival rates in the two logged watersheds following logging.

---

[21] / The Ecosystem Diagnosis and Treatment (EDT) model is used throughout the Pacific Northwest to help assess the performance of salmon populations in relation to habitat condition. http://www.mobrand.com/MBI/edt.html

Table 2. Summary of survival from egg deposition to fry emergence for coho salmon in the Alsea River (Oregon Coast) study streams averaged over eight years (Moring and Lantz 1975).

Measure	Deer Cr.	Flynn Cr.	Needle Br.	Mean
No. of redds trapped	32	30	32	
% survival for successful emergence only	37.9%	25.7%	34.6%	32.7%
% survival including zero emergence	33.5%	20.8%	29.8%	28.0%

Tagart (1984) assessed survival from redds in tributaries to the Clearwater River (Olympic Peninsula, Washington) during a period of active logging in the watershed. Most of the logging in his study streams had occurred within a period of 1-10 years prior to his study. Over two years, he monitored survival in 19 redds. The average survival for all redds monitored was 29.8% (arithmetic mean). Tagart reported a geometric mean of 22.1%. Tagart cautioned, however, that redds were selected in the study on the basis of how he felt they would aid in developing a relationship between intergravel sediment load and survival. Redds were not selected randomly to assess mean survival to emergence in the river system. Moreover, he specifically excluded redds for trapping that were determined to be subject to scour. Jeff Cederholm[22] (*personal communications*, cited in WDF and Quinault Treaty Tribes [1982]) reviewed Tagart's study and concluded that Tagart's arithmetic mean of 29.8% was a reasonable estimate of average survival in the river system at that time, including redds with no successful emergence.

Prior to logging, the average estimated survival to emergence for coho salmon in Carnation Creek (Vancouver Island) was 29.1% (Scrivener and Brownlee 1989), a value nearly identical to the estimates for Clearwater and Alsea tributaries. It should be noted that Carnation Creek and all of the study streams in the Clearwater and Alsea watersheds are small streams, characteristic of many coho spawning streams.

Sandercock (1991) stated that Briggs (1953) reported in a California study that "average egg-to-fry survival was 74.3%" based on 22 coho redds sampled. However, Sandercock failed to identify that Briggs had not estimated survival to emergence. Briggs employed egg and alevin pumping to obtain estimates of the ratio of live to live plus dead at the time of pumping. The estimates did not take into account dead eggs that had disintegrated nor the loss that would have occurred from that time until emergence. Koski (1966) suggested that much of the mortality that occurs in redds is due to pre-emergent fry being prevented from emerging successfully from the redd. Thus, it appears that Briggs' estimates do not reflect survival to emergence comparable to the other studies cited above.

---

[22] / Jeff Cedarholm was Project Leader for the Clearwater River effects of logging studies conducted by the Fisheries Research Institute of the University of Washington. Tagart's study was part of this project.

Data collected in the Alsea watershed study streams (Oregon Coast) suggest that survival to emergence of coho salmon generally lacks a density-dependent effect. Relationships between the numbers of emigrant fry trapped in the lower end of the three study streams and numbers of female spawners are linear across the range of spawners seen during the eight year study period (Figure 25). Linearity in these relationships indicates that survival to emergence is density-independent in these streams. This means that over the range of spawners seen that the availability of spawning area was sufficient to minimize any effect of competition for redd sites and redd superimposition.

Two factors are most often cited as affecting the survival to emergence of coho salmon: fine sediment loading and bed scour. A third factor, presence of an egg-eating oligochaete worm, has also been found to have significant effects on survival to emergence in some areas of Northern California. A brief summary of the magnitude of these effects is useful here.
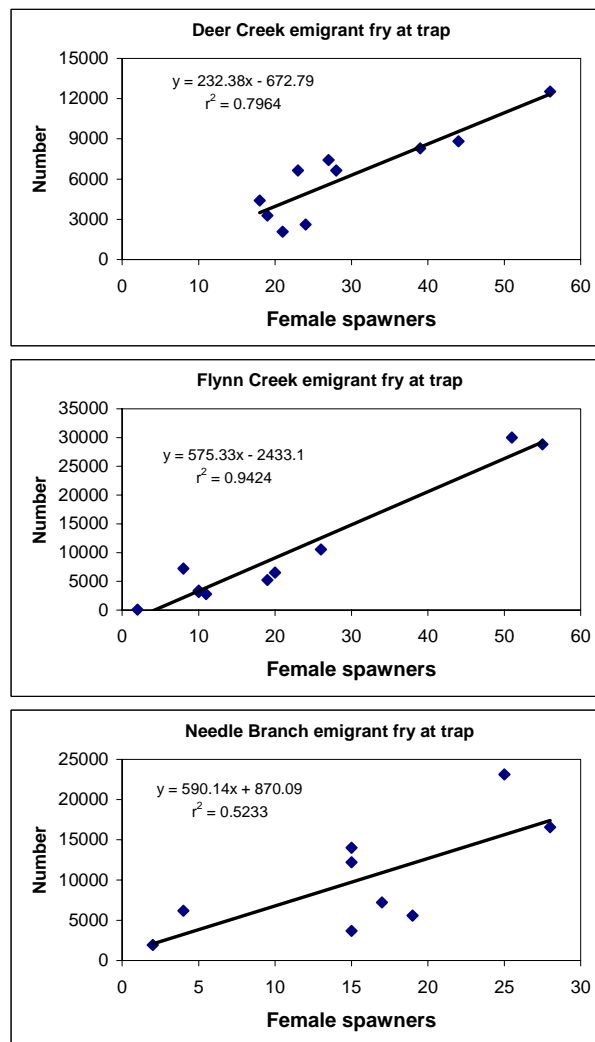
Figure 25. Relationships between female coho salmon spawners and emigrant fry captured in traps at the downstream ends of study streams in the Alsea watershed (Oregon Coast). Emigrant fry data from Au (1972). Spawner abundance data from Knight (1980).

Following logging, the estimated average survival to emergence of coho salmon in Carnation Creek was approximately half that prior to logging. Average survival was estimated to have declined from 29.1% to 16.4% (Scrivener and Brownlee 1989). This was attributed primarily to sediment loading. Mortality likely occurred both as a result of reduced oxygenation associated with increased fine sediment and to increased bed scour associated with the greater sediment load. Scrivener and Tripp (1998) provided updated estimates of survival for Carnation Creek. They listed 25% as the unlogged average and 19% as the logged average in the absence of mass wasting. With mass wasting, they estimated survival to emergence to be 15%. Cause of mortality was listing as being both reduced oxygenation and increased bed scour.

Tagart (1984) characterized the relationship between fine sediment and survival to emergence for coho salmon as curvilinear across the range of fines examined (Figure 26). Relatively small increases in fine sediment within the intermediate range of values produced a steep decline in survival. At higher levels of fines, the rate of decline in survival slowed substantially, suggesting that egg pocket structure affords some protection against further degradation as fines within the surrounding redd environment increase to higher levels. Chapman (1988) predicted that egg pocket structure within natural redds would afford such protection.

Koski (1966) characterized the relationship between sand sized particles and survival to emergence for coho salmon within the Alsea watershed study streams (Oregon Coast) as being linear (Figure 27). Variability in survival increased at higher levels of sand concentrations.

$$Y = 934.109(X)^{-1.19633}$$
$$r = -.776$$
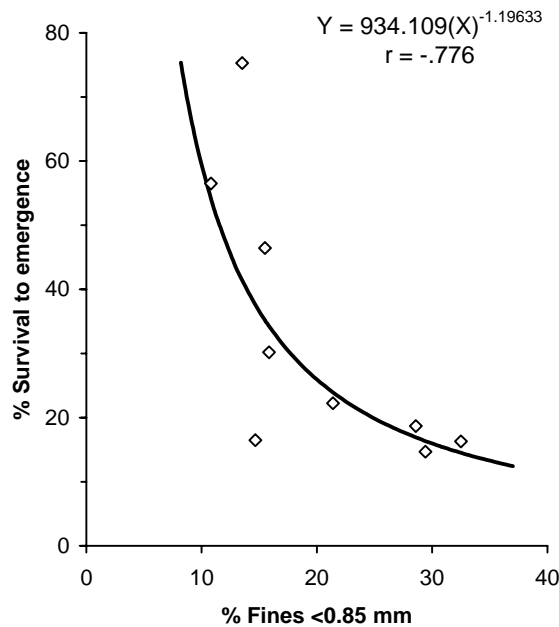
Figure 26. Relationship between percent of substrate <0.85 mm in size and percent survival to emergence of coho salmon in the Clearwater River (Olympic Peninsula, Washington). From Tagart (1984).

The relationships between fines/sand and survival shown in Figures 26-27 apply where flow through the redd is downwelling. Tributaries in the Clearwater River watershed are little affected

by spring sources and flow through salmon redds is downwelling (i.e., water flow moves from the surface flow down through the redd).

In streams fed largely by springs, salmonid spawning can occur at sites with upwelling due to the groundwater influx occurring through a reach (Figure 28). When spawning occurs in upwelling groundwater, the adverse effects of sediment on eggs and emerging fry are largely negated, resulting in high survival, provided the groundwater is not low in dissolved oxygen (Bjornn and Reiser 1991; Waters 1995; Garrett et al. 1998). Spawning areas at these locations can be very high in fines. This explains why salmonids can have very high rates of reproduction in some streams despite excessive deposits of fine sediment. Coho salmon will spawn heavily in groundwater channels if available (personal observations of author).
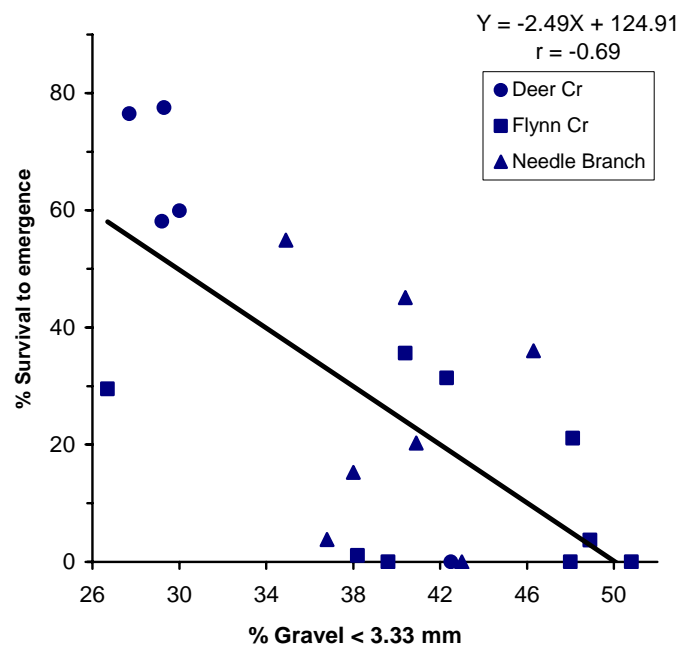
Figure 27. Relationship between percent of substrate <3.33 mm in size and percent survival to emergence of coho salmon in the Alsea River study streams (Oregon Coast). From Koski (1966).

Bed scour can have very high adverse effects on incubating salmon eggs. On the Queen Charlotte Islands, Tripp and Poulin (1986) cite bed scour as being a significant factor affecting survival to emergence of coho salmon. It is most damaging to egg survival in relatively high gradient streams having little large woody debris. It is made worse following logging that leads to mass wastage. If the loss of eggs to scouring is assumed to be directly related to depth of the incubating eggs, mortality due to scouring alone could be greater than 70% for coho salmon in many streams on the Queen Charlottes (Scrivener and Tripp 1998).

Montgomery et al. (1996) found that even minor increases in depth of bed scour due to land use practices can significantly reduce salmon embryo survival. Scour and fill of gravel beds is a normal physical process that occurs during high flow events, but watershed development can change their rates and associated equilibria. Schuett-Hames and Adams (2003) reported that the

depth of bed scour in salmonid spawning tributaries of the upper White River (Western Washington) is a function of peak flow (Figure 29). They projected significant egg losses for spring Chinook due to bed scour. Channel simplification and loss of stable large woody debris (LWD) appears to have increased the extent of bed scour at flow in those streams. Peak flows also appear to have increased as a result of timber harvest and road building.
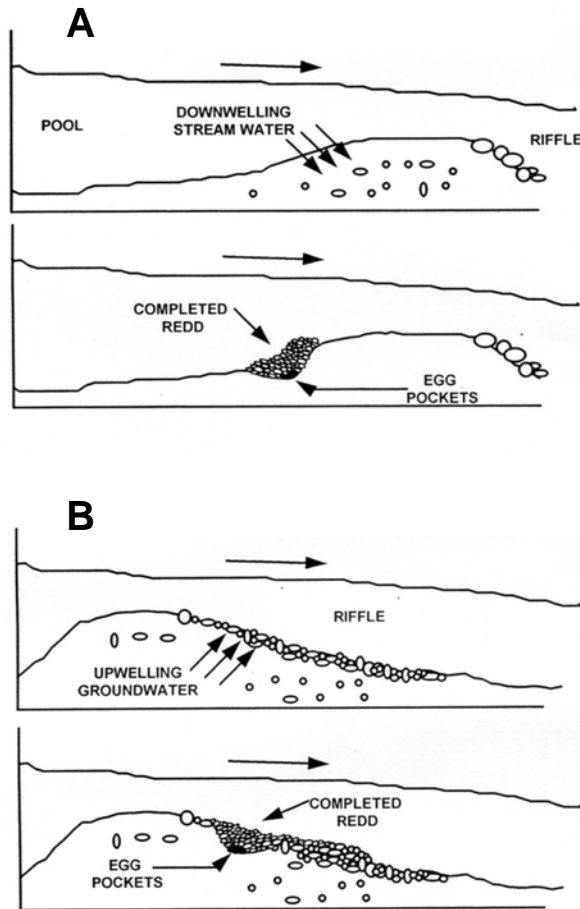
Figure 28. Salmonid redd construction in relation to sites of downwelling (A) and upwelling (B). From Waters (1995).
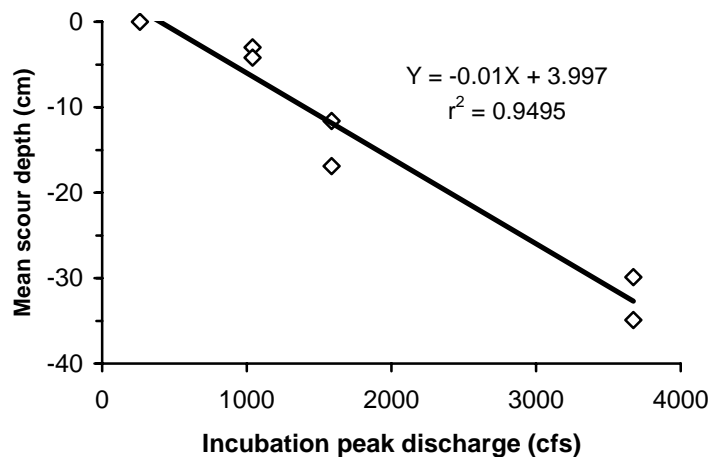
Figure 29. Relationship between mean scour depth at spring Chinook redd sites (averaged by reach) and peak flow during incubation period in a spawning tributary of the upper White River (Western Washington). The White River drains the north slopes of Mt. Rainier. Adapted from Schuett-Hames and Adams (2003).

Rates of scour and fill within a stream segment can be highly variable due to widely differing site specific conditions (Montgomery et al. 1999; Rennie and Millar 2000). For example, side channels provide much greater bed stability than found in the main channel. Stable LWD can also provide favorable spawning sites, protected from high velocities in exposed areas during freshet conditions. Shellberg (2002) reported that in streams having high flows during fall and winter that bull trout redds were scoured in stream reaches lacking features that protect from instability (e.g., side channels and stable LWD). He concluded that loss of LWD and channel simplification had increased the probability for redd scour in some streams.

Montgomery et al. (1996) studied bed scour and chum salmon egg pocket depths in two streams, one located in Puget Sound (Kennedy Creek). They concluded that close correspondence found between egg burial depths and scour depths implies a finely tuned adaptation to long-term rates of sediment transport. Further, they said that changes in gravel transport rates, as can occur with land use, can dramatically affect egg survival because egg pockets tend to be just below the usual depth of scour in pristine streams. They reported that egg pocket depths averaged about 22 cm for chum salmon (median = 20 cm), although the range between the shallowest and the deepest was quite large (10 to 49 cm). Egg pocket depths reported are the distances from the level of stream bed to the ceiling of the egg pocket. Their results demonstrated that relatively small increases in scour depth would jeopardize the majority of egg pockets (Figure 30). Depths of egg pockets for coho salmon are very similar to those of chum salmon (DeVries 1997).

Montgomery et al. (1999) examined the spawning distributions of Chinook and coho salmon and trout species in several rivers of Washington and Oregon to assess the role of geomorphic factors on distribution. They concluded that the spawning distributions of all fall spawning salmon species in rain-dominated stream systems are strongly affected by channel gradient and valley floor width. Bed scour generally increases with channel gradient and the degree of channel confinement. In rain dominated systems, these authors concluded that coho salmon would infrequently spawn in streams with gradients greater than 3% or in highly confined channels because bed scour would usually be prohibitively high to sustain the population.
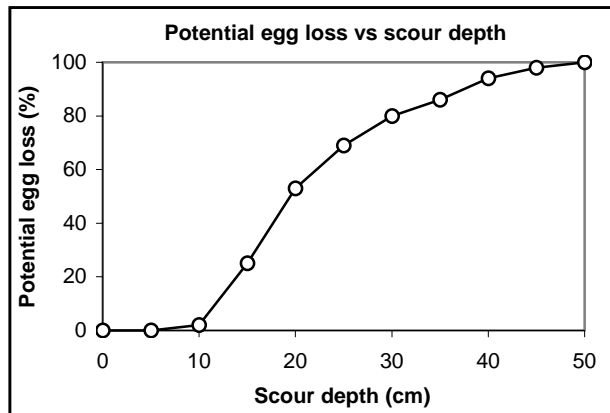
Figure 30. Potential egg loss (as a percent of egg deposition) for chum salmon in Kennedy Creek (Puget Sound region, Washington). From Montgomery et al. (1996). Egg pocket depths of coho salmon are similar to those of chum salmon (DeVries 1997).

Another mortality factor found to significantly affect coho survival to emergence in some streams in Northern California, is an oligochaete worm (Briggs 1953; Sparkman 2003). The worm, *Haplotaxis ichthyophagous*, can kill eggs with copious mucous secretions, although Sparkman (2003) found evidence that the worms also consume portions of live eggs. When worms are present survival to emergence can be reduced to 0%. Sparkman reported that two factors best explained survival to emergence in natural redds within the Prairie Creek watershed in Northern California—amount of fine sediment and presence/absence of the oligochaete worm. In artificially constructed redds, egg survival averaged 9% and 78% when worms were present and not present, respectively. The distribution of this worm species outside Prairie Creek is unknown. Egg mortality associated with the worm has not been reported outside of Northern California (Sparkman 2003).

3.2.4 Fry Colonization

Upon emergence coho fry move quickly to slow velocity habitats, typically along the channel margin, or they continue to move downstream. They have a strong affinity for very slow velocity water (Figure 11) and generally move there as rapidly as possible. Fry emergence can be very protracted, which can help facilitate dispersal (Mason 1976b).

Fish that emerge during high flows can be swept downstream (Chapman and Bjornn 1969; Hartman and Holtby 1982; Holtby 1988; Shirvell 1990; Fausch 1993), in some situations moving them to less suitable habitats, increasing bioenergetic costs, and increasing predation exposure. In rivers with abundant floodplain habitat, emergence during high flows (i.e., spring runoff) can be beneficial if fry gain access to those habitats, then subsequently return to the main river without being stranded (Sommer et al. 2001; Henning 2004; Lestelle et al. 2005). Backwaters and bank edges along vegetated shorelines during spring runoff are also important refuge sites for emergent fry. However, in streams lacking suitable velocity refugia, fry survival is likely diminished if emergence occurs during periods of prolonged high flow (Shirvell 1990; Smith 2000; Fausch et al. 2001; Lestelle et al. 2006).

Young fry are most often found in shallow, slackwater along stream margins and often associated with some form of bank cover—particularly back eddies, or behind fallen trees, undercut tree roots, and other well-protected areas (Mundie 1969; Lister and Genoe 1970).

Nickelson et al. (1992) reported that coho fry densities in small streams on the Oregon Coast were by far highest in backwater pool units (Figure 31) compared to other habitat types, although they could be found along the margins of virtually all types. They were not present in off-channel habitats (alcoves) as fry, presumably because these habitats were not well connected to the stream during time of emergence. Of the habitat types inhabited, backwater units had the slowest water velocities.

Mundie (1969) reported that newly emerged coho fry were relatively scarce in large mainstem rivers like the Stamp River on Vancouver Island (Figure 32). He stated: "Contrary to appearances large coastal rivers like this one are not important feeding areas for coho. The food produced in them is sparse, and the recently emerged fry are confined to marginal slack water out of reach of the main stream drift." Mundie's observations suggest that low velocity refugia are limited in this river.

Following emergence, some fry move longer distances than others (Au 1972), partly as a result of emigration due to intraspecific competition (Chapman 1962). This effect can result in moving some fish into larger streams and lakes downstream of natal tributaries. In some cases, emergent fry may move upstream into a lake if spawning occurs in the lake's outlet stream (Swain and Holtby 1989).

In cases where spawning is not distant from the sea, some fry can move into stream mouth estuary (Tschaplinski 1988; Nielsen 1994), as described earlier in this report. These movements are typical of coho fry and serve as a dispersal mechanism. However, large numbers of fry sometimes captured at stream trapping facilities, usually assumed to be fry emigrants (Au 1972), are apparently often merely moving a short distance downstream of the trapping site (Lindsay 1974). In such cases, emergence sites are likely not far upstream of trapping sites. This suggests that the distance traveled from natal sites as fry is typically not extensive for coho salmon.

Young coho fry that move to larger rivers can subsequently move into off-channel habitats as a result of their need for calm, slow velocity water. Peterson and Reid (1984) reported trapping small fry moving into off-channel ponds via low velocity egress channels connected to the outlets of the ponds. This movement is the likely source of juvenile coho found in many off-channel habitats during summer—both in coastal regions (e.g., Sedell et al. 1984; Coe 2001) and interior regions (Brown 2002).

Water temperature is generally not an issue to young coho fry in the Pacific Northwest and California because of their emergence timing during spring.
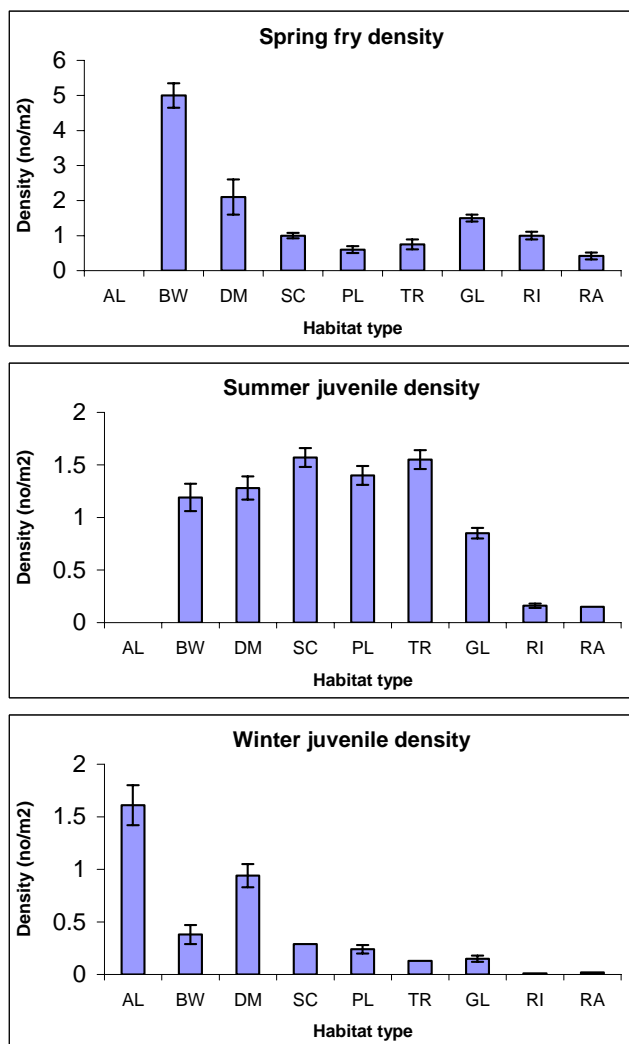
Figure 31. Mean density (+/- SE) of juvenile coho salmon by habitat type during spring, summer, and winter reported for Oregon coastal streams. AL = alcove; BW = backwater pool; DM = dammed pool; SC = scour pool; PL = plunge pool; TR = trench pool; GL = glide; RI = riffle; RA = rapid. Adapted from Nickelson et al. (1992).

Survival during the fry colonization stage is likely mostly density-independent because of the short time period involved. Estimated survival rates for Deer Creek in the Alsea watershed study (Oregon Coast) show a modest density-dependent effect (Figure 33 – derived from data in Au 1972). An estimate of the density-independent component of survival can be obtained from Figure 33 by simply extending the regression line to the Y-axis (zero density), giving a value of 81%. This represents the average survival rate for the fry colonization phase for Deer Creek—a small coho stream—absent any effect of fry density.

Figure 32. Stamp River, Vancouver Island. Mundie (1969) reported that this river is of a size that keeps it from being an important nursery area for coho salmon fry. Fry in rivers like this one must remain confined to marginal, slow velocity water, which is generally limited in amount and distribution.
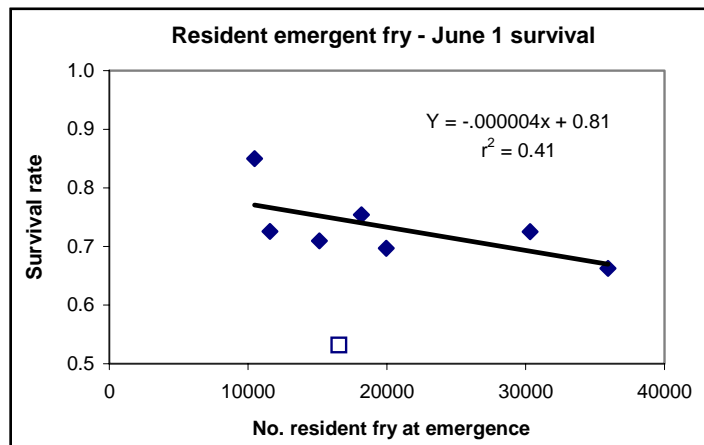
Figure 33. Relationship between the number of newly emerged, resident coho fry (total emergent fry minus fry emigrants) and survival to June 1 in Deer Creek, Alsea watershed (Oregon Coast). Survival shown is for the fry colonization phase for resident fry. Derived from data in Au (1972). Estimated density-independent survival is the point where the regression line would cross the Y-axis (0.81). The open square symbol was assumed to be an outlier and was not used in the regression.

3.2.5 Subyearling Summer Rearing

Juvenile coho reside in a wide variety of stream types and sizes during summer, in addition to connected lakes where present. They are typically found in highest densities within their natal streams since the majority of fry usually do not migrate long distances from spawning sites

(Lindsay 1974), unless the natal stream has a high gradient promoting longer distance movement (Lestelle et al. 1993a).

The need for slow velocity water by juvenile coho remains strong during this life stage (Figure 11). In larger streams, juvenile Chinook and steelhead are more frequently associated with some surface water turbulence than coho salmon, as seen in a study of velocity-depth preferences in the Trinity River in the Klamath basin (Hampton 1988)(Figure 34). Juvenile Chinook and steelhead are often found feeding near velocity shears within main channels, while coho remain more closely associated with the shoreline or dense cover of woody debris. This pattern—seen across the species' range—indicates a much stronger affinity for slow velocity by coho salmon than the other species during this life stage. All of the foraging phenotypes described by Nielsen (1992a, 1992b, 1994) are closely associated with habitat types having slow water velocities.
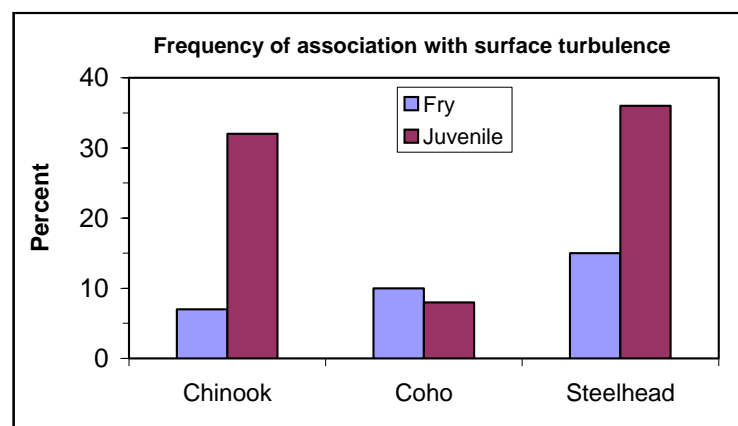
Figure 34. Percent of observations of fry (<50 mm) and juvenile (>50 mm) Chinook, coho, and steelhead found occurring with surface turbulence in the Trinity River in the Klamath River basin (Northern California). Recreated from Hampton (1988).

Juvenile coho are most often found in pools as shown in data for the Oregon Coast (Figure 23)(Nickelson et al. 1992). In smaller streams, they are found in highest densities in all pool types, intermediate densities in glides, and lowest densities in riffles and cascades. It is important to note that these densities occur where fry recruitment is high (i.e., high spawning escapements) and habitat quality is not degraded. This pattern of habitat selection occurs throughout their range (Hartman 1965; Bisson et al. 1988b; Schwartz 1991; Lau 1994; Sharma and Hilborn 2001; Brakensiek 2002).The densities reported by Nickelson et al. (1992) are very consistent with those predicted for key habitats (pools) using relationships developed for coho salmon in British Columbia (Ptolemy 1993). Those relationships show, however, that density can be strongly affected by stream productivity, i.e., by the amount of food it produces to support salmonids. Highly productive streams can support higher juvenile coho densities than less productive ones (Mason 1976a; Ptolemy 1993; Ward et al. 2003)

The highest densities of juvenile coho during this life stage are usually found in the smallest streams (Rosenfeld et al. 2000). Although utilization patterns have not been well defined for all habitat types in large streams, qualitative descriptions indicate that densities drop sharply in large

streams (Allen 1969; Mundie 1969; Marshall and Britton 1980; Murphy et al. 1989; Jepsen and Rodgers 2004; Jepsen 2006).

The most extensive data set comparing densities between low and high order streams (i.e., small versus large streams) occurs in Jepsen and Rodgers (2004) and Jepsen (2006). This study, the Western Oregon Rearing Project, provides a quantitative comparison based on an exceptionally large number of pools sampled by snorkeling in late summer in watersheds spread across the Oregon coast (Table 3; Figure 35). Spawning escapements for brood years that produced these data were high compared to earlier years (PFMC 2006). The large differences seen between densities of small and large streams occurs because a smaller proportion of the total cross-section in large streams affords depths and velocities preferred by juvenile coho salmon, though other factors are also operative. This largely explains why average coho smolt production for different sizes of watersheds between Southeast Alaska and California has been found to be linearly correlated with the total utilized stream length in a watershed (Bradford 1997; Bocking and Peacock 2004).[23]

Within the SONCC Coho ESU, extensive sampling for juvenile salmonids occurred annually in the mainstem Rogue River between 1974-1983 to evaluate the effects of Lost Creek Dam on salmonids. Sites were sampled between the dam site (RM 157) and the river mouth throughout spring, summer, and fall. Prior to the return of hatchery coho to Cole Rivers Hatchery, few subyearling coho were captured each year in the mainstem river, suggesting that this species was rearing almost entirely within the tributaries (Cramer and Martin 1978; Cramer and Martin 1979; McPherson and Cramer 1981; Cramer et al. 1985). Following the return of adult hatchery to Cole Rivers Hatchery near the dam, more juvenile coho than in previous years—though still small numbers—were captured in the upper part of the mainstem (within approximately 25 miles of the dam)(McPherson and Cramer 1983). The researchers believed that this was due to stray hatchery adults spawning in the mainstem river below the dam (Cramer et al. 1985).

---

[23] / The linear relationship suggests that, on average, the same number of smolts is produced in a mile of a large river as in a mile of a small tributary to that river. Substantial variability is evident about the relationship, indicating effects of stream type, geomorphology, climate, habitat quality, nutrients, etc. For example, in stream systems with substantial ponds or lakes, smolts produced per mile of stream is linearly correlated with the percentage of total wetted surface area in the system comprised of ponds or lakes (Baranski 1989; Lestelle et al. 1993b). It should be noted that within large watersheds, the large majority of stream miles utilized are found in tributaries to the mainstem river.

Table 3. Densities (fish/m² pool) and SE of means of juvenile coho salmon in two size groups of streams on the Oregon Coast: 1ˢᵗ-3ʳᵈ order (small streams) and 4ᵗʰ-5ᵗʰ order (large streams). Data were collected by snorkeling in late summer. Ratios of density for small streams to large streams, maximum and minimum observed densities, number of reaches sampled, and number of pools sampled are also shown. Only sites where coho were found are included in statistics. Data from Jepsen and Rodgers (2004) and Jepsen (2006).

Year	Measure	Stream order		Ratio
		1st-3rd	4th-5th	
2002	Ave density (fish/m²)	0.68	0.03	0.038
	Standard error	0.077	0.009	
	Range	0.00-6.37	0.00-0.29	
	No. reaches sampled	179	44	
	No. pools sampled	2800	448	
2003	Ave density (fish/m²)	0.48	0.08	0.164
	Standard error	0.060	0.041	
	Range	0.00-7.75	0.00-1.78	
	No. reaches sampled	251	52	
	No. pools sampled	4008	409	
2004	Ave density (fish/m²)	0.31	0.03	0.104
	Standard error	0.032	0.012	
	Range	0.00-3.32	0.00-0.59	
	No. reaches sampled	231	55	
	No. pools sampled	3877	404	
Mean	Overall ave density	0.49	0.05	0.100

Juvenile coho that rear in mainstem rivers usually remain in close association with the shoreline (Mundie 1969; Marshall and Britton 1980; Beechie et al. 2005). Beechie et al. (2005) assessed the relative utilization by juvenile salmonids, including coho, of mainstem habitat units in the Skagit River (Western Washington). The researchers concluded that juvenile coho were largely using edge habitats with very little use of mid channel habitats. This pattern was evident during both summer and winter. Among the three edge unit types, juvenile coho were found primarily in bank and backwater units during both summer and winter, with little use of bar edges in either season (Figure 36A). During summer, they were almost always closely associated with cover comprised of wood or aquatic plants—little use was made of cobble cover (Figure 36C).[24] In winter, only wood appeared to provide suitable cover. Banks had the most abundant wood cover, whereas backwaters contained aquatic plants and wood cover. Bars contained mainly cobble-boulder cover. Among edge units, bars and banks tended to have similar velocity distributions, with backwaters comprised exclusively of low velocity points. While juvenile coho were found

---

[24] / For purposes of this study, wood was defined as anchored brush, bank roots, debris piles or jams, root wads, logs, and branches. Aquatic plants were defined as live, non-woody aquatic vegetation.

associated with both low and medium velocity classes in summer (Figure 36B), they were almost always found within the low velocity class in winter.
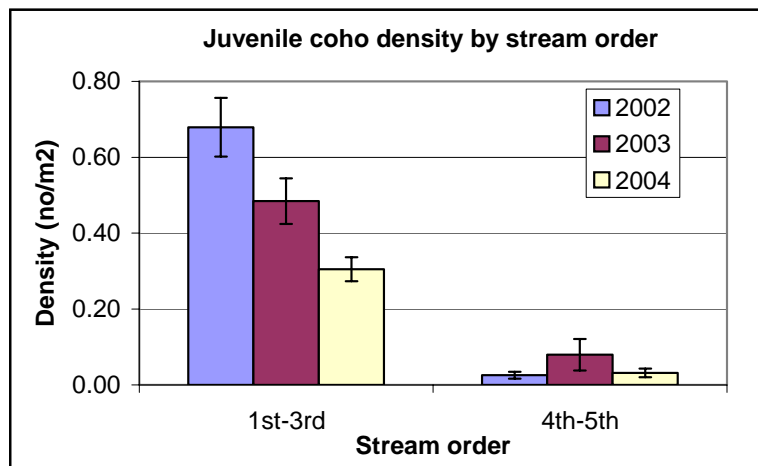
Figure 35. Densities (fish/m2 pool +/- SE) of juvenile coho salmon in two size groups of streams on the Oregon Coast: 1st-3rd order (small streams) and 4th-5th order (large streams). Data from Jepsen and Rodgers (2004) and Jepsen (2006).

In large rivers, secondary channels (i.e., side channels and off-channel habitats) provide important rearing areas for juvenile coho. Murphy et al. (1989) determined utilization rates of various channel and habitat types in the lower Taku River, Alaska during mid to late summer. Within the main river, they sampled channel edges, backwater pools, braids, and side channels (called sloughs by the authors). On the valley floor off the main river (i.e., off-channel habitat), they sampled terrace tributaries (type of groundwater channel), tributary mouths, upland sloughs (type of groundwater channel), and off-channel beaver complexes. Within the main river (including side channels), habitats beyond the channel edge were too swift to sample and were assumed to not hold rearing juveniles because of fast current.[25] Coho and Chinook generally occupied different habitats. Juvenile Chinook were more abundant in main river channel and habitat types than coho salmon, whereas the latter were more abundant in off-channel habitats (Figures 37 and 38). Coho salmon occupied significantly slower current than Chinook. Coho densities were highest in still or slow water (<10 cm/s), whereas Chinook density was highest in slow-to-moderate current (1-20 cm/s). Both species were virtually absent from areas with currents > 30 cm/s. Coho almost exclusively occupied off-channel habitats and were consistently scarce in river habitats, even those with slow water.

---

[25] / Although this assumption could not be verified through actual observation in the river, it is extremely unlikely that coho juveniles were rearing in this large, swift mainstem river.

A
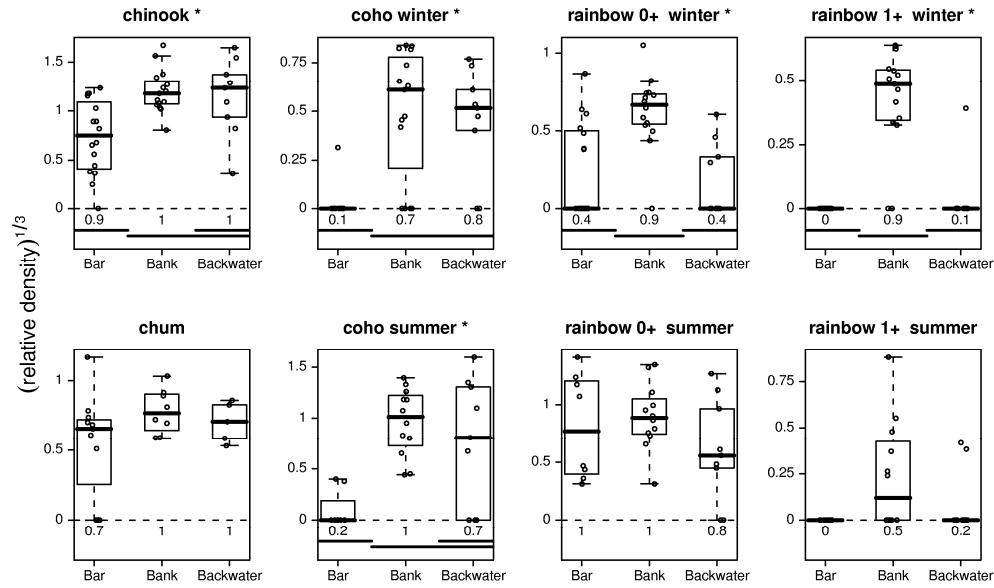
B
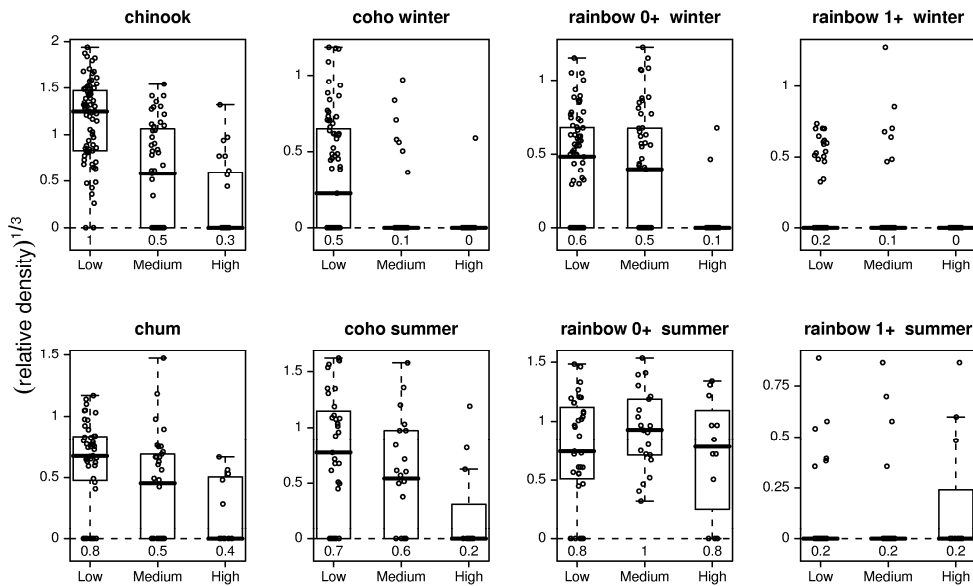
Figure 36. Relative fish density (fish per point standardized by year) by species-age class and (A) edge unit type, (B) water velocity class, and (C – continued to next page) cover type in the Skagit River (Western Washington). Asterisk indicates statistically significant difference among unit types (a = 0.05). Numbers below x-axis indicate the proportion of points at which fish of that species were captured. Bars below x-axis indicate results of multiple comparisons (bars at similar elevation indicate that differences are not significant). See Figure 15 for edge unit types. Velocity classes defined as high (>45 cm/s), medium (15 - 45 cm/s), and low (<15 cm/s). Relative densities are not comparable between species. From Beechie et al. (2005).

C
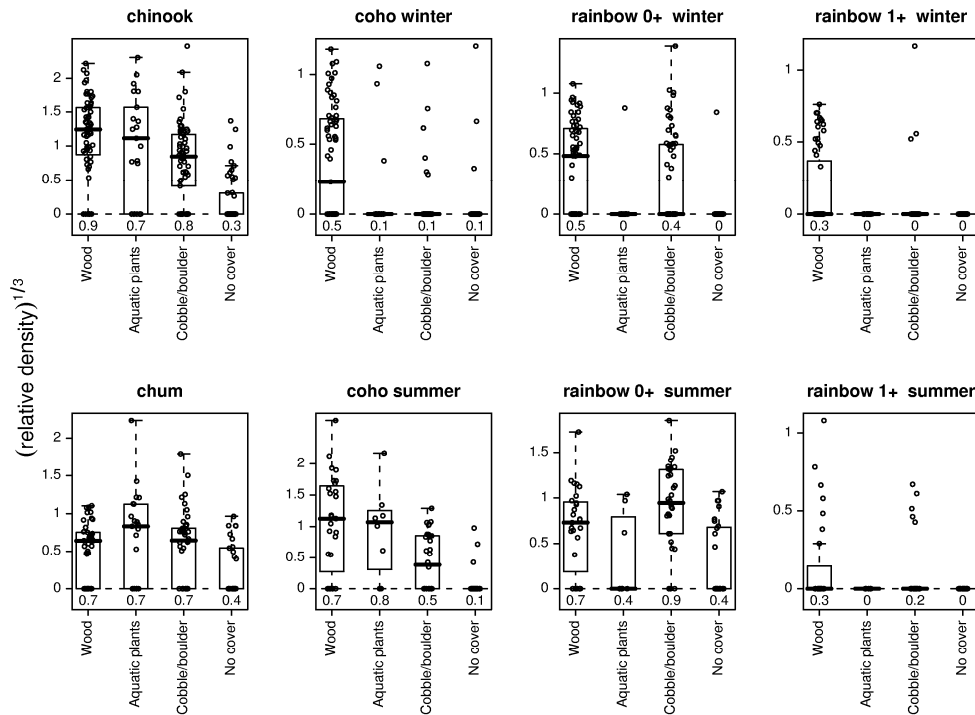
Figure 36 C – *continued from previous page*. **Relative fish density by species-age class and cover type in the Skagit River (Western Washington).**

The importance of side channels and groundwater channels of large rivers to juvenile coho during summer has been described in several studies in Washington State. Juvenile coho are often found in small side channels to mainstem rivers (Sedell et al. 1984; Rot 2003; Pess et al. 2005), together with juvenile Chinook and steelhead trout. Juvenile coho can occur in especially high densities (0.8 fish/m2 total area) in stable side channels, i.e., those protected at their head end by large blocking log jams (Sedell et al. 1984). In groundwater channels, juvenile coho are frequently found in larger numbers than in surface water fed side channels. Groundwater channels are usually utilized almost exclusively by coho salmon, rarely by juvenile Chinook or steelhead trout (Sedell et al. 1984; Rot 2003; Pess et al. 2005). Both of these channel types can be major rearing areas for juvenile coho during summer in some parts of large river systems (Sedell et al. 1984). Both types, particularly groundwater channels, provide low velocity rearing habitat. In addition, groundwater channels normally have cooler water temperatures in summer than occur in mainstem rivers and their side channels. Stanford and Ward (1993) described groundwater channels as being exceptionally productive for some salmonid species—as seen by this author for juvenile coho in this channel type along the mainstem Queets River (Olympic Peninsula, Washington). In rivers of Western Washington, coho salmon utilize groundwater channels more than any other species.
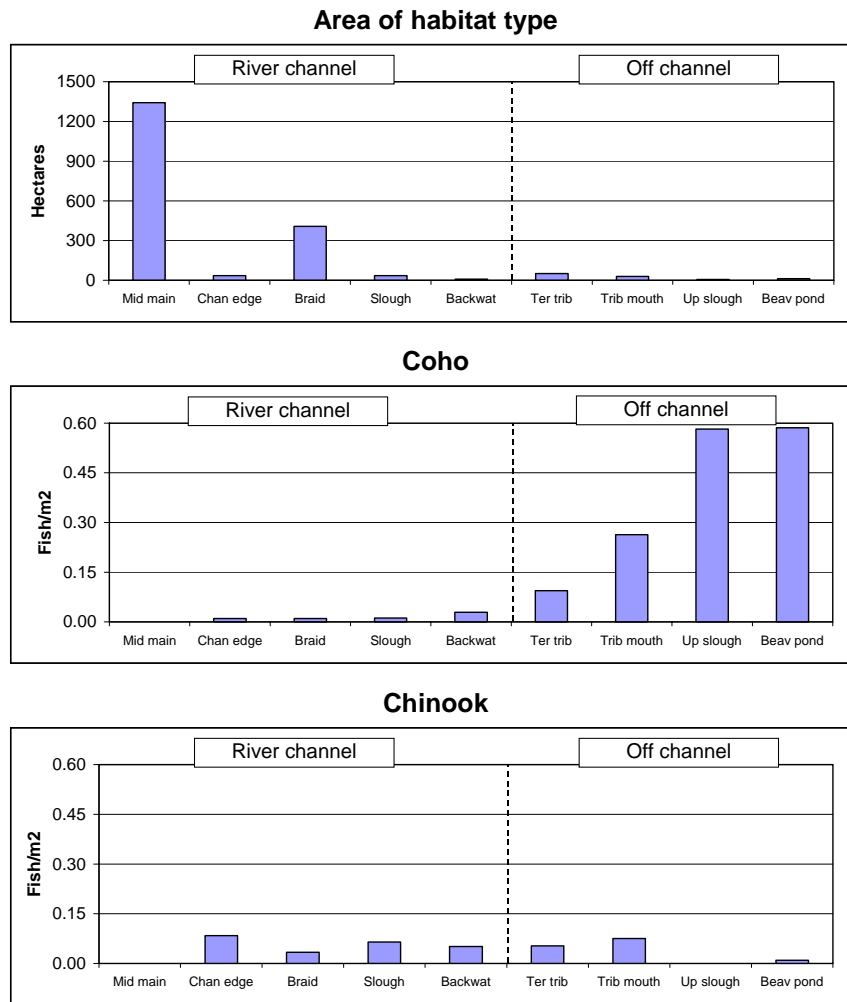
Figure 37. Wetted area (hectares) of different channel and habitat types in the lower Taku River (Alaska)(top) and corresponding mean densities (mid to later summer) of juvenile coho and Chinook (adapted from Murphy et al. (1989). Channel and habitat types are: mid channel of main river channel and side channels (Mid main), channel edge of main river and side channels (Chan edge), braid (Braid), slough (Slough), backwater (Backwat), terrace tributary (Ter trib), tributary mouth (Trib mouth), upland slough (Up slough), and beaver pond (Beav pond).
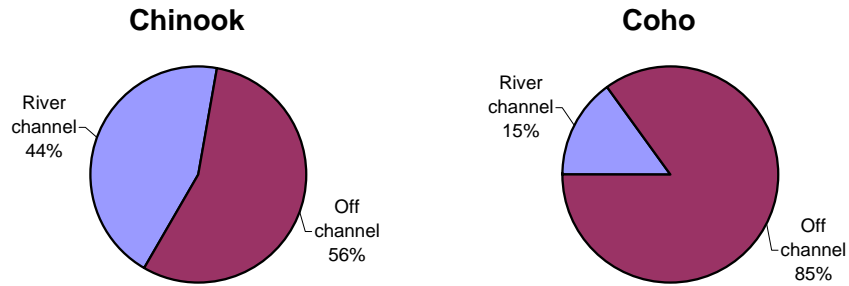
Chinook

Coho

Figure 38. Distribution of juvenile Chinook and coho salmon between river channel and off-channel habitats in the lower Taku River (Alaska) in mid to late summer. Derived from Murphy et al. (1987).

The influence of wood on coho rearing densities during summer is not the same across all stream types and sizes and its role in this life stage is not altogether clear (Giannico and Healey 1999). Some studies have reported that juvenile coho densities in smaller streams during summer are positively correlated with quantity of large woody debris (Hartman and Scrivener 1990; Koski 1992; Roni and Quinn 2001)(Figure 39) while others have not found strong association (Grette 1985; Bugert et al. 1991; Fransen et al. 1993; Spalding et al. 1995; Cederholm et al. 1997b). Part of the discrepancy appears to be due to whether authors distinguish the role that wood has in pool formation from its role as cover. Greater amounts of large wood often equate to more frequent and larger pools (as seen in the study of Roni and Quinn 2001), which in turn, results in a greater number of juvenile coho per channel length (reported by Roni and Quinn 2001). Cover in small streams can be provided by other stream components besides large wood, such as undercut banks, overhanging riparian vegetation, macrophytes—these items may dilute the role of large wood as cover in some streams during summer (Grette 1985; Bugert et al. 1991). There is also evidence that the affinity of juvenile coho salmon for wood accumulations increases through the summer with growth (Hartman 1965; Dolloff and Reeves 1990; Fransen et al. 1993; Peters 1996)(Figure 40). Therefore, differences between studies may be partly due to within season variation.
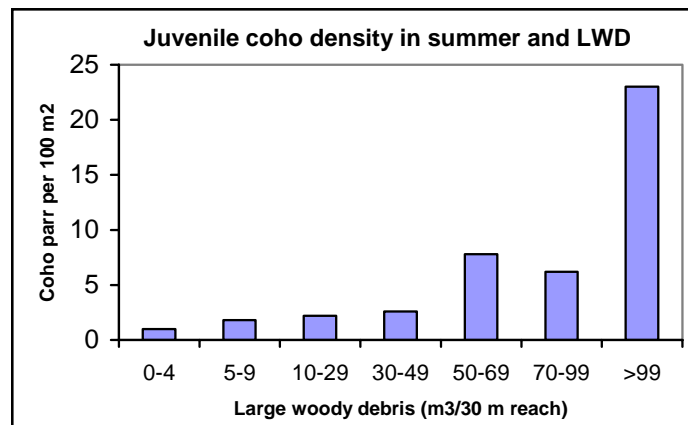
Figure 39. Density of juvenile coho salmon during summer in streams in Southeast Alaska, expressed as number of fish per square meter of total wetted channel area in relation to volume of large woody debris (LWD). Recreated from Koski (1992).
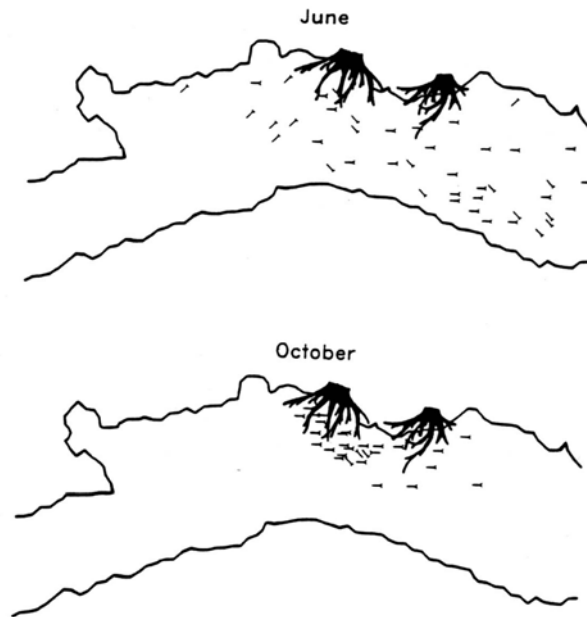
Figure 40. Location of juvenile coho in June and early October in a lateral scour pool relative to rootwads in Huckleberry Creek (Western Washington). The pool was at low flow when observations were made. From Fransen et al. (1993).

In mainstem rivers during summer the presence of large wood appears to be much more important than in small streams for juvenile coho salmon. Peters (1996)—in the most extensive study of mainstem coho utilization known to this author—found that juvenile coho rearing in the mainstem Clearwater River (Washington) was strongly associated with large wood (Figure 41). Highest juvenile coho densities were associated with the most complex wood matrices sampled. Areas containing sparse wood had few juvenile coho present. John McMillan with the Center for Wild Salmon in Washington State has conducted extensive snorkeling surveys of several rivers on the Olympic Peninsula (Washington). His findings (*personal communications*) are comparable to those of Peters (1996). Areas of no or little wood have few juvenile coho relative to sites with dense large wood. Hartman (1965) reported very similar findings for the mainstem Chilliwack River (British Columbia); association with wood increased as juveniles grew and by late summer and fall juveniles were almost always associated with log jams.
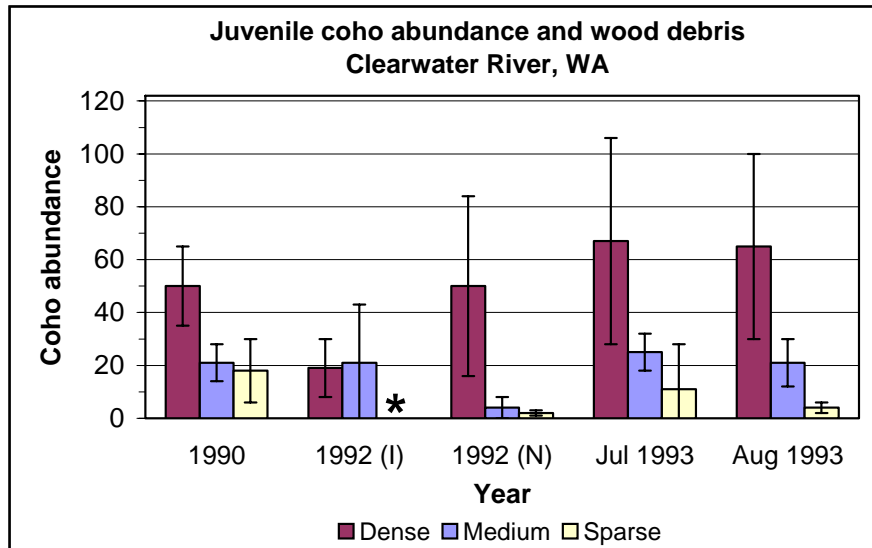
Figure 41. Mean (+/- 2 SE) coho salmon abundance (#/debris accumulation) at natural and introduced woody debris (combined) accumulations of different density during 1990 and 1993 and natural (N) and introduced (I)(separate) debris accumulations during 1992 in the mainstem Clearwater River (Washington). Recreated from Peters (1996). (* = no stations classified as sparse) Wood is classified by its relative accumulation as dense, medium, or sparse.

Peters (1996) concluded that the reason why juvenile coho were so tightly associated with wood in the mainstem river during summer was not simply to avoid higher water velocities. Many debris accumulations were located in sites with current velocities well below those preferred by juvenile coho (10 cm/s in Murphy et al. 1989; 20 cm/s in Dollof and Reeves 1990). In most cases wood was located such that water velocities were not appreciably different within wood matrices than outside them. Peters hypothesized that the attraction of wood during summer in mainstem rivers is due to its providing refuge cover from predators and not primarily as water velocity refuge. In his study, the attraction of wood increased as coho grew larger, i.e., wood association was greater later in the summer—identical to the findings of Hartman (1965) cited above. (As noted earlier, this same pattern is also evident in streams smaller than the Clearwater River – see Figure 40). Peters concluded that as juvenile coho grow they become more wary of predators, seeking greater association with dense wood. He stated:

> "This is supported by the observation that juvenile coho salmon are less willing than other Pacific salmon to take risks during feeding (Abrahams and Healey 1993), which results in reduced attack distance to food following the presentation of model predators (Dill and Fraser 1984)."

This suggests that not only are juvenile coho poor swimmers in swift water, they are much less daring than other salmonid species in their willingness to move away from cover to feed. In larger and swifter rivers than the one studied by Peters (1996), large wood is also likely important as velocity refuge, suggested in other aspects of Hartman's (1965) study (described below for the overwintering life stage).

High water temperatures during summer can be an important factor affecting the distribution, growth, and survival of juvenile coho salmon.[26] Preferred temperatures in this life stage are 12-14°C (Brett 1952) with optimum temperatures for growth at about 14-18°C (Sullivan et al. 2000). Food availability is an important determinant in how well juvenile salmon can cope with elevated temperatures (Brett et al. 1982; McCullough et al. 2001). As food abundance increases, they are better able function (e.g., grow) with higher temperatures, but within limits. The maximum temperature that juvenile coho can tolerate without mortality is less clear because of the many ways that temperature can affect performance (McCullough 1999; Sullivan et al. 2000).

Eaton et al. (1995) used an extensive database of stream temperatures and species presence to estimate the weekly mean temperatures (daily maximums) that species can tolerate. For coho salmon, the value was estimated to be 23.4°C but it was not made clear what level of mortality could be expected above that point. This value is below laboratory-determined lethal temperature limits. Although it is clear that juvenile coho can tolerate higher temperatures under some natural conditions, it is evident that performance is usually adversely affected. Adverse effects have also been described at lower temperatures in various field investigations. Welsh et al. (2001) concluded that the findings of Eaton et al. (1995) for coho salmon were skewed by data representing large (and presumably diverse) river reaches and by use of less sensitive life stages. In a field investigation relating water temperature to juvenile coho distribution in the Mattole River (Northern California), the authors found that temperatures in the warmest tributaries containing juvenile coho salmon were 18°C or less (maximum weekly maximum temperature or MWMT). The study suggests that MWMT greater than 18.1°C would preclude coho presence. Madej et al. (2006) reported that the coho distribution in Redwood Creek (Northern California) is currently limited to the lowermost 12 miles of the stream, a point downstream of where the MWMT ranges between 23 to 27°C; historically coho migrated upstream another 45 miles. Frissell (1992) found juvenile coho salmon to be absent or rare in stream segments where temperatures exceeded 21°C in Sixes River (Southern Oregon).

In stark contrast to the findings of Welsh et al. (2001) and Frissell (1992), Bisson et al. (1988a) reported that juvenile coho showed no evidence of mortality or lethargy when temperatures exceeded 24.5°C during extended periods in streams near Mount St. Helens (Washington). In that case, water temperatures peaked at 29.5°C. Bisson et al. (1988a) hypothesized that an unusually high abundance of food may have enabled the juvenile coho to survive. However, these streams had extreme diurnal fluctuations in temperature (Martin et al. 1986) that likely afforded some measure of relief. The authors did not attempt to identify potential thermal refuge sites as described by Nielsen (1992a) or Ebersole et al. (2003a).

High water temperatures apparently can trigger movement of juvenile coho salmon during summer, when little movement typically occurs, as reported on the South Fork Umpqua River (Oregon Coast)(Figure 6; Kruzic 1998). It is not clear from the study results what the sole effect of elevated temperatures was on juvenile movement (compared to flow and initial fry dispersal) but it is strongly evident that a temperature effect was occurring. Temperatures when movement

---

[26] / A separate report addressing coho salmon performance in the Klamath River authored by Cramer Fish Sciences (in preparation) provides a thorough review of the effects of water temperature on coho salmon. This issue is dealt with only briefly in this report.

occurred ranged between 15-23°C. High temperature also appears to trigger downstream movement of juvenile coho in the Klamath River basin (Chesney and Yokel 2003).

One way that juvenile salmonids cope with high temperatures is to find thermal refuge sites. Groundwater channels described earlier can provide such refuge. Ebersole et al. (2003a) described four cold water patch types in streams of the Grande Ronde basin (Northeast Oregon): cold alcoves, floodplain springbrooks (type of groundwater channel), cold side channels, and lateral seeps. All of these tended to be small. Ebersole et al. (2003b) reported that the abundances of juvenile Chinook and rainbow trout abundance were affected by the frequency of occurrence of coldwater patches. Higher frequency of occurrence of patches increased abundance, suggesting that survival is related to the probability that juveniles can successfully find patches. Ebersole et al. (2001) reported that patches appeared to be able to accommodate limited number of juvenile rainbow trout, suggesting that patch size may limit how many juveniles will survive even if patches can be readily located. Ebersole et al. (2003b) found no evidence that patch size affected abundance of juvenile Chinook salmon.

Juvenile coho have been found to use thermal refuge sites in Northern California streams. Nielsen (1992a) reported that juvenile coho used cool water pools at confluences with cool tributaries and coldwater seeps along hillslopes where some groundwater influence exists. One coho foraging phenotype, called "early emerging" (see Table 1), exhibited a unique feeding behavior that relied on cold water seeps for refuge during hours of high temperature.

Juvenile coho are found to be restricted to thermal refugia in the mainstem Klamath River during extended periods of the summer (Belchik 1997; Sutton et al. 2002; Deas and Tanaka 2006). Deas and Tanaka (2006) provided detailed observations on how subyearling coho, in addition to juvenile Chinook and steelhead, were distributed in several thermal refuge sites in the mainstem river in relation to water temperature. Figure 42 shows juvenile salmonid counts made by snorkeling within a thermal refuge site (Beaver Creek confluence) on the mainstem Klamath River at RM 162, showing fish numbers of each species within a sampling grid. The figure also shows temperature patterns at the time of the fish counts, made on July 28, 2005 at 7 pm. More examples are provided in the Deas and Tanaka report. Figure 43 is a photograph of the site taken on December 19, 2005, showing the backwater pool seen mapped in Figure 42 in relation to other channel and related flow features (flows are much higher in the December photo). Figure 42 shows that the distributions of the three species appear to be related to the thermal pattern. It also appears, in consideration of flow features seen in Figure 43, that the distributions were affected by flow velocities. Note that the juvenile coho show little association with where the velocity shear line would be expected to be (along the outer edge of the thermal refuge), in contrast to the other species. The authors noted that the juvenile coho were closely associated with an "algae mat" on the backwater pool (remnant of the mat is visible in Figure 43); the pool also contained abundant small woody debris on the substrate as well as rooted aquatic vegetation. No large wood pieces are present at the site. The composition of cover types in this backwater unit is comparable to that described earlier for backwaters in the Skagit River.
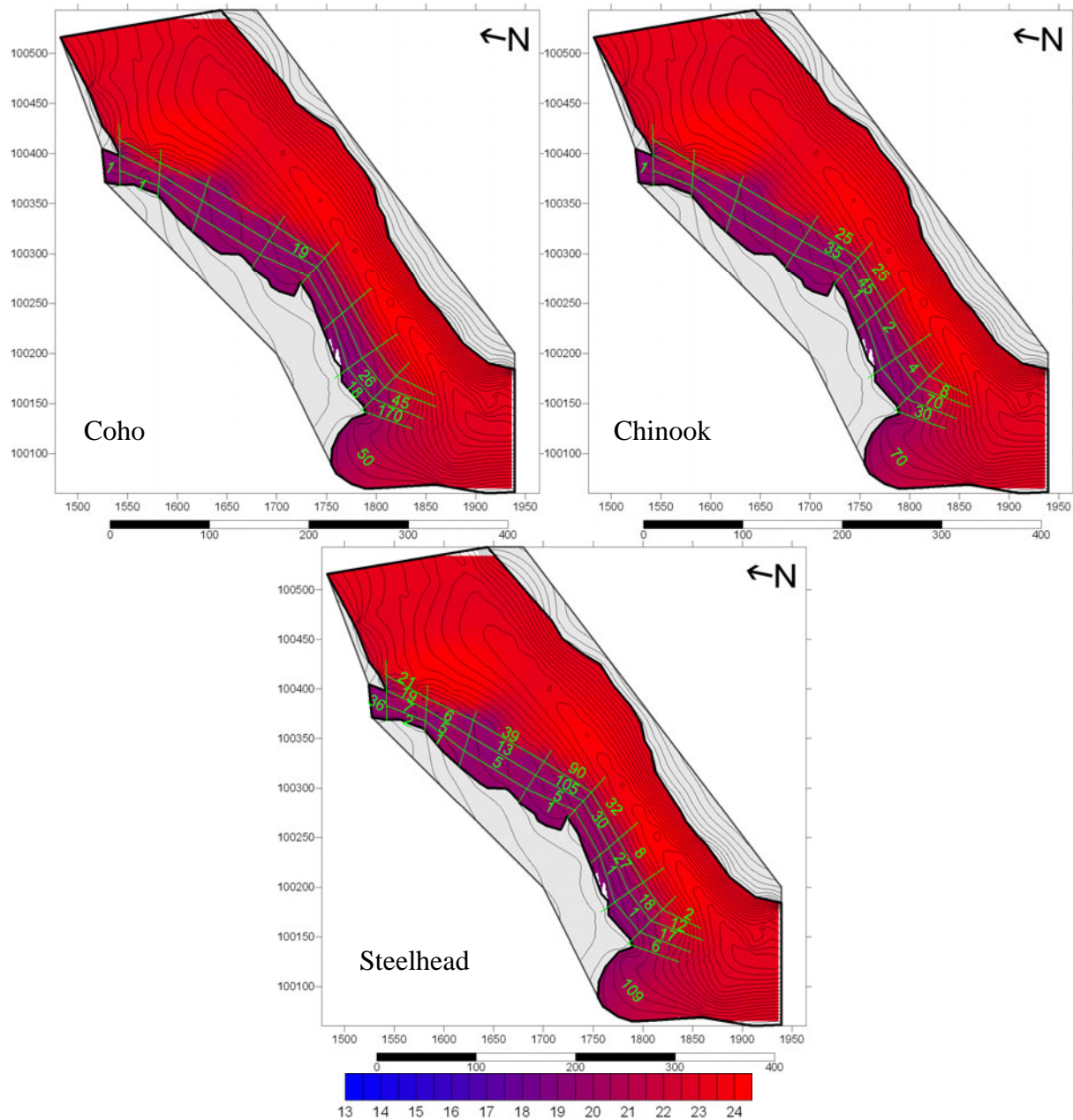
Figure 42. Fish counts by species at a thermal refuge site in the mainstem Klamath River (Northern California) on July 28, 2005 at 7:00 pm. Beaver Creek enters the mainstem river at upper left, shown as a cool water plume. Cool water also emerges along the gravel bar downstream of the mouth of Beaver Creek. A backwater pool is located in the bottom of the figure. Water temperatures are shown by the color scale. From Deas and Tanaka (2006). See Figure 43 for photograph of site.

Figure 43. Beaver Creek thermal refuge site in the Klamath River illustrated in Figure 42. Photograph taken on December 19, 2005. Backwater pool unit is plainly evident in lower left quadrant; remnant algae mat covers the inner part of the pool.

Survival of juvenile coho salmon during summer can be strongly density-dependent (Au 1972; Marshall and Britton 1980; Fransen et al. 1993; Quinn 2005). Competition for shrinking space—due to declining flows in late summer—and limited food results in reduced survival at higher juvenile abundance (Figure 44). Thus, the amount of suitable living space during summer can limit the size of a coho population in a watershed. Such limitations can be plainly evident in smaller watersheds where the population does not exhibit extensive redistributions between life stages. This is readily seen in the relationship between summer low flow and smolt yield in the following spring in some streams in the Puget Sound region (Figure 45). Relationships like this one are found in streams that have an abundance of overwintering habitat (Lestelle et al. 1993b).[27] In streams with little overwintering habitat, smolt yield is often controlled by winter conditions, thereby obscuring the effects of summer low flow on abundance.

Figure 44, derived from data for Deer Creek in the Alsea watershed study (Au 1972), provides an estimate of the density-independent component of survival for the stream by extending the regression line to the Y-axis (zero density), giving a value of 86%. This represents the average survival rate for the summer rearing phase for Deer Creek between June 1 and October 15 absent any effect of juvenile density. The Deer Creek watershed was partly logged approximately halfway during the study. Combined with the density-independent rate reported earlier in this document for the fry colonization phase the overall rate absent density effects for this stream would be 70% (multiplying 0.81 times 0.86).

---

[27] / In streams that lack abundant overwintering habitat, such as occurs for many streams on the Oregon Coast (Solazzi et al. 1990), coho production from strreams is not correlated with summer low flow (Scarnecchia 1981). A lack of correlation is also evident in Washington streams where overwintering habitat is not abundant (Lestelle et al. 1993b).
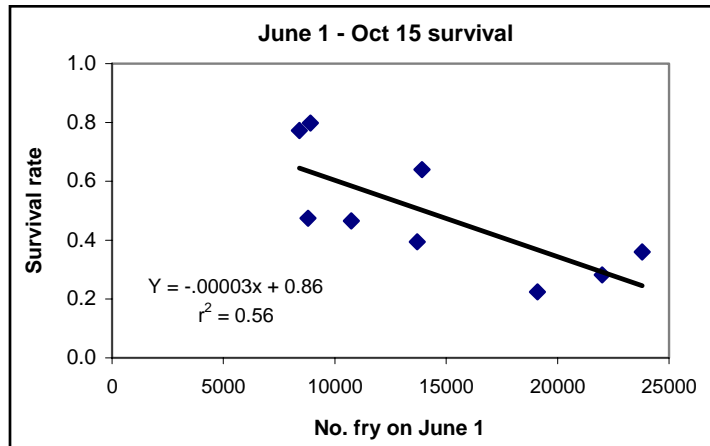
Figure 44. Relationship between the number of resident coho fry present on June 1 and survival to October 15 in Deer Creek, Alsea watershed (Oregon Coast). Survival shown is for the summer life stage for resident juveniles. Derived from data in Au (1972). Estimated density-independent survival is the point where the regression line would cross the Y-axis (0.86).
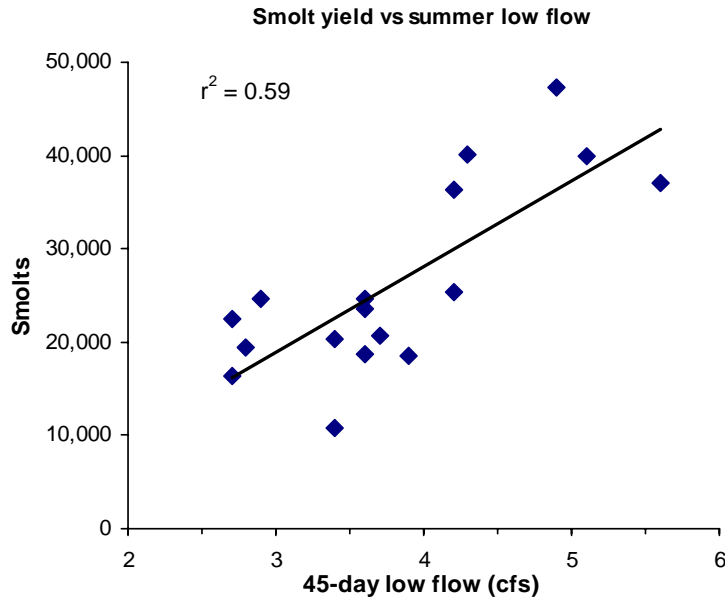
Figure 45. Relationship between the 45-day average lowest summer flow and coho smolt yield the following spring in Big Beef Creek (Western Washington). From Lestelle et al. (1993b).

3.2.6 Fall Redistribution and Overwintering

In many streams, some juvenile coho salmon move from their summer rearing locations in fall, triggered by increased flows associated with autumn rainfall. This movement is another demonstration of the affinity that these fish have for slow velocity water. Water velocities increase in main stream habitats with rising flow, either dislodging juveniles from summer rearing sites or stimulating them to move to find more favorable habitats prior to the coming of larger, more frequent winter storms (Tschaplinski and Hartman 1983). Moyle (2002) suggests that the availability of overwintering habitat is one of the most important and least appreciated factors influencing the survival of juvenile coho in streams.

This pattern of downstream movement in fall associated with rising flow has been reported in the Klamath River (USFWS 1998; Toz Soto, Karuk Department of Natural Resources *personal communications*), Oregon coastal streams (Rodgers et al. 1987)(Figure 46); Western Washington streams (Allee 1974; Peterson 1982), and British Columbia streams (Tschaplinski and Hartman 1983; Brown 2002). In some cases, juveniles captured at the head of tidal influence (Rodgers et al. 1987; Allee 1974; IMWSOC 2006) have been found to continue moving into estuarine habitat (Miller and Sadro 2003). It is evident, however, that these fish have not undergone smoltification and are not prepared for survival in full strength seawater (Rodgers et al. 1987). Miller and Sadro (2003) found them to reside into winter in the extensive upper parts of the Coos Bay estuary (i.e., within the estuary-freshwater ecotone) (Oregon Coast). In rivers that have minimal estuarine habitat, such as rivers on the Washington North Coast (e.g., Queets River), juvenile coho swept into the ocean during fall freshets likely perish.[28]

---

[28] / Some uncertainty remains regarding the fate of fall emigrants that move into the marine environment. This author believes that probability of survival is related to whether the juveniles can find low salinity habitats along the nearshore environment or whether they can locate and reenter nearby streams to overwinter. This topic is being researched in streams along the western portion of the Strait of Juan de Fuca (see IMWSOC 2006)—a significant downstream emigration of juvenile coho past a trap site immediately above tide water has been found in East Twin River between mid October and mid December. East Twin River and other streams in the immediate vicinity have very small stream mouth estuaries—the streams discharge directly into the outer coast of Strait of Jaun de Fuca. Data on East Twin River is being analyzed as part of a Master's Thesis by Todd Bennett (University of Washington).
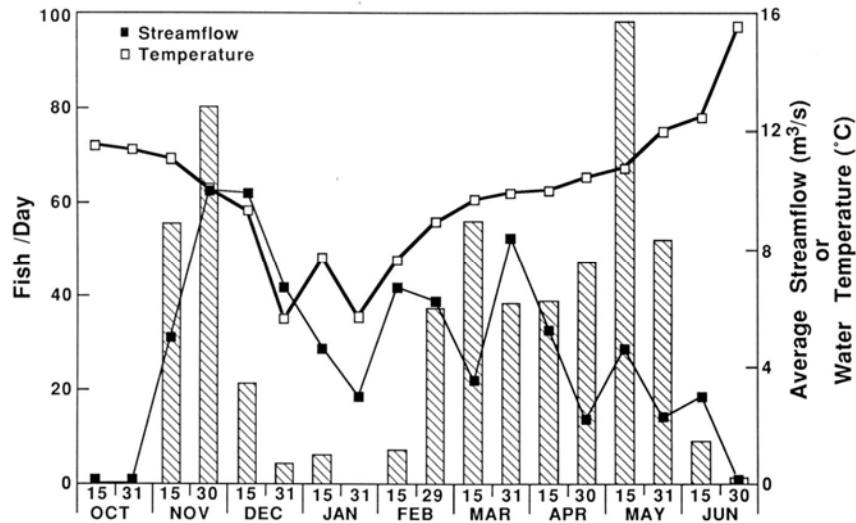
Figure 46. Pattern of juvenile coho downstream movement in Knowles Creek, Oregon. From Rodgers et al. (1987). Average catch per day of fish trapped near the head of tidewater is shown. Fish captured in fall reflect the pattern of redistribution seen in many streams. Fish captured after February are smolts moving seaward.

During this period of redistribution, some juvenile coho salmon immigrate into off-channel habitats. These habitats provide refuge from high flow velocities. Peterson (1982a) and Peterson and Reid (1984) described extensive movements of juvenile coho out of the mainstem Clearwater River (Washington Coast) into off-channel ponds (Figure 47). Thousands of juvenile coho salmon can move upstream through a tiny egress channel into a single pond within a short period of time—showing this to be a very striking pattern of migration for this species. Juvenile Chinook and steelhead trout do not generally exhibit such a movement into these habitats (Brown 2002; Lestelle et al. 2005). Once coho juveniles have moved into these sites, few move back out into the main stream during the winter—the large majority stay for the duration and emigrate in the spring as smolts. Their overwinter survival in these sites is typically high (approximately 70%) although it can apparently be less in very shallow ponds (Peterson 1982b; Peterson and Reid 1984). Similar movements occur by juvenile coho into off-channel alcoves along small streams (Nickelson et al. 1992; Bell et al. 2001). Bell et al. (2001) reported very high fidelity of overwintering coho to alcoves in Prairie Creek (Northern California), a finding comparable to the lack of movement out of riverine ponds until smolt emigration. Winker et al. (1995) suggested that stable residency within a habitat type is indicative of high quality habitat.
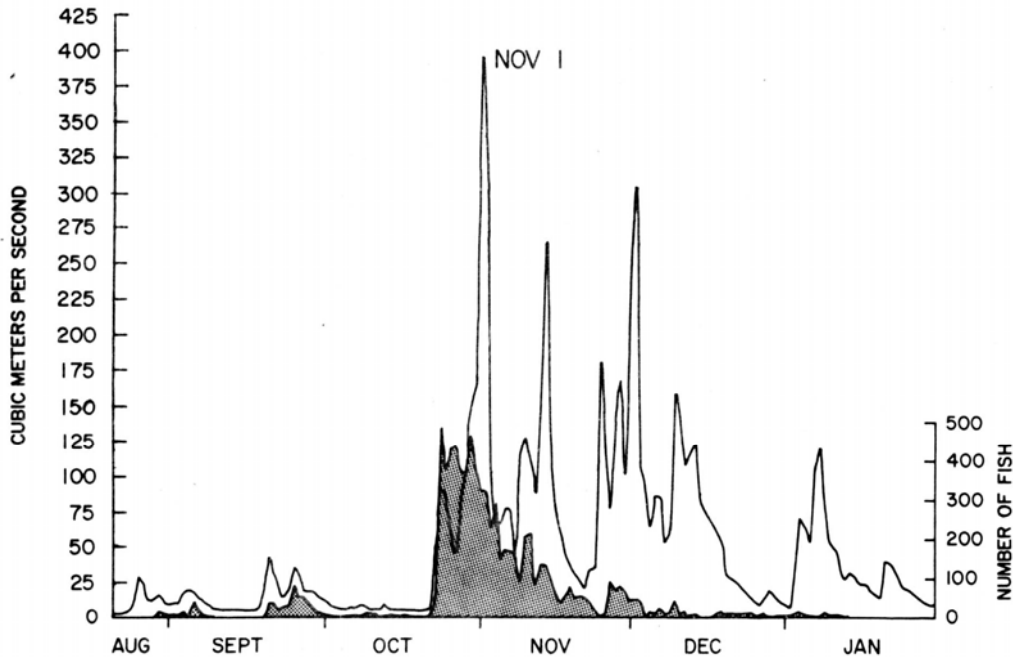
Figure 47. Pattern of trap catches of juvenile coho salmon moving into an off-channel pond along the Clearwater River (Washington) in relation to stream discharge in the mainstem river. From Peterson (1982a).

To aid the reader in visualizing the differences in the quality of different habitats for overwintering coho, three reference photos are provided here. Figure 48-top shows the Clearwater River (the river where Peterson conducted his studies) during moderately low winter flow—the reach shown is typical of the river. Figure 48-middle shows the Smith River in Oregon, comparable to the Clearwater River in size, during a flow event exceeding bankfull. Figure 48bottom shows a riverine pond habitat on the Clearwater River—conditions shown exist throughout the winter. These pictures illustrate the extreme differences in conditions between in-channel and off-channel habitats during winter.

Figure 48. Winter habitat conditions in rivers used by juvenile coho salmon. (Top) Clearwater River (Washington) during moderately low winter flow. (Middle) Lower Smith River (Oregon Coast) during flood event—this river is comparable in size to the Clearwater River. (Bottom) Riverine pond adjacent to the Clearwater River. Smith River photo is courtesy of Ron Rasmussen, U.S. Forest Service.

The same type of movement observed by Peterson is also found into groundwater channels (or small spring-fed floodplain tributaries)(Skeesick 1970; Giannico and Hinch 2003). Skeesick (1970) summarized the results of monitoring the movements of juvenile coho out of the mainstem Wilson River (Oregon Coast) into a small spring-fed floodplain tributary over a period of ten years. Immigrants were marked at the time of their capture in fall so that overwinter survival could be assessed; surviving smolts were enumerated in late winter and spring at the time of their emigration as smolts. Overwinter survival for the ten year period ranged between 46% to 91% and averaged 72%.

Bustard and Narver (1975) and Tschaplinski and Hartman (1983) monitored coho juveniles moving out of the mainstem Carnation Creek (Vancouver Island) into a series of small beaver ponds on the stream's floodplain. As found by Peterson (1982a), once fish moved into the site they generally did not leave again until late winter and spring. Tschaplinski and Hartman (1983) estimated the average overwinter survival over a six year period to be either 67% or 72% (using two methods of estimation).

Overwinter survival in off-channel habitats has been found to be improved if cover in the form of wood is added (Giannico and Hinch 2003), although the effect is not as evident in relatively warm groundwater channels. Apparently fish remain more active in warmer groundwater channels and may be more effective at evading predation. Juvenile coho have a greater cover-seeking response in very low temperatures (Bustard and Narver 1975; Taylor 1988).

Besides moving into off-channel habitats, juvenile coho salmon will also move from large streams (mainstem rivers) into small tributaries during this period of redistribution (Cederholm and Scarlett 1982; Scarlett and Cederholm 1984; Bramblett et al. 2002). In the Clearwater River (Washington), Cederholm and Scarlett monitored the movements of juvenile coho from the mainstem river into small tributaries. These streams are not spring fed—they are perennial runoff tributaries (1-1.5% channel gradients) that respond rapidly to rainfall events. Fish were found to move up to 1,100 meters upstream of the mainstem Clearwater River into these streams. The pattern of residency appeared to be different than reported for ponds by Peterson (1982a) and Tschaplinski and Hartman (1983). In the runoff tributaries, fish exhibited a greater amount of movement through the winter—fish appeared to be arriving and departing more often than seen in the ponds. This suggests that fish were leaving the mainstem in an effort to find improved conditions, then continued that search to other areas during the course of winter. This may reflect an urgency to leave the large mainstem river when conditions are particularly harsh, followed later by more movement to escape conditions found unfavorable for continued residency. It suggests a transient residency pattern of fish that have not found high quality overwintering sites.

This movement of juvenile coho salmon from mainstem streams during fall and winter appears to be due to fish leaving unfavorable areas in search of improved survival conditions. Within mainstem streams, they evacuate sites with high exposure to high velocities. In Carnation Creek (Vancouver Island), sites within the main channel jammed with logs, undercut banks, and deep pools filled with upturned tree roots and other forest debris contained almost all of the juvenile coho remaining in the main stream during the winter (Tschaplinski and Hartman 1983). The large reductions in the main stream population in fall coincided with the largest movement of juvenile coho into the off-channel sites. No coho were found in midstream locations within the

stream and they did not inhabit areas under banks unless the sites contained tree roots or other lodged debris (Figure 49), consistent with the findings of Beechie et al. (2005) in the Skagit River described above (Figure 36C). Bustard and Narver (1975) reported the same pattern for cover use in Carnation Creek in earlier work than that of Tschaplinski and Hartman as seen in Figure 50, which nicely contrasts species differences in cover type preferences. Juvenile steelhead, in addition to also overwintering in wood accumulations (yearling and older fish), utilize cobble substrates. Young of the year steelhead predominantly utilize cobble or boulder substrates for overwintering, which coho rarely use (Ruggles 1966; USFWS 1988; McMahon and Hartman 1989).

Grette (1985) reported similar results for small streams on the Olympic Peninsula (Washington), stating:

> "During winter, coho were observed to be closely associated with instream cover, especially debris-related instream cover. Often, the majority of the coho population in a particular pool would be found near debris cover along a slow velocity stream margin. Although cover appeared to be important, the single most important factor determining distribution of coho during winter appeared to be velocity. A slow velocity pool with instream cover (often even a very small area of cover) was likely to have coho present, while a high velocity habitat with abundant instream cover often had no coho."
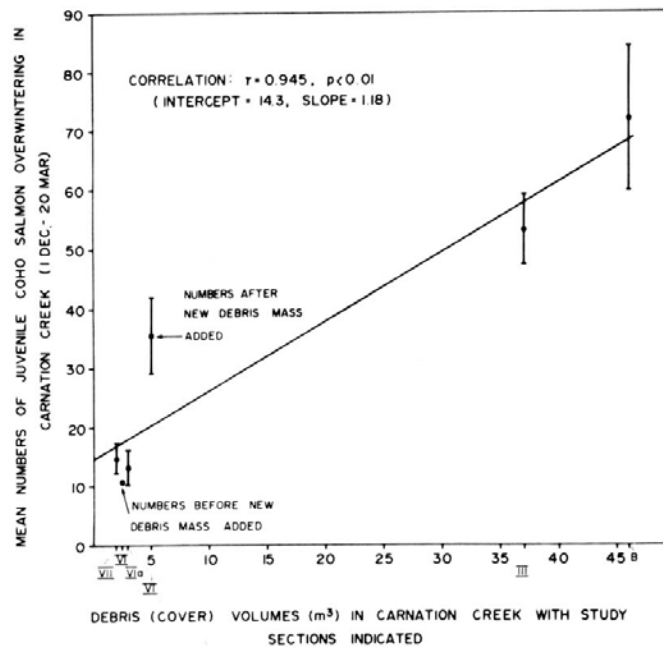
Figure 49. Relationship between instream wood volume and numbers of juvenile coho salmon overwintering at sites in Carnation Creek (Vancouver Island). From Tschaplinski and Hartman (1983).
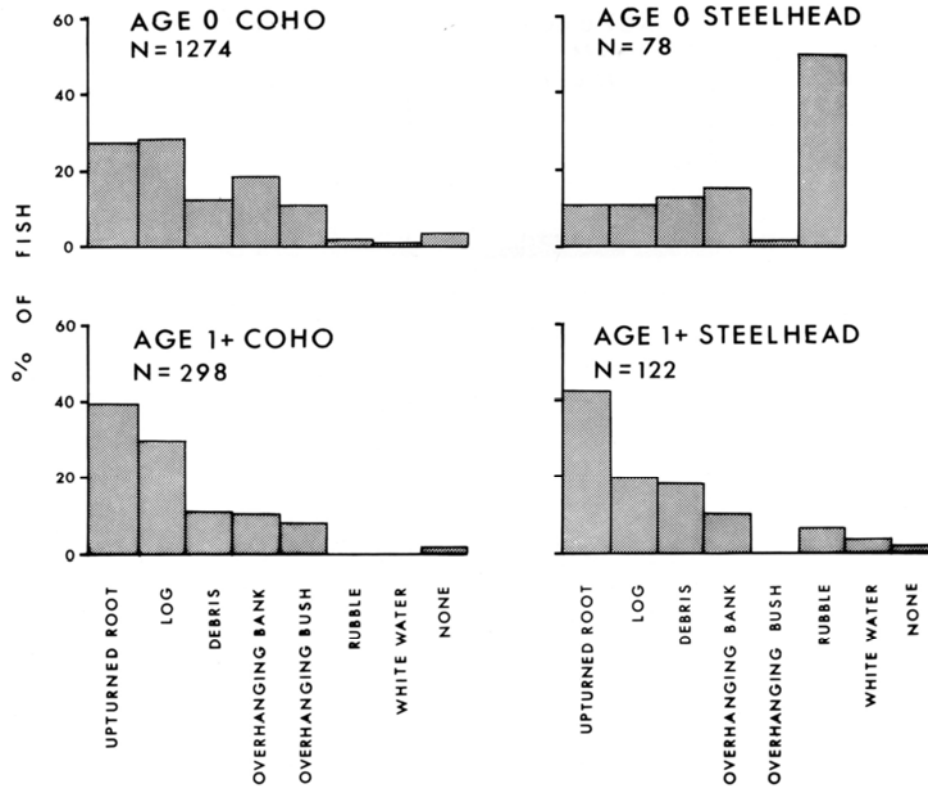
Figure 50. Cover types selected by juvenile coho and steelhead at water temperatures of 7 °C or less during winter in Carnation Creek (Vancouver Island). From Bustard and Narver (1975).

The USFWS (1988) investigated habitat types used by overwintering juvenile coho and steelhead in the Trinity River within the Klamath River basin. Juvenile coho were found overwintering in side channels in "still water with aquatic vegetation or woody debris as the main cover type." Juvenile coho were rarely observed holding underneath cobbles as was the common behavior for juvenile steelhead. The researchers noted that "use of large woody debris by juvenile coho salmon would have probably been greater had this type of cover been available in greater quantities within the study sites or the Trinity River in general."

The association between juvenile coho and cover increases as water temperature drops. Distance between individual juvenile coho and nearest cover diminishes with falling temperature, as seen in Carnation Creek. (Figure 51). At temperatures <3 °C, virtually all individuals were found tight within cover. Toz Soto (Karuk Department of Natural Resources *personal communications*) has observed a similar pattern in snorkeling surveys in tributaries to the Klamath River. Juvenile coho, like several salmonid species, are nocturnal at low temperatures during winter months (McMahon and Hartman 1989; Roni and Fayram 2000).

Hartman (1965) described the importance of large, stable instream wood to juvenile coho overwintering in main stream habitats in British Columbia)(Hartman 1965). The Chilliwack River, the focus study stream, at the time contained numerous large wood accumulations. Hartman's study is particularly notable in how he performed his sampling within this mainstem

river—he used "Prima Cord" explosives to sample for small fish at various sites within the river. This proved to be an effective way to sample under log jams. Sampling was conducted in all seasons, including winter. To this author's knowledge, it is the only study to conduct such a rigorous sampling of log jam sites. Hartman reported that the large majority of juvenile coho found at sampling sites in the mainstem river during fall were located in close association with log jam cover. During winter, nearly all coho juveniles were associated with log jams.
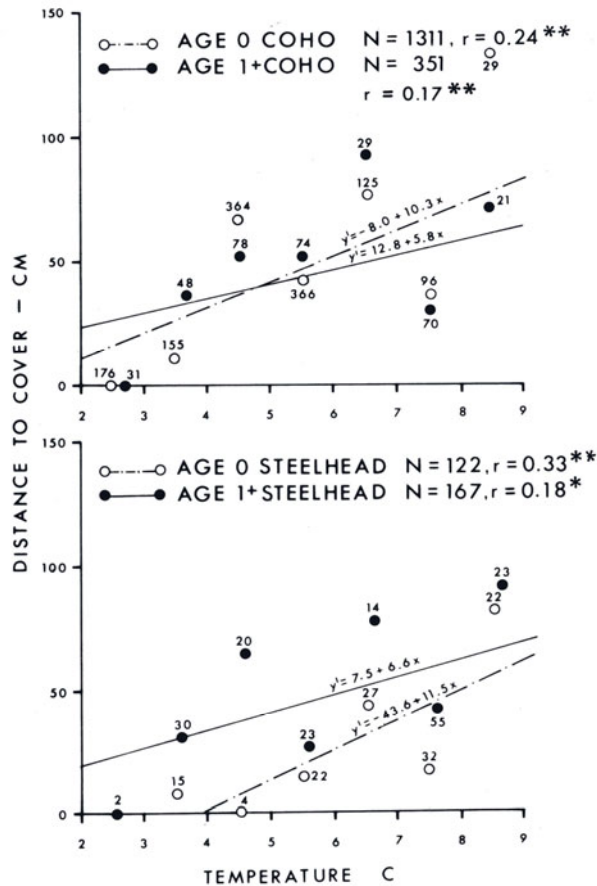
Figure 51. Mean distance to cover of juvenile coho and steelhead in relation to water temperature during winter in Carnation Creek (Vancouver Island). From Bustard and Narver (1975). Sample size is indicated by the associated numbers. Regression lines were derived from N observations.

The importance of large wood to overwintering coho salmon has also been documented in Porter Creek, tributary to the Chehalis River (Washington)(Cederholm et al. 1997b). This study looked at the effect of wood enhancement on numbers of coho and juvenile steelhead produced in this medium sized creek. Although wood enhancement also increased pool quantity in the stream, smolt numbers were much more responsive to wood than merely to changes in pool quantity (Figure 52).
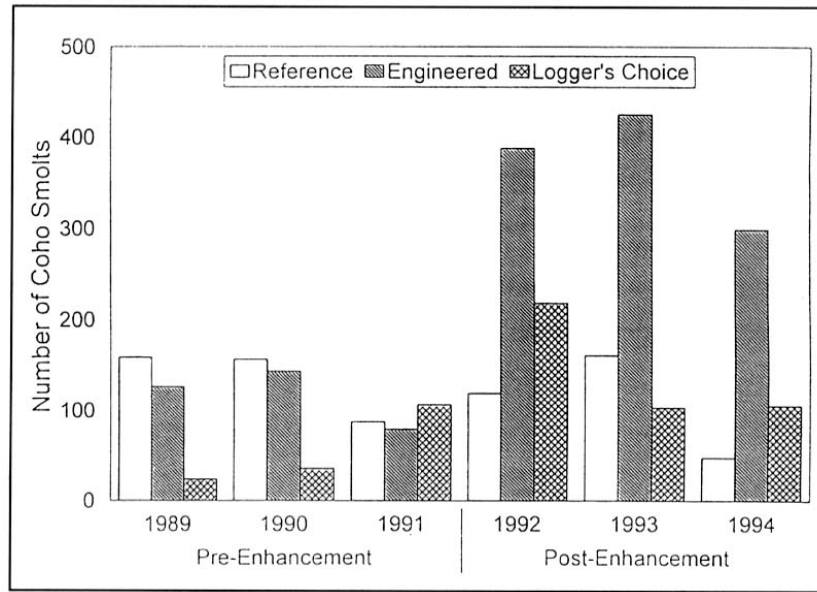
Figure 52. Results of large wood enhancement in Porter Creek, Washington. Juvenile coho smolt numbers are compared between reference (control) reaches, reaches with wood placed strategically (engineered), and reaches where loggers chose to add wood. From Cederholm et al. (1997b).

It bears noting that the size and density of large, stable wood in stream channels varies greatly by channel size, channel type, and available wood sources (Abbe and Montgomery 1996; Bilby and Bisson 1998; Montgomery et al. 2003). Small channels retain wood much more readily than large channels (Figures 53-54). Wood is much more easily transported in large channels. Channel type (i.e., extent of confinement) also influences how much wood is retained in a channel—confined channels with boulder or bedrock substrate contain about half or less number of pieces of wood found in similarly sized, unconfined reaches with small substrate (Bilby and Wasserman 1989; Bilby and Bisson 1998). The amount and sizes of wood that are recruited into a stream channel also greatly affects the extent of wood retained within a channel (Hyatt and Naiman 2001). Where riparian forests have been reduced by development or where they are composed of small trees, stream channels contain much less wood compared to heavily forested areas with large trees (Montgomery et al. 2003). Large wood jams are still abundant on a few large rivers of the Pacific Northwest, as seen on the Queets River within the Olympic National Park (Washington)(Figure 55)—a river subject to extreme flood conditions associated with high precipitation but still able to retain large wood volumes within its channel.
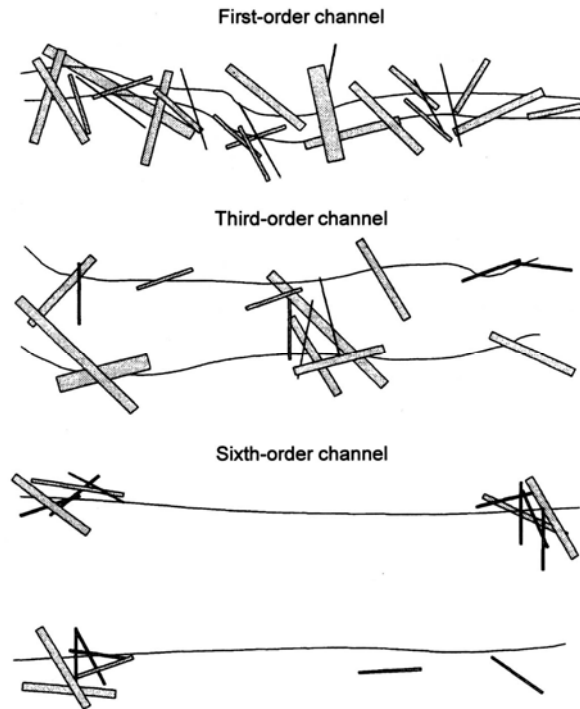
Figure 53. Typical distribution of large woody debris in channels of various sizes. From Bilby and Bisson (1998).

In smaller mainstem streams on the Oregon Coast, Nickelson et al. (1992) reported that juvenile coho predominantly overwinter in pools—particularly dammed pools and backwater pools—and in alcoves (Figure 31), all having low velocities. Densities are highest in alcoves. Nickelson et al. (1992) reported that riffle habitats hold virtually no coho juveniles during winter.

Researchers on the Oregon Coast concluded on the basis of various analyses (e.g., Reeves et al. 1989) that coho salmon in Oregon coastal streams were largely limited by the amount of suitable overwintering habitat compared to available summer habitat. This entire region has been subject to extensive logging in the past; habitats have been altered and wood loads are far below historic levels. A project was initiated in several streams to add winter habitat, primarily by increasing the amount of alcoves and dammed pools (Solazzi et al. 2000). The well designed study monitored two reference streams and two treatment streams over a period of eight years. A key response variable considered was overwinter survival of juvenile coho salmon. Overwinter survival was increased significantly in both treatment streams as a result of habitat modifications. This study provides some of the best evidence that overwinter survival is related to the availability of low velocity habitat. Prior to treatment and including the reference streams, average survival in these streams was in the range of 10-20%. Average overwinter survival in the two treatment streams following habitat modification was 39%. These post-treatment survivals are similar to overwinter survivals estimated in Prairie Creek (Northern California, a nearly pristine stream within old growth redwood forest) of 45% (Brakensiek 2003) and in Carnation Creek prior to logging of 35% (Bustard and Narver 1975).
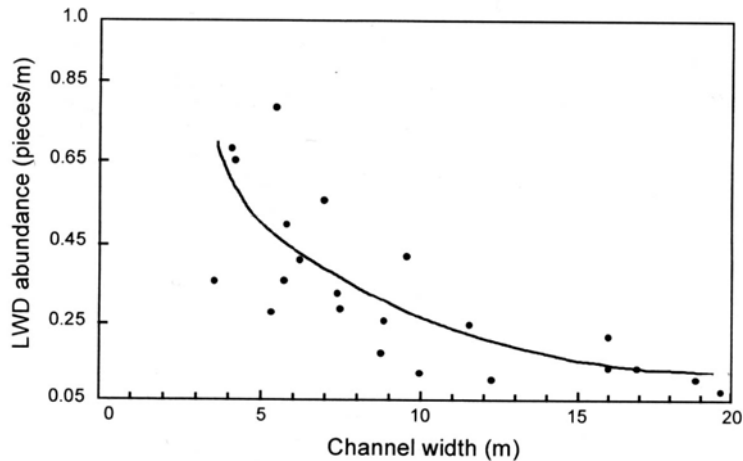
Figure 54. Abundance of large woody debris in relation to channel size in old-growth forests in southeastern Washington. From Bilby and Bisson (1998) as modified from Bilby and Ward (1989).

The role of winter conditions to the performance of Oregon coastal coho has also been demonstrated in an analysis of winter flows and smolt yields. Knight (1980) found smolt yields in the three Alsea River study streams to be significantly correlated to the level of high flow during the overwintering period (Figure 56). These results provide further evidence that the quantity and quality of winter habitats limit coho production on the Oregon Coast. At high flows, the distinction between pools and riffles can be obscured. Gordon et al. (2004), in their excellent book on stream hydrology, describe it as follows:

> "As kayakers are well aware, the water surface slope, depth of flow and speed of the current become more uniform over the stream reach at high flows. At these times, it becomes questionable whether the terms 'pool' and 'riffle' are even applicable. As discharge increases, velocity and depth rise more rapidly in pools than in riffles, and energy loss becomes more uniform. The shear stress in pools can eventually exceed that in riffles."

Figure 55. Abundant log jams still exist on some rivers in the Pacific Northwest as seen in the Queets River within Olympic National Park (Washington). Dense accumulations of wood, built on large key pieces, provide cover and velocity refugia for small salmonids. Note the young alder trees growing from a large key piece (middle picture), indicating a degree of interannual stability of jams, despite extreme flow fluctuations within this river due to high precipitation.

This suggests that the effective size of pools shrinks—from the perspective of the coho—as winter flows increase; hence Figure 56 suggests that smolt yields in effect decline as pools become less effective as velocity refuge sites. Grette (1985), in describing the role of pools for overwintering coho, reported that some habitats classified as pools during summer were recognized as riffles during winter flows for the reasons described by Gordon et al. (2004). This dynamic of how velocities change in main channel pools also highlights the importance of off-channel habitats to coho that need low velocity habitats. Moreover, it emphasizes the importance of large, stable wood for fish residing in the main channel during winter.

Figures 57 and 58 and Table 4 summarize estimates made of overwinter survival for juvenile coho salmon in streams of the Pacific Northwest and California. The estimates are presented corresponding to the major channel type (main stream or off-channel) utilized by coho in each study. There is a clear pattern showing much higher survivals for off-channel sites. Figure 58 separates the estimates further into altered main stream channels (by land use practices), pristine main channel habitat, and several types of off-channel habitats.

Another factor that can affect overwinter survival of juvenile coho is fish size in fall, just prior to the redistribution movement. Overwinter survival can be higher for larger fish at the end of the summer rearing period (Holtby 1988; Quinn and Peterson 1996). In a small Puget Sound stream, Quinn and Peterson (1996) reported that juvenile coho in larger size-classes had significantly higher overwinter survival rates than smaller fish in the winter of 1990-1991 but not in 1991-1992—though a pattern for increasing survival with size was still evident in the second year (Figure 59). Maximum daily flows during the winter of 1990-1991 were almost twice as high as those in 1991-1992, suggesting that the benefit of fish size is greatest during winters with high peak flows. This further suggests that the effect of fish size is demonstrated most in runoff-type streams as opposed to within off-channel habitats where velocity effects are minimal. Moreover, juvenile coho that rear during summer in mainstem rivers are usually larger than those rearing in small tributaries (Marshall and Britton 1980; Scarlett and Cederholm 1984; Peterson and Reid 1984), except when mainstem temperatures are extremely high, which limits growth. Hence, where juvenile coho find favorable conditions in mainstem rivers for summer growth and remain there overwinter, their larger size may compensate to some degree for harsher winter conditions that often exist there compared to smaller tributaries. Quinn and Peterson (1996) suggested that the superior survival of larger fish during winter may be explained by some combination of size-biased predation and resistance to displacement by floods.
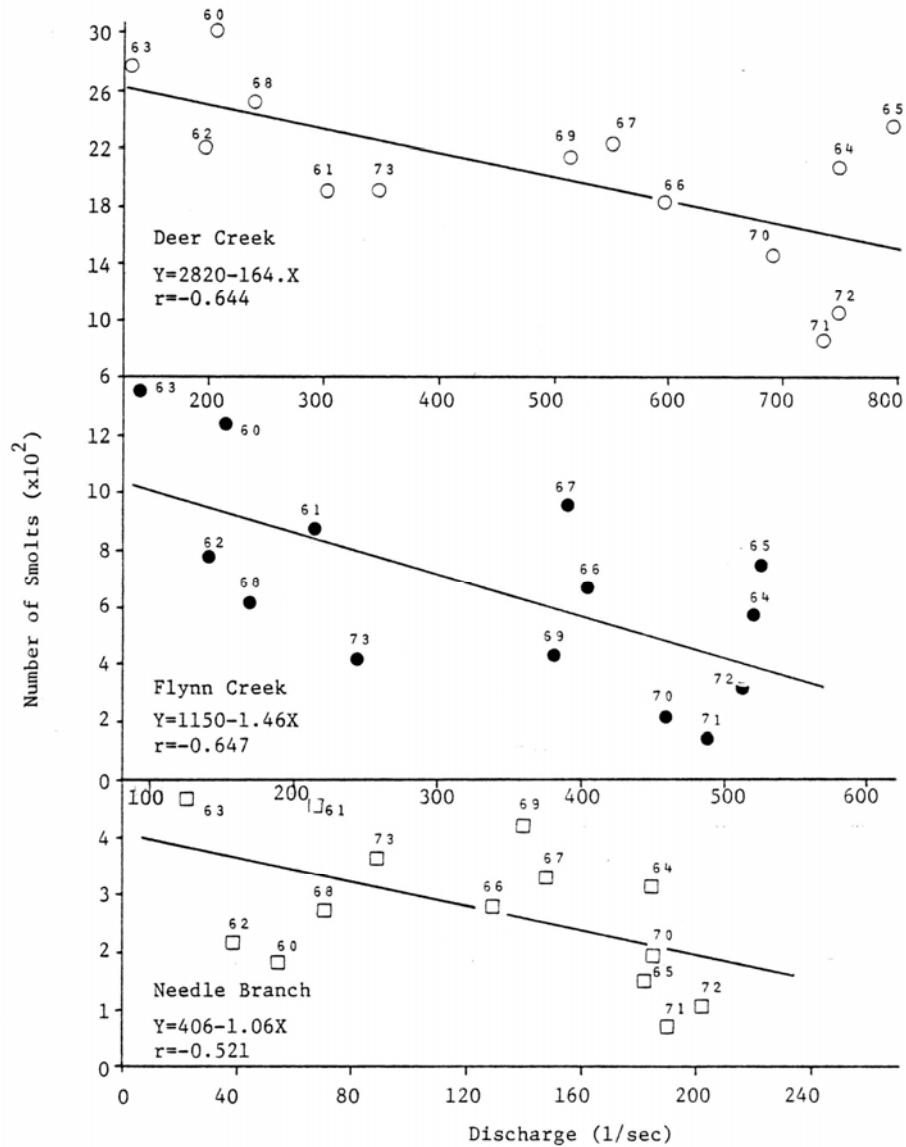
Figure 56. Relationships between coho smolt yields and mean January discharge during the overwintering life stage in Deer Creek, Flynn Creek, and Needle Branch within the Alsea River system (Oregon Coast). Data labels indicate smolt year. The three streams were subject to different levels of logging. The Needle Branch watershed was clearcut in 1966, leaving no buffer strip along the stream. The Deer Creek watershed was patchcut (three patches) with 25% of the area being logged in 1966. Partial buffer strips were left. Flynn Creek was not logged and served as a control watershed during the study period. From Knight (1980).
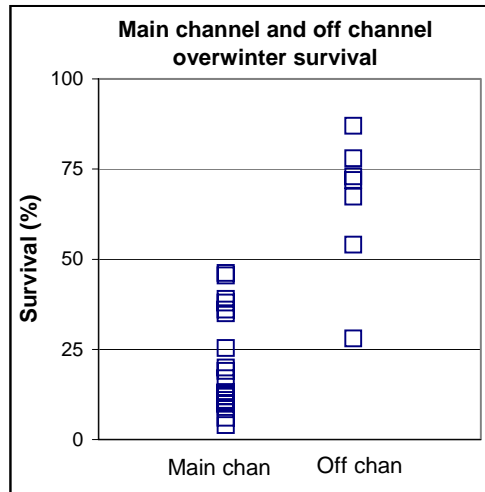
Figure 57. Comparison of overwinter survival estimates for juvenile coho in main stream habitats and off-channel habitats. See Table 3 for a list of studies used to create the chart.
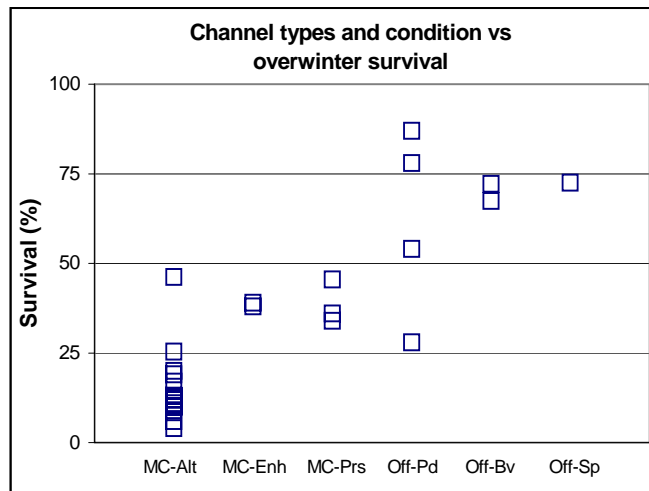
Figure 58. Comparison of overwinter survival estimates for juvenile coho in altered main stream habitats (MC-Alt), enhanced main stream habitats (MC-Enh), pristine main stream habitats (MC-Prs), off-channel ponds (Off-Pd), off-channel beaver complexes (Off-Bv), and off-channel spring sites (Off-Sp). See Table 1 for a list of studies used to create the chart.

Table 4. Summary of estimated overwinter survival rates for juvenile coho salmon in streams of Alaska, British Columbia, Washington, Oregon, and California.

Channel type	Basin	Status	Region	Survival	Source	Comment
In channel	Alsea R.	Previously logged; pre treatment	Oregon Coast	0.13	Solazzi et al. (2000)	Two year mean
In channel	Alsea R.	Previously logged; reference-pre treatment	Oregon Coast	0.17	Solazzi et al. (2000)	Two year mean
In channel	Alsea R.	Previously logged; post treatment	Oregon Coast	0.38	Solazzi et al. (2000)	Two year mean
In channel	Alsea R.	Previously logged; reference-post treatment	Oregon Coast	0.20	Solazzi et al. (2000)	Two year mean
In channel	Nestucca R.	Previously logged; pre treatment	Oregon Coast	0.11	Solazzi et al. (2000)	Two year mean
In channel	Nestucca R.	Previously logged; reference-pre treatment	Oregon Coast	0.19	Solazzi et al. (2000)	Two year mean
In channel	Nestucca R.	Previously logged; post treatment	Oregon Coast	0.39	Solazzi et al. (2000)	Two year mean
In channel	Nestucca R.	Previously logged; post treatment	Oregon Coast	0.10	Solazzi et al. (2000)	Two year mean
In channel	WF Smith R.	Previously logged	Oregon Coast	0.04 - 0.13	J. Ebersole personal communications	Survivals of groups from 9 locations
In channel	Big Beef Cr.	Previously logged	Hood Canal	0.25	Quinn and Peterson (1996)	High flow winter
In channel	Big Beef Cr.	Previously logged	Hood Canal	0.46	Quinn and Peterson (1996)	Moderate flow winter
In channel	Sashin Cr.	Pristine	SE Alaska	0.35	Crone and Bond (1976)	Three year mean
In channel	Carnation Cr.	Pristine	Vancouver Is.	0.35	Bustard and Narver (1975)	One year
In channel	Prairie Cr.	Pristine	North CA	0.45	Brakensiek (2002)	One year; estimate for standardized fish length
In channel			Mean	0.20		

Channel type	Basin	Status	Region	Survival	Source	Comment
Off channel – beav ponds	Carnation Cr.	Pristine	Vancouver Is.	0.72	Tschaplinski and Hartman (1973)	Mean of several years
Off channel – beav ponds	Carnation Cr.	Post logging	Vancouver Is.	0.67	Tschaplinski and Hartman (1973)	Mean of several years
Off channel - spring creek	Wilson R.	Not known	Oregon Coast	0.72	Skeesick (1970)	Mean of nine years (range 0.46-0.91)
Off channel - pond	Clearwater R.	Pristine	Wash Coast	0.78	Peterson (1982)	One year; deep pond
Off channel - pond	Clearwater R.	Pristine	Wash Coast	0.28	Peterson (1982)	One year; shallow pond
Off channel - pond	Coldwater R.	Not known	Fraser R.	0.54	Swales et al. (1986)	One year
Off channel - pond	Coldwater R.	Not known	Fraser R.	0.87	Swales et al. (1986)	One year
Off channel			Mean	0.66		
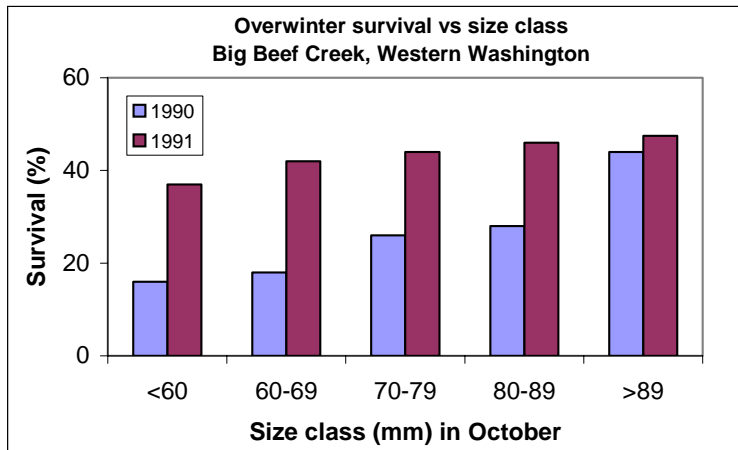
Figure 59. Overwinter survival of juvenile coho of different sizes tagged at the end of summer in Big Beef Creek (Western Washington) in 1990 and 1991. From Quinn and Peterson (1996).

Figure 60 summarizes in graphic form effects of environmental factors on the overwinter survival of juvenile coho salmon. Most of these factors relate to how easily juvenile coho can find low velocity habitats during winter.
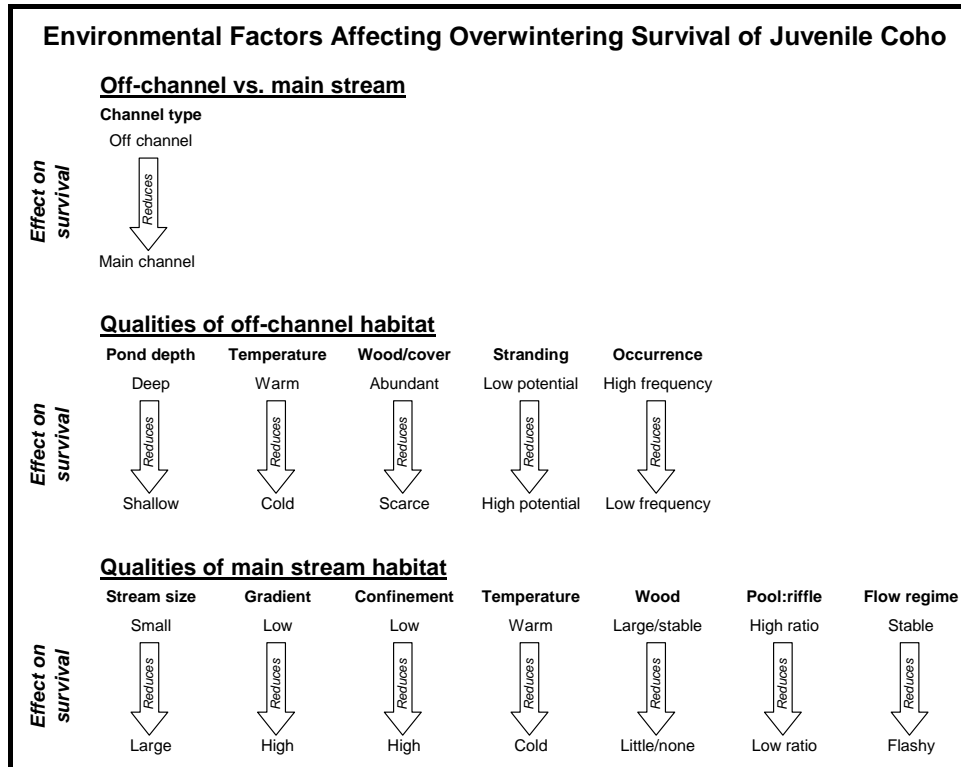
Figure 60. Summary of factors that affect overwinter survival of juvenile coho salmon.

Coho Salmon Life History Patterns   82

3.2.7 Smolt Migration

Juvenile coho salmon that attain a certain size by late winter or spring undergo smoltification—the physiological transformation necessary for surviving at sea. Minimum fork length needed during this time period to facilitate the transformation appears to be 75-80 mm based on studies cited by Sandercock (1991). Fish that do not reach this size within the critical time window delay their outmigration until the next year. As noted earlier in this document, the fate of especially small yearling migrants associated with the margin-backwater foraging type described by Nielsen (1994) remains unknown. The large majority of coho smolts in California, Oregon, and Washington are yearlings.

Smoltification and the corresponding smolt migration begins earlier in the southerly part of the species' geographic range (Sandercock 1991; Spence 1995). Shapovalov and Taft (1954) reported that in California the outmigration of smolts begins as early as mid March, peaking in mid May. Similar timing patterns exist in Oregon and Washington streams (Au 1972; Seiler et al. 2004). In contrast, in the Resurrection Bay area of Alaska, the mid point of the outmigration can occur in mid June (Sandercock 1991 citing McHenry 1981). Spence (1995) suggests that one reason for the relationship between smolt timing and latitude is that ocean upwelling and seasonal increase in productivity occurs progressively later with increasing latitude. Also, migrations of northern populations tend to be of short duration (majority migrating over a 5-10 day period), while 50% of the fish from southern populations migrate over a 2-5 wk period. Spence (1995) suggests that the migration of southern populations spans a greater time period because greater variation occurs in the timing of increased spring-time ocean productivity in the southern end of the species' range. While positive relationships between smolt timing and latitude are strong, considerable variation in timing has been observed among populations at any given latitude (Spence 1995). This variation may be partly the result of the type of streams where data has been collected within the data set that Spence used in his analysis.

Of particular interest for this review is the wide range of smolt outmigration patterns that can occur in a single watershed within the overall critical time window for smoltification. While the onset and duration of smoltification are largely controlled by day length and water temperature (Hoar 1976), both migration timing and rate of migration can be affected by smolt size, location in the watershed at the start of the migration, migration distance, and stream flow (Quinn 2005). This overview is focused primarily on free-flowing rivers. It is beyond the scope in this report to consider factors affecting migration timing and travel rates through reservoirs, such as in the Columbia system, though some information from that system is included here where useful.

Larger salmonid smolts, for several species including coho salmon, generally begin their migration earlier than smaller ones, presumably because smaller ones require additional time to gain size necessary for smoltification and for improved marine survival (Irvine and Ward 1989; Seiler et al. 2004; Quinn 2005). This pattern is seen in the Queets River system on the Washington coast (the Clearwater River seen in Figure 2 is a major tributary to the Queets River). Studies have been underway in this river system since 1981 to annually assess natural coho smolt yields from various tributaries and from the watershed as a whole. The studies provide a means to assess outmigration timing, rates of migration, and production of wild smolts

originating in various habitats around the basin (Lestelle and Curtwright 1988; Lestelle et al. 1993a).

The coho smolt migration in the Queets system typically begins first for fish emigrating from riverine ponds, followed by fish from runoff tributaries (Figure 61). Smolts coming from off-channel ponds are consistently larger than fish that overwinter and emigrate from runoff tributaries and small groundwater channels (Figure 62). Consequently, the emigration from overwintering ponds occurs earliest and ends well before it is completed in runoff streams. While emigration timing from ponds is earlier than runoff streams, considerable variability can exist between ponds (Figure 63). Differences in timing seen in Figure 63 are not due to variation in smolt size because both the earliest and latest patterns shown consisted of exceptionally large fish of comparable size.
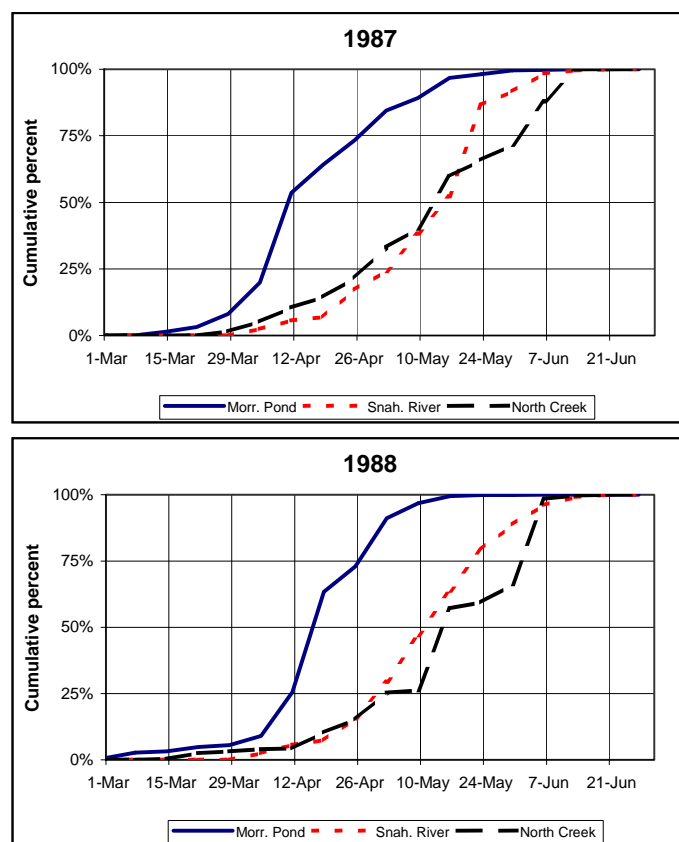
Figure 61. Timing of coho smolt emigration from three channel types in the Queets River system in 1987 and 1988: a riverine pond (Morrison Pond), a runoff stream (Snahapish River), and a groundwater fed stream (North Creek). Data from Lestelle and Curtwright (1988) and QDNR (1989a).

Another pattern usually seen with Queets coho smolts shows that early emigrants, though large, move downstream more slowly than fish that emigrate late in the migration. Figure 64 illustrates this pattern, comparing the timing of wild fish marked when they departed either a pond or a runoff tributary with their recapture timing at a seining site near the head of tidewater. The pond and runoff tributary trap sites where marking occurred were 6.8 and 27.6 miles upstream of the

seining site, respectively. Travel rates computed using the median dates when smolts were marked and released, then recaptured near the head of tidewater were 0.6 and 5.5 miles per day for pond and runoff tributary fish respectively (1.0 and 8.9 km/day). A different depiction of this pattern is seen by comparing the release timing of all marked fish to their recapture timing at a scoop trap near the mouth of the Clearwater River (Figure 65). Smolts departing tributary streams and ponds later in the season migrated more quickly to the scoop trap than earlier migrants. It bears noting that more rapid migration of later-timed fish in this river occurs during a receding hydrograph—the flow regime is rainfall dominated with winter peak flows.
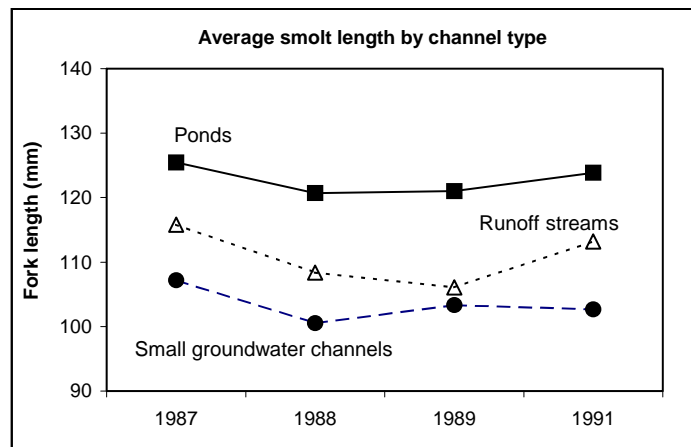
Figure 62. Average lengths of coho smolts emigrating from ponds, runoff streams, and small groundwater channels in the Queets River system in 1987, 1988, 1989, and 1991. Data for 1990 in the sequence of years shown were not used here due to experimental supplementation fish present that year. Multiple trapping sites for each channel type are included. Data from Lestelle and Curtwright (1988) and QDNR (1989a, 1989b 1992).
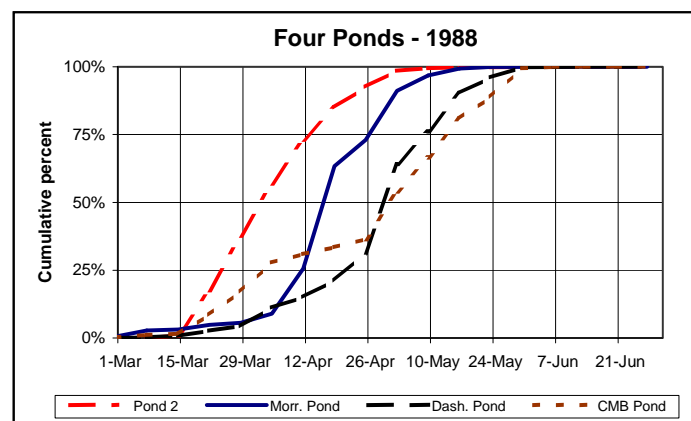
Figure 63. Timing of coho smolt emigration from four riverine ponds along the Clearwater River (Queets River system) in 1988: Pond 2, Morrison Pond, Dashers Pond, and Coppermine Bottom Pond (CMB). Data from QDNR (1989a).
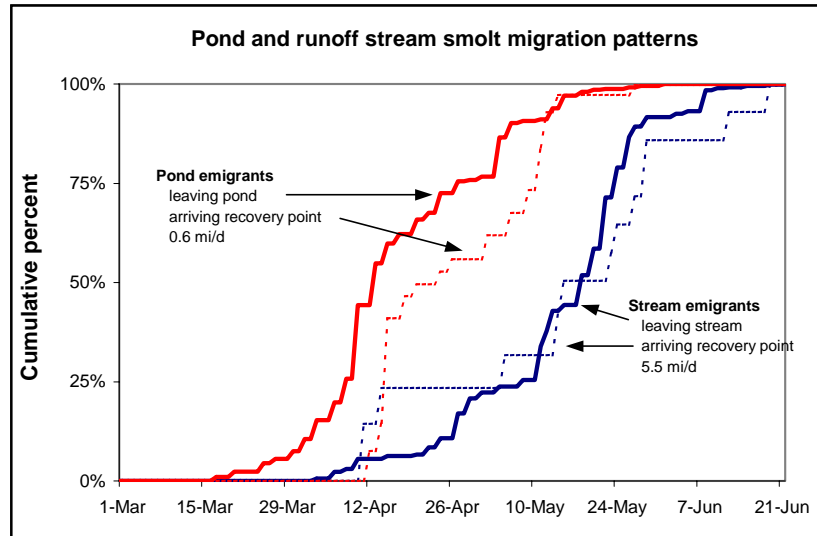
Figure 64. Emigration timing patterns of marked coho smolts from a riverine pond (Morrison Pond) and a runoff tributary (Snahapish River) in the Clearwater watershed and recapture patterns of the same marked smolts at the Queets River seining site near the head of tidewater in 1987. Computed average migration rates associated with the times of 50% of marks released and marks recaptured are shown in miles traveled per day. The trap sites where smolts were marked are located 6.8 and 27.6 miles upstream of the seining site respectively. Adapted from Lestelle and Curtwright (1988).

This pattern of early migrating smolts moving more slowly downstream than later migrants has been documented elsewhere and it appears to occur for salmonid species in general (Quinn 2005). Dawley et al. (1986) documented the pattern for hatchery coho salmon released at Ice Harbor Dam on the Snake River. Fish released later in the season migrated more quickly than those released earlier (Figure 66). Similar results were reported by Giorgi et al. (1997) for hatchery and wild yearling Chinook smolts and steelhead smolts in the Columbia River and by Pyper and Smith (2005) for spring Chinook yearling and coho smolts in the Yakima River.

Another factor that can affect migration rate of salmonid smolts is migration distance to the river mouth (Quinn 2005). Smolts that begin their migration far from the estuary generally travel downstream much faster than those that begin closer. A multiple regression analysis of coho smolt release data in Dawley et al. (1986)(Table 18 in that report-excluding releases prior to March 15 and after June 15) for the Columbia River shows significant effects ($P<0.05$) of both date released (Julian day) and distance between release site and the recovery point on travel time. Similarly, data presented here in Table 6 show the same type of effects for wild coho smolts in the Clearwater River—though the scale in distance being traveled by smolts is much less in this case. Multiple regression analysis between release date (Julian day) and distance to the recapture site as independent variables and travel time (dependent variable) shows significant effects ($P<0.05$) for both independent variables in combination ($R^2 = 0.73$). This effect of distance on travel time is intriguing—Quinn (2005) states that it raises the question of whether there is a genetic adaptation in travel time to the distance that a population has to migrate.
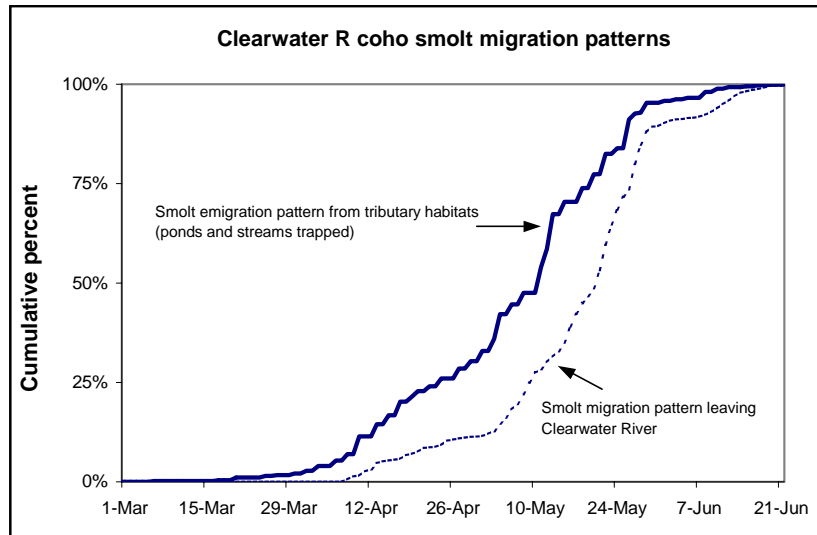
Figure 65. Emigration timing patterns of marked coho smolts released at all tributary trap sites combined and at a scoop trap near the Clearwater River mouth in 1987. Adapted from Lestelle and Curtwright (1988).
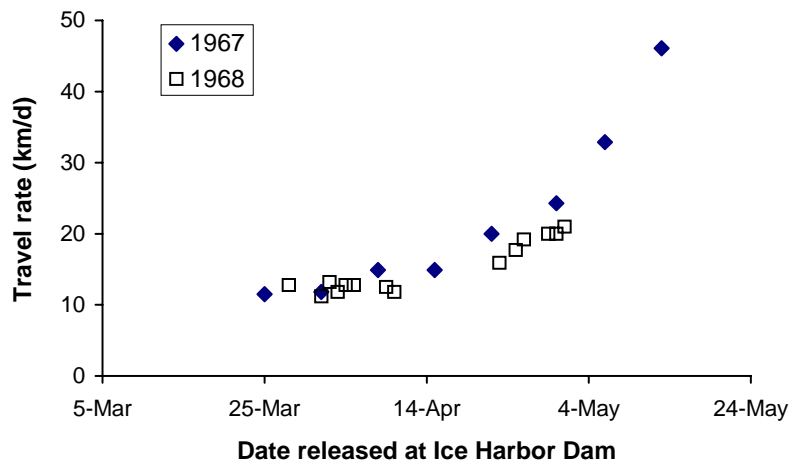
Figure 66. Travel rate of coho salmon smolts released at Ice Harbor Dam on the Snake river and captured at Jones Beach on the lower Columbia River (463 km downstream—288 miles). Data from Dawley et al. (1986); figure recreated from Quinn (2005).

Flow is another factor that can affect migration timing and migration rate (Fast et al. 1991; Berggren and Filardo 1993; Williams et al. 2005; Quinn 2005). The effect of flow on smolt migration patterns through the reservoir system of the Columbia is reasonably well established—river flow has been demonstrated to make the greatest contribution to explaining smolt travel time among various factors examined (Berggren and Filardo 1993). Williams et al. (2005) summarized available information relating flow level to smolt migration rates of yearling

Chinook under pre-dam and post-dam conditions on the Columbia and Snake rivers (Figure 67). Flow levels are shown as affecting travel time between Lewiston, Idaho and Bonneville Dam (317 miles) under both pre-impoundment and post-impoundment conditions. Travel time over this distance prior to dams during high flow conditions was estimated to be approximately half the time required during low flow conditions (based on Raymond 1979).

Factors that can affect the survival rates of migrant smolts in fresh water have been extensively studied in the Columbia and Snake rivers—and intensely debated. Much of the debate has focused on the relationship between mainstem flow and outmigrant survival. It is well known that predation can be high on juvenile salmonids as they outmigrate through impounded systems such as the Columbia River (Beamesderfer et al. 1996) and in systems with multiple water diversions with fish bypasses like the Yakima River (Fast et al. 1991). These rivers have large populations of northern pikeminnow (*Ptychocheilus oregonensis*) and exotic predatory fishes. It has often been assumed in these cases that the travel rate of smolts, affected by flow, determines predation rates by regulating the amount of time that juvenile migrants are exposed to the predators. More recent research, however, indicates that while migration rate is affected by flow, survival appears to be largely a function of migration distance and not travel rate (Muir et al. 2001; Smith et al. 2002; Williams et al. 2005). This is particularly the case for yearling and older smolts (as reported for yearling Chinook and yearling and older steelhead)(Anderson 2003a; Williams et al. 2005).

Anderson (2003b) explains that the effect of predatory fishes on yearling and older smolts acts essentially through a gauntlet effect: "observations on migrating prey (juvenile salmon) through a field of predators (pisivors) reveals that mortality depends mostly on distance traveled and only weakly on travel time…At the other extreme, if prey and predators move randomly within an enclosed habitat, mortality is time dependent." The latter case could be applied to the effect of predators on subyearling Chinook as they move slowly seaward through a large river like the Columbia River, consistent with conclusions of Anderson (2003a).

Within the mainstem Columbia River hydrosystem, another factor shown to be important to the survival of outmigrant yearling smolts is water temperature (Anderson 2003a; Conner et al. 2003; Smith et al. 2003). Anderson (2003a) suggests that for yearling spring Chinook smolts that temperature operates mainly by affecting the activity of predatory fishes. As water temperatures rise, feeding rates of predatory fishes typically increase (within temperature limits tolerable to the species).

Travel time to Bonneville Tailrace

Travel rate Bonneville Tailrace
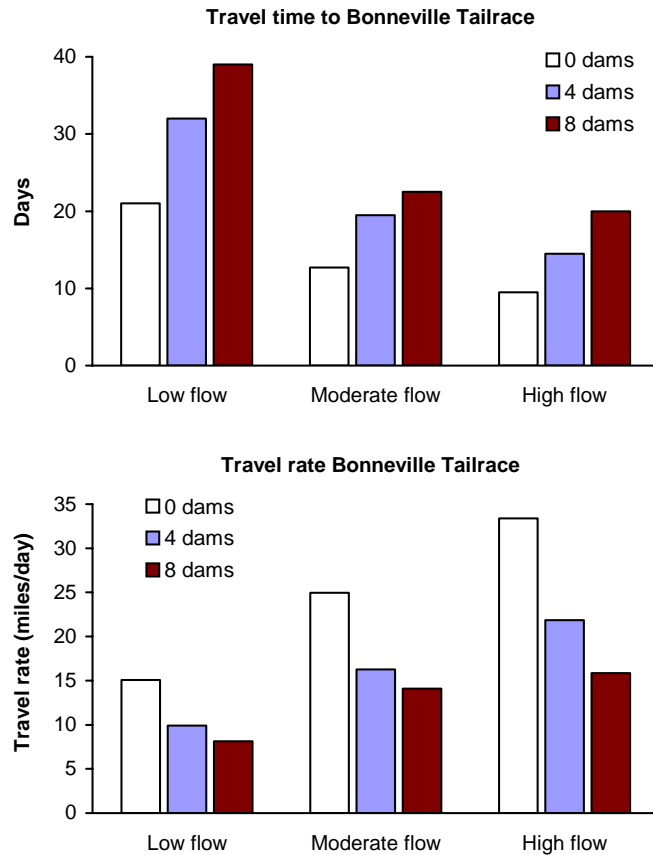
Figure 67. Estimated average travel times (top) and travel rates (bottom) for yearling Chinook smolts through the section of the lower Snake and Columbia rivers now inundated by mainstem dams (approximately from Lewiston, Idaho to Bonneville Dam). Estimates for the 0- and 4- dam scenarios are derived from Raymond (1979). Data for 8 dams were derived from PIT-tagged fish between 1997 and 2003. Top chart is from Williams et al. (2005). Bottom chart was adapted from the top chart.

The effect of migration distance on yearling smolt survival has also been demonstrated for free-flowing streams upstream of Lower Granite Dam on the Snake River. A strong inverse relationship exists between survival and migration distance for hatchery spring Chinook smolts released at various hatchery sites in the Snake River system (Figure 68)(Williams et al. 2005). The fish experienced only free-flowing river conditions from their points of release until they arrived at the top end of the Lower Granite Dam reservoir—they were assessed for survival just below the dam. Williams et al. (2005) also reported survival rates for PIT-tagged wild and hatchery yearling Chinook released at two sites upstream of Lower Granite Dam (Table 5). It is important to note that the free-flowing section of the Snake River below the tributaries where these releases were made, the lower ends of the tributaries, and the Lower Granite reservoir contain northern pikeminnow and other exotic predatory fish species. Anderson (2003b) concluded that water temperature during the period of migration did not help explain mortality within the free-flowing tributaries to the Snake River, suggesting that temperature has a stronger role in the prey-predator dynamics within the extensive reservoir system downstream. Anderson (2003b) determined that only migration distance affected smolt survival to Lower Granite Dam.

Table 5. Summary of average survivals for wild and hatchery yearling Chinook smolts released at two sites upstream of Lower Granite Dam (LGD) on the Snake River, 1993-2003. Fish released at the Salmon River trap experienced free-flowing river conditions until they arrived at the Lower Granite reservoir. Fish released at the Snake River trap at the head of the reservoir experienced impounded water conditions to the point of tag detection at the dam. Data from Williams et al. (2005).

Release site	Distance to LGD (km)	Survival to LGD	
		Hatchery	Wild
Salmon River (White Bird) trap	233	77.7%	86.2%
Snake River trap – head of LG reservoir	52	92.9%	93.5%

Less data exists on predation rates on free-flowing rivers in the Pacific Northwest where pikeminnow and exotic predators are not present. One example is for streams on Vancouver Island where mergansers are the primary predator on migrant smolts. Wood (1987) reported maximum estimates of mortality rate due to adult mergansers to be less than 2% for hatchery coho salmon during their seaward migration in the Big Qualicum River.

Lestelle and Curtwright (1988) evaluated survival of wild coho smolts during their migration downstream from traps within the Clearwater River system on the Olympic Peninsula. This river, like those reported on by Wood (1987), is used extensively by mergansers. Groups of wild coho smolts captured in tributary traps were uniquely branded to identify recaptured fish at a scoop trap located near the mouth of the river. A total of 18 mark groups in nine pairs were released to learn whether survival was affected by release time (day or night) or release site (distance traveled)(Table 6). No significant differences in recapture rates were found between release sites nor between day and night releases. The results suggested that little or no mortality occurred between release and recapture for all groups. The closest release site was 1.3 miles upstream of the scoop trap, while the most distant site was 22.6 miles upstream. It is noteworthy that this river, as the name implies, is a clear water river and generally has very low turbidity through much of the smolt migration. It is a rainfall-dominated stream and is moderately confined over much of its length. During the smolt migration, the river has virtually no flooded shorelines containing grasses and willows that might provide cover. It also has a relatively low wood load, unlike the Queets River, which it joins.

Taken together, the studies described above for free-flowing rivers suggest that smolt survival during their outmigration is typically very high. The data reported in Table 5 for the Snake River, combined with results in Table 6, are construed to mean that most or all of the mortality on fish released at the head of the Lower Granite Dam was due to the presence of pikeminnow and exotic fishes inhabiting the impoundment. This suggests that survival with distance is much higher in the absence of pikeminnow and for entirely free-flowing reaches than seen in Table 5.
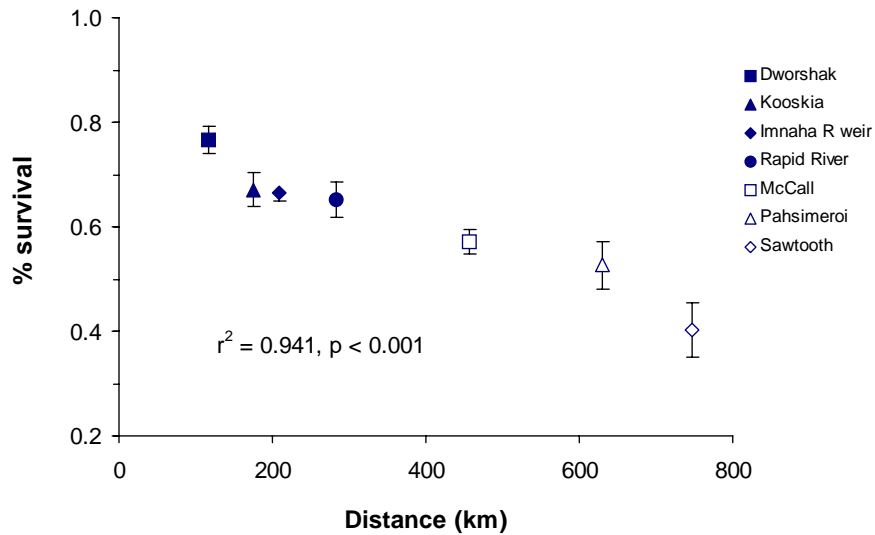
Figure 68. Estimated survivals (+/- SE) of yearling Chinook smolts from release at Snake River basin hatcheries to Lower Granite Dam tailrace, 1993-2003, versus distance (km) to Lower Granite Dam. Correlation between survival and migration distance is shown. From Williams et al. (2005).

The results of the marking experiments in the Clearwater River (Table 6) show another pattern worth noting. Smolts emigrating from an individual tributary on any given date exhibited wide ranges in the number of days that it took to arrive at the river mouth. For example, smolts trapped and released on May 14 at the mouth of Miller Creek, 11 miles above the downstream scoop trap, took between 1 to 28 days with a median of 13 days to travel that distance. For all groups combined, the range in days required to migrate to the scoop trap was 1 to 37 days. These results show that smolts tended not to travel rapidly between the tributary of origin and the point of departure from the mainstem river. These findings are consistent with patterns of wild coho smolt migrations seen elsewhere.

In Carnation Creek (Vancouver Island), McMahon and Holtby (1992) reported that coho smoltification and associated downstream emigration occurs progressively within a stream system, even small ones as Carnation Creek. Fish emigrating from tributaries moved progressively—as if in stages—downstream as smoltification developed. Smolts were typically aggregated in groups >5 fish, with aggregation size increasing significantly over the course of the smolt run. Smolts exhibited few agonistic interactions. The groups exhibited a high degree of cohesiveness. Typically, fish were quite secretive, milling about in dark, low velocity areas under cover with occasional forays to the edge of cover to feed on invertebrate drift. The most often used cover type was large woody debris associated with pools. Movement downstream in this short stream required several weeks once movement had been initiated. These findings indicate that smolt emigration by individual fish is not rapid once initiated, but occurs progressively with fish continuing to forage and use instream cover during periods of rest and short-term residency at stop-over sites. McMahon and Holtby stated that shelter from high velocities during spring freshets is likely important to prevent premature displacement.

Table 6. Summary results of mark-recapture experiments with wild coho smolts captured in outmigrant traps in tributaries to the Clearwater River in 1982. All groups were marked with unique brands. Fish were released within 24 hrs of their capture at the tributary traps to test for differences in recapture rates between day and night release. Recaptures were made at a scoop trap near the mouth of the river. Table is recreated from Lestelle and Curtwright (1988). No significant (*P*>0.05) differences in recapture rate were found between any release site.

Release site	mi from scoop trap	Pair no.	Date	Time	No. released	No. recaptured	Percent recaptured	First	Median	Last
								Days from release		
Hurst Cr.	1.3	1	14-May	day	211	52	24.6%	1	3	23
			15-May	night	101	14	13.9%	2	5	22
		2	25-May	day	213	56	26.3%	1	5	19
			26-May	night	205	58	28.3%	1	3	12
Miller Cr.	11.0	3	14-May	day	166	39	23.5%	1	13	28
			15-May	night	88	17	19.3%	2	13	28
		4	25-May	day	244	73	29.9%	1	7	23
			26-May	night	245	72	29.4%	1	8	23
Christmas Cr.	12.5	5	15-May	day	30	6	20.0%	3	7	18
			15-May	night	30	8	26.7%	4	10	24
Bull Cr.	18.5	6	15-May	day	37	15	40.5%	9	33	37
			15-May	night	37	5	13.5%	3	25	32
Snahapish R.	22.6	7	14-May	day	212	41	19.3%	4	17	25
			15-May	night	141	19	13.5%	4	15	27
		8	25-May	day	501	134	26.7%	5	14	24
			25-May	night	343	88	25.7%	5	14	23
		9	3-Jun	day	215	40	18.6%	5	7	11
			3-Jun	night	213	50	23.5%	5	8	16
		Total day releases			1,829	456	24.9%			
		Total night releases			1,403	331	23.6%			
		Grand total releases			3,232	787	24.4%			

Quinn (2005) described the downstream migration of coho smolts as not continuous but interspersed by periods of holding. Radio tracking of wild coho smolts in the Chehalis River (Western Washington) suggested that migrants spent about 40% of the time moving and 60% holding during their outmigration (Moser et al. 1991). Smolts rested in back eddies and even in off-channel habitats, consistent with observations of McMahon and Holtby (1992).

A multi-year study is being conducted in the Klamath River by the U.S. Fish and Wildlife Service to investigate coho smolt emigration patterns and associated survivals using radiotelemetry. First year results (Stutzer et al. 2006) have shown an outmigration pattern similar to those described above where wild smolts display periods of holding interspersed with downstream movement. While smolts were found to hold in a variety of habitat types, they appeared to prefer those with low water velocities. Unlike juvenile coho at younger life stages, however, fish were frequently found to be occupying velocity shear zones. Moreover, unlike the observations of McMahon and Holtby (1992) in Carnation Creek where fish were found in close association with shelter, smolts in the mainstem Klamath River were more removed from margin cover when holding. Holding smolts were generally still associated with shoreline habitats, 75% of habitat use was within 20 ft of the shoreline. The migration rate of smolts was also found to accelerate as fish moved further down the river.

McMahon and Holtby (1992) described the progressive downstream movement pattern of smolts as one of transitioning to a behavior adapted to open-water life (i.e., away from cover)—a pattern seen in the Klamath River observations. It is logical to expect that as smolts leave small streams (such as the size of Carnation Creek) and emigrate down large rivers, their association with instream cover would diminish.

4.0 Discussion and Conclusions

Two underlying questions have been considered throughout this report as they relate to how coho salmon utilize physical habitats within a watershed. How similar are coho life history patterns across the species' range? And what kinds and extent of variation occur with respect to these patterns, particularly as variation might relate to the SONCC Coho ESU and Klamath River coho?

These questions relate to Moyle's statements about coho salmon in his book "Inland Fishes of California":

> "…evolutionary forces keep coho salmon (and other salmon) surprisingly uniform in morphology and life history throughout their range, while producing runs that show strong, genetically based adaptations to local or regional environments. In California coho populations are the southernmost for the species, and they have adapted to the extreme conditions (for the species) of many coastal streams."

The extensive coverage of coho life histories in Sandercock (1991), augmented by the works of Moyle (2002) and Quinn (2005), provide much material that addresses the two questions of primary interest here. This report provides additional information, mostly as it pertains to how

physical habitat is used and associated survival rates. Variations in life history traits that relate to habitat use have been described here to the extent that information is available.

On its surface, Moyle's statement may seem contradictory. He concludes that coho salmon show a high degree of uniformity (or similarity) in life history patterns across their range, yet he asserts there is also significant variation and local adaptation. In context, Moyle is saying that coho salmon—like other salmonid species—exhibit significant variation in life histories, but the range of variation remains within what he sees as unifying life history themes for the species. The central themes of life history similarity are morphology, age structure, spatial distribution within a watershed, general timing patterns of migrations and other movements, development and growth patterns, foraging patterns, effects of environmental stressors, and habitat use patterns—among others. But significant variations exists within these unifying themes, enabling considerable adaptation to local conditions.

One unifying theme in the freshwater life history of juvenile coho is their affinity for slow velocity habitats in all life stages. Body morphology, fin sizes, and behavior are generally adapted to life in these habitats—notwithstanding variations that exist between stream-type and lake-type fish and coastal and interior forms (discussed further below). Their affinity for slow water is evident across the species' range—in both northern and southern regions and coastal and interior regions. Juveniles in all life stages—though to a lesser extent during the smolt stage—primarily rear and seek refuge in slow velocities associated with pools, channel margins, backwaters, and off-channel sites (alcoves, ponds, and groundwater channels). This tends to segregate them to some degree from juvenile Chinook and steelhead, though overlaps in space occur. Their affinity for low velocity water is strongest during the fry (very young fry) and overwintering life stages.

This association with low velocity habitats tends to result in several patterns of distribution within a watershed. Juvenile rearing—particularly in summer—occurs to a large extent within the natal streams. These streams usually tend to be relatively small and low in gradient, thus they often have a substantial amount of low velocity habitat. Emergent fry generally remain relatively close to their natal areas, though some dispersal downstream typically occurs. The maximum extent that dispersal occurs downstream is not known. Spawning which occurs in higher gradient streams appears to result in a greater downstream dispersal of fry. In that case, the young move—or are displaced by high velocity flows—to low velocity habitats in reaches of lower gradient.

Another related distribution pattern is the association that juvenile coho have for physical cover. Cover types within the water column or overhead are preferred (wood, rooted macrophytes, roots, overhead structure), as opposed to substrate cover provided by cobbles or turbulence cover associated with velocity shears. Preferred cover types provide shelter from high water velocities and predators, and match feeding behaviors keyed to aquatic drift and terrestrial organisms on the water surface (instead of benthos feeding). In smaller streams, cover is not a strong determinant of habitat selection in summer, though association with it grows by summer's end. Physical cover appears to be a much greater determinant of habitat selection in large rivers, probably due to the likelihood for higher water velocities and more predators.

The affinity for low velocity habitats is particularly strong during winter. This season often brings rapidly changing, adverse conditions within a stream—both in coastal and interior regions—whether due to flow fluctuations or extreme cold and icing. Survival appears to be strongly related to how successful juvenile coho are in locating suitable refuge from harsh conditions. One characteristic of coho seen throughout their range is for some individuals within the population to move during fall to sites that offer some degree of refuge. The number of fish that move, and the extent of their movement, appears to be related to the suitability of their locations to provide shelter from high velocities. Movement seems to be volitional, or when flows are high, due to displacement. In dynamic rivers, redistribution to overwintering sites can be quite dramatic in terms of distances traveled and numbers of fish that move. Off channel sites (alcoves, ponds, groundwater channels) are particularly desirable overwintering habitats throughout the Pacific Northwest and California. These provide the highest survival rates compared to other habitats. Low velocity locations within main stream channels having undercut banks with exposed root masses or sites of large wood accumulations also provide refuge habitat. Side channels with low velocities and some form of cover are also used. Juvenile coho rarely use cobble substrate for overwintering cover, as commonly occurs for juvenile steelhead.

Lestelle et al. (2005) considered how these patterns of distribution would be manifested in a large river system, one with a fairly extensive floodplain along the mainstem river. For the sake of illustration, they compared the expected distribution pattern of coho salmon to one that could be expected for ocean-type Chinook (i.e., fall Chinook). The patterns, shown in Figures 69 and 70, are based on a summary of habitat use patterns given in that paper. The patterns are those that would be expected in a largely unaltered watershed. They are consistent with the conclusions being presented here.

Another set of utilization patterns showing how species use a stream system has been derived using the Intrinsic Potential Method (Agrawal et al. 2005). The method assumes that three indicators of landform and hydrology—channel gradient, valley width (degree of confinement), and mean annual discharge—constrain channel morphology and hence the potential of a reach to express habitat characteristics favorable for specific salmonid species and life stages. The method was originally developed for coho and steelhead in watersheds draining the Coast Range of Oregon (Burnett 2001; Burnett et al. 2003). Burnett's (2001) study was conducted in the Elk River (Southern Oregon), which is encompassed by the SONCC Coho ESU. Figure 71 displays suitability of stream reaches to support coho, Chinook, and steelhead using this method. If these patterns were to be recast in the form of Figures 69 and 70, they would yield similar patterns as seen in those figures.

Coho Utilization Pattern
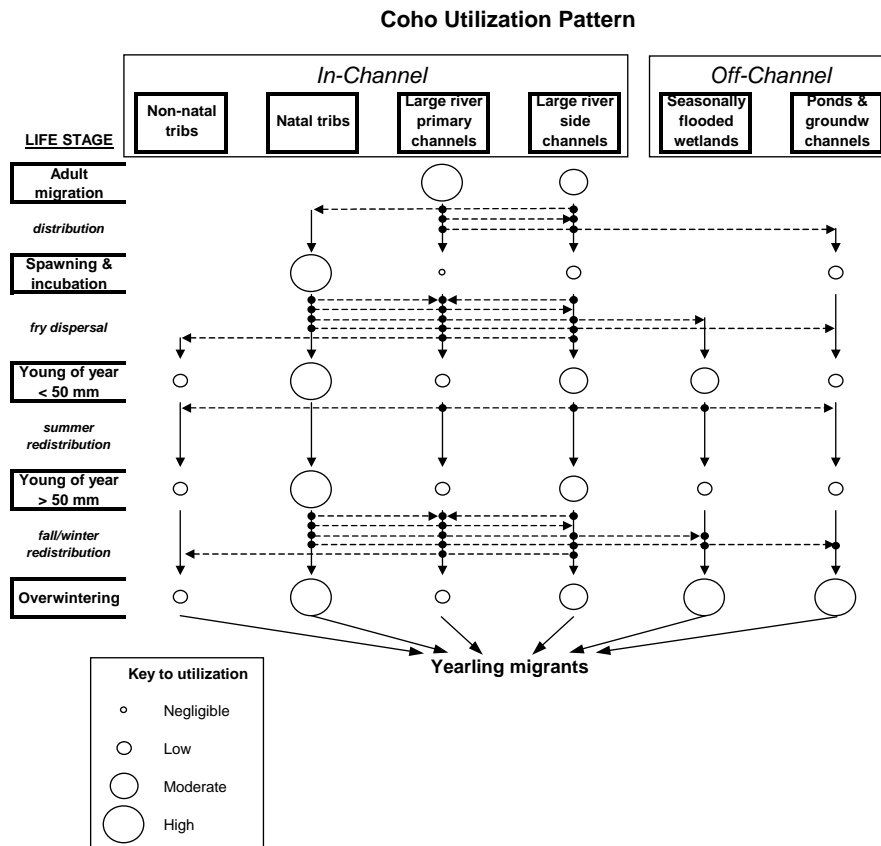
Figure 69. Summary of expected habitat utilization pattern for coho salmon in a generally unaltered large river system. A moderate to high spring runoff is assumed. It is assumed that the mainstem river is flowing across a wide floodplain. Circle size reflects relative amounts of production attributed to each area. Dashed lines show movements of fish from one area (dot) to another area (arrow). From Lestelle et al. (2005).

Variations on the central themes of coho life history exist and several types could affect habitat utilization patterns. Juvenile coho in the southern part of the range can exhibit a summer movement pattern different from what is seen further north. This movement pattern appears to be a redistribution to find thermal refugia. There is no evidence that fish in the southern region have a higher thermal tolerance than fish further north, though some greater tolerance may exist. Little or no movement by juveniles in mid summer is typically seen in more northern populations, but temperatures are less severe. Trapping in some streams in California and Oregon show that substantial numbers of fish can move in early to mid summer during periods of increasing temperature. While the fate of these fish has not been determined, some do successfully arrive at cooler water sites. It is unknown what level of mortality or loss in other performance measures might occur while moving to refugia or the distance that fish can travel. Nielsen (1992a, 1994) described a foraging phenotype (termed "early-emerging") in Northern California that appears to provide some measure of adaptation to high temperature. These fish display no obvious dominance hierarchy and have a crepuscular (i.e., associated with dawn or twilight) foraging pattern, where they move out from refuges to feed then return. Nielsen (1992a) concluded that this foraging phenotype is the dominant one during periods of drought, when streams are

particularly warm with limited flow. Perhaps this phenotype is suited for movement during early to mid summer to seek out refugia. Their larger size than other foraging phenotypes would be advantageous for such movement. Habitat utilization in warm water streams will reflect overlapping areas of tolerable temperatures and water velocities.
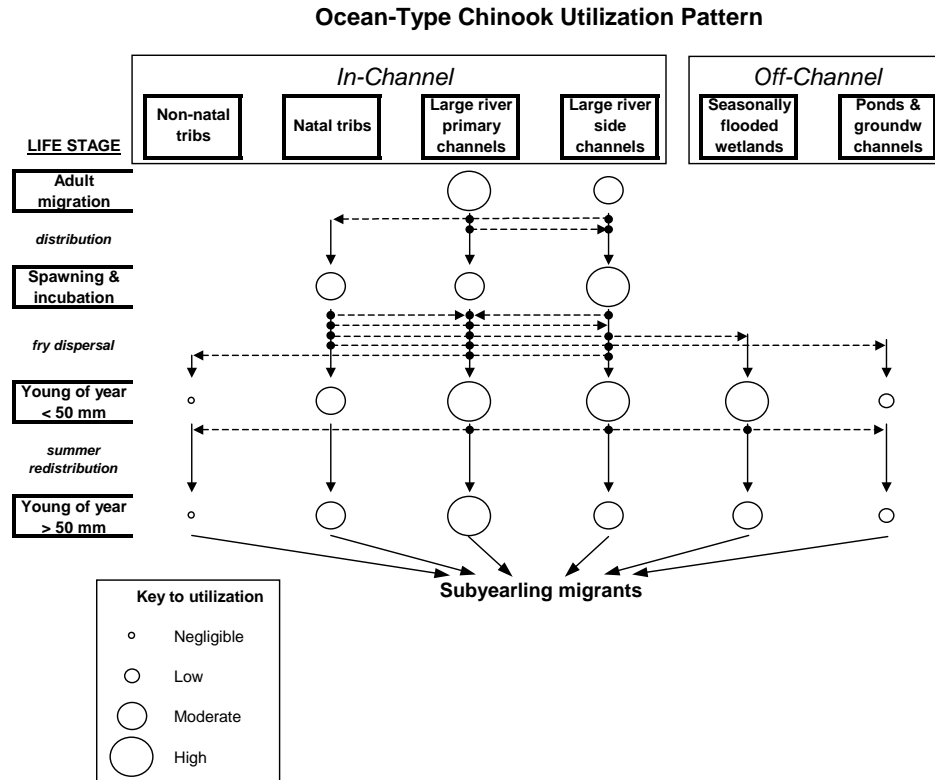
Figure 70. Summary of expected habitat utilization pattern for ocean type Chinook salmon in a generally unaltered large river system. A moderate to high spring runoff is assumed. It is assumed that the mainstem river is flowing across a wide floodplain. Circle size reflects relative amounts of production attributed to each area. Dashed lines show movements of fish from one area (dot) to another area (arrow). From Lestelle et al. (2005).

Another life history variation is seen in differences in body morphology and fin sizes between coastal and interior populations and associated swimming performances (see Taylor 1985a and b). It is not known how far south such a coastal-interior distinction might extend. Do both forms exist within the Klamath River basin? There is no evidence that these morphological forms have different habitat requirements, i.e., does the interior form, which has greater swimming stamina, have less of an affinity for slow water habitats than the coastal form? Or do cover type preferences differ between the forms? Evidence shows that both forms exhibit the same selection for slow water habitat types and cover types (e.g., Bratty 1999). Taylor and McPhail (1985a and b) suggest that the adaptive benefit of these variations to interior coho (more streamlined body, smaller fins, greater swimming stamina) is in their ability to negotiate long in-river migrations, both as smolts and adults. Richard Bailey's (Fisheries and Oceans Canada, *personal communications*) hypothesis that Thompson River juvenile coho travel from the upper Thompson River to the lower Fraser River to overwinter recognizes that these fish may be

adapted for a fall redistribution on such a scale. An interior-type body form would presumably aid upper Klamath River coho in their movements within the mainstem Klamath River, if this body form occurs there. This author, on seeing the nature of the mainstem Klamath River downstream of the Scott River, wondered whether juveniles could successfully negotiate the distance and turbulent water conditions to travel to the very lower parts of the river to overwinter. In light of what Thompson River fish would encounter during a fall redistribution of the scale mentioned, the Klamath scenario would be much more feasible. A multi-year study was initiated in fall 2006 to investigate the fall redistribution and overwintering patterns of juvenile coho in the lower Klamath River and the lower reaches of its small tributaries.[29]
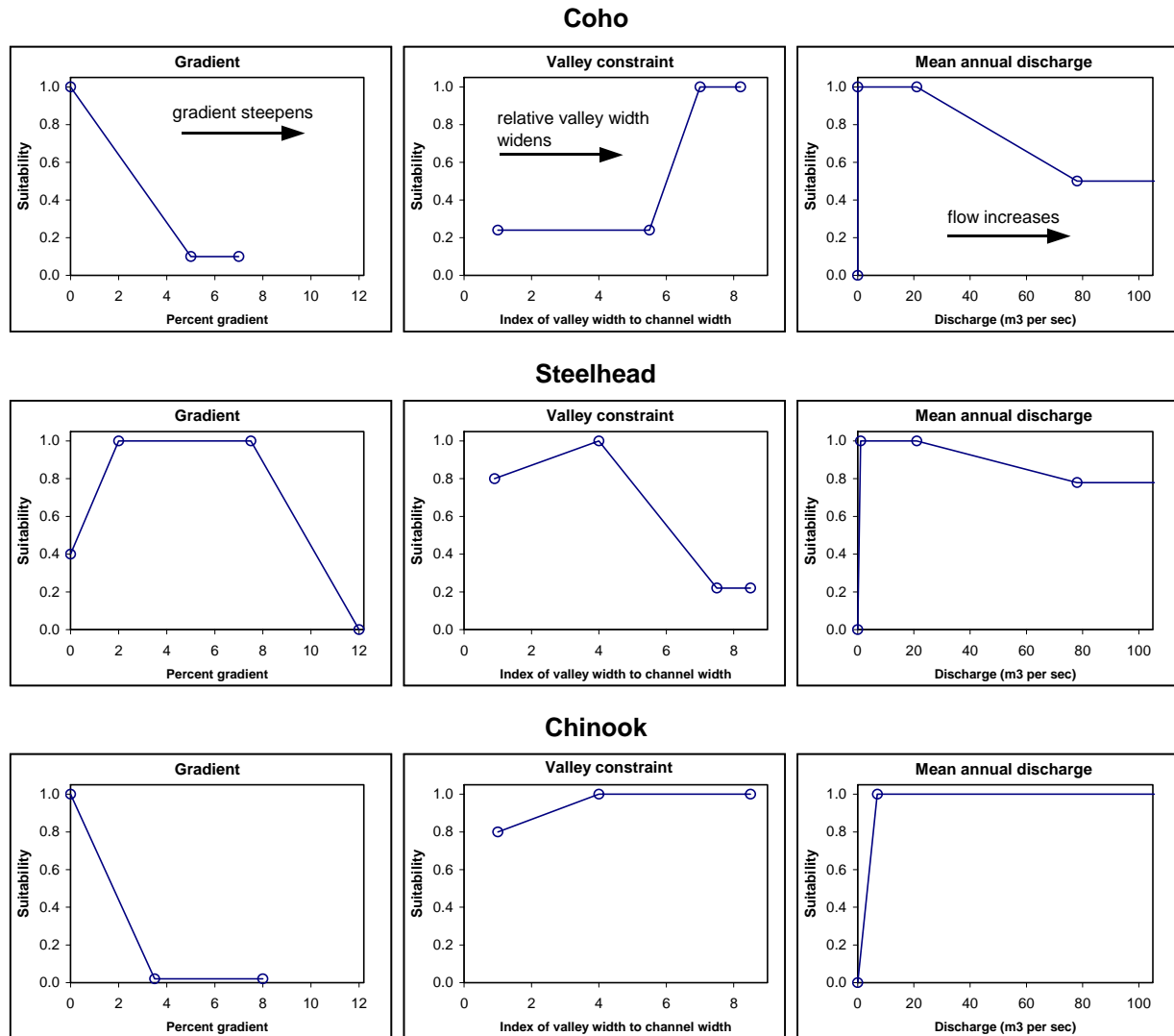
Figure 71. Suitability curves for each of the three components of the Intrinsic Potential Method (gradient, valley constraint, and discharge) for coho, steelhead, and Chinook juveniles. Recreated from Agrawal et al. (2005).

Perhaps the most obvious variation in life history patterns seen in southern coho populations is their ability to delay river entry timing during periods of drought or late arriving rainfall, particularly when sand bars are formed that block entry. In the extreme, river entry can apparently be stalled several months. This would thereby delay spawning and would presumably have cascading effects on emergence timing and subsequent growth and habitat use patterns. This may be a factor in variation of freshwater age structure seen in Prairie Creek (see Bell et al. 2001). Sand bars can often block entry to smaller streams in Northern California but on occasion also form on large rivers in that region such as the Klamath River. While these features may only rarely delay entry timing into rivers like the Klamath (Walt Duffy, Humboldt State University *personal communications*), it is noteworthy that delayed rainfall can affect the ability of adult coho to enter spawning tributaries in such large rivers. In such cases, delayed rainfall can force adults to spawn to a greater extent in the mainstem; spawning maturation would likely not be delayed.[30]

Coho salmon exhibit a wide variety of life history patterns in large, diverse watersheds. These patterns are phenotypic expressions of the interaction of genotype and environmental factors. Among others, these factors include flow characteristics, gradient, water temperature, and habitat structure. Diverse phenotypic expressions enable the species to utilize a wide variety of physical habitats across a range of gradients, habitat sizes, and qualities—but within limits set by the species' genetic blueprint. To understand the performance of a species in any watershed requires a life history perspective, seen across the full cycle (Lichatowich et al. 1995).

---

[30] / Once adult coho enter freshwater, maturation would probably develop on a normal schedule (see Hodgson and Quinn 2002).

Literature Cited

Abbe, T.B., and D.R. Montgomery. 1996. Large woody debris jams, channel hydraulics and habitat formation in large rivers. Regulated Rivers Research and Management 12:201-221.

Abrahams, M.V., and M.C. Healey. 1993. A comparison of the willingness of four species of Pacific salmon to risk to a predator. Oikos 66:439–446.

Agrawal, A., R.S. Schick, E.P. Bjorkstedt, R.G. Szerlong, M.N. Goslin, B.C. Spence, T.H. Williams, and K.M. Burnett. 2005. Predicting the potential for historical coho, Chinook and steelhead habitat in Northern California. NOAA Technical Memo NMFS-SWFSC-379.

Allee, B.J. 1974. Spatial requirements and behavioral interactions of juvenile coho salmon (*Oncorhynchus kisutch*) and steelhead trout (*Salmo gairdneri*). Ph.D. Thesis, University of Washington, Seattle, WA.

Allen, K.R. 1969. Limitations on production in salmonid populations in streams. Pages 3-18 *in* T.G. Northcote (ed.) Symposium on Salmon and Trout in Streams. University of British Columbia, Vancouver, BC.

Anderson, J.J. 2003a. Toward a resolution of the flow/survival debate and the impacts of flow augmentation and water withdrawal in the Columbia/Snake River system. White Paper, Columbia Basin Research, School of Aquatic and Fishery Science, University of Washington, Seattle, WA.

Anderson, J.J. 2003b. An analysis of smolt survival with implications to flow management. White Paper, Columbia Basin Research, School of Aquatic and Fishery Science, University of Washington, Seattle, WA.

Au, D. W. K. 1972. Population dynamics of the coho salmon and its response to logging in three coastal streams. Ph.D. Thesis, Oregon State University, Corvallis, OR.

Baranski, C. 1989. Coho smolt production in ten Puget Sound streams. Technical Report No. 99, Washington Department of Fisheries, Olympia, WA.

Beamer, E.M., A. McBride, R. Henderson. 2004. Lone Tree Pocket Estuary Restoration 2004 Fish sampling and pre-restoration project monitoring report. Unpublished report of the Skagit River System Cooperative, LaConner, WA.

Beamesderfer, R.C.P., D.L. Ward, and A.A. Nigro. 1996. Evaluation of the biological basis for a predator control program on northern squawfish (*Ptychocheilus oregonensis*) in the Columbia and Snake rivers. Canadian Journal of Fisheries and Aquatic Sciences 53:2898-2908.

Beamish, R., D. Noakes, G. MacFarlance, W. D. Pinnix, R. Sweeting, J. King, and M. Folkes. 2000. Trends in coho marine survival in relation to the regime concept. Fisheries Oceanography 9(1):114-119.

Beamish, R.J., R.M. Sweeting and C.M. Neville. 2004. Improvement of juvenile Pacific salmon production in a regional ecosystem after the 1998 climatic regime shift. Transactions of the American Fisheries Society 133:1163–1175.

Beecher, H.A., B.A. Caldwell, and S.B. DeMond. 2002. Evaluation of depth and velocity preferences of juvenile coho salmon in Washington streams. North American Journal of Fisheries Management 22 (3):785-795.

Beechie, T.J., M. Liermann, E.M. Beamer, R. Henderson. 2005. A classification of habitat types in a large river and their use by juvenile salmonids. Transactions of the American Fisheries Society, 134:717-729.

Behnke, R.J. 2002. Trout and Salmon of North America. Free Press, Simon and Shuster, Inc. New York, NY.

Belchik, M. 1997. Summer locations and salmonid use of cool water areas in the Klamath River: Iron Gate Dam to Seiad Creek, 1996. Unpublished report, Yurok Tribal Fisheries Program. Klamath, CA.

Bell, E. 2001. Survival, growth and movement of juvenile coho salmon (*Oncorhynchus kisutch*) over-wintering in alcoves, backwaters, and main channel pools in Prairie Creek, California. Master's Thesis. Humboldt State University, Arcata, CA.

Bell, E., W.G. Duffy, and T.D. Roelofs. 2001. Fidelity and survival of juvenile coho salmon in response to a flood. Transactions of the American Fisheries Society 130:450-458.

Berggren, T.J., and M. Filardo. 1993. An analysis of variables influencing the migration of juvenile salmonids in the Columbia River basin. North American Journal of Fisheries Management 13:48-63.

Bilby, R.E., and P.A. Bisson. 1998. Function and distribution of large woody debris. Pages 324-346 *in* R.J. Naiman and R.E. Bilby (eds.) River Ecology and Management: Lessons from the Pacific Coastal Ecoregion. Springer, New York, NY.

Bilby, R.E., and L.J. Wasserman. 1989. Forest practices and riparian management in Washington State: data based regulation development. Pages 87-94 *in* R.E. Gresswell, B.A. Barton, and J.L. Kershner (eds.) Practical approaches to riparian resource management: an educational workshop. USDI Bureau of Land Management, Billings, MT.

Bisson, P.A., J.L. Nielsen, R.A. Palmason, and L.E. Grove. 1982. A system of naming habitat types in small streams, with examples of habitat utilization by salmonids during low streamflow. *In* N.B. Armantrout (ed.) Acquisition and Utilization of Aquatic Habitat Inventory Information: Proceedings of the Symposium. Portland, OR.

Bisson, P. A., J. L. Nielsen, and J. W. Ward. 1988. Summer production of coho salmon stocked in Mount St. Helens streams 3-6 years after the 1980 eruption. Transactions of the American Fisheries Society 117: 322-335.

Bjornn, T.C., and D.W. Reiser.1991. Habitat requirements of salmonids in streams. Pages 83-138 *in* W. R. Meehan (ed.) Influences of forest and rangeland management on salmonid fishes and their habitats. American Fisheries Society Special Publication No. 19, Bethesda, Maryland.

Bocking, R.C., and D. Peacock. 2004. Habitat based production goals for coho salmon in Fisheries and Oceans Statistical Area 3. Fisheries and Oceans Canada. Canadian Science Advisory Secretariat Research Document 2004/129.

Bradford, M.J., G.C. Taylor, and J.A. Allan. 1997. Empirical review of coho salmon smolt abundance and the prediction of smolt production at the regional level. Transactions of the American Fisheries Society 126:49-64.

Brakensiek, K.E. 2002. Abundance and survival rates of juvenile coho salmon (*Oncorhynchus kisutch*) in Prairie Creek, Redwood National Park. Master's thesis. Humboldt State University, Arcata, CA.

Bramblett, R.G., M.D. Bryant, B.E. Wright, and R.G. White. 2002. Seasonal use of small tributary and main-stem habitats by juvenile steelhead, coho salmon, and Dolly Varden in a Southeastern Alaska drainage basin. Transactions of the American Fisheries Society 131:498-506.

Bratty, J.M. 1999. The winter ecology of juvenile coho salmon (*Oncorhynchus kisutch*) in interior British Columbia streams. Master's Thesis, University of British Columbia, Vancouver, B.C.

Brett, J.R. 1952. Temperature tolerance in young Pacific salmon, genus *Oncorhynchus*. Journal of the Fisheries Research Board of Canada 9:265-323.

Brett, J.R., W.C. Clarke, and J.E. Shelbourn. 1982. Experiments on thermal requirements for growth and food conversion efficiency of juvenile chinook salmon, *Oncorhynchus tshawytscha*. Canadian Technical Report Fisheries and Aquatic Sciences 1127.

Briggs, J.C. 1953. The behavior and reproduction of salmonid fishes in a small coastal stream. California Department of Fish and Game, Marine Fisheries Branch, Fish Bulletin No. 94.

Brown, T.G. 2002. Floodplains, flooding, and salmon rearing habitats in British Columbia: A review. Canadian Science Advisory Secretariat Research Document 2002/007.

Brown, L.R., and P.B. Moyle. 1991. Status of coho salmon in California. Report to the National Marine Fisheries Service. Department of Wildlife and Fisheries Biology, University of California, Davis, CA.

Brown, L.R., P.B. Moyle, and R.M. Yoshiyama. 1994. Historical decline and current status of coho salmon in California. North American Journal of Fisheries Management 14:237-261.

Buffington, J.M., R.D. Woodsmith, D.B. Booth and D.R. Montgomery. 2003. Fluvial processes in Puget Sound Rivers and the Pacific Northwest. Pages 46-78 *In* D.R. Montgomery, S. Bolton, D.B. Booth and L. Wall (eds.) Restoration of Puget Sound Rivers. University of Washington Press, Seattle, WA.

Bugert, R.M., T.C. Bjornn, and W.R. Meehan. 1991. Summer habitat use by young salmonids and their responses to cover and predators in a small southeast Alaska stream. Transactions of the American Fisheries Society 120:474-485.

Burnett, K.M. 2001. Relationships among juvenile anadromous salmonids, their freshwater habitat, and landscape characteristics over multiple years and spatial scales in the Elk River, Oregon. Ph.D. Thesis, Oregon State University, Corvallis, OR.

Burnett, K. M., G. H. Reeves, D. Miller, S. E. Clarke, K. C. Christiansen, and K. Vance-Borland. 2003. A first step toward broad scale identification of freshwater protected areas for Pacific salmon and trout. Pages 144-154 *in* J. Beumer, A. Grant, and D.C. Smith (eds.) Aquatic Protected Areas: what works best and how do we know? Proceedings of the World Congress on Aquatic Protected Areas, Cairns, Australia, August 14-18, 2002. Australian Society for Fish Biology, University of Queensland, Australia.

Bustard, D.R., and D.W. Narver.1975. Aspects of the winter ecology of juvenile coho salmon (*Oncorhynchus kisutch*) and steelhead trout (*Salmo gairdneri*). Journal of the Fisheries Research Board of Canada 32:667-680.

California Department of Fish and Game (CDFG). 2002. Status review of California coho salmon north of San Francisco: Report to the California Fish and Game Commission. California Department of Fish and Game, Sacramento, CA.

California Department of Fish and Game (CDFG). 2004. September 2002 Klamath River fish kill: final analysis of contributing factors and impacts. California Department of Fish and Game, Northern California-North Coast Region.

Cederholm, C.J., and W.J.. Scarlett. 1982. Seasonal immigrations of juvenile salmonids into four small tributaries of the Clearwater River, Washington, 1977-1981. Pages 98-110 *in* E.L. Brannon and W.O. Salo (eds.). Proceedings of the Salmon and Trout Migratory Behavior Symposium. School of Fisheries, University of Washington, Seattle, WA.

Cederholm, C.J., L.G. Dominguez, and T.W. Bumstead. 1997a. Rehabilitating stream channels and fish habitat using large woody debris. In Watershed Restoration Technical Circular No. 9. Ministry of Environment, Lands and Parks and Ministry of Forests. Chapter 8.

Cederholm, C.J., R.E. Bilby, P.A. Bisson, T.W. Bumstead, B.R. Fransen, W.J. Scarlett, and J.W. Ward. 1997b. Response of juvenile coho salmon and steelhead to placement of large woody

debris in a coastal washing stream. North American Journal of Fisheries Management 17:947-963.

Chapman, D.W. 1962. Aggressive behavior in juvenile coho salmon as a cause of emigration. Journal of the Fisheries Research Board of Canada 19:1047-1080.

Chapman, D.W., and T.C. Bjornn. 1969. Distribution of salmonids in streams with special reference to food and feeding. Pages 153-176 *in* T. G. Northcoate (ed.) Symposium on Salmon and Trout in Streams. H.R. MacMillan Lectures in Fisheries, University of British Columbia, Vancouver, BC.

Chesney, W.R., and E.M. Yokel. 2003. Annual report: Shasta and Scott River juvenile salmonid outmigrant study, 2001-2002. Project 2a1. California Department of Fish and Game, Northern California - North Coast Region, Steelhead Research and Monitoring Program. Arcata, CA.

Coe, T.A. 2001. Contrasting discharge patterns, juvenile salmonid use, and fish community structure in off-channel floodplain habitats, Queets River, Washington, during summer low-flow. Master's Thesis, University of Washington, Seattle, WA.

Collins, B.D., D.R. Montgomery, and A.J. Sheikh. 2003. Reconstructing the historical riverine landscape of the Puget lowland. Pages 79-128 *in* D.R. Montgomery, S. Bolton, D. B. Booth, and L. Wall (eds.) Restoration of Puget Sound Rivers. University of Washington Press, Seattle, WA.

Coronado, C., and R. Hilborn. 1998. Spatial and temporal factors affecting survival in coho salmon (*Oncorhynchus kisutch*) in the Pacific Northwest. Canadian Journal of Fisheries and Aquatic Sciences 55:2067-2077.

Cramer, S.P., T.D. Satterwaite, R.B. Boyce, and B.P. McPherson. 1985. Lost Creek Dam fisheries evaluation, impacts of Lost Creek Dam on the biology of anadromous salmonids in the Rogue River. Oregon Department of Fish and Wildlife, Fish Research Project DACW57-77-C-0027, Phase I Completion Report, Volume 1. Portland, OR.

Cramer, S.P., and J.T. Martin. 1978. Rogue basin evaluation program, juvenile salmonid studies. Oregon Department of Fish and Wildlife, Fish Research Project DACW57-77-C-0027, Annual Progress Report, Portland, OR.

Cramer, S.P., and J.T. Martin. 1979. Rogue basin evaluation program, juvenile salmonid studies. Oregon Department of Fish and Wildlife, Fish Research Project DACW57-77-C-0027, Annual Progress Report, Portland, OR.

Crone, R.A., and C.E. Bond. 1976. Life history of coho salmon *Oncorhynchus kisutch*, in Sashin Creek, southeastern Alaska. Fisheries Bulletin 74:897-923.

Deas, M.L., and S.K. Tanaka. 2006. Klamath River thermal refugia study: flow and temperature characterization – final project temperature report. Watercourse Engineering, Inc., prepared for

U.S. Bureau of Reclamation in cooperation with the U.S. Bureau of Reclamation, Karuk Tribe, and Yurok Tribe. Klamath Falls, OR.

DeVries, P. 1997. Riverine salmonid egg burial depths: review of published data and implications for scour studies. Canadian Journal of Fisheries and Aquatic Sciences 54:1685-1698.

Dill, L.M., and H.G. Fraser. 1984. Risk of predation and the feeding behavior of juvenile coho salmon (*Oncorhynchus kisutch*). Behavioral Ecological Sociobiology 16:65-71.

Dolloff, C.A., and G.H. Reeves. 1990. Microhabitat partitioning among stream-dwelling juvenile coho salmon, *Oncorhynchus kisutch*, and Dolly Varden, *Salvelinus malma*. Canadian Journal of Fisheries and Aquatic Sciences 47: 2297-2306.

Dykaar, B.D. 2000. A hydrogeomophic index for river-floodplain habitat assessment in the Willamette Basin. Prepared for Oregon Department of Fish and Wildlife by EcoHydrology, Inc, Santa Cruz, CA; January 2000 Contract Report, 139 pages.

Eaton, J.G., J.H. McCormick, B.E. Goodno, D.G. O'Brien, H.G. Stefany, M. Hondzo, and R.M. Scheller. 1995. A field information-based system for estimating fish temperature tolerances. Fisheries 20:10–18.

Ebersole, J.L., W.J. Liss, and C.A. Frissell. 2001. Relationship between stream temperature, thermal refugia, and rainbow trout *Oncorhynchus mykiss* abundance in arid-land streams of the northwestern United States. Ecology of Freshwater Fish 10:1–10.

Ebersole, J.L., W.J. Liss, and C.A. Frissell. 2003a. Cold water patches in warm streams: physiochemical characteristics and the influence of shading. Journal of the American Water Resources Association 39:355–368.

Ebersole, J.L., W.J. Liss, and C.A. Frissell, 2003b. Thermal heterogeneity, stream channel morphology and salmonid abundance in northeast Oregon streams. Canadian Journal of Fisheries and Aquatic Sciences 60:1266-1280.

Edie, B.G. 1975. A census of juvenile salmonids of the Clearwater River basin, Jefferson County, Washington, in relation to logging. Master's Thesis. University of Washington, Seattle, WA.

Fast, D., J. Hubble, M. Kohn, and B. Watson. 1991. Yakima River spring chinook enhancement study. Yakima Indian Nation Fisheries Resource Management, Final Report to the Bonneville Power Administration, Portland, OR.

Fausch, K.D. 1993. Experimental analysis of microhabitat selection by juvenile steelhead (Oncorhynchus mykiss) and coho salmon (*O. kisutch*) in a British Columbia stream. Canadian Journal of Fisheries and Aquatic Sciences 50:1198-1207.

Fausch, K.D., Y. Taniguchi, S. Nakano, G.D. Grossman, and C.R. Townsend. 2001. Flood disturbance regimes influence rainbow trout invasion success among five Holarctic regions. Ecological Applications 11:1438-1455.

Fedorenko, A.Y., and R.J. Cook. 1982. Trapping and coded wire tagging of wild coho juveniles in the Vedder-Chilliwack River, 1976 to 1979. Canadian Manuscript Report of Fisheries and Aquatic Sciences 1678.

Fransen, B.R., P.A. Bisson, J.W. Ward, and R.E. Bilby. 1993. Physical and biological constraints on summer rearing of juvenile coho salmon (*Oncorhynchus kisutch*) in small Western Washington streams. Pages 271-288 *in* L. Berg and P.W. Delaney (eds.) Proceedings of the coho workshop. British Columbia Department of Fisheries and Oceans, Vancouver, BC.

Frissell, C.A., W.J. Liss, C.E. Warren and M.D. Hurley. 1986. A hierarchical framework for stream habitat classification: viewing streams in a watershed context. Environmental Management 10:199-214.

Frissell, C.A. 1992. Cumulative effects of land use on salmonid habitat on southwest Oregon streams. Ph.D. Thesis, Oregon State University, Corvalis, OR.

Garrett, J.W., D.H. Bennett, F.O. Frost, and R.F. Thurow. 1998. Enhanced incubation success for Kokanee spawning in groundwater upwelling sites in a small Idaho stream. North American Journal of Fisheries Management 18:925–930.

Giannico, G.R. and Healey, M.C. 1999. Ideal free distribution as a tool to examine juvenile coho salmon habitat choice under different conditions of food abundance and cover. Canadian Journal of Fisheries and Aquatic Sciences. 56:2362-2373.

Giannico, G.R., and S.G. Hinch. 2003. The effect of wood and temperature on juvenile coho salmon winter movement, growth, density and survival in side-channels. River Research and Applications 19: 219-231.

Glova, G.J. 1986. Interaction for food and space between experimental populations of juvenile coho salmon (*Oncorhynchus kisutch*) and coastal cutthroat trout (*Salmo clarki*) in a laboratory stream. Hydrobiologia 132:155-168.

Gordon, N.D., McMahon T.A., Finlayson B.L., Gippel C.J. and Nathan R.J. 2004. Stream Hydrology – An Introduction for Ecologists. 2nd edition. John Wiley and Sons, West Sussex, UK.

Grette, G.B. 1985. The abundance and role of large organic debris in juvenile salmonid rearing habitat in small streams. Master's Thesis. University of Washington, Seattle, WA.

Groot, C., and Margolis, L. (Eds.). 1991. Pacific Salmon Life Histories. University of British Columbia Press, Vancouver, B.C.

Hamilton, J.B., G.L. Curtis, S.M. Snedaker, and D.K. White. 2005. Distribution of anadromous fishes in the Upper Klamath river watershed prior to hydropower dams - a synthesis of the historical evidence. Fisheries 30(4):10-20.

Hampton, M.. 1988. Development of habitat preference criteria for anadromous salmonids of the Trinity River. U.S. Dept. Int., Fish Wildlife Serv., Div. Ecol. Serv., Sacramento, California.

Hardy, T.B., and R.C. Addley. 2001. Evaluation of interim instream flow needs in the Klamath River, Phase II Final Report. Institute for Natural Systems Engineering. Utah Water Research Laboratory. Utah State University, Logan, UT.

Hartman, G.F. 1965. The role of behavior in the ecology and interaction of underyearling coho salmon (*Oncorhynchus kisutch*) and steelhead trout (*Salmo gairdneri*). Journal of the Fisheries Research Board of Canada 22:1035-1081.

Hartman, G.F., B.C. Anderson, and J.C. Scrivener. 1982. Seaward movement of coho salmon (*Oncorhynchus kisutch*) fry in Carnation Creek, an unstable coastal stream in British Columbia. Canadian Journal of Fisheries and Aquatic Sciences 39:588–597.

Hartman, G.F. and L.B. Holtby. 1982. An overview of some biophysical determinants of fish production and fish population responses to logging in Carnation Creek, British Columbia. Pages 348-374 *in* Hartman (ed.) Proceedings Carnation Creek Workshop: A 10-year review. Pacific Biological Station, Nanaimo, B.C.

Hartman, G.F., and J.C. Scrivener. 1990. Impacts of forestry practices on a coastal stream ecosystem, Carnation Creek, British Columbia. Canadian Bulletin of Fisheries and Aquatic Sciences No. 223.

Hartman, G.F., D.B. Tripp, and T.G. Brown. 1998. Overwintering habitats and survival of juvenile salmonids in coastal streams of British Columbia. Pages 141-154 *in* Hogan, D.L., P.J. Tschaplinski, and S. Chatwin (eds) Carnation Creek and Queen Charlotte Islands Fish/Forestry Workshop: Applying 20 Years of Coastal Research to Management Solutions. B.C. Ministry of Forests, Research Program, Land Management Handbook No. 41, Victoria, B.C.

Hassler, T.J. 1987. Species profiles: life histories and environmental requirements of coastal fishes and invertebrates (Pacific Southwest) -- coho salmon. U.S. Fish Wildl. Serv. Biol. Rep. 82 (11.70). U.S. Army Corps of Engineers, TR EL-82-4.

Hawkins, C.P., and 10 coauthors. 1993. A hierarchical approach to classifying stream habitat features. Fisheries 18(6): 3-12.

Healey, M.C. 1991. Life history of chinook salmon (*Oncorhynchus tshawytscha*). Pages 311-349 *in* C. Groot and L. Margolis (eds.) Pacific Salmon Life Histories. University of British Columbia Press, Vancouver, B.C.

Henning, J. 2004. An evaluation of fish and amphibian use of restored and natural floodplain wetlands. Final Report EPA Grant CD-97024901-1. Washington Department of Fish and Wildlife, Olympia, WA.

Hillemeier, D. 1999. An assessment of pinniped predation upon fall-run chinook salmon in the Lower Klamath River, CA, 1997. Unpublished report of the Yurok Tribal Fisheries Program. Klamath, CA.

Hoar, W.S. 1976. Smolt transformation: evolution, behavior, and physiology. Journal of the Fisheries Research Board of Canada 33:1233-1252.

Hodgson, S., and Quinn, T.P. 2002. The timing of adult sockeye salmon migration into fresh water: adaptations by populations to prevailing thermal regimes. Canadian Journal of Zoology 80:542–555.

Holtby, L.B. 1988. Effects of logging on stream temperatures in Carnation Creek, British Columbia, and associated impacts on the coho salmon (*Oncorhynchus kisutch*). Canadian Journal of Fisheries and Aquatic Sciences 45:502-515.

Holtby, B., K. Simpson, and S. Baillie. 1993. How important are lakes to coho production? Page 289 *in* L. Berg and P.W. Delaney (eds.) Proceedings of the coho workshop. British Columbia Department of Fisheries and Oceans, Vancouver, BC.

Holtby, L.B., G.F. Hartman, and J.C. Srivener. 1984. Stream indexing from the perspective of the Carnation Creek experience. Pages 87-111 *in* P.E.K. Symons and M. Waldichuck (eds.) Proceedings of the Workshop on Stream Indexing for Salmon Escapement Estimation, West Vancouver, British Columbia, 2-3 February, 1984. Canadian Technical Report Fisheries and Aquatic Sciences 1326.

Hyatt, T.L., and R.J. Naiman. 2001. The residence time of large woody debris in the Queets River, Washington, USA. Ecological Applications 11:191-202.

Intensively Monitored Watersheds Scientific Oversight Committee (IMWSOC). 2006. Study plan for the Intensively Monitored Watershed Program. Submitted to the Salmon Recovery Funding Board by member agencies and companies belonging to the IMWSOC, Olympia, WA.

Irvine, J.R. 2002. COSEWIC status report on the coho salmon *Oncorhynchus kisutch* (Interior Fraser population) in Canada. Committee on the Status of Endangered Wildlife in Canada. Ottawa.

Irvine, J.R., and B.R. Ward. 1989. Patterns of timing and size of wild coho smolts (*Oncorhynchus kisutch*) migrating from the Keogh River watershed on northern Vancouver Island. Canadian Journal of Fisheries and Aquatic Sciences 46:1086-1094.

Jepsen, D.B. 2006. Abundance monitoring of juvenile salmonids in Oregon coastal streams, 2004. Monitoring Program Report Number OPSW-ODFW-2006-1, Oregon Department of Fish and Wildlife, Salem, OR.

Jepsen, D.B., and J.D. Rodgers. 2004. Abundance monitoring of juvenile salmonids in Oregon coastal streams, 2002-2003. Monitoring Program Report Number OPSW-ODFW-2003-1, Oregon Department of Fish and Wildlife, Portland, OR.

Kahler, T.H., P. Roni, T.P. Quinn. 2001. Summer movement and growth of juvenile anadromous salmonids in small western Washington streams. Canadian Journal of Fisheries and Aquatic Sciences 58:1947–1956.

Keenleyside, M.H., and F.T. Yamamoto. 1962. Territorial behaviour of juvenile Atlantic salmon (*Salmo salar* L.). Behaviour 19:139-168.

Knight, N.J. 1980. Factors affecting the smolt yield of coho salmon (*Oncorhynchus kisutch*) in three Oregon streams. Master's Thesis, Oregon State University, Corvallis, OR.

Knighton, D. 1998. Fluvial Form and Processes. Wiley and Sons, New York, NY.

Koski, K.V. 1966. The survival of coho salmon (*Oncorhynchus kisutch*) from egg deposition to emergence in three Oregon coastal streams. Master's Thesis, Oregon State University, Corvallis, OR.

Koski, K V. 1992. Restoring stream habitats affected by logging activities. Pages 344-397 *in* G. Thayer (ed.) Restoring the Nation's Coastal Environment, University of Maryland Sea Grant Proceedings, Symposium on Habitat Restoration. NOAA, Washington, DC.

Kruzic, L.M. 1998. Ecology of juvenile coho salmon within the upper south Umpqua Basin, Oregon. Master's Thesis. University of Idaho, Moscow, ID.

Landers, D., A. Fernald, and C. Andrus. 2002. Off channel habitats. *In* D. Hulse, S. Gregory, and J.Baker (eds) Willamette River Basin Atlas: Trajectories of Environmental and Ecological Change. The Pacific Northwest Ecosytem Research Consortium, Oregon State University Press, Corvallis, OR.

Lau, M.R. 1984. Habitat utilization, density, and growth of steelhead trout, coho salmon, and Pacific Giant Salamander in relation to habitat types in a small coastal redwood stream. Master's Thesis. University of California Davis, Davis, CA.

Laufel, J.C., G.B. Pauley, and M.F. Shepard. 1986. Species profiles: life histories and environmetal requirements of coastal fishes and inverterbrates (Pacific Northwest) - coho salmon. USFWS Biological Report 82 (11.48). US Army Corps of Engineers, TR EL-82-4.

Leidy, R.A. 1984. Distribution and ecology of stream fishes in the San Francisco Bay drainage. Hilgardia 52:1-175.

Lestelle, L.C., and S. Curtwright. 1988. Queets River coho indicator stock study: 1987 smolt tagging and yield studies. Quinault Department of Natural Resources Annual Report for FY 1987 - Contract No. 30000-632 to the Northwest Indian Fisheries Commission, Taholah, WA.

Lestelle, L.C., B. Watson, and G. Blair. 2006. Species-habitat rules: supporting documentation for updated flow rules for application to EDT – Supplemental report to information structure of Ecosystem Diagnosis and Treatment (EDT) and habitat rating rules for Chinook salmon, coho salmon, and steelhead trout. Report to U.S. Bureau of Reclamation, Mobrand-Jones and Stokes, Vashon, WA

Lestelle, L.C., G.R. Blair, S.A. Chitwood. 1993a. Approaches to supplementing coho salmon in the Queets River, Washington. Pages 104-119 *in* L. Berg and P.W. Delaney (eds.) Proceedings of the coho workshop. British Columbia Department of Fisheries and Oceans, Vancouver, BC.

Lestelle, L.C., M.L. Rowse, and C. Weller. 1993b. Evaluation of natural stock improvement measures for Hood Canal coho salmon. TR 93-1, Point No Point Treaty Council, Kingston, WA.

Lestelle, L.C., W.E. McConnaha, G. Blair, and B. Watson. 2005. Chinook salmon use of floodplain, secondary channel, and non-natal tributary habitats in rivers of western North America. Report prepared for the Mid-Willamette Valley Council of Governments, U.S. Army Corps of Engineers, and Oregon Department of Fish and Wildlife. Mobrand-Jones and Stokes, Vashon, WA and Portland, OR.

Lichatowich, J. 1999. Salmon Without Rivers – A History of the Pacific Salmon Crisis. Island Press, Washington D.C., Covelo, CA.

Lichatowich, J., L. Mobrand, L. Lestelle, and T. Vogel. 1995. An approach to the diagnosis and treatment of depleted Pacific salmon populations in Pacific Northwest watersheds. Fisheries 20(1):10-18.

Lindsay, R.B. 1974. Distribution and survival of coho salmon fry after emigration from natal streams. Master's Thesis. Oregon State University, Corvallis, OR.

Lindsay, R.B., W.J. Knox, M.W. Flesher, B.J. Smith, E.A. Olsen, and L.S. Lutz. 1986. Study of wild spring chinook salmon in the John Day River system. Oregon Department of Fish and Wildlife 1985 Final Report. Prepared for U.S. Department of Energy, Bonneville Power Administration, Portland, Oreg. Project 79-4. Contract DE-AI79-83BP39796.

Lister, D.B., and H.S. Genoe. 1970. Stream habitat utilization by cohabiting underyearlings of chinook (*Oncorhynchus tshawytscha*) and coho (*O. kisutch*) salmon in the Big Qualicum River, British Columbia. Journal of the Fisheries Research Board of Canada 27:1215-1224.

Madej, M.A., C. Currens, V. Ozaki, J. Yee, and D.G. Anderson. 2006. Assessing possible thermal rearing restrictions for juvenile coho salmon (*Oncorhynchus kisutch*) through thermal

infrared imaging and in-stream monitoring, Redwood Creek, California. Canadian Journal of Fisheries and Aquatic Sciences 63:1384-1396.

Marshall, D.E. and E.W. Britton. 1980. Carrying capacity of coho streams. Fisheries and Oceans Manuscript Report, Vancouver, B.C.

Martin, D.J., L.J. Wasserman, and V.H. Dale. 1986. Influence of riparian vegetation on post-eruption survival of coho salmon fingerlings on the westside streams of Mount St. Helens, Washington. North American Journal of Fisheries Management 6:1-8.

Mason, J.C. 1976a. Response of underyearling coho salmon to supplemental feeding in a natural stream. Journal of Wildlife Management 40:775-778.

Mason, J.C. 1976b. Some features of coho salmon, *Oncorhynchus kisutch*, fry emerging from simulated redds and concurrent changes in photobehavior. Fishery Bulletin 74:167-175.

McCullough, D.A. 1999. A review and synthesis of effects of alterations to the water temperature regime on freshwater life stages of salmonids, with special reference to chinook salmon. Published as EPA 910-R-99-010 . Prepared for the U.S. Environmental Protection Agency (EPA), Region 10. Seattle, WA.

McCullough, D.A., S. Spalding, D. Sturdevant, and M. Hicks. 2001. Issue Paper 5: Summary of technical literature examining the physiological effects of temperature on salmonids. U.S. Environmental Protection Agency EPA 910-D-01-005.

McElhany, P., M.H. Ruckelshaus, M.J. Ford, T.C. Wainwright, and E.P. Bjorkstedt. 2000. Viable salmonid populations and the recovery of evolutionarily significant units. U.S. Dept. Commerce, NOAA Tech. Memo. NMFS-NWFSC-42, Seattle, WA.

McMahon, T.E., and G.F. Hartman. 1989. Influence of cover complexity and current velocity on winter habitat use by juvenile coho salmon (*Oncorhynchus kisutch*). Canadian Journal of Fisheries and Aquatic Sciences 46:1551–1557.

McMahon, T.E., and L.B. Holtby. 1992. Behaviour, habitat use, and movements of coho salmon (*Oncorhynchus kisutch*) smolts during seaward migration. Canadian Journal of Fisheries and Aquatic Sciences 49:1478-1485.

McPhail, J.D., and C.C. Lindsey. 1970. Freshwater fishes of northwestern Canada and Alaska. Fisheries Research Board of Canada, Bulletin 173, Ottawa, Ontario.

McPherson, B.P., and S.P. Cramer. 1981. Rogue basin evaluation program, juvenile salmonid studies. Oregon Department of Fish and Wildlife, Progress Report, Fish Research Project DACW57-77-C-0027, Portland, OR.

McPherson, B.P., and S.P. Cramer. 1983. Rogue basin evaluation program, juvenile salmonid studies. Oregon Department of Fish and Wildlife, Fish Research Project DACW57-77-C-0027, Annual Progress Report, Portland, OR.

Miller, B.A. 2005. West Fork Smith River salmonid life-cycle monitoring. Final Report for 2004-2005 (FY 2004 allocation), BLM Contract Number HAC991021, Western Oregon Research and Monitoring Program, Oregon Department of Fish and Wildlife, Charleston District Office, Charleston, OR.

Miller, B.A., and S. Sadro. 2003. Residence time and seasonal movements of juvenile coho salmon in the ecotone and lower estuary of Winchester Creek, South Slough, Oregon. Transactions of the American Fisheries. Society 132:546-559.

Mobrand, L. E., L.C. Lestelle, J.A. Lichatowich, and T.S. Vogel. 1996. Examples of the use of a trivariate performance measure. Mobrand Biometrics Inc, compiler. Report 7 of 8 in Applied ecosystem analysis - background, EDT: the ecosystem diagnosis and treatment method. Bonneville Power Administration, Portland, OR.

Mobrand, L.E., J.A. Lichatowich, L.C. Lestelle, and T.S. Vogel. 1997. An approach to describing ecosystem performance "through the eyes of salmon." Canadian Journal of Fisheries and Aquatic Sciences 54: 2964-2973.

Montgomery, D.R., E.M. Beamer, G.R. Pess, and T.P. Quinn. 1999. Channel type and salmonid distribution and abundance. Canadian Journal of Fisheries and Aquatic Sciences 56:377-387.

Montgomery, D.R., J.M. Buffington, N.P. Peterson, D. Schuett-Hames, and T.P. Quinn. 1996. Streambed scour, egg burial depths, and the influence of salmonid spawning on bed surface mobility and embryo survival. Canadian Journal of Fisheries and Aquatic Sciences 53:1061-1070.

Montgomery, D.R., and J.M. Buffington. 1998. Channel processes, classification, and response. Pages 13-42 *in* R.J. Naiman and R.E. Bilby (eds.) River Ecology and Management – Lessons from the Pacific Coastal Ecoregion. Springer-Verlag, New York, NY.

Montgomery, D.R., B.D. Collins, T.B. Abbe, and J.M. Buffington. 2003. Geomorphic effects of wood in rivers. Pages 21-47 *in* S.V. Gregory, K.L. Boyer, and A. Gurnell (eds.) The Ecology and Management of Wood in World Rivers. American Fisheries Society Symposium 37, Bethesda, MD.

Moring, J.R., and R.L. Lantz. 1975. The Alsea watershed study: effects of logging three headwater streams of the Alsea River, Oregon, Part I. Biological Studies. Oregon Department of Fish and Wildlife Research Report 9:1-39.

Moser, M.L., A.F. Olson, and T.P. Quinn. 1991. Riverine and estuarine migratory behavior of coho salmon (*Oncorhynchus kisutch*) smolts. Canadian Journal of Fisheries and Aquatic Sciences 48:1670-1678.

Moyle, P.B. 2002. Inland Fishes of California. University of California Press, Berkeley, CA.

Muir, W.D., S.G. Smith, J.G. Williams, E.E. Hockersmith, and J.R. Skalski. 2001. Survival estimates for migrating yearling chinook salmon and steelhead tagged with passive integrated transponders in the Lower Snake and Lower Columbia Rivers, 1993-1998. North American Journal of Fishery Management 21:269-282.

Mullan, J.W. 1984. Overview of artificial and natural propagation of coho salmon (*Oncorhynchus kisutch*) on the mid-Columbia River. Rept. No. FRI/FAO-84-4. USFWS Leavenworth, WA.

Mundie, J.H., 1969. Ecological implications of the diet of juvenile coho salmon in streams. Pages 135-152 *in* T.G. Northcote (ed.) Symposium on Salmon and Trout in Streams, University of British Columbia, Vancouver, B.C.

Murphy, M.L., J. Heifetz, J.F. Thedinga, S.W. Johnson, and K.V. Koski. 1989. Habitat utilization by juvenile Pacific salmon (*Onchorhynchus*) in the glacial Taku River, southeast Alaska. Canadian Journal of Fisheries and Aquatic Sciences 46:1677-1685.

Murphy, M.L., J.F. Thedinga, K.V. Koski, and G.B. Grette. 1984. A stream ecosystem in an old-growth forest in southeastern Alaska. Part V: seasonal changes in habitat utilization by juvenile salmonids. Pages 89–98 in W.R. Meehan, T.R. Merrell, Jr., and T.A. Hanley (eds.) Fish and wildife relationships in old-growth forests. American Institute of Fisheries Research Biologists, Juneau, AK.

Nicholas, J.W. and D.G. Hankin. 1988. Chinook salmon populations in Oregon coastal river basins: description of life histories and assessment of recent trends in run strengths. Oregon Department of Fish and Wildlife, Information Report 88-1, Corvallis, OR.

Nickelson, T.E., Rodgers, J.D., Johnson. S.L., and Solazzi, M.F. 1992. Seasonal changes in habitat use by juvenile coho salmon (*Oncorhynchus kisutch*) in Oregon coastal streams. Canadian Journal of Fisheries and Aquatic Sciences 49: 783-789.

Nielsen, J.L. 1992a. The role of cold-pool refugia in the freshwater fish assemblage in northern California rivers. Pages 79-88 *in* Proceedings, Symposium on Biodiversity in Northwestern California, 28-30 October 1991, Santa Rosa, California. Report 29, Wildland Resources Center, Division of Agriculture and Natural Resources, University California, Berkeley, CA.

Nielsen, J.L. 1992b. Microhabitat-specific foraging behavior, diet, and growth of juvenile coho salmon. Transactions American Fisheries Society 121:617-634.

Nielsen, J.L. 1994. Invasive cohorts: impacts of hatchery-reared coho salmon on the trophic, developmental, and genetic ecology of wild stocks. Pages 361-385 *in* D.J. Stouder, K.L. Fresh, and R.J. Feller (eds) Theory and Application in Fish Feeding Ecology. Belle W. Baruch Library in Marine Sciences Number 18, University of South Carolina Press

National Research Council (NRC). 2004. Endangered and Threatened Fishes in the Klamath River Basin – Causes of Decline and Strategies for Recovery. The National Academies Press, Washington, DC.

Pacific Fishery Management Council (PFMC). 2006. Review of 2005 ocean salmon fisheries. Pacific Fishery Management Council, Portland, OR.

Pakkasmaa, S., and J. Piironen. 2001. Water velocity shapes juvenile salmonids. Evolutionary Ecology 14:721-730.

Pearcy, W.G. 1992. Ocean Ecology of North Pacific Salmonids. University of Washington Press, Seattle, WA.

Pess, G.R., S.A. Morley, J.L. Hall, and R.K. Timm. 2005. Monitoring floodplain restoration. Pages 127-166 *in* P. Roni (ed.) Methods for Monitoring Stream and Watershed Restoration. American Fisheries Society, Bethesda, Maryland.

Peters, R.J. 1996. An evaluation of habitat enhancement and wild fry supplementation as a means of increasing coho salmon production of the Clearwater River, Washington. Ph.D. Thesis, University of Washington, Seattle, WA.

Peterson, N.P. 1982a. Immigration of juvenile coho salmon (*Oncorhynchus kisutch*) into riverine ponds. Canadian Journal of Fisheries and Aquatic Sciences 39:1308-1310.

Peterson, N.P. 1982b. Population characteristics of juvenile coho salmon (*Oncorhynchus kisutch*) overwintering in riverine ponds. Canadian Journal of Fisheries and Aquatic Sciences 39:1303-1307.

Peterson, N.P., and L.M. Reid. 1984. Wall-base channels: their evolution, distribution, and use by juvenile coho salmon in the Clearwater River, Washington. Pages 215-225 *in* J.M. Walton and D.B. Houston (eds).Proceedings of the Olympic Wild Fish Conference. Peninsula College and Olympic National Park, Port Angeles, WA.

Pinnix, W.D. 1999. Climate and coho: a Puget Sound perspective. Master's Thesis. University of Washington, Seattle, WA.

Ptolemy, R.A. 1993. Maximum salmonid densities in fluvial habitats in British Columbia. Pages 223-250 *in* L. Berg and P.W. Delaney (eds.) Proceedings of the coho workshop. British Columbia Department of Fisheries and Oceans, Vancouver, BC.

Quinault Department of Natural Resources (QDNR). 1989a. Queets River coho indicator stock study: 1988 smolt tagging and yield studies. Quinault Department of Natural Resources Annual Report for FY 1988 - Contract No. 30000-632 to the Northwest Indian Fisheries Commission, Taholah, WA.

Quinault Department of Natural Resources (QDNR). 1989b. Queets River coho indicator stock study: 1988 smolt tagging and yield studies with a summary of 1989 fry supplementation activities. Quinault Department of Natural Resources Annual Report for FY-89 - Contract No. 30000-633 to the Northwest Indian Fisheries Commission, Taholah, WA.

Quinault Department of Natural Resources (QDNR). 1992. Queets River coho indicator stock study – data analysis. Quinault Department of Natural Resources Annual Report for FY-91 - Contract No. 3107 to the Northwest Indian Fisheries Commission, Taholah, WA.

Quinn, T.P. 2005. The Behavior and Ecology of Pacific Salmon and Trout. American Fisheries Society and University of Washington Press, Seattle and London.

Quinn, T.P., and N.P. Peterson. 1996. The influence of habitat complexity and fish size on over-winter survival and growth of individually marked juvenile coho salmon (*Oncorhynchus kisutch*) in Big Beef Creek, Washington. Canadian Journal of Fisheries and Aquatic Sciences 53:1555-1564.

Quinn, T.P, and K.W. Myers. 2005. Anadromy and the marine migrations of Pacific salmon and trout: Rounsefell revisited. Reviews in Fish Biology and Fisheries 14:421–442.

Puckett, K.J., and L.M. Dill. 1985. The energetics of feeding territoriality in juvenile coho salmon (*Oncorhynchus kisutch*). Behaviour 92:97–111.

Pyper, B.J., and D.L. Smith. 2005. Evaluation of salmonid survival resulting from flow alterations to the lower Yakima River. S.P. Cramer and Associates. Report prepared for Kennewick Irrigation District and U.S. Bureau of Reclamation, Yakima Operations Office, Yakima, WA.

Raymond, H.L. 1979. Effects of dams and impoundments on migrations of juvenile Chinook salmon and steelhead from the Snake River, 1966 to 1975. Transactions of the American Fisheries Society 108:505–529.

Reeves, G.H., F.H. Everest, and T.E. Nickelson. 1989. Identification of physical habitats limiting the production of coho salmon in Western Oregon and Washington, United States Forest Service. USFS General Technical Report PNW-GTR-245.

Rennie, C.D., and R.G. Millar. 2000. Spatial variability of stream bed scour and fill: a comparison of scour depth in chum salmon (*Oncorhynchus keta*) redds and adjacent bed. Canadian Journal Fisheries and Aquatic Sciences 57:928-938.

Rodgers, J.D., R.D. Ewing, and J.D. Hall. 1987. Physiological changes during seaward migration of wild juvenile coho salmon (*Oncorhynchus kisutch*). Canadian Journal of Fisheries and Aquatic Sciences 44:452-457.

Roni, P., and A. Fayram. 2000. Estimating winter salmonid abundance in small western Washington streams: a comparison of three techniques. North American Journal of Fisheries Management 20: 683-692.

Roni, P., and T.P. Quinn. 2001. Density and size of juvenile salmonids in response to placement of large woody debris in western Oregon and Washington streams. Canadian Journal of Fisheries and Aquatic Sciences 58:282-292.

Rosenfeld, J.S., M. Porter, and E. Parkinson. 2000. Habitat factors affecting the abundance and distribution of juvenile cutthroat trout (*Oncorhynchus clarki*) and coho salmon (*Oncorhynchus kisutch*). Canadian Journal of Fisheries and Aquatic Sciences 57:766-774.

Rosenfeld, J.S., T. Leiter, G. Lindner, and L. Rothman. 2005. Food abundance and fish density alters habitat selection, growth, and habitat suitability curves for juvenile coho salmon (*Oncorhynchus kisutch*). Canadian Journal of Fisheries and Aquatic Sciences 62:1691-1701.

Rot, B. 2003. The evolving Dungeness River: Juvenile salmon and their use of side channel habitat, a comparison of data collected 1997/1998 vs. 1999/2000. Unpublished report, Jamestown S'Klallam Tribe, WA.

Ruggerone, G.T., and C.J. Harvey. 1994. Age-specific use of habitat by juvenile coho and other salmonids in the Chignik Lakes watershed, Alaska. Pages 45-60 *in* M.L. Keefe (ed.) Salmon Ecosystem Restoration: Myth and Reality. Proceedings of the 1994 Northeast Pacific Chinook and Coho Salmon Workshop. Eugene, OR.

Ruggerone, G.T., and D.E. Rogers. 1992. Predation on sockeye salmon fry by juvenile coho salmon in the Chignik Lakes, Alaska: implications for salmon management. North American Journal of Fisheries Management 12:87-102.

Saldi-Caromile, K., K. Bates, P. Skidmore, J. Barenti, D. Pineo. 2004. Stream habitat restoration guidelines. Co-published by the Washington Departments of Fish and Wildlife and Ecology and the U.S. Fish and Wildlife Service. Olympia, WA.

Sandercock, F.K. 1991. Life history of coho salmon (*Oncorhynchus kisutch*). Pages 396-445 *in* C. Groot and L. Margolis (eds.) Pacific Salmon Life Histories. University of British Columbia Press, Vancouver, B.C.

Scarlett, W.J., and C.J. Cederholm. 1984. Juvenile coho salmon fall-winter utilization of two small tributaries of the Clearwater River, Jefferson County, Washington. Pages 227-242 *in* J. M. Walton and D.B. Houston (eds). Proceedings of the Olympic Wild Fish Conference. Peninsula College and Olympic National Park, Port Angeles, WA.

Scarnecchia, D.L. 1981. Effects of streamflow and upwelling on yield of wild coho salmon (*Oncorhynchus kisutch*) in Oregon. Canadian Journal of Fisheries and Aquatic Sciences 38:471-475.

Schuett-Hames, J., and D. Adams. 2003. Upper White River basin spring chinook redd scour and cross-section assessments: 1995-2001. Publication No. 03-10-071, Washington Department of Ecology, Olympia, WA.

Schwartz, J.S. 1990. Influence of geomorphology and land use on distribution and abundance of salmonids in a coastal Oregon basin. Master's Thesis, Oregon State University, Corvallis, OR.

Schwartz, J.S., and E.E. Herricks. 2005. Fish use of stage-specific fluvial habitats as refuge patches during a flood in a low-gradient Illinois stream. Canadian Journal of Fisheries and Aquatic Sciences 62:1540-1552.

Scrivener, J.C., and D.B. Tripp. 1998. Changes of spawning gravel characteristics after forest harvesting in Queen Charlotte Islands and Carnation Creek watersheds and the apparent impacts on incubating salmonid eggs. Pages 135-140 *in* Hogan, D.L., P.J. Tschaplinski, and S. Chatwin (eds) Carnation Creek and Queen Charlotte Islands Fish/Forestry Workshop: Applying 20 Years of Coastal Research to Management Solutions. B.C. Ministry of Forests, Research Program, Land Management Handbook No. 41, Victoria, B.C.

Scrivener, J.C., and M.J. Brownlee. 1989. Effects of forest harvesting on spawning gravel and incubation survival of chum (*Oncorhynchus keta*) and coho salmon (*O. kisutch*) in Carnation Creek, British Columbia. Canadian Journal of Fisheries and Aquatic Sciences 46:681-696.

Sedell, J., and L. Froggatt. 1984. Importance of streamside forests to large rivers: The isolation of the Willamette River, Oregon, U.S.A., from its floodplain by snagging and streamside forest removal. Verh. Internat. Verin. Limnol. 22: 1828-1834.

Sedell, J.R., J.E. Yuska, and R.W. Speaker. 1984. Habitats and salmonid distribution in pristine, sediment-rich river valley systems: S. Fork Hoh and Queets rivers, Olympic National Park. Pages 33-46 *in* W. R. Meehan, T. R. Merrell, and T. A. Hanley (eds.) Fish and wildife relationships in old-growth forests. American Institute of Fisheries Research Biologists, Juneau, AK.

Seiler, D., G. Volkhardt, L. Peterson, L. Fleischer, S. Newhauser, P. Hanratty, and L. Kishimoto. 2004. 2003 Juvenile salmonid production evaluation and adult escapement: intensively monitored watersheds (IMW). Annual report to the Washington Salmon Recovery Funding Board, Washington Department of Fish and Wildlife, Fish Science Division, Olympia, WA.

Shapovalov, L., and A.C. Taft. 1954. The life histories of the steelhead rainbow trout (*Salmo gairdneri gairdneri*) and silver salmon (*Oncorhynchus kisutch*) with special reference to Waddel Creek, California, and recommendations regarding their management. Fish Bulletin No. 98. State of California, Department of Fish and Game. Sacramento, CA.

Sharma, R., and R. Hilborn. 2001. Empirical relationships between watershed characteristics and coho salmon (*Oncorhynchus kisutch*) smolt abundance in 14 western Washington streams. Canadian Journal of Fisheries and Aquatic Sciences 58:1453-1463.

Sharma, R., G. Morishima, S. Wang, A. Talbot, and L. Gilbertson. 2006. An evaluation of the Clearwater River supplementation program in western Washington. Canadian Journal of Fisheries and Aquatic Sciences 63: 423-437.

Shellberg, J.G. 2002. Hydrologic, geomorphic, and biologic influences on redd scour in bull trout (*Salvelinus confluentus*) spawning streams. Master's Thesis, University of Washington, Seattle, WA.

Shirvell, C.S. 1990. Role of instream rootwads as juvenile coho salmon (*Oncorhynchus kisutch*) and steelhead trout (*O. mykiss*) cover habitat under varying streamflows. Canadian Journal of Fisheries and Aquatic Sciences 47: 852–861.

Skeesick, D.G. 1970. The fall immigration of juvenile coho salmon into a small tributary. Research Report 2. Fish Commission of Oregon, Portland, OR.

Smith, B.D. 2000. Trends in wild adult steelhead (*Oncorhynchus mykiss*) abundance for snowmelt-driven watersheds of British Columbia in relation to freshwater discharge. Canadian Journal of Fisheries and Aquatic Sciences 57:285-297.

Smith, S.G., W.D. Muir, J.G. Williams, and J.R. Skalski. 2002. Factors associated with travel time and survival of migrant yearling Chinook salmon and steelhead in the lower Snake River. North American Journal of Fisheries Management 22:385–405.

Solazzi, M.F., T.E. Nickelson, S.L. Johnson, and J.D. Rodgers. 2000. Effects of increasing winter rearing habitat on abundance of salmonids in two coastal Oregon streams. Canadian Journal of Fisheries and Aquatic Sciences 57:906-914.

Sommer, T. R., M. L. Nobriga, W. C. Harrell, W. Batham, and W. J. Kimmerer. 2001. Floodplain rearing of juvenile chinook salmon: evidence for enhanced growth and survival. Canadian Journal of Fisheries and Aquatic Sciences 58:325-333.

Southwood, T.R.E. 1977. Habitat, the templet for ecological strategies? Journal of Animal Ecology 16:337-365.

Spalding, S., N.P. Peterson, and T.P. Quinn. 1995. Summer distribution, survival, and growth of juvenile coho salmon under varying experimental conditions of brushy instream cover. Transactions of the American Fisheries Society 124:124-130.

Sparkman, M.D. 2003. Negative influences of predacious egg-eating worms, *Haplotaxis ichthyophagous*, and fine sediments on coho salmon, *Oncorhynchus kisutch*, in natural and artificial redds. Master's Thesis, Humboldt State University, Arcata, CA.

Spence, B.C. 1995. Geographic variation in timing of fry emergence and smolt migration of coho salmon (Oncorhynchus kisutch). Ph.D. Thesis, Oregon State University, Corvallis, OR.

Stanford, J.A., and J.V. Ward. 1992. Management of aquatic resources in large catchments: Recognizing interactions between ecosystem connectivity and environmental disturbance. Pages 91-124 *in* R.J. Naiman (ed.) Watershed Management – Balancing Sustainability and Environmental Change. Springer-Verlag, New York, NY.

Stanford, J., E. Snyder, M. Lorang, D. Whited, P. Matson, and J. Chaffin. 2002. The Reaches Project. Project No. 1997-04700, BPA Report DOE/BP-00005854-1, Portland, OR.

Stearns, S.C. 1992. The Evolution of Life Histories. Oxford University Press, Oxford, UK.

Stein R.A, P.E. Reimers, and J.D. Hall. 1972. Social Interaction between juvenile coho (*Oncorhynchus kisutch*) and fall chinook salmon. (*O. tshawytscha*) in Sixes River, Oregon. Journal of the Fisheries Research Board of Canada 29:1737-1748.

Stutzer, G.M., J. Ogawa, N.J. Hetrick, and T. Shaw. 2006. An initial assessment of radiotelemetry for estimating juvenile coho salmon survival, migration behavior, and habitat use in response to Iron Gate Dam discharge on the Klamath River, California. Arcata Fisheries Technical Report TR2006-05, U.S. Fish and Wildlife Service, Arcata, CA.

Sullivan, K., D.J. Martin, R.D. Cardwell, J.E. Toll, and S. Duke. 2000. An analysis of the effects of temperature on salmonids of the Pacific Northwest with implications for selecting temperature criteria. Sustainable Ecosystems Institute. Portland, OR.

Sutton, R., M. Deas, M.R. Belchik, and S.M. Turo. 2002. Klamath River thermal refugia study. Report for the United States Bureau of Reclamation, Mid-Pacific Region, Klamath Falls, CA.

Swain, D.P., and L.B. Holtby. 1989. Differences in morphology and behavior between juvenile coho salmon (*Oncorhynchus kisutch*) rearing in a lake and in its tributary stream. Canadian Journal of Fisheries and Aquatic Sciences 46:1406-1414.

Swales, S., R.B. Lauzier, and C D. Levings. 1986. Winter habitat preferences of juvenile salmonids in two interior rivers in British Columbia. Canadian Journal of Zoology 64:1506-1514.

Tagart, J.V. 1984. Coho salmon survival from egg deposition to fry emergence. Pages 173-182 *in* J.M. Walton and D.B. Houston (eds.) Proceedings of the Olympic Wild Fish Conference. Peninsula College Fisheries Technology Program and Olympic National Park, Port Angeles, WA.

Taylor, E.B. 1988. Water temperature and velocity as determinants of microhabitats of juvenile chinook and coho salmon in a laboratory stream. Transactions of the American Fisheries Society 117:22-28.

Taylor, E.B., and J.D. McPhail. 1985a. Variation in body morphology among British Columbia populations of coho salmon, *Oncorhynchus kisutch*. Canadian Journal of Fisheries and Aquatic Sciences 42:2020-2028.

Taylor, E.B., and J.D. McPhail. 1985b. Variation in burst and prolonged swimming performance among British Columbia populations of coho salmon, *Oncorhynchus kisutch*. Canadian Journal of Fisheries and Aquatic Sciences 42:2029-2032.

Tockner, K., F. Malard, P. Burgherr, C.T. Robinson, U. Uehlinger, R. Zah, and J.V.Ward. 1998. Physico-chemical characterisation of channel types in a glacial floodplain ecosystem (Val Roseg, Switzerland). Archiv für Hydrobiologie 140:433-463.

Tockner, K., A. Paetzold, U. Karaus, C. Claret, J. Zettel. *In press*. Ecology of braided rivers. *In* Proceedings of Conference on Braided Rivers 2003. Center for Water Research, University of Birmingham, UK.

Tripp, D., and V.A. Poulin. 1986. The effects of logging and mass wasting on salmonid spawning habitat in streams on the Queen Charlotte Islands. Land Management Report No. 50. British Columbia Ministry of Forests and Lands. Vancouver, B.C.

Tschaplinski, P.J. 1988. The use of estuaries as rearing habitats by juvenile coho salmon. Pages 123–142 *in* T.W. Chamberlin (ed.) Proceedings of the workshop: applying 15 years of Carnation Creek results. Department of Fisheries and Oceans Canada, Pacific Biological Station, Nanaimo, B.C.

Tschaplinski, P.J., and G.F. Hartman. 1983. Winter distribution of juvenile coho salmon (*Oncorhynchus kisutch*) before and after logging in Carnation Creek, British Columbia, and some implications for overwinter survival. Canadian Journal of Fisheries and Aquatic Sciences 40:452-461.

U.S. Fish and Wildlife Service (USFWS). 1988. Trinity River flow evaluation – annual report. U.S. Fish and Wildlife Service, Division of Ecological Services, Sacramento, CA.

U.S. Fish and Wildlife Service (USFWS). 1998. Klamath River (Iron Gate Dam to Seiad Creek) life stage periodicities for chinook, coho and steelhead. U.S. Fish and Wildlife Service, Coastal California Fish and Wildlife Office. Arcata, CA.

Vogel, D.A. 2003. Salmon rearing habitats in the main stem Klamath River. Natural Resource Scientists, Inc. Red Bluff, CA.

Volkhardt, G., P. Hanratty, D. Rawding, P. Topping, M. Ackley, C. Kinsel, K. Kiyohara, and L. Kishimoto. 2007. 2007 wild coho forecasts for Puget Sound and Washington coastal systems. Unpublished report, Science Division, Washington Department of Fish and Wildlife, Olympia, WA.

Ward, B.R., D.J.F. McCubbing, and P.A. Slaney. 2003. Evaluation of the addition of inorganic nutrients and stream habitat structures in the Keogh River watershed for steelhead trout and coho salmon. Pages 127-147 in J.G. Stockner (ed.). Nutrients in Salmonid Ecosystems: Sustaining Production and Biodiversity. American Fisheries Society, Symposium 34, Bethesda, MD.

Ward J.V., F. Malard, K. Tockner, and U. Uehlinger. 1999. Influence of ground water on surface water conditions in a glacial flood plain of the Swiss Alps. Hydrological Processes 13:277-293.

Waters, T.F. 1995. Sediment in Streams--Sources, Biological Effects, and Control. American Fisheries Society Monograph 7, Bethesda, MD.

Welsh, H.H., Jr., G.R. Hodgson, B.C. Harvey, and M.F. Roche. 2001. Distribution of juvenile coho salmon in relation to water temperatures in tributaries of the Mattole River, California. North American Journal of Fisheries Management 21:464-470.

Williams, J.G., S.G. Smith, R.W. Zabel, W.D. Muir, M.D. Scheuerell, B.P. Sandford, D.M. Marsh, R.A. McNatt, and S. Achord. 2005. Effects of the federal Columbia River power system on salmonid populations. U.S. Department of Commerce, NOAA Technical Memorandum, NMFS-NWFSC-63.

Williams, T.H., E.P. Bjorkstedt, W. Duffy, D. Hillemeier, G. Kautsky, T. Lisle, M. McCain, M. Rode, R.G. Szerlong, R. Schick, M. Goslin, and A. Agrawal. 2006. Historical population structure of coho salmon in the Southern Oregon/Northern California Coasts Evolutionarily Significant Unit. U.S. Department of Commerce, NOAA Technical Memorandum, NMFS-SWFSC-390.

Williamson, K., and D. Hillemeier. 2001. An assessment of pinniped predation upon fall-run chinook salmon in the Lower Klamath River, CA, 1999. Unpublished report of the Yurok Tribal Fisheries Program, Klamath, CA.

Winker, K., J. H. Rappole, and M. A. Ramos. 1995. The use of movement data as an assay of habitat quality. Oecologia 101: 211-216.

Wood, C.C. 1987. Predation of juvenile Pacific salmon by the common merganser (*Mergus merganser*) on eastern Vancouver Island. I: Predation during the seaward migration. Canadian Journal of Fisheries and Aquatic Sciences 44:941-949.

Wright, S.G. 1968. Origin and migration of Washington's chinook and coho salmon. Washington Department of Fisheries, Information Booklet No. 1, Olympia, WA.

Young, K.A. 2001. Habitat diversity and species diversity: testing the competition hypothesis with juvenile salmonids. Oikos 95:87-93.

Zah R., M. Niederöst M. and U. Uehlinger. 2000. Application of photogrammetry in freshwater ecology: analysing the morophology of a high alpine floodplain. International Archives of Photogrammetry and Remote Sensing 33:1739-1746.

Zhou, S. 2000. Stock assessment and optimal escapement of coho salmon in three Oregon coastal lakes. Information Report Number 2000-7. Oregon Department of Fish and Wildlife. Portland, OR.

Personal Communications

Bailey, Richard.   Fisheries and Oceans Canada, Kamloops, British Columbia.

Cederholm, Jeff C.   Washington State Department of Natural Resources, Olympia, Washington.

Duffy, Walt G.   Humboldt State University, Arcata, California.

Ebersole, Joseph L.   U.S. Environmental Protection Agency, Corvallis, Oregon.

McMillian, John.   The Wild Salmon Center, Forks, Washington.

Nielsen, Jennifer L.   U.S. Geological Survey, Anchorage, Alaska.

Soto, Toz.   Department of Natural Resources, Karuk Tribe, Orleans, California.