

PRELIMINARY DRAFT

A review of coho salmon life history to assess potential limiting factors and the implications of historical removal of large woody debris in coastal Mendocino County

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May 1997



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Background

This technical report on coho salmon is designed to support the efforts of Louisiana-Pacific (L-P) to develop Sustained Yield Plans (SYP) and a Habitat Conservation Plan (HCP) for the company's timberlands in coastal Mendocino and Humboldt counties.

The fisheries resource of particular interest in coastal areas of Mendocino County, California is coho salmon (*Oncorhynchus kisutch*), because of its importance for sport and commercial harvest, and its status as a federally listed threatened species. The suitability of coastal streams for coho salmon can be heavily influenced by land management actions, because such actions may cause changes in fine sediment loads, stream cover conditions, and channel morphology that can have a pronounced effect on the quality of coho salmon habitat. L-P's fisheries mitigation and monitoring approach considers coho salmon as a key species of special emphasis. Actions taken to protect, enhance, and monitor habitat conditions for coho are assumed to provide benefits to other resident and anadromous species as well. The SYP and HCP will also address the need for specific actions directed towards aquatic species other than coho salmon.



Coho Salmon Literature Review

Introduction

Coho salmon (*Oncorhynchus kisutch*) is one of two species of Pacific salmon in California (the other being chinook salmon, *O. tshawytscha*) historically supporting important commercial and sport fisheries. Coho salmon are anadromous, and thus occupy freshwater, estuarine, and ocean habitats during different stages of their life cycle. As a result, the coho salmon population is subject to impacts from a variety of sources, including climatic shifts, ocean and freshwater fishing pressure, and natural or man-made habitat changes. Land management activities of various types have the potential to dramatically affect the suitability of coastal streams for the production of coho salmon. During the freshwater portions of their life cycle, salmon may act as a keystone food resource for terrestrial vertebrate predators and scavengers, and thus they form a critical link between the aquatic and terrestrial ecosystems (Houston 1983, Cederholm et al. 1989, Willson and Halupka 1995). Declines in anadromous fish species such as coho salmon may therefore result in cascading effects through food webs in both aquatic and adjacent terrestrial ecosystems.

Declines in the population of coho salmon in California have led to increased regulatory pressure on many activities that potentially affect coho salmon habitat. The California Department of Fish and Game (CDFG) currently considers coho salmon a candidate for listing as threatened under the California Endangered Species Act (CDFG 1994). On July 25, 1995, the National Marine Fisheries Service (NMFS) issued a proposed rule to list three Evolutionarily Significant Units (ESUs) of coho salmon as threatened under the Federal Endangered Species Act (NMFS 1995). The three ESUs include the Oregon coast, southern Oregon/northern California, and central California coast populations (NMFS 1995). The present state of these populations is believed to be a result of human-induced conditions (commercial fishing, habitat degradation, and introduction of hatchery fish) serving to exacerbate adverse recent environmental conditions such as drought and poor ocean conditions (NMFS 1995). Degradation of freshwater spawning and rearing habitat is suspected of being the most important factor causing long-term declines of coho productivity and the recent declines in escapement (Pearcy et al. 1992).

The potentially adverse impacts of various land management activities, particularly timber harvesting related activities, on spawning and rearing habitat for coho salmon have led to their special consideration in Louisiana Pacific's (L-P) Sustainable Forestry Program, and in components of L-P's Sustained Yield Plan.

Methods

Information on coho salmon was obtained through contacts with professionals involved in coho salmon research and management, and through extensive scientific literature review from both published and unpublished sources. Literature sources included university libraries, resource agency files, and Stillwater Sciences's scientific literature database of over 8,000 entries on salmonid ecology. Selected publications were reviewed in detail to gather information pertinent to coho salmon habitat management in coastal streams of northern California. The literature review concentrates on those aspects of the life history most relevant to understanding the effects of land management on coho salmon and most useful for modeling the responses of coho populations to habitat alterations.



***Coho Salmon General
Description***

Physical Description

Coho salmon is one of five species of Pacific salmon (Genus *Oncorhynchus*) distributed along the coast of North America, the others being chinook salmon, sockeye salmon (*O. nerka*), pink salmon (*O. gorbuscha*), and chum salmon (*O. keta*). Lengths and weights of adult coho typically range from 45 to 60 cm and 3-6 kg, respectively (Shapovalov and Taft 1954, Godfrey 1965, Scott and Crossman 1973, Meehan and Bjornn 1991), although coho of over 12 kg have been caught (Meehan and Bjornn 1991). Adult coho salmon are generally smaller than chinook salmon and are most easily distinguished from them by their white gum line (versus a black gum line in chinook). Dark spots on the back, dorsal fin, and upper lobe of the tail distinguish coho salmon from chum and sockeye salmon (Hassler 1987), and lack of oval blotches on the lower lobe of the tail distinguish them from pink salmon (Moyle 1976).

Coho salmon are also referred to as “silver” salmon, particularly in California where silver salmon was adopted by the State as the official name prior to the widespread usage of the name “coho” (Hassler 1987). Coho salmon is the common name adopted by the American Fisheries Society.

Taxonomic Relationships

All five Pacific salmon species are found in California, although chinook and coho are by far the most numerous. Unlike chinook salmon, coho salmon do not appear to have genetically distinct, temporally segregated runs (Moyle et al. 1989). Coho salmon populations can be divided into “big river” and “short-run” fish, with big river coho migrating up into main river systems 60-120 miles or more to spawn in the main stem or tributaries (Moyle et al. 1989). Short-run coho salmon migrate up smaller coastal streams or tributaries in the lower reaches of larger rivers, and rarely migrate more than 60 miles upstream. Much of the natural production of big river coho has now been supplemented by hatchery populations, whereas short-run coho are more dependent on natural reproduction.

Taylor and McPhail (1985) also categorized coho salmon into two forms based on the body morphology of fish found from the upper Columbia River north to Alaska. The “coastal” form was characterized by large median fins and a deep robust body; the “interior” form had smaller median fins and a more streamlined body. The interior form was thought to be adapted for longer, more arduous migrations in fresh water, and would be comparable to the “big river” group described by Moyle et al. (1989). The coastal form exhibited greater morphological variation within and between river systems, which suggests that straying rate, and hence gene flow, may be greater among coastal-type coho (Sandercock 1991).

Strong homing abilities in natural populations of coho salmon appear to coexist with the ability to rapidly recolonize newly accessible habitat (NMFS 1995). Separate populations of coho salmon are currently considered as “species” under the Endangered Species Act (ESA) based on a policy published by the NMFS in 1991 that addresses how the agency applies the definition to anadromous salmonids. The NMFS considers a salmon population as “distinct, and hence a species under the ESA, if it represents an ESU of the biological species” (NMFS 1995). In order to be considered an ESU, a salmon population (1) must be reproductively isolated from other conspecific population units, and



(2) must represent an important component in the evolutionary legacy of the biological species. Reproductive isolation need not be absolute in order for a population to qualify as an ESU, however, it must be strong enough to permit evolutionarily important differences to accrue in different population units. The second criterion is met “if the population contributes substantially to the ecological/genetic diversity of the species as a whole” (NMFS 1995). Local spawning populations of coho salmon do not meet the criterion of strong reproductive isolation under guidelines for determining ESUs, however, local populations within watersheds may experience substantial long-term isolation from other such groups (NMFS 1995). Studies of the genetic relationships among coho salmon populations show a strong geographic component and several major stock groupings have been identified (NMFS 1995). In southern Oregon and California, two major geographic clusters are separated by a relatively large genetic distance, although there is considerable genetic diversity within both groups (NMFS 1995).

Distribution The largest numbers of coho salmon in California are currently found along the north coast in the Klamath, Trinity, Mad, Noyo, and Eel rivers. Other populations are located in smaller coastal streams from the Oregon border to as far south as the San Lorenzo River in Santa Cruz County (Moyle et al. 1989). Coho salmon are rare in the Sacramento River, although attempts have been made to establish populations there (Hallock and Fry 1967). High summer water temperatures probably limit the freshwater distribution of coho salmon in California (Fry 1977). Ocean distribution of coho typically extends as far south as Monterey Bay (Sandercock 1991), although coho have been documented as far south as Baja California.

Population Trends Coho no longer occupy many of the streams in California in which they used to occur, and remaining populations in other streams are greatly reduced (Hassler et al. 1991). In a recent survey, only 54% of 248 streams (43% of the 582 streams historically occupied by coho) were still found to contain coho salmon (Brown et al. 1994). Brown et al. (1994) estimated that coho populations have decreased to less than 6% of 1940 populations, and there has been a decline of at least 70% since the 1960s. Most coho produced in California come from hatcheries (Greenley 1985, Baker and Reynolds 1986). Historical populations in the southern part of the coho’s range appear to have shown the greatest declines, with a few coho occupying coastal streams south of, or in the vicinity of, San Francisco Bay. Brown et al. (1994) report that peak spawner densities of coastal coho populations now rarely exceed 1–2 adult fish per mile. In many streams, runs have been reduced in frequency to only once every three years, indicating that two of the three brood cycles have already become extinct (Hope 1993, Brown et al. 1994). Brown et al. (1994) estimate that less than 5,000 native coho salmon now spawn in California streams. Those river basins still supporting spawning runs of wild coho have annual spawning populations of fewer than 100 to 1,300 adults (the latter population estimate is from the South Fork Eel River.)

Coho Salmon Life History

Spawning Migration Over 95% of coho salmon in Washington, Oregon, and California mature in their third year of life (NMFS 1995) after having spent about 3 to 4 months within the gravels as eggs and salmon larvae (alevins), and up to 15 months rearing in fresh water, followed by a 16-month growing period in the ocean (Sandercock 1991). These three-year-old coho adults are considered to be age 1.1, having spent one winter in fresh water and one win-



ter in the ocean. In addition, spawning runs of coho usually include males that return after spending only six months at sea; these males are commonly referred to as “jacks” (age 1.0). Scale readings of Mendocino coast rivers have shown that female coho may return at two years of age as well (Nielsen et al. 1991). Nielsen et al. (1991) found that 73% of a sample of returning adult coho released as fry into the South Fork Noyo River returned at age three, with the remainder returning at age two.

After attaining sexual maturity in the summer following one or two winters at sea, adult coho migrate to the vicinity of their natal stream during late summer and fall (Sandercock 1991). Since heavy rains typically arrive sooner in the more northern portions of the state, coho salmon runs in the more northern streams generally occur earlier than in streams farther south. In southern Oregon and northern California, adult coho begin to enter the rivers in September and October, while entry from the Klamath River Basin south to the Mattole River occurs in November and December, and from mid-December to mid-February in rivers farther south (NMFS 1995). Spawning in southern Oregon and northern California occurs primarily in December; south of the Mattole River, spawning occurs most frequently in January (NMFS 1995). Coho salmon of central California thus spend far less time in the river as adults prior to spawning than those in populations farther north (NMFS 1995). In individual streams, upstream migration is dependent upon the condition of a particular stream. Coho salmon do not all enter the stream system at one time, but instead arrive throughout the spawning season in a pattern that reflects the occurrence of storms that increase flow in the spawning streams (Shapovalov and Taft 1954). Shapovalov and Taft (1954) found that 96% of the upstream migration in Waddell Creek, California took place during the nine week period from December 10 to February 10. Since many California coastal streams are blocked at their mouths by sand bars during the dry season, migration into freshwater is precluded until after sufficient rainfall has occurred to increase stream discharge to a point where the sand barriers are broken. Coho salmon may concentrate in the ocean near the spawning stream during the late summer and fall, in preparation for upstream migration as soon as the sand bars are breached (Hassler 1987).

There may be some selective advantage to spawning late in the run, because these fish often dig up eggs deposited in the gravel (“redd superimposition”) by females arriving earlier that have since died subsequent to spawning.

The early part of the coho salmon run is dominated by males, with females returning in greater numbers during the latter part of the run (Shapovalov and Taft 1954, Moyle et al. 1989). The male population includes both three-year-old males (age 1.1), as well as two-year-old jacks (age 1.0). There is usually a slight excess of females over males in the age 1.1 spawners, but an excess of males over females if both jacks and age 1.1 males are combined (Shapovalov and Taft 1954, Salo and Bayliff 1958, Fraser et al. 1983). This is probably due to relatively higher ocean survival of jacks than three-year-old males because of their shorter exposure to ocean fisheries. However, the sex ratio for all of the spawning adult coho salmon of a given cohort (those fish deriving from a single brood year) is close to 50:50.

Most adult coho migrate upstream during daylight hours rather than at night (Sandercock 1991, Neave 1943), with peak activity usually occurring at dawn and sunset (Fraser et al. 1983). Since adult coho are vulnerable to predation while migrating through shal-



low riffle areas, they move through these areas as quickly as possible and seek deeper, quieter pools in which to rest before migrating further upstream (Sandercock 1991).

Briggs (1953) observed coho moving across riffles where the water depth was only 2 inches. Under proper conditions, vertical leaps of more than 6 feet are possible to surmount instream barriers (Reiser and Peacock 1985). Maximum non-sustainable swimming speeds of over 30 feet per second have been recorded for adult coho salmon (Ellis 1962), so it is unlikely that excessive water velocity would physically block upstream migration in most situations. However, migration is reported to be retarded at velocities of over 10–13 feet per second (Reiser and Bjornn 1979).

Homing of coho and other Pacific salmon to their natal streams is well-documented in the literature. Straying rates in natural populations of salmon are usually less than 5% (Hasler and Scholz 1983). Coded-wire-tag recoveries of wild adult coho indicate that straying rates may be in the range of 0.1–2.0% (Sandercock 1991, Labelle 1992). Salmon that are blocked from access to their native tributary may die before choosing an alternative location to spawn (Ricker and Robertson 1935, Hartman and Raleigh 1964).

Bell (1986) reported that water temperatures ranging from 7.2°C to 15.6°C were suitable for adult migration. However, other researchers report that temperatures over 12.7°C may result in a marked increase in disease infection rates of adult coho (Fryer and Picher 1974, Holt et al. 1975, Groberg et al. 1978). Wedemeyer (pers. comm., as cited in McMahon 1983) stated that water temperatures below 13°C minimize pre-spawning mortality of adult coho. Temperatures of 25.5°C or over are considered lethal to adult migrants (Bell 1983). Dissolved oxygen levels below about 6.5 mg/l, which tend to co-occur with elevated water temperatures may reduce swimming performance of adult coho and/or cause avoidance reactions during upstream migration (Davis 1975, Davis et al. 1963).

Spawning

Females select a nest site after arriving on the spawning ground, and defend the area against other females. Redd construction behavior is similar to that displayed by other salmonid species, with the female excavating a depression in the gravel by turning on her side and using her body and tail to displace the gravel downstream. Digging activity may last as long as five days, during which time the female will dig up to seven egg pockets in succession, progressing in an upstream direction (Shapovalov and Taft 1954, Tautz 1977, van den Berghe and Gross 1984, Sandercock 1991). Egg pockets range from 50–70 cm in diameter and from 9–24 cm deep (Tautz 1977, van den Berghe and Gross 1989). The average number of eggs deposited per egg pocket ranges from 300 to 1,200, with the most frequent number being 800 to 900 (Sandercock 1991). Fecundity and egg size generally increase with the size of the female (Allen 1958, Ivankov and Andreyev 1969, Stauffer 1976). Shapovalov and Taft (1954) derived the following formula for estimating total egg production per female coho for Scott Creek, California:

$$\text{Number of Eggs} = 0.01153 \times \text{fork length (cm)}^{2.9403}$$

Published fecundity estimates are summarized in Table 1. Beacham (1982) found significant regional and annual variability in the fecundity of coho salmon, in addition to the relationship between fecundity and length. Beacham and Murray (1993) examined data for 40 coho salmon populations and found only a weak association between fecundity and latitude. The results suggested that female coho salmon in long-migrating, upper



Table 1: Coho Salmon Fecundity Estimates

Location	Number of eggs	Source	Notes
British Columbia (Oliver Creek)	2,267	Foerster (1944)	
British Columbia (Beadnell Creek)	2,789	Foerster (1944)	
British Columbia	2,500–5,000	Hart (1973)	55 -70 cm long
British Columbia	2,100–2,789	Scott and Crossman (1973)	
British Columbia (Nile Creek)	2,310	Wickett (1951)	
British Columbia (Cultus Lake)	2,300	Foerster and Ricker (1953)	
British Columbia	2,699	Neave (1948)	Several stocks
British Columbia (Big Qualicum River)	2,574	Fraser et al. (1983)	Range \pm 549; 14 year average
Washington (Minter Creek)	2,500	Salo and Bayliff (1958)	Range 1,900–3,286; 18 year average
Washington	1,400–5,700	Scott and Crossman (1973)	40–70 cm long
Oregon (Fall Creek)	1,983	Koski (1966)	n=92
California (Scott Creek)	1,000–3,550	Shapovalov and Taft (1954)	Range found for females 56 - 76 cm fork length
California	1,000–5,000	Moyle (1976)	
California	1,400–5,700	Moyle et al. (1989)	
California	2,610	Beacham and Murray (1993)	Standardized for female of 520 mm postorbital-hypural length
California (Jolly Giant Creek, Humboldt County)	3,184	Miyamoto (1979)	Mean fecundity at mean postorbital-hypural length of 55.5 cm (n=14) (cited in Beacham 1982)
California (Jolly Giant Creek, Humboldt County)	3,040	Miyamoto (1979)	Fecundity adjusted to 53.6 cm postorbital-hypural length (cited in Beacham 1982)

river locations were smaller and less fecund than those in more coastal streams due perhaps to a greater allocation of energy reserves to migration rather than gonadal development. Standardized fecundities for females of 520 mm postorbital-hypural length were found to be lowest in California (2,610 eggs/female), Vancouver Island, British Columbia (2,470 eggs/female), and Queen Charlotte Island, Alaska (3020 eggs/female). Ocean conditions may also influence fecundity. Johnson (1988) reported reduced fecundity of Oregon coho salmon related to the 1982-83 El Nino episode that affected conditions in the northeast Pacific. Because coho exhibit little variation in marine residency period,



ocean conditions favoring increased growth and thus higher fecundity upon maturity (van den Berghe and Gross 1989, Fleming and Gross 1990) may result in greater competition among the next generation of fry (Quinn 1994).

Two separate tactics may be used by male coho in fertilizing the eggs laid by a female, depending upon whether the male is a two-year-old jack or a three-year-old adult (Gross 1985). Adult, or “hooknose” males are adapted for fighting other males to achieve dominance over other males and the opportunity to fertilize a defended female’s eggs. Jacks employ a “sneaking” tactic, using refuges such as rocks, debris, or shallow areas near females that are constructing redds and rushing in to fertilize some of the eggs during the act of spawning between a female and a dominant “hooknose” male. The eggs of a female may thus be fertilized by more than one male (Gross 1984, Sargent et al. 1987). Gross (1985) estimated that the separate fitnesses of these alternative life history strategies approaches equality, thus suggesting that each exists in a “mixed evolutionarily stable strategy” with the other.

Larger juvenile or smolt coho salmon tend to return as jacks (Wallis 1968, Hager and Noble 1976, Gross 1991). Factors that may influence juvenile body size include genetics, egg size, time of hatching, water flow, temperature, quality of feeding territory, productivity of stream, predation pressure, and population density (Gross 1991).

There are indications that fertilization rates under natural conditions are very high, close to the percent ages of eggs found fertilized under the ideal conditions existing in hatcheries (Shapovalov and Taft 1954). Hobbs (1937) found that various species of salmonids had average fertility rates of over 99% under natural conditions.

Suitable temperatures for spawning adult coho salmon range from 4.4–9.4°C, according to Bell (1986). Adult coho in Oregon have been observed spawning at temperatures ranging from 2.5°C to 12.0°C (Burner 1951). Briggs (1953) reported coho salmon spawning in California at temperatures of 5.6°C to 13.3°C.

The total number of eggs deposited per female depends on the number of eggs which are retained by the spawned out fish. Shapovalov and Taft (1954) estimated that fewer than 50 eggs were left in the female after spawning, and hypothesized that the number of unspawned eggs is independent of the size of the fish. Since this number is small relative to the egg production of the female, Shapovalov and Taft (1954) made no adjustment in their productivity estimates for undeposited eggs. Other investigations have reported even fewer eggs remaining in spawned out females, with averages of 4 eggs per female in Prairie Creek, California (Briggs 1953); 4 eggs per female in Fall Creek, Oregon (Koski 1966); and 7–16 eggs per female in Kamchatka, Russia (Semko 1954).

Females continue to guard the redd and prevent superimposition by other females until they are too weak to maintain position in the current (Briggs 1953). Various studies have reported that the post-spawning survival time for females averages from 8 to 13 days (Briggs 1953, Willis 1954, Crone and Bond 1976, van den Berghe and Gross 1986). Larger females appear to be able to guard for a longer period perhaps because of their greater energy reserves (van den Berghe and Gross 1986, 1989).

Redd Characteristics

The hydraulic characteristics of the redd aid in keeping the majority of the eggs in the gravel during laying and prevent loss of eggs due to the current. Shapovalov and Taft



(1954) estimated that 97% of the eggs spawned lodge in the pit and are properly buried. Authors studying other salmonids similarly found very high percent ages of eggs to lodge in the redd, with studies by Hobbs (1937) concluding that at least 97.5% of brown trout eggs lodged in the redds at the time of spawning.

Burner (1951) reported that the average area of a coho salmon redd was 2.8 m², similar to the value (2.6 m²) reported by Crone and Bond (1976) as the average area of gravel disturbed by a spawning coho. Burner (1951) found that the area required by a spawning pair of coho was 11.7 m², and Sandercock (1991) reported that inter-redd space is usually about three times the size of the redd (see Table 2).

Table 2: Coho Salmon Redd Size Estimates

Redd size (m ²)	Source	Comments
2.8	Burner (1951)	
1.5	Sandercock (1991)	Summarized from Briggs (1953) and Gribanov (1948)
2.6	Crone and Bond (1976)	
5.2	Buck and Barnhart (1986)	“Completed redd (containing several nests)”

Van den Berghe and Gross (1984) found that larger coho females in a wild population in Washington dug significantly more egg pockets than smaller females. In addition, larger females dug deeper redds, burying their eggs as much as 2.5 times deeper than smaller females. Because females compete aggressively on the spawning grounds for suitable redd sites, and later-arriving or better-competing females may dig up eggs laid by previous spawners, broods of larger females are probably less susceptible to redd superimposition because there are fewer potential competitors that can dig as deep (Van den Berghe and Gross 1984). Thus, the authors concluded that there was likely to be a selective advantage to larger bodied females. Holtby and Healey (1986) however, concluded that large size was not necessarily always selected for, which would help explain the range of adult female sizes they observed in the spawning run. Small females may be more likely to spawn in sites with lower flows and smaller gravels; these sites may be less susceptible to scour than sites selected by the larger females (Holtby and Healey 1986).

Gravel sizes used by coho salmon for construction of redds range from 1.3 to 10.2 cm in diameter, based on criteria formed for other Pacific salmon species (Bjornn and Reiser 1991). Burner (1951) reported that 85% of coho salmon redds found in the Columbia River occurred in gravels of 15 cm diameter or smaller; only 10% of redds occurred in gravels of larger size. In studies of coho salmon conducted in laboratory aquaria, Dill and Northcote (1970) reported higher egg-to-fry survival (52–94%, depending on egg density and burial depth) in gravels of 3.2–6.3 cm diameter than in smaller gravels of 1.9–3.2 cm diameter.

In the smaller streams typical of coastal coho salmon spawning habitat, redds are typically located in the faster water of the transitional area at the downstream end (or “tail”) of pools where they feed into riffles (Hazzard 1932; Hobbs 1937; Smith 1941; Briggs 1953; Stuart 1953). The downstream end of pools is where flow tends to intrude into the gravel, thereby resulting in good intergravel flow and smaller amounts of fines,



which may explain the preference shown for this habitat (Platts et al. 1979). Thompson (1972) reported that spawning coho select depths > 18 cm and velocities of 30–91 cm/s. Smith (1973) recorded similar depths and velocities in riffles, observing a minimum depth of 15 cm for redds and velocities at preferred redd sites ranging from 21–70 cm/s.

Incubation and Emergence

Following deposition in the gravel, coho salmon eggs incubate for 35–50 days (Shapovalov and Taft 1954). Incubation time is inversely related to water temperature. In hatcheries, eggs hatch in about 38 and 48 days at average temperatures of 11° and 9°C, respectively (Hassler 1987). Shapovalov and Taft (1954) report similar incubations periods from Waddell Creek, California of 38 days at 10.7°C and 48 days at 8.9°C. Laufle et al. (1986) reported that 86–101 days were required for hatching when water temperatures drop to 4.5°C. The degree days (the sum of the number of degrees [°C] over zero of the incubation water, accumulated on a daily basis) required for hatching were found to be 418 to 432 by Hassler (1987), 407 to 427 by Shapovalov and Taft (1954), and approximately 421 by Laufle et al. (1986). These findings were fairly consistent, averaging about 421 degree days.

Water temperature affects not only the length of time to hatching, but also the survival of the eggs. Recommended water temperatures for coho salmon egg incubation are 4–13.3°C (Davidson and Hutchinson 1938, Bell 1973; Reiser and Bjornn 1979), although eggs will develop normally at lower temperatures if initial development has progressed to where the eggs are tolerant of cold (Reiser and Bjornn 1979). Beacham and Murray (1990), compiling data from Velsen (1987) and additional sources, noted that coho salmon are apparently adapted to low water temperatures during incubation, showing the highest survival rates of all five Pacific salmon species at incubation temperatures of 1.5°C. Coho also appear to be among the most poorly adapted of the five species for surviving high incubation temperatures. Data compiled by Beacham and Murray (1990) indicated that constant incubation temperatures of 13.5°C resulted in 50% embryo mortality. In addition, although egg size was more important in determining salmon alevin weight, incubation temperature was found to be more important in determining alevin length. Coho alevin and fry were found to be proportionately larger when incubated at temperatures of 4°C than at 8°C or 12°C. The authors relate these findings to the fact that coho are among the latest spawning of the Pacific salmon species. Critical ranges of water temperatures for incubation and other life stages reported by various authors are summarized in Table 3.

After hatching, salmon larvae (alevins) remain in the gravel while undergoing further development and absorption of the yolk sac. Because alevins can move while in the gravel, they have the advantage over eggs of being able to alter the environmental conditions under which further development takes place. Coho salmon alevins are initially photonegative, although this response appears to progressively weaken during gravel incubation (Dill 1969, Mason 1976b). The resulting downward movement appears to be an adaptive mechanism to prevent premature emergence of alevins that are located close to the surface of the gravel bed (Sandercock 1991).

Emergence begins 2–3 weeks after hatching, and may continue for an additional 2–7 weeks (Shapovalov and Berrian 1940). In California streams, emergence occurs from March until May (Hassler 1987). Fraser et al. (1983) found that the total heat requirement for incubation in gravel (spawning to emergence) was $1,036 \pm 138$ degree days.



Table 3: Water Temperature Relationships For Coho Salmon

Life stage	Temperature Range (°C)	Comments	Source
Adult Migration	7.2–15.6	Suitable for upstream migration	Bell (1986)
Adult Migration	> 12.7	Disease infection rates in coho increase markedly	Fryer and Pilcher (1974), Holt et al. (1975), Groberg et al. (1978)
Adult Migration	≤ 13	Recommended to minimize prespawning mortality	Wedemeyer (pers. comm.), as cited by McMahon (1983)
Adult Migration	≥ 25.5	Lethal to migrating adults	Bell (1973)
Spawning	2.5–12.0	Observations in Oregon	Burner (1951)
Spawning	4.4–9.4	Considered suitable	Bell (1986)
Spawning	5.6–13.3	Observations in California	Briggs (1953)
Incubation	4.4–13.3	Considered optimum	Bell (1973); Reiser and Bjornn (1979)
Incubation	4–11	Considered optimum	Davidson and Hutchinson (1938)
Rearing	5–17	Growth occurs	Brungs and Jones (1977)
Rearing	9–13	High growth rate observed	Stein et al. (1972)
Rearing	18	Growth rate slowed considerably	Stein et al. (1972)
Rearing	> 20	Decreases in swimming speed occur	Griffiths and Alderdice (1972)
Rearing	> 20.3	Growth ceases	Bell (1973)
Rearing	22.9–25.0	Upper incipient lethal temperature at acclimation temperatures of 5–23°C	Brett (1952)
Smolt	< 10	Prevents accelerated smolting	Wedemeyer et al. (1980)
Smolting and Emigration	< 12	Prevents shortened duration of smoltification and onset of desmoltification and disease infection	Wedemeyer et al. (1980)

Many alevins emerge at night (Shapovalov and Taft 1954, Mason 1976b), which presumably decreases vulnerability to predation (Shapovalov and Berrian 1940, Bams 1969, Mason 1976b, Godin 1980).

Survival to emergence of salmonid eggs and alevins is closely related to the quality of spawning gravels available to them. Eggs and alevins require sufficient amounts of dissolved oxygen for good survival and normal development. The size distribution of the gravels affects their permeability—the relative resistance to flow through the gravels. Permeability of gravels, in combination with flow (actually—hydraulic head) and dissolved oxygen concentration, determine the delivery of dissolved oxygen to the eggs and alevins and thus their survival. Fine sediments within the gravels tend to decrease their permeability and reduce the amounts of dissolved oxygen reaching incubating eggs and developing alevins (Wickett 1954, Coble 1961, McNeil 1962a, 1966, Ringler and Hall 1975, Woods 1980). Fine sediments may also impede or obstruct the emergence of



alevins; this occurrence, known as “entombment” is often associated with a seal or cap of fine sediments that are deposited in the upper layers of gravel after redd construction is completed.

Survival of coho salmon eggs and alevins is strongly influenced by the dissolved oxygen supply within the redd (Mason 1976b). Dissolved oxygen requirements appear to be highest in the period during and following hatching of the eggs (Alderdice and Brett 1957, Fast et al. 1982). A positive correlation between intergravel dissolved oxygen within the redds and survival of coho salmon embryos was observed in the field by Phillips and Campbell (1961) who determined that dissolved oxygen levels must average 8 mg/l for embryos and alevins to survive well. Survival of coho salmon eggs and alevins drops significantly at dissolved oxygen levels at or less than 6.5 mg/l and levels below 3 mg/l have been found to cause very high rates of mortality (Coble 1961, Shumway et al. 1964, Davis 1975). Reductions in levels of dissolved oxygen can result in delayed hatching and emergence, smaller size of emerging fry, and increasing incidence of developmental abnormalities (Alderdice et al. 1958, Coble 1961, Silver et al. 1963, Shumway et al. 1964, Mason 1976b). Several studies have shown that Pacific salmon embryos subjected to chronic low dissolved oxygen concentrations hatch later and result in smaller fry than those from embryos incubated at higher dissolved oxygen concentrations (Silver et al. 1963, Shumway et al. 1964, Chapman 1988). Reiser and Bjornn (1979) recommend that dissolved oxygen levels be maintained at or near saturation and temporary reductions fall no lower than 5 mg/l for successful incubation. Table 4 shows egg deposition to emergence survival estimates for coho salmon in the literature.

Gravel permeability, generally measured with a standpipe, has been shown to be directly related to the survival of coho salmon eggs and alevins (Cloern 1976). Permeability of spawning gravels may be affected by gravel characteristics such as porosity, size, shape, depth, and arrangement of gravel particles, and, perhaps most importantly, amount of fine sediments (Vaux 1962, McNeil and Ahnell 1964, Cooper 1965). Fine sediments (also referred to as “fines”) such as silt, clay, and sand reduce gravel permeability by filling in the interstices of the gravel particles. The intrusion of fines into spawning gravels can result in marked effects on gravel permeability (McNeil and Ahnell 1964, Peters 1965, Moring 1975). Fines are often measured as a percentage of the spawning gravel by weight of sediment that is smaller in diameter than some designated size. The proportions of fines that have the potential to result in detrimental effects may vary within and among streams; to a large extent because permeability is a function of the full range of sediment particles represented, not just the fines (Moring 1975). Moring (1975) suggested that the direct measurement of permeability by use of a standpipe may be more useful in evaluating spawning gravel quality than methods relying on determination of proportion of fines present because it more directly assesses the extent to which interstitial flow has been reduced.

Most studies have used percent fines as a proxy for permeability measurements. In the Clearwater River of Washington, Tagart (1976) found that dissolved oxygen in nine redds was inversely related to the percentage of fines under 0.85 mm diameter. The amount of fine sediments less than 3.3 mm in diameter occurring naturally in gravels used by spawning coho was found to vary from 27.0–54.9% in unlogged Oregon watersheds (Koski 1966, Moring and Lantz 1974). An inverse relationship between the proportion of fines less than 3.3 mm diameter in spawning gravels and subsequent survival



Table 4: Egg-To-Emergence Survival Estimates for Coho Salmon

Location	Percent survival	Source	Notes
Waddell Ck., California	65 to 85	Shapovalov and Taft (1954)	Good conditions
	75	Harrison (1923)	
California	74.3	Briggs (1953)	22 redds
Oregon coastal streams	54.4	Koski (1966)	Maximum survival of 21 natural redds in most productive of 3 streams sampled
	53.7	Carl (1940)	
Oregon coastal streams	45	Koski (1966)	In natural redds with 20% fines
Alesea River, OR tributaries	23.7-37.9	Moring and Lantz (1975)	In areas affected by increased sedimentation
Clearwater River, WA	32	Tagart (1976)	In redds in which 20% of fines were smaller than 0.85 mm diameter
Clearwater River, WA	30	Cederholm et al. (1981)	Survival at about 15% fines < 0.85 mm in diam.
Oregon coastal streams	27.1	Koski (1966)	Mean survival
	15 to 27	Neave (1949), Crone and Bond (1976)	Average conditions
Oregon coastal streams	27.1	Koski (1966)	21 coho redds, coastal streams
Oliver Ck. and Beadnell Ck., B.C.	24.3	Foerster (1944)	Average from 8 years data
Clearwater River, WA	20	Cederholm et al. (1981)	Survival at about 20% fines < 0.85 mm in diam.
	16.2	Shaw and Maga (1943)	Some silting present in gravels
Clearwater River, WA	15	Cederholm et al. (1981)	Survival at about 25% fines < 0.85 mm diam.
Clearwater River, WA	13.6	Cederholm et al. (1981)	Minimum survival in poorest stream
	10.2	Shapovalov and Berrian (1940)	Heavy silting
	0.9 to 77.3	Tagart (1984)	19 redds

to emergence of coho salmon fry has been well-documented (Koski 1966, Hall and Lantz 1969, Cloern 1976). Lower survival to emergence of coho salmon was documented by Tagart (1984) at higher concentrations of and fine sediment (particle size < 0.85 mm), and survival was positively correlated with gravel sizes between 3.35 mm and 26.9 mm in diameter. Survival to emergence of fry has been found to be high in laboratory and natural stream investigations where the percentage of fines is less than 5% (Koski 1966, Hall and Lantz 1969, Cloern 1976). In all of the above studies, survival to emergence was observed to drop sharply at over 15% fines.

The construction of a redd by a female salmon will generally reduce the amount of fines within the gravels (Burner 1951, Kondolf et al. 1993). After the redd is completed, fine sediments, particularly sands transported as bedload, can intrude into the gravels of the



redd and reduce permeability or form a seal (Einstein 1968) that can result in entombment. In Koski's (1966) study, he postulated that much of the mortality in the redds within the streams studied was caused by the inability of fry to emerge from the gravel. Phillips et al. (1975) tested the percentage of emergence of swim-up coho fry placed in various gravel-sand mixtures. Mean emergent survival was 96% in control groups without sand, but decreased precipitously when levels of sand were above 20%. Additional studies have shown that mortality may be caused by entombment rather than low levels of dissolved oxygen (White 1942, Cooper 1965, Phillips and Campbell 1961, 1975, Hausle and Coble 1976, Turnpenny and Williams 1980). Selective mortality against larger fry may occur in substrates containing higher amounts of sand or smaller gravels, because smaller fry can move through the smaller interstitial spaces present in these substrates (Koski 1975).

On the basis of numerous studies, Reiser and Bjornn (1979) provided general habitat guidelines for salmonid incubation that recommend less than 25% by volume of fines \leq 6.4 mm diameter. Table 5 shows the results of studies that have investigated the effects of fines on spawning success in both natural streams and laboratories

Table 5: Percent Fines Present In Spawning Gravels And Effects on Coho Salmon Emergence

Percent Fines	Location	Source	Notes
30% fines 1–3 mm diam.	laboratory	Phillips et al. 1975	40% emergent survival of planted fry (fry were not incubated in the gravels)
20% fines 1–3 mm diam.	laboratory	Phillips et al. 1975	65% emergent survival (planted fry that were not incubated in these gravels)
20% fines	OR	Koski 1966	45% survival to emergence
20% fines < 0.85 mm diam.	Clearwater River, WA	Cederholm et al. 1981	20% survival to emergence
25% fines < 0.85 mm diam.	Clearwater River, WA	Cederholm et al. 1981	This proportion of fines resulted in 15% survival to emergence in natural redds.
15% fines < 0.85 mm diam.	Clearwater River, WA	Cederholm et al. 1981	This proportion of fines resulted in 30% survival to emergence in natural redds.
13% fines < 0.85 mm diam.	laboratory	Cederholm et al. 1981	This proportion of fines resulted in 15% survival to emergence in laboratory troughs.
10% fines < 0.85 mm diam.	laboratory	Cederholm et al. 1981	This proportion of fines resulted in 30% survival to emergence in laboratory troughs.
> 20% of fines < 0.85 mm diam.	Clearwater River, WA	Tagart 1976	18% survival to emergence from redds in which more than 20% of fines < 0.85
\geq 15% fines < 0.84 mm diam.	Wisconsin	Cloern 1976	No survival to hatching occurred when eggs were planted in study redds with this proportion of fines.
\leq 20% of fines < 0.85 mm diam.	Clearwater River, WA	Tagart 1976	32% survival to emergence occurred from redds.

Other factors which affect egg survival include gravel movements during floods, low flows, freezing, bird and insect predators, and fungal infections (Sandercock 1991). In coastal California, floods are probably the most important of these sources of mortality. Gravel mobilization can cause scouring of eggs from the gravels during incubation or



cause mortality by physically injuring embryos that are in the extremely sensitive stages following fertilization (Gangmark and Bakkala 1960). Several researchers have concluded that movements of gravel can be very detrimental to survival during incubation (Neave and Wickett 1953, Wickett 1958, Skud 1958, McNeil 1962b). Management activities that reduce roughness of the stream channel (i.e., the streambed becomes finer) may result in more frequent mobilization of spawning gravels and increased egg mortality.

Because the level of fines in spawning gravels is an important component of salmonid incubation success, land management activities which affect this parameter can have a significant effect on salmonid populations. Upslope activities such as livestock grazing, timber harvesting, or road construction can lead to accelerated soil erosion and sedimentation, thereby increasing the fine sediment load in downstream areas. The increased fine sediment load causes deposition of fines in spawning habitat such as pool tail outs and glides, which results in decreased spawning success for salmonid species.

Rearing Coho salmon populations are generally believed to be limited by density dependent mechanisms operating within the freshwater environment (Allen 1969, Chapman 1962, 1966, McFadden 1969, Marshall and Britton 1990, Meehan and Bjornn 1991). As House and Boehne (1985) pointed out: “Streams have finite carrying capacities for salmonids, producing similar numbers of young annually if spawning and rearing habitat is not degraded and stocks overfished”; this has been demonstrated for coho salmon in Pacific Northwest streams (Wickett 1951, Salo and Bayliff 1958, Hunter 1959, Chapman 1965). The availability of suitable rearing habitat is believed to be the limiting factor that governs the number of juvenile coho salmon that can be produced from a stream system (Larkin 1988, Chapman 1962, 1966). Juvenile coho select habitat primarily on the basis of water velocity (Shirvell 1990), preferring low velocity habitats throughout the juvenile rearing period. In coastal streams, low velocity habitat conditions are primarily produced by large woody debris (LWD). Depth and light intensity also influence juvenile coho habitat selection, but to a lesser degree than velocity (Shirvell 1990). It has been shown that juvenile coho prefer the cover afforded by woody debris to that provided by rocks and substrate (steelhead parr show the opposite affinity) (Bustard and Narver 1975a, Bugert 1985). The presence or absence of LWD in streams thus has overwhelming influence on the suitability of these streams for rearing coho salmon. McMahon and Reeves (1989) postulate that LWD could be considered a “keystone” habitat feature for salmonids because of its overwhelming influence on channel morphology (e.g., pool creation, bank condition), sediment and organic matter retention, water velocities, and cover availability. Numerous studies on juvenile coho salmon published in the past ten years have investigated the relationship between juvenile coho habitat and LWD. The following discussion reviews the literature on habitat use and preferences of rearing coho salmon and discusses the role of LWD.

Low velocity stream habitats preferred by juvenile coho include pools, beaver ponds, and off channel habitats such as side channels, backwaters, and tributaries on floodplains or terraces (Everest et al. 1985, Glova 1986, Taylor 1988, Bugert and Bjornn 1991). Smaller coastal mountain streams tend to have more confined channels and less availability of off channel habitats; in these streams, pools constitute the primary rearing habitat in streams for coho salmon. Large woody debris creates pool habitat in streams by influ-



encing channel morphology (Bisson et al. 1987, Andrus et al. 1988, Bilby and Ward 1989, Robinson and Beschta 1990a, 1990b, Sedell and Beschta 1991) and provides areas of reduced velocity under high flows. In all seasons it also provides conditions of reduced light intensity that are of use for protection against predation. In coastal streams throughout the coho's range, LWD is said to be the primary factor governing stream habitat diversity (Swanson et al. 1976, Lisle 1981, Bryant 1982, Beschta and Platts 1986). Several field studies have related density of juvenile salmonids to pools or hydraulic conditions associated with LWD (Bisson et al. 1988, Dolloff and Reeves 1990, Bugert et al. 1991, Taylor 1991).

Large, deep pools appear to be the most preferred, although pools as shallow as 0.3 m may be used (Nickelson et al. 1992b). Positive correlations between standing crop of juvenile coho salmon and pool volume have been reported by Nickelson and Reisenbichler (1977) and Nickelson et al. (1979). Studies by Nickelson (pers. comm., as cited in McMahon 1983) in Oregon indicate that pools of 10–80 m³ or 50–250 m² in size that have sufficient riparian canopy for shading are optimum for juvenile coho production. As juvenile salmonids age and grow, they tend to be associated with the deepest pools available to them (Dolloff 1983, Dolloff and Reeves 1990).

In summer, when flows are low and most growth of juvenile coho occurs, pools are important for feeding since they constitute the most efficient foraging areas available. In the winter, during the period of lower temperatures, higher flows, and freshets, coho reduce or stop feeding; pools are important during this period as shelter from high water velocities that may result in downstream displacement. Deeper pools may also be helpful for mediating temperature extremes in both summer and winter. The availability of suitable pool habitat in a stream may limit juvenile coho production during either season, depending upon local conditions.

Other instream habitats—such as riffles, glides, and runs—may be occupied by juvenile coho during the summer, but the densities found in these habitats are usually much lower than those found in pool or off channel habitats (Edie 1975, Everest et al. 1985). Riffles play an important role in coho stream productivity because these areas are the source for much of the aquatic invertebrate production of a stream. A pool/riffle ratio of 1:1 has been proposed as optimum for providing food and cover for rearing coho salmon (Ruggles 1966). Human disturbances that result in loss of LWD tend to increase amount of riffle areas in streams while decreasing pool area; therefore, availability of riffle habitat is not believed to be often limiting to coho populations.

Table 6 shows the range of densities of rearing juvenile coho reported in the literature.

Summer Habitat Preferences

During the summer, juvenile coho salmon prefer pool habitats but may also utilize glides and riffles to a lesser extent (Everest et al. 1985, Glova 1986, Bugert and Bjornn 1991). Everest et al. (1985) found very low summer densities of juvenile coho to occur in glide and riffle habitat (average 0.04 fish/m²) when compared to densities found in beaver ponds (average 1.43 fish/m²). Since low velocities are more common throughout the channel in summer, distribution with regards to LWD distribution may not be as apparent as it is in winter. In addition, some studies have indicated that cover, such as that provided by LWD and/or riparian vegetation, is not as important in influencing juvenile dis-



Table 6: Juvenile Coho Salmon Rearing Densities

Season	Density (fish/m ²)	Source	Notes
Summer	0.745	Murphy et al. (1986)	Fry + parr, old growth, from 6 streams in southeast Alaska
Summer	1.776	Murphy et al. (1986)	Fry + parr, from 6 streams with buffer strips in southeast Alaska
Summer	1.696	Murphy et al. (1986)	Fry + parr, clear-cut, from 6 streams in southeast Alaska
Winter	0.085	Murphy et al. (1986)	Fry + parr, old growth, from 4 streams in southeast Alaska
Winter	0.205	Murphy et al. (1986)	Fry + parr, from 4 streams with buffer strips in southeast Alaska
Winter	0.087	Murphy et al. (1986)	Fry + parr, clear-cut, from 4 streams in southeast Alaska
Summer	4.3	Shirvell (1990)	Fry, Kloiya Ck., British Columbia. Average among different rootwad conditions
	0.07-1.31	Beechie et al. (1994)	Smolt, production from side-channel slough
	0.27	Beechie et al. (1994)	Smolt, production from tributary areas that were not slough-like
Summer	1.7	Beechie et al. (1994)	Parr, rearing density in highest quality summer habitat-average winter water temperatures ≥ 7 C
Winter	1.8	Beechie et al. (1994)	Parr, rearing density in highest quality winter habitat-average winter water temperatures ≥ 7 C
Summer	1.7	Beechie et al. (1994)	Parr, rearing density in highest quality summer habitat-average winter water temperatures < 7 C
Winter	5.0	Beechie et al. (1994)	Parr, rearing density in highest quality winter habitat if average winter water temperatures are < 7 C [reflects smaller amount of useable habitat (pools)]
Summer	0.04	Everest et al. (1985)	Parr, average density in riffle/glide habitats (1982-85) in Fish Creek, Oregon
Summer	1.43	Everest et al. (1985)	Parr, average density in beaver ponds (1982-85) in Fish Creek, Oregon
	0.85	Mundie and Traber (1983)	Smolt, densities in side-channel pools
June	1.3	Nielsen (1992)	Parr, density calculated for pools; Washington
August	1.1	Nielsen (1992)	Parr, density calculated for pools; Washington
	0.1-1.0	Allen (1969)	Age 1+ salmonids 7-10 cm in length
	0.17	Allen (1969)	Age 1+ salmonids 10 cm in length



tribution during the summer (Bustard and Narver 1975a, Grette 1985, Murphy et al. 1986, Taylor 1988, Nielsen 1992, Fausch 1993), while other studies show that coho prefer areas of reduced light intensity in summer (Bugert and Bjornn 1991). Distribution with regards to LWD or other cover during the summer may vary depending on the relative type and intensity of predation threat present (Bugert et al. 1991).

In late summer or fall, when stream temperatures are highest and flows lowest, the juvenile coho move into deeper pools and feeding rate is diminished (Shapovalov and Taft 1954). Low summer flows result in reduced rearing area, increased vulnerability to predators, increased stranding, and increased water temperature. Availability of pool habitat at this time may limit coho production in some streams, especially those that tend to have very low flows or high temperatures in the summer or those where stranding and/or predation may tend to occur (Smoker 1955, Nickelson et al. 1979, Peterson and Quinn 1994). Burns (1971) found that the highest mortality of juvenile coho during summer occurred in the periods of lowest flow. Correlations of low summer flow to low catches of adult coho two years later have been demonstrated in work by Neave (1948, 1949) and Smoker (1953). Therefore, even though juvenile coho may not be selecting habitat conditions (low velocities, reduced light intensities) based on LWD cover in the summer, the distribution of coho is directly influenced by LWD, because it creates the pools which may constitute the only available habitat during low summer flows.

Although some studies indicate that summer pool area may be limiting to coho production in some streams, other studies have shown that winter habitat is ultimately limiting. An experiment by Mason (1976a) that increased summer low flow biomass by seven fold through supplemental feeding, but that did not result in higher smolt production than what might be expected from expected natural levels in the following spring illustrates this well (Cederholm and Peterson 1989). Availability of high quality summer habitat is unquestionably important because most growth occurs within this period; overwinter survival of salmonids has been shown to increase with larger size (Hartman et al. 1987, Hartman Scrivener 1990), and size at smolting has been correlated with ocean survival of anadromous salmonids (Peterman 1982, Bilton et al. 1982, Ward et al. 1989). Therefore, survival and fitness of coho are likely to be dependent on the quality of summer habitat and foraging positions in some streams (Fausch 1993).

Water temperatures suitable for juvenile coho are determined by both preferences shown by juvenile coho or by temperatures that result in growth. Brett (1952) reported that coho showed preference for temperatures around 12–14°C. Brungs and Jones (1977) reported growth of juvenile coho at temperatures from 5°C to 17°C. High growth rates were observed by Stein et al. (1972) at temperatures from 9°C to 13°C. Growth may increase with higher temperatures as long as food supplies are not limiting; however, increases of only 4°C have been shown in laboratory streams to decrease productivity for coho salmon where food is limiting (Hughes and Davis 1986).

With low summer flows and high ambient air temperatures, water temperatures can approach or exceed the upper lethal temperature of 25°C for juvenile coho. Brett (1952) found that exposure to temperatures in excess of 25°C or a quick rise in temperature from less than 20°C or a quick rise in temperature from less than 20°C to 25°C resulted in a high mortality rate. High water temperatures that are below those considered to be lethal may also result in negative impacts to rearing coho. Stein et al. (1972) reported that growth rate in juvenile coho salmon slows considerably at 18°C, and Bell (1973)



reported that growth of juvenile coho ceases at 20.3°C. Decreases in swimming speed may occur at temperatures over 20°C (Griffiths and Alderdice (1972). During smolting, juvenile coho are very sensitive to increases in temperature. Wedemeyer et al. (1980) reported that smoltification and the onset of desmoltification may accelerate at temperatures over 10°C and recommended that water temperatures during the smolt period remain below 12°C to prevent shortened duration of smoltification, onset of desmoltification, and increases in disease infection.

Winter Habitat Preferences

In the winter, availability of LWD and pools associated with this material are crucial to juvenile coho salmon survival in coastal streams. Although juvenile coho use pools in all seasons, they show a preference for certain natural pool types in the winter that afford cover and the greatest refuge from high water velocities. Mid-channel pools or glides without LWD which hold large numbers of coho fry in the summer may become largely unsuitable in the winter because of increased flows (Grette 1985, Sullivan 1986). Other stream habitats, such as riffles, glides, or pools without cover were not found to be used by overwintering coho in a study by Heifetz et al. (1986) in Alaskan streams. Bustard and Narver (1975) and Tschaplinski and Hartman (1983) found juvenile coho to be generally absent from habitats lacking cover in the winter.

An experiment by Ruggles (1966) indicated that coho do not utilize rubble as overwinter cover. Juvenile coho may migrate into secondary channels on floodplains or terraces (Cederholm and Scarlett 1982, Peterson and Reid 1984), or may travel long distances to overwinter in tributaries to the spawning stream (Peterson 1982a, 1982b, Cederholm and Scarlett 1982) to escape high or fluctuating flows in the main channel.

The majority of juvenile coho in coastal streams appear to overwinter in deep pools within the stream channel that have substantial amounts of cover in the form of woody debris (Bustard and Narver 1975a, Scarlett and Cederholm 1984, Murphy et al. 1986, Brown and Hartman 1988). Swimming ability decreases with temperature and as water temperatures fall below 9°C, juvenile coho become less active (Mason 1966). Feeding is reduced and growth is negligible during the winter period of higher flow and lower temperatures (Shapovalov and Taft 1954). Numerous studies have shown that pools with adequate cover are the most important habitat elements used by juvenile coho in the winter (Hartman 1965, Bustard and Narver 1975a, 1975b, Tschaplinski and Hartman 1983, Murphy et al. 1984, Bisson et al. 1985, 1988, Everest et al. 1985, Glova 1986, Heifetz et al. 1986, Swales et al. 1986, Hartman and Brown 1987, Cederholm et al. 1988, McMahon and Hartman 1989, Shirvell 1990, Nickelson et al. 1992b). Instream cover and areas of slow water are essential for protection against displacement by high flows, and cover from predation (Bustard and Narver 1975a, Mason 1976b, Hartman et al. 1982). Deep (>45 cm), slow (<15 cm/s) areas in or near (<1 m) instream cover of roots, logs, and flooded brush appear to constitute preferred habitat (Hartman 1965, Bustard and Narver 1975a), especially during freshets (Tschaplinski and Hartman 1983, Swales et al. 1986, McMahon and Hartman 1989). Underwater observations by Shirvell (1990) found that 99% of all coho salmon fry observed were occupying positions downstream of natural or artificial rootwads during artificially created drought, normal, and flood streamflows.

Because juvenile coho show narrower preferences for pool habitat types in the winter than in the summer, habitat limitations may be more common in the winter. Lack of



suitable winter habitat may result in poor survival and many studies indicate that availability of winter habitat may be the ultimate factor limiting to coho in rearing areas (Chapman 1966, Mason 1976b, Chapman and Knudsen 1980, McMahon 1983, Nickelson et al. 1992b). Tschaplinski and Hartman (1983) documented substantial decreases in juvenile coho salmon numbers in fall and winter, particularly in response to seasonal freshets. The authors found that habitats such as deep pools, logjams, and undercut banks with woody debris lost fewer fish during high flow events and maintained higher juvenile populations over the winter. Rodgers (1986) (as cited by House et al. 1991) found only 9% of the juvenile coho found during the summer remaining as smolts in Knowles Creek, a stream system that lacked good overwintering habitat.

Further evidence for the importance of LWD for juvenile coho comes from numerous studies where human disturbances to the stream have resulted in the absence of this habitat element. Removal of LWD generally leads to loss of those habitat features most important to rearing juvenile coho and a decline in salmonid abundance (Bryant 1980, Toews and Moore 1982, Lestelle and Cederholm 1984, Dolloff 1986, Elliott 1986, Fausch and Northcote 1992).

LWD in forested streams has been lost primarily by activities such as splash damming, stream cleaning, streamside logging and snagging, agricultural conversion, and fire (McMahon and Reeves 1989). Sedell and Luchessa (1982) document the extensive removal of LWD and debris jams from streams in the past 150 years. Stream channels tend to become simpler and less stable after the removal of LWD, and the habitat complexity that provides substrate diversity, refuges from current velocity, and cover used by spawning, feeding, and resting salmonids is also lost (McMahon and Reeves 1989). Several studies have shown that removal of LWD results in wider and shallower channels with little pool volume available at low flows (Bilby 1984, Bisson and Sedell 1984, Heifetz et al. 1986). Cutting of streamside vegetation and LWD removal has been observed to decrease pool habitat and increase riffle area (Bryant 1980, Everest and Meehan 1981, Bisson and Sedell 1984). In clear-cut areas, Bisson and Sedell (1984) observed that the frequency of both pools and riffles appeared to decline, suggesting that the normally stepped stream profile had changed to a steeper gradient.

Juvenile survival of coho salmon is often substantially reduced in disturbed streams when compared with undisturbed streams. Many studies have documented reductions in rearing habitat as a result of the removal of LWD (Tschaplinski and Hartman 1983, Bisson and Sedell 1984, Koski et al. 1984, House and Boehne 1987). The number of overwintering coho is low in stream reaches where debris abundance has been reduced by removal associated with streamside logging (Tschaplinski and Hartman 1983, Murphy et al. 1986) or other disturbance (Martin et al. 1986). Tschaplinski and Hartman (1983) and McMahon and Holtby (1992) found that the estimated capacity of streams for coho smolts was reduced in clear-cut reaches of their study areas—debris volume and smolt abundance were significantly lower than in reaches bordered by a forested buffer strip. Nickelson et al. (1992b) found that pool habitat that had been enhanced by the addition of large woody debris supported significantly higher coho densities than pools without woody debris. Their addition of woody debris to artificially-dammed pools increased the density of juvenile coho inhabiting the pools to levels found in naturally dammed pools. Older or larger juvenile coho appear to benefit most from availability of deeper pools and cover. A study of sections of a British Columbia stream found that standing crop of age



1+ coho was significantly greater in pools with complex cover, and was positively correlated to pool volume in a given section of stream (Fausch and Northcote 1992).

Presence or absence of woody debris may also affect mating strategies used by coho salmon. Gross (1991) notes that streams with less LWD may favor hooknose males over jacks while increase in either debris (that serves as hiding cover) or shallow water (that is less accessible to large males) may favor jacks and their sneaking mating strategy.

Researchers sometimes quantify the amount of LWD in streams by using the number of pieces per 100 m that are large enough to influence the channel characteristics. House and Boehne (1986) estimated that, in a relatively undisturbed section of a small stream in Oregon, there were 18 pieces of LWD per 100 m large enough to influence the channel. Sedell et al. (1982, 1984) found that five (1982 study) and four (1984 study) pieces of LWD per 100 m either dammed the stream channel or directly influenced it by creating pool habitat in undisturbed channels of the South Fork Hoh River, Washington. Bilby and Ward (1989) surveyed characteristics of LWD in western Washington streams and found that size of stable pieces of LWD increases with stream size. Their values suggest that streams under 5 m in width require trees of about 30–35 cm in diameter to be useful as fish habitat and to be able to persist as stable LWD in the channel. Streams of about 10 m in width require larger trees of about 45 cm in diameter. In a basin in which over 50% of the forest had been logged in the past 20 years, House and Boehne (1986) found that the reduction of large conifers in the riparian zone resulted in only 0.4 pieces per 100 m of LWD large enough to influence channel morphology.

Outmigration

Coho salmon smolts in California begin to migrate to the ocean in the spring, approximately one year after emergence. Shapovalov and Taft (1954) noted that nearly all of the outmigration in Waddell Creek, California took place during the months of April and May. Outmigration was observed to begin as early as mid-March in some years. Coho appear to have a more protracted outmigration period than other salmon species (Holtby et al. 1989). Holtby et al. (1989) found that, out of 17 years of trapping smolts in Carnation Creek, British Columbia, there was only one year in which 50% of the smolts emigrated in less than 14 days. During their study, the period which 50% of smolts emigrated usually lasted at least 21 days. As the emigration is made up of larger yearling salmonids, there may be less predation pressure that would make synchronized movement a survival advantage.

Throughout their range in North America, coho usually migrate downstream as yearling smolts. A smaller portion of the outmigration is made up of age 0+ fish migrating downstream as fry, but these fish are believed to have low probability of surviving to adulthood (Otto 1971, Crone and Bond 1976, Hartman et al. 1982). In some river systems, mostly in the more northern parts of their range, coho may rear in freshwater for an additional year or more before migrating to sea, but the proportion is generally low.

Photoperiod, temperature, and water flow are among the environmental factors influencing smoltification (Parry 1960, Hoar 1965, Wagner 1974, Clarke et al. 1978, 1981, Wedemeyer et al. 1980, Clarke and Shelbourn 1981). Juvenile coho must generally reach a fork length of about 100 mm for successful smoltification (Drucker 1972, Crone and Bond 1976). Conte et al. (1966) found that maximum salinity tolerance in coho salmon corresponded to a 90 mm threshold size. Shapovalov and Taft (1954) found outmigrat-



ing smolts to measure an average size of from 103.11 to 116.61 mm in Waddell Creek, California.

Downstream movements of salmon smolts have been found to correspond to changes in water temperature, flow, and perhaps lunar or tidal phase. Unlike other salmon species that migrate as fry or that smolt at only a few months of age, coho smolts migrating downstream as yearlings may be less vulnerable to predation and therefore may not need to employ synchronous migration as a predator swamping tactic. McMahon and Holtby (1992) found that the number of coho salmon smolts migrating over a counting fence in Carnation Creek, British Columbia was not influenced strongly by stream discharge or lunar phase. They did find a significant increase between numbers of migrants during temperature declines. Coho smolts outmigration may be influenced by local factors which signal favorable conditions for rearing downstream within estuaries. Holtby et al. (1989) found that variability in stream temperatures during spring accounted for 60% of the variability in the median date of coho emigration in Carnation Creek. They hypothesized that this timing/temperature relationship and the timing of adult spawning were adaptations for synchronizing outmigration with “windows of opportunity” or advantageous conditions in the ocean or rearing environment. Low flows and/or high temperatures have been observed to accelerate smoltification and advance the timing of outmigration (Shapovalov and Taft 1954, Wedemeyer et al. 1980).

Behavioral changes from those observed during the summer have been found to accompany smoltification. Territories may be defended less vigorously and coho appear to migrate downstream in small schools (Hoar 1951, Shapovalov and Taft 1954, McMahon and Holtby 1992). Hoar (1951) observed that coho salmon undergoing smoltification in laboratory experiments showed a decline in aggression and associated territorial and hierarchical behavior and formed aggregations presumably adaptive for life in the sea. In Carnation Creek, British Columbia, McMahon and Holtby (1992) found 95% of smolts to be aggregated in groups of five or more fish. During the smolt outmigration, aggregation size increased and was significantly greater in the estuary than in stream sections. Large coho salmon smolt aggregations have been observed beneath docks in Oregon estuaries (McAllister 1988) and in low water areas of a Washington estuary having log pilings (Moser et al. 1991). McMahon and Holtby (1992) believed that schooling and cover-seeking behavior of smolts was a continuation of winter parr behavior. When temperatures in the spring increased above 7 °C, they did not observe the return to territorial behavior typical for parr rearing in the summer.

McMahon and Holtby (1992) found that smolts tended to be distributed near large woody debris in Carnation Creek study reaches. Over 80% of smolts (1260 observations) were within 1 m of debris, and 95% were within 2 m of debris. The debris jam sites were characterized by deep (> 1 m), slow-moving (< 15 cm/s) water, overhead shade, and structurally complex cover afforded by rootwads, undercut banks, and submerged logs. Most smolts were associated with debris having volumes > 14 m³. Smolts were noticeably scarce in areas having deep pools and/or bankcover that lacked large debris. The authors theorized that the cover and velocity refuges afforded by woody debris would be important for avoiding predation and preventing displacement into the ocean prior to completion of smoltification.



Outmigration generally has been observed to occur at night in coho salmon (Shapovalov and Taft 1954) and in anadromous salmonids in general (Meehan and Siniff 1962, Mace 1983); this is likely a predator avoidance tactic as piscivorous fish generally rely on sight for prey capture.

After reaching the estuary, coho salmon may remain for a few months residency. McMahon and Holtby (1992) found that coho smolts remained in the Carnation Creek estuary for about 2 months (April and May). A similar period of estuarine residency was found for an Oregon estuary (Myers and Horton 1982). Even a short period of residency in the estuary may result in enhanced survival as growth appears to be very rapid in this habitat. Coho sampled in nearshore areas have measured 140–220 mm (Berg 1948, Fisher et al. 1984). The rapid growth during estuary rearing may reduce vulnerability to nearshore predators, which are believed to be a major source of ocean mortality for coho salmon (Holtby et al. 1990). Once smolts reach the estuary and nearshore ocean waters they may encounter several new predators in addition to those they encountered during their freshwater rearing stage (juvenile steelhead, cutthroat trout, herons, mergansers, and mink). New predators include fish such as dogfish (*Squalus acanthias*), lamprey (*Lampetra* spp.), and sharks (e.g. *Lamna ditropis*); piscivorous birds such as gulls (*Larus* spp.), and loons (*Gavia* spp.); and marine mammals such as harbor seals (*Phoca vitulina*), sea lions (*Eumetopias jubatus* and *Zalophus californianus*) and orcas (*Orcinus orca*). Salmon appear to constitute only a small proportion of the diet of most marine mammals, however (Bowlby 1981, Sandercock 1991).

Ocean Life

Diet

During the coho salmon's first few months at sea they are opportunistic feeders consuming a wide variety of zooplankton and fish prey, depending on the season or area of collection (Brodeur 1992). In early summer (May-July), while still relatively small, their fish prey tend to be small planktonic larvae; later in the summer they become more piscivorous and the diversity in their diets decreases, consisting mainly of juvenile marine fishes (Brodeur 1992). There is a general trend of increasing fish prey in the diet with increasing body size (Brodeur 1991). In most northeast Pacific coastal estuaries and bays, coho and chinook salmon consume mainly invertebrate prey while smaller in size (McCabe et al. 1983, MacDonald et al. 1987, as cited by Brodeur 1991). The diets of coho and chinook salmon at sea are more piscivorous than other Pacific salmon; this is reflected in the morphology of their gill rakers, which are fewer in number, shorter, and more widely spaced than those of sockeye and pink salmon (Beacham 1986). Some differences in diet between chinook and coho may be attributable to the differences in depths utilized by the two species. Beacham (1986) reported that coho were most abundant at depths of less than 18 m, while chinook were most abundant at depths greater than 18 m. By far the most dominant invertebrate prey are euphasiids; in Beacham's (1986) sample of 1,364 non-empty stomachs, 54% of total stomach contents were made up of invertebrate prey with 51% of total contents comprised of euphasiids. Larger salmon may switch from smaller sand lance to larger herring and juvenile rockfish as they grow (Beacham 1986). Sand lance were found to occur in 27% of all non-empty stomachs and comprised 27% of total stomach volume. Herring comprised less than 1% of stomach contents of coho under 40 cm fork length, but made up 25% of total stomach volume for coho over 60 cm fork length (Beacham 1986). Prey consumed by coho



salmon are generally less than one-fifth their length, but can be up to one-half of the salmon's length (Brodeur 1991).

There are conflicting opinions about whether or not density-dependent mechanisms are operating at sea for coho salmon. Emlen et al. (1990) found some evidence that coho salmon smolts interact in the nearshore area in a way that generates density feedback on survival. They reported this data mainly to caution against the discounting of density-dependent mortality at sea. If density-dependent mortality controls coho numbers at sea, hatchery programs to enhance fishery production may be largely ineffective. McGie (1984) had concluded that density-dependent mortality was important in years of low upwelling, but that it was absent in years of high upwelling, when ocean conditions are more favorable for salmon. Pearcy and Fisher (1988) report that most variation in ocean mortality of coho salmon apparently occurs during the first few weeks of ocean residence. Nearshore conditions during late spring and early summer along the coasts of Washington, Oregon, and California may dramatically affect year-class strength (Scarnecchia 1981). Coho along the California and Oregon coasts may be more sensitive to ocean conditions as these areas do not have the extensive bays, straits, and estuaries found in Washington and Alaska. These landscape features may serve to buffer oceanographic effects (Bottom et al. 1986).

Ocean Distribution and Migration

Coho salmon are found in the ocean along the Pacific coast from Chamula Bay, Mexico (Miller and Lea 1972), to Point Hope, Alaska, through the Aleutians, and from the Anadyr River, USSR, south to Hokkaido, Japan (Scott and Crossman 1973). Coded-wire-tag (CWT) marked coho salmon from southern Oregon and northern California are usually recovered from California coastal waters (65–92%) with some recoveries off of the Oregon coast (7–34%) (NMFS 1995). The genetic characteristics of individual coho salmon stocks, along with environmental factors, probably determines the timing and pattern of seaward dispersal (Heard 1991). Seasonal movements of salmon at sea are complex and not as yet linked with any major oceanographic feature (Burgner 1991). Homeward migration to the natal stream, however, is strongly oriented, rapid, and precise (Cury 1994). Salmon migrating to their home stream may travel at speeds approaching those maximum for sustainable swimming (Burgner 1991).

Population Trends and Threats

Populations of anadromous salmonids in the Pacific Northwest and California, have declined in recent years (Brown et al. 1994), as indicated by decreased commercial and sport harvests (Lufkin 1991; Nehlsen et al. 1991). Coho salmon have shown substantial coastwide decreases in freshwater distribution and abundance (Konkel and McIntyre 1987). Postulated reasons for decline of coho salmon populations in California include: stream degradation related to poor land use practices, genetic breakdown of native stocks, introduced diseases, overfishing, floods and drought, and climatic change (Brown et al. 1994).

Loss of stream habitat is widely acknowledged as the single biggest cause of declines of anadromous salmonids in general in the Pacific Northwest, and of coho salmon in particular (Nehlsen et al. 1991; Reeves and Sedell 1992; The Wilderness Society 1993). Most of the habitat loss has been the result of watershed disturbances associated with logging, livestock grazing, urbanization, agriculture, mining, and other human activities (Brown et al. 1994, NMFS 1995). These activities typically result in the loss of complex stream



habitat that is characteristic of coho salmon streams (Sandercock 1991), particularly when there is a reduction in the amount of large woody debris and an increase in fine sediment input to the watershed.

Effects of Logging and
Road Construction

Northwest and central coastal California have very erodible soils (Judson and Ritter 1964, as cited in CDFG 1994). Logging and associated road building are some of the primary human disturbances that may result in increased erosion within watersheds. Increased levels of sediment transport may fill in pools, reducing juvenile coho rearing habitat. Embeddedness of substrates with fine sediments may reduce production (Crouse et al. 1981), primarily by reducing aquatic invertebrate production. The filling in the coastal estuaries reduces the area very high quality rearing habitat available to coho before going to sea; filling in of estuaries has been documented in north coastal California rivers (Puckett 1977, Hofstra 1983, Smith 1987). Aggradation of streams from erosion may result in less stable spawning gravels and mortality of eggs and embryos due to gravel mobilization during freshets (Nawa et al. 1990). Gravel instability may also affect colonization of the streamside area by riparian vegetation. Extremely aggraded streams may have surface flows that are reduced or are completely lacking in the summer (CDFG 1994). Large accumulations of sediment may block juvenile and adult migrations where tributaries join main rivers (Payne and Associates 1989). Intrusion of fine sediments from logging activities can cause profound effects on spawning gravel permeability (McNeil and Ahnell 1964, Peters 1965, Moring 1975).

Water temperatures in streams may increase both through removal of the streamside canopy as well as through increased sedimentation. Removal of riparian canopy exposes more of the stream channel to direct solar radiation. Sedimentation was reported by Hagans et al. (1986) to cause increased stream temperatures by replacing the reflective gravel substrate with darker sediment that could store more solar radiation. In addition, sedimentation can reduce intergravel flow and more of the water column will therefore be exposed to solar radiation (Hagans et al. 1986). Higher temperatures during the incubation period can cause coho to emerge earlier and be displaced by winter freshets (Scrivener and Anderson 1984). Temperatures in over 25% of the pools of the main fork of the Eel River were found to be over 26.7°C in the summer (Kubicek 1977). These temperatures are reported as lethal to juvenile coho and even temperatures that are 7°C lower would be expected to result in reduced growth and survival. In addition to its effects on stream temperatures, removal of the riparian canopy also results in reduced input of terrestrial invertebrates and litterfall to the stream, reducing allochthonous input used in stream production.

Effects of Hatcheries and
Introductions of
Non-Native Stocks

The genetic integrity of native coho salmon stocks has been affected by the introduction of large numbers of hatchery fish and transplants of different stocks in California. Coho salmon stocks from the Columbia River basin, Alsea River, Washougal River and others were transferred by the California Department of Fish and Game (CDFG) in the past to supplement runs or restore populations (CDFG 1994). Bartley et al. (1992) noted that transplants of different stocks within California, and plantings of Oregon and Washington stocks, may have effects such as disruption of locally adapted gene complexes, swamping and homogenization of native gene pools, and transmittal of nonadaptive traits from hatchery stocks to native stocks. Differences in the genetic structure of native and



hatchery stocks can potentially lead to lower survival of subsequent hybrid generations compared with pure wild fish (Steward and Bjornn 1990; Hindar et al. 1991).

Studies have shown lower survival of juvenile coho that were offspring of hatchery strays or hatchery-wild hybrids (Smith et al. 1985, Chilcote et al. 1986). Hatcheries have not proven successful in the restoration of native coho stocks (Withler 1982, Solazzi et al. 1993, Nickelson 1986). The CDFG now has an internal policy that seeks to minimize interactions between wild and hatchery populations.

Stocking of juvenile coho may reduce survival of native stocks through increased competition for limited space or food in rearing streams (Nickelson 1986). Survival of juvenile hatchery fish has been shown to be lower than that of native coho (Nickelson 1986). Competition for spawning sites can occur when the number of native spawners are swamped by larger numbers of hatchery reared fish. The accelerated growth of fry in hatcheries may result in increased incidence of juvenile coho that return as jacks (Gross 1991). The interaction of hatchery and native stocks also increases disease potential, since native stocks may be exposed to disease organisms originating from hatcheries that they would not be exposed to under normal conditions. Some California hatcheries with coho stocks used for providing eggs (Iron Gate, Trinity River, Mad River, and Warm Springs hatcheries) and coho stocks from the Noyo River and Big Creek that provide eggs for artificial propagation are known to harbor Bacterial Kidney Disease (BKD), a chronic and slow developing infection that can have adverse effects on coho smolts (CDFG 1994, NMFS 1995).

Effects of Ocean Harvest

Overfishing is often mentioned as a major factor contributing to the decline of coho salmon, but its effects are poorly known because catch of wild and hatchery fish are rarely separated (Steward and Bjornn 1990). Ocean commercial and sport fishing harvest salmon stocks in a nondiscriminating fashion. Harvest levels that may be appropriate for hatchery stocks to sustain may not be able to be sustained by depressed wild stocks. If conditions within freshwater spawning and rearing areas are poor, salmonid fishes cannot rebound quickly from overfishing and ocean harvest may therefore become an impediment to recovery of populations (CDFG 1994). Coho salmon in California are particularly vulnerable to overfishing because most females have a strict 3-year life span; populations therefore lack resilience to withstand excessive harvest occurring over successive years than would be provided by a wider range of ages. Overharvest in a single year can decimate the entire population of a stream that has only one strong year class remaining. Although commercial and recreational fisheries have been severely restricted or closed along much of the Pacific coast for the past few years, these measures have not resulted in increased returns of coho (NMFS 1995).

This may be due to continuing habitat degradation and decreasing productivity in streams (Pearcy et al. 1992).

An intensive commercial fishery that preferentially captures the larger and older “hooknose” male coho salmon may enhance jack mating success on the spawning grounds and subsequently increase the frequency of jacks in the population since jack maturity appears to be heritable (Iwamoto et al. 1983, Gross 1991). Reductions of populations may also increase the frequency of coho returning as jacks (Gross 1991) since growth rates may increase at the lower densities found in depressed populations (Bilby and Bisson 1992).



Effects of Ocean
Conditions and Climate

Natural changes in climatic conditions may also have had an adverse effect on the coho salmon population as evidenced by the decline associated with ocean warming trends in the northeast Pacific during the period of 1976–1983 (Nickelson 1986; Lawson 1993; Brown et al. 1994). Generally favorable conditions prevailed during the period from about 1945–1975, but upwelling along the Oregon coast has declined in the past 20 years, and coho salmon marine survival has declined at a similar rate (Bottom et al. 1986, Pearcy et al. 1992, Lawson 1993). The evidence for the positive effects of upwelling is not always strong and the mechanisms that may create benefits to coho survival from coastal upwelling are not always clear (Scarnecchia 1981, Holtby et al. 1990, reviewed by Pearcy 1992). Upwelling along the Pacific coast may be driven by 40-60 year cycles in wind patterns (Ware and Thompson 1991).

Ocean warming along the British Columbia and California coasts has been reported for the last fifty years (Freeland 1990, Roemmich 1992). During periods of climate change such as this, El Nino events may become particularly intense (Quinn et al. 1986). El Nino events are associated with unusually warm ocean surface temperatures and changes in coastal currents and upwelling (NMFS 1995). These ocean conditions lead to decreased primary and secondary productivity and changes in the distributions of predator and prey species resulting in reduced growth, survival, and fecundity of salmon (Johnson 1988, NMFS 1995). The 1982–83 El Nino episode had widespread effects on the northeast Pacific and was associated with an estimated 58% reduction in adult coho survival and a 24–27% reduction in fecundity in populations that rear off of the Oregon coast and south (Johnson 1988). If climate warming continues as predicted, there may be a progressive deterioration of marine habitat for salmonids that could forestall or curtail the recovery of more favorable ocean conditions subsequent to El Nino episodes (Lawson 1993).

Changes in the marine food web may also contribute to a decline in coho salmon marine survival. Pacific sardine and hake populations, both of which are used as food by coho salmon, have collapsed during the last century and have not recovered in the most recent period of more favorable ocean conditions (Ware and Thompson 1991). Reductions in ocean food supply and intensive hatchery planting may lead to density dependent ocean mortality (Bordeur 1990).

Oceanic effects have been compounded by droughts in 1976–1977 and 1986–1992, which have completely dried up some streams, and restricted access to or degraded spawning and rearing conditions in other streams (Brown et al. 1994). Lack of sufficient rainfall during the period of October through January may affect migration of adult coho. Access to streams through estuaries may be delayed if the opening of the sandbar does not occur when adults are ready for upstream migration. Low flows during migration periods may result in greater vulnerability to predation (CDFG 1994). The long duration of the recent drought may have resulted in the loss of some local populations because of the three year life span of most adult coho (CDFG 1994). Floods have had deleterious effects as well (such as those occurring in 1964), scouring the stream channel and decreasing spawning success and rearing habitat. Although catastrophic drought and flood events have always occurred, they have been made more serious in recent years by the compounding effects of human-induced stream degradation.

Effects of Predation

Predation is not believed to be a major factor affecting the decline of coho populations, although it may retard recovery when populations are severely depressed (CDFG



1994). Introduced Sacramento squawfish in the Eel River are known to prey on juvenile salmonids and may be expected to increase in numbers if the warming of the main river channel continues; increased predation rate on juvenile coho could result (CDFG 1994). The loss of habitat complexity in streams may make juvenile coho more vulnerable to avian predation by such species as kingfishers and herons. A study by Lonzarich and Quinn (1994) showed that predation losses may be up to 50 percent higher in the simplest habitat type available, indicating the importance of pools having adequate cover and/or depth. Some marine mammals feed on both juvenile and adult salmonids, however Bowlby (1981) found salmon to comprise only a minor part of harbor seal and sea lion diets in the Klamath River estuary.

***Stream Habitat
Enhancement and
Restoration***

The science of stream habitat restoration and enhancement is still relatively new and rapidly evolving. Attempts to increase salmonid production in streams must include careful evaluation of each system in order to identify those aspects of habitat that are limiting to the population. Increasing the availability of habitat for one salmonid life history stage may not result in increased overall production if habitat is actually limiting at a later life stage. Limiting factors may change from year to year depending on conditions within the watershed and may also interact with other habitat elements (Reeves et al. 1991). Furthermore, stream rehabilitation may be effective in the long term only if the watershed is protected from continuing degradation. A stream and its valley are an inseparable ecological unit (Hynes 1975), and therefore protection of riparian habitat within the watershed is by far the most effective stream restoration and enhancement technique (Reeves et al. 1991). The following reviews coho salmon habitat enhancement and restoration efforts that have been documented in the literature.

Management activities such as stream cleaning and timber harvesting that have resulted in the loss of large woody debris (LWD) in streams (and reduced recruitment from valley slopes) may result in decreased habitat complexity in stream channels and reduced cover available to rearing coho salmon. Stream channel morphology may also change in response to LWD removal, with pools becoming reduced in area and frequency. Because LWD is an important component of juvenile coho salmon habitat (Koski et al. 1984, Sedell and Swanson 1984, Sedell et al. 1984, Bisson et al. 1987, House and Boehne 1987), and its role as a determinant of physical stream dynamics has been well documented (Swanson et al. 1976, Bryant 1983, Bilby 1984, Beschta and Platts 1986, Lienkaemper and Swanson 1987), stream habitat restoration and enhancement efforts aimed at increasing coho smolt production have been largely focused on the addition of LWD or structures to imitate the effects of LWD.

Habitat enhancement efforts designed to increase coho salmon production are generally aimed at providing increased summer and winter rearing habitat for juveniles, or increasing the quality and/or quantity of spawning gravels. Successful enhancement of rearing habitat often involves creating or augmenting existing habitat complexity and cover, and creating off-channel or nearshore habitats, and deep pools. Since juvenile coho salmon prefer low-velocity areas for overwintering (see rearing section), velocity-reducing structures and habitats such as dammed pools, alcoves, and off-channel or nearshore areas can be effective in providing increased winter rearing potential for coho. Numbers of rearing and spawning coho, and other salmonids, increased substantially in East Fork Lobster Creek, a coastal Oregon stream, following installation of V-shaped rock gabions (House



and Boehne 1985). The gabions increased the diversity of the stream bed, trapped gravel, and created shallow gravel bars and deep, covered pools. The gabion structures increased the size and number of pools at treated sites, and improved pool quality. Newly created pool habitat in treated areas consisted of dammed pools upstream from gabions and plunge, secondary channel, and backwater pools located downstream from gabions, as well as side channels, scour pools, and undercut banks. A later study by the same authors used gabions to simulate LWD in a section of Tobe Creek, Oregon where logging had resulted in almost total removal of LWD (House and Boehne 1986). Installation of gabions resulted in a three-fold numerical increase in juvenile coho salmon, and increased salmonid density to levels found in an unlogged section of stream containing large amounts of LWD. These results indicated that the coho salmon rearing capabilities of Tobe Creek could be improved by adding some type of structure to act as a scouring agent for pool formation.

Creation of pools by blasting and excavating into sandstone bedrock substrate successfully increased numbers and size of coho salmon rearing in Vincent Creek, located in the Smith River basin on the central Oregon coast (Anderson and Miyajima 1975, Anderson 1981). Temperatures in the enhanced pool were lower than in the riffles during summer and the peak high temperature period was shorter. In a small mud substrate tributary to the Clearwater River on the Washington coast, explosives were used to create pool habitat for juvenile coho salmon, and cover was provided by addition of bundles of woody debris (Cederholm et al. 1988). A low dam was created to keep the pond inundated. Two years of monitoring before and after the pond construction (4 years total) indicated that 90% of coho smolts produced after the habitat construction came from the constructed pond. Average overwinter survival of marked juvenile coho salmon increased from 11 percent before to 56 percent after pond construction. Length and weight of smolts were also increased as a result of the project. The authors attributed the increased survival at least in part to extensive shallow areas that are ideal for aquatic food production and winter rearing habitat.

Everest et al. (1985) studied the benefits to overwintering coho of a pond constructed on a flood terrace adjacent to Fish Creek, Oregon. The pond made a significant contribution to smolt production—although it only represented about 25% of the habitat area it contributed an addition of 18.9% to the total smolt run. Overwinter survival in the pond appeared to exceed 50% survival while overwinter survival in Fish Creek was observed to be only half that.

Spawning gravel enhancement has also been an important component of stream habitat restoration and enhancement. Most gravel enhancement has focused on the cleaning of gravels to reduce effects of sedimentation and the addition of gravels or specially engineered spawning channels where gravel availability is limiting. Suitable spawning gravels may be limiting in a coho salmon stream if the watershed has experienced increased erosion and sedimentation due to timber harvest and road building, mining, livestock grazing, or other human activities in the basin. Dams or large debris jams may interfere with the recruitment of new gravels into the stream from upstream sources, and extreme flow events may result in lapses in gravel availability due to bedload movements. Benefits gained by cleaning of gravels are usually only temporary unless the sources of sedimentation are identified and the problem solved (Reeves et al. 1991).



If there is adequate movement of the gravel bedload, structures designed to catch and hold gravels may be used to increase spawning habitat. Gabions have been the most successful and widely used structures for gravel catchment, especially with recent design modifications and placement methods resulting in structures capable of withstanding the force of stream flows and creating the desired outcomes (Anderson and Cameron 1980, Anderson et al. 1984, as cited by Reeves et al. 1991). The most successful use of gabions has been in a V-shaped structure with the point facing downstream and the ends toed 1–1.5 m into the stream banks and riprapped in order to prevent the stream from flowing around the structure. A 1% slope of the structure from bank to midstream allows it to dissipate the energy of the stream and create better pools than a structure perpendicular to the flow. These V-shaped structures are best placed in a series, with the bottom of the upstream structure level with the top of the downstream structure. The upstream structure acts to dissipate the stream's energy and creates a pool downstream, while the downstream gabion accumulates and retains gravel (Reeves et al. 1991). Gabion series such as these have achieved most success in stream gradients of less than 1.5%, but have also been used in steeper areas (Reeves et al. 1991).

In addition to the use of structures such as gabions to increase gravel catchment, gravel placement has been successful in improving spawner density in some situations (West et al. 1965a, 1965b, Gerke 1973, 1974, as cited in Reeves et al. 1991). In Alaska, a ground-water tributary was enhanced to provide habitat for coho spawning and rearing by deepening the stream, adding gravels, and developing a 1.5% gradient (Bachen 1984, as cited by Reeves et al. 1991). These techniques, developed in British Columbia (Lister et al. 1980, as cited by Reeves et al. 1991), were successful in maintaining water levels sufficient for both spawning and rearing of coho salmon.

Gravel cleaning machines (Mih 1978, Mih and Bailey 1981) and bulldozers (Reeves and Roelofs 1982, Heiser 1972, West 1984, as cited in Reeves et al. 1991) have been used in attempts to reduce the amount of fine sediment present in spawning gravels. These methods have achieved mixed results. Adult salmon appear to avoid recently cleaned gravels, which perhaps are more unstable than undisturbed substrates (Wilson 1976, as cited by Reeves et al. 1991). A small amount of fine sediment may actually be desirable in spawning gravels for retaining and stabilizing the larger material (Reeves et al. 1991).

Management of the streamside or riparian zone is another critical component of efforts to maintain coho salmon habitat. Benefits of streamside management zones cited by Hicks et al. (1991) include:

- 1 Maintenance of stable stream banks, with overhanging cover and undercut banks.
- 2 Protection for stable large wood in the channel.
- 3 Provision for a continuing source of large wood for the future.
- 4 Maintenance of stable streambed and channel, minimizing increased sedimentation.
- 5 Prevention of substantial modification of stream temperature.

Riparian zone enhancement activities include riparian plantings or revegetation and fine sediment management. Sedell and Beschta (1991) stress the need for additional research and administrative studies “to understand how various tree species, root systems, debris sizes, etc., function through time with channels of different widths, gradients, and valley form. Such information is necessary to aid decisions regarding where, what kind, and



how many trees (or shrubs) are to be selectively planted or maintained in riparian areas to optimize fish habitat requirements over the long term...For a wide variety of resource values, including fisheries, reestablishing the functional attributes of streamside vegetation is crucial to improving the bank characteristics and riparian conditions for streams and rivers...”



Large Woody Debris Removal

Relationship Of Large Woody Debris To Coho Salmon Production

Essential to the development of effective mitigation and monitoring plans is identifying the factors that are most important in controlling the salmon population size. One of the working hypotheses concerning coho salmon ecology and management in Mendocino County streams is that large woody debris (LWD), and the rearing habitat that it provides, may currently be the most important factor limiting coho populations. The well-documented role of LWD in coho salmon ecology, combined with the observation that the recent decline of coho salmon in California appears to be somewhat coincident with large-scale LWD removal programs led quite naturally to this hypothesis.

To explore and develop this hypothesis L-P attempted to document the history of LWD removal in Mendocino County. In particular, L-P hoped to identify as closely as possible where and when LWD was removed and the objectives of the different LWD removal programs (e.g., to provide fish passage through selective removal of LWD or complete removal of all LWD). This analysis, by providing an estimate of the extent and magnitude of LWD removal in different watersheds, allows L-P to begin assessing the biological significance of LWD removal and the extent to which the removal programs may have contributed to the decline of coho salmon. In addition, knowing which streams have been cleared, and to what extent, greatly assisted us in evaluating both the degree to which current habitat conditions reflect past LWD removal programs and the potential for using LWD for habitat enhancement.

Some of the investigations that were conducted as part of preparing the SYP had as one of their objectives to begin evaluating this hypothesis. One component of the stream geomorphology investigation was to assess, for each of the different channel types, the pool-forming processes and the resulting morphology (especially pool depth) with and without LWD. This assists in evaluating the potential of different channels to provide more habitat if LWD were present. The fish habitat investigation collected data that could be used to begin assessing whether the availability of spawning gravels or rearing habitat provided by LWD is more important in limiting coho salmon populations in different watersheds.

If this hypothesis proves to be true, the management of LWD should play a central role in any coho salmon mitigation or enhancement strategy.

History Of Large Woody Debris Removal In Mendocino County

Logging of forests in Mendocino County began following the establishment of Ft. Bragg in 1854. Before railroads were constructed for logging, streams were used to transport logs to the mills. Trees were felled and bucked on the hillsides, and the logs were transported by teams of oxen along skid roads to the streams. The first log skidding used teams of oxen. Oxen were eventually replaced by the "steam donkey," and later by the tractor. Skid roads were excavated by hand into the hillsides, and skidding was sometimes aided by half-burying logs side by side to form a path (sometimes referred to as a corduroy road) along which the oxen could more easily drag the logs.

At the stream, one of two methods would be used to transport the logs to the mill. The first method involved stacking the logs in the stream bed, in anywhere from five to 40 tiers (Jackson 1975). This was done throughout the drier months of summer and fall in preparation for the winter rains and releases from upstream dams which would supply



enough water to carry them downstream (Jackson 1975). The second method, which was primarily used in larger streams, involved loading the logs into lakes that formed behind temporary splash dams (Jackson 1975). Sometimes, topography permitting, trees were felled directly into the lakes. When water conditions were right, the splash dams would be breached, often with the concurrent release of upstream dams for added water. If the head of water generated from the dam release was sufficient to get the logs moving, they would be floated all the way downstream to the mills on the coast, scouring the stream beds and banks as they went. Both of these techniques required "channel improvement" to allow logs to flow freely down the channels. Channel improvement involved removing anything in or along the channel that could obstruct a log drive. This included riparian vegetation, large boulders, sunken logs, and anything else that would create an obstruction or complex flow conditions (Napolitano 1996).

Tractors used extensively in the late 1940s and 1950s after conclusion of World War II enabled access to large tracts of forested land which were previously difficult to log, and accelerated the rate of logging. Use of the tractors facilitated temporary road construction into logging areas via side cuts in the steep slopes or along the stream courses. Landings were constructed in lower slope areas adjacent to or in the stream channels, and marketable timber transported from the landings or nearby roads to the sawmills via trucks.

Since regulation of forest practices during this time period was largely non-existent, protection or rehabilitation of forest land and stream channels during or after logging operations was not practiced. As a result, many of the streams were left with enormous amounts of woody debris in the channel and substantial loads of fine sediment which continued to erode from the unprotected hillsides and road failures. These conditions largely precluded the continued use of some streams by anadromous salmonids such as coho, steelhead, or chinook salmon, since the woody debris formed insurmountable migration barriers and the fine sediment rendered the spawning areas useless.

The California Department of Fish and Game (CDFG) initiated the Sports Fish Restoration Program (funded by Dingle-Johnson legislation) in the 1950s to facilitate rehabilitation of many fisheries that had been impacted by various timber, land use, and water use practices. One of the objectives of the program was to restore access to anadromous fish streams that were blocked by accumulations of woody debris left over from the logging operations. The perspective of fishery managers at that time is reflected in the following writings from one of the proposals for LWD removal:

“Stream damage has been of two types that can be helped through a stream clearance program. Both consist of adding material to the streambed that does not belong there—logging debris in the form of wood materials and soil. The logging debris may pollute the water, making it unsuitable for fish life, block migrations of fish, cover over a stream area making it unsuitable for either spawning or food production or holding the soil in the streambed. Some streambeds have been built up several feet with soil and gravel so that during periods of low flow in late summer there is little or no surface flow. Removal of much of this logging debris changes some streambeds from a low producing, stinking mud bottom to a clean gravel bottom of higher food producing nature. The actual streambed changes are made by high velocity winter flows after key material is removed. In some cases fol-



low-ups are necessary to clean out two or more layers of logging debris. It is only fair to the logging industry to say that a good deal of material in some streams got there in a natural way without assistance from logging activity. Regardless of how the material got there, its removal is beneficial to salmon and steelhead trout (CDFG ca 1970).”

The enormity of the LWD problem caused by logging practices in the logging boom of the 1940s and 1950s led to a focus on LWD removal to restore access to many miles of spawning habitat that had been blocked by LWD jams. This emphasis on LWD removal was not without merit, as substantiated by the maps and tables contained in proposal documents which described 51 migration barriers out of 835 logjams which totaled an estimated 336,791 ft³ of woody debris. For example, on Hayworth Creek in the headwaters to the Noyo River, biologists documented the presence of 17 logjams over a two mile reach. Of the 17, ten were considered to be upstream passage barriers up to 15 ft in height. One of the largest jams was estimated to be 100 ft long x 100 ft wide x 8 ft high, containing approximately 40,000 ft³ of wood.

California Department of Forestry (CDF) inmate crews were used for much of the LWD removal work, and cleared significant portions of the streams of all debris that could accumulate to form a migration barrier or act as a sediment trap. Five original documents dated between 1959 and about 1970 that proposed LWD clearance projects in Mendocino County were obtained from CDFG personnel (T. Wooster). The documents detailed the level of effort that would be required for LWD clearance of specific streams. The number of miles of stream that were currently accessible to anadromous fish and the miles that would be accessible once clearance activities were completed was documented. In many instances the upstream extreme of viable anadromous fish spawning and rearing habitat was also documented. Typically, the streams would be walked by fisheries biologist and the location and size of debris jams would be noted on topographic maps. Traced copies of many of these maps were included with the documents. The required effort for clearance was calculated by classifying the stream (Table 7) and estimating the number of stream miles needing clearance. In many instances the level of scattered debris between major logjams was also noted so that effort estimates could be adjusted accordingly.

Subsequent flood flows through these areas cleared away remaining woody debris and removed large accumulations of fine sediment. Since the stream channels had been damaged by timber harvest and much of the stream structure provided by logs had been removed, the floods resulted in significant in-channel scouring and lowered the thalweg elevation in some stream sections by as much as 10–20 feet (pers. comm., Bob Snyder, CDFG).

Areas where LWD removal operations were planned in the 1950s and 1960s are documented on Map 8 in the maps provided in the *Map Atlas: Sustained Yield Plan for Coastal Mendocino County* (L-P 1997). Confirmation that all of these operations were completed is not available in the historical record, although the current lack of LWD accumulations in most or all of these areas indicates the planned removal operations were carried out.

Because stream clearance programs occurred on such a large percentage of Northern California coastal streams and the intent was to remove all wood within the bankful



Table 7: Stream classification scheme for stream clearance activities. (Source: CDFG undated).

Classification	Description
I	Small tributaries of headwater areas having undergone extensive logging damage. Many debris areas and smaller logjams exist in this classification. The method of stream clearance will be to remove all material from the stream bed above high water mark. The estimated labor and equipment cost for this classification is \$800 per mile plus travel time.
II	Small tributaries or headwater areas having undergone moderate logging damage. Scattered small logjams and debris areas will occur in this classification. The method of stream clearance will be to remove all material from the stream bed above high water mark. The estimated labor and equipment cost for this classification is \$300 per mile plus travel time.
III	Small tributaries or headwater areas having undergone little logging damage, still having a few logjams needing to be removed. The method of stream clearance will be to remove all material from the stream bed above high water mark. The estimated labor and equipment cost for this classification is \$300 per mile plus travel time.
IV	Larger streams or stream sections having undergone extensive logging and having many larger logjams. The method of removal will be to cut the key logs or long logs into short lengths and allow winter rains to wash away. Burning of the logjams will also be used where there is an advantage. Estimated labor and equipment costs is \$200 per mile plus travel time.
V	Larger streams or stream sections having a few larger logjams needing to be removed. They will be removed by cutting the key logs or long logs into short lengths and allowing winter rains to wash them away. Burning of the logjams will also be used where there is an advantage. Estimated labor and equipment costs is \$100 per mile plus travel time.

channel, natural or not, it seems reasonable to conclude that there was an enormous reduction in LWD in the streams most important to coho salmon.

Subsequent to the stream clearing projects of the 1950s and 1960s, the importance of large woody debris (LWD) for the maintenance of channel structure and fish habitat (particularly for coho salmon) became more widely recognized. The Stream and Lake Improvement Program (a part of the Sport Fish Restoration Program) initiated by CDFG now includes an element that evaluates the need for any LWD removal. Debris jams which are documented barriers to upstream migration are currently modified to allow passage, but there is no longer any large scale removal of woody debris from the channel. Woody debris that enhances fish habitat and provides channel structure and stability is left in place, and restoration projects which use LWD to improve fish habitat have been implemented. Documented cases of more recent stream clearance projects conducted in the 1970s, 1980s, and 1990s are also included in Map 8 in the *Map Atlas: Sustained Yield Plan for Coastal Mendocino County* (L-P 1997).

Louisiana-Pacific acquired numerous tracts of land in Mendocino County from Georgia Pacific in 1972–1973, and has been managing the forest for timber harvest since that time. Current forest practice rules prohibit or restrict most of the harvest practices that originally resulted in the more severe stream degradation and woody debris problems described above. Cooperative efforts between L-P and resource agencies, such as CDFG, are underway to reverse much of the damage to the fisheries habitat caused by



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former land use practices. In addition, conservation strategies, which in many cases go beyond the current forest practice rules, are being developed as part of L-P's SYP and HCP planning efforts to help insure that future forest management activities maintain or enhance stream habitat for coho salmon and other native aquatic species.



6. References

- Alderdice, D. F., W. P. Wickett, and J. R. Brett. 1958. Some effects of temporary exposure to low dissolved oxygen levels on Pacific salmon eggs. *Journal of the Fisheries Research Board of Canada* 15: 229-250.
- Alderdice, D. F., and J. R. Brett. 1957. Some effects of kraft mill effluent on young Pacific salmon. *Journal of the Fisheries Research Board of Canada* 14: 783-795.
- Allen, G. H. 1958. Notes on the fecundity of silver salmon (*Oncorhynchus kisutch*). *The Progressive Fish-Culturist* 21: 163-169.
- Allen, K. R. 1969. Limitations on production in salmonid populations in streams. T. G. Northcote, editor. *Symposium on salmon and trout in streams*. H. R. MacMillan Lectures in Fisheries, University of British Columbia, Vancouver.
- Altukhov, Y. P., and E. A. Salmenova. 1986. Stock transfer relative to natural organization, management, and conservation of fish populations. N. Ryman and F. Utter, editors. *Population genetics and fishery management*. University of Washington Press, Seattle.
- Anderson, J. W. 1981. Anadromous fish projects 1981: USDI - BLM Coos Bay District. Pages 109-114 in T. J. Hassler, editor. *Propagation, enhancement, and rehabilitation of anadromous salmonid populations and habitat in the Pacific Northwest symposium*. Humboldt State University, California Cooperative Fishery Research Unit, Arcata.
- Anderson, J. W., and J. J. Cameron. 1980. The use of gabions to improve aquatic habitat. Technical Note 342. U. S. Bureau of Land Management, Denver, Colorado.
- Anderson, J. W., and L. Miyajima. 1975. Analysis of the Vincent Creek fish rearing pool project. Technical Note 274. U. S. Bureau of Land Management, Coos Bay District, Oregon.
- Anderson, J. W., R. A. Ruediger, and W. F. Hudson, Jr. 1984. Design, placement and fish use of instream structures in southwestern Oregon. Pages 165-180 in T. J. Hassler, editor. *Proceedings, Pacific Northwest stream habitat management workshop*. California Cooperative Fishery Research Unit, Humboldt State University, Arcata.
- Andrus, C. W., B. A. Long, and H. A. Froehlich. 1988. Woody debris and its contribution to pool formation in a coastal stream 50 years after logging. *Canadian Journal of Fisheries and Aquatic Sciences* 45:2080-2086.
- Armstrong, R. W., and A. W. Argue. 1977. Trapping and coded-wire tagging of wild coho and chinook juveniles from the Cowichan River system, 1975. Technical Report Service PAC/T-77-14. Field Operations Directorate, Pacific Region.
- Bachen, B. A. 1984. Development of salmonid spawning and rearing habitat with groundwater-fed channels. Pages 51-62 in T. J. Hassler, editor. *Proceedings of the Pacific Northwest stream habitat management workshop*. California Cooperative Fishery Research Unit, Humboldt State University, Arcata.
- Baker, P., and F. Reynolds. 1986. Life history and status of coho salmon in California. California Department of Fish and Game Report to the California Fish and Game Commission.
- Bams, R. A. 1969. Adaptations of sockeye salmon associated with incubation in stream gravels. Pages 71-87 in T. G. Northcote, editor. *Symposium on salmon and trout in streams*. H. R. MacMillan Lectures in Fisheries, University of British Columbia, Vancouver.
- Bartley, D. M., B. Bentley, P. G. Olin, and G. A. E. Gall. 1992. Population genetic structure of coho salmon (*Oncorhynchus kisutch*) in California. *California Fish and Game* 78: 88-104.
- Beacham, T. D. 1982. Fecundity of coho salmon (*Oncorhynchus kisutch*) and chum salmon (*O. keta*) in the northeast Pacific Ocean. *Canadian Journal of Zoology* 60: 1463-1469.
- Beacham, T. D. 1986. Type, quantity, and size of food of Pacific salmon (*Oncorhynchus*) in the Strait of Juan de Fuca, British Columbia. *Fishery Bulletin* 84: 77-89.
- Beacham, T. D., and C. B. Murray. 1990. Temperature, egg size, and development of embryos and alevins of five species of Pacific salmon: a comparative analysis. *Transactions of the American Fisheries Society* 119: 927-945.
- Beacham, T. D., and C. B. Murray. 1993. Fecundity and egg size variation in North American Pacific salmon (*Oncorhynchus*). *Journal of Fish Biology* 42: 485-508.
- Beechie, T., E. Beamer, and L. Wasserman. 1994. Estimating coho salmon rearing habitat and smolt production losses in a large river basin, and implications for habitat restoration. *North American Journal of Fisheries Management* 14: 797-811.
- Bell, M. C., editor. 1973. *Fisheries handbook of engineering requirements and biological criteria*. Contract DACW57-68-C-0086. Fisheries-Engineering Research Program, U. S. Army Corps of Engineers, North Pacific Division, Portland, Oregon.



PRELIMINARY DRAFT - COHO SALMON LIFE HISTORY

- Bell, M. C., editor. 1986. Fisheries handbook of engineering requirements and biological criteria. Fisheries-Engineering Research Program, U. S. Army Corps of Engineers, North Pacific Division, Portland, Oregon, NTIS AD/A167-877.
- Berg, L. S. 1948. Freshwater fishes of the USSR and adjacent countries. Translated from the Russian, 1962, Israel Program for Scientific Translations, Jerusalem.
- Beschta, R. L., and W. S. Platts. 1986. Morphological features of small streams: significance and function. *Water Resources Bulletin* 22: 369-379.
- Bilby, R. E. 1984. Removal of woody debris may affect stream channel stability. *Journal of Forestry* 82: 609-613.
- Bilby, R. E., and P. A. Bisson. 1992. Allochthonous versus autochthonous organic matter contributions to the trophic support of fish populations in clear-cut and old-growth forested streams. *Canadian Journal of Fisheries and Aquatic Sciences* 49:540-551.
- Bilby, R. E., and J. W. Ward. 1989. Changes in characteristics and function of woody debris with increasing size of streams in western Washington. *Transactions of the American Fisheries Society* 118: 368-378.
- Bilton, H. T., D. F. Alderdice, and J. T. Schnute. 1982. Influence of time and size at release of juvenile coho salmon (*Oncorhynchus kisutch*) on returns at maturity. *Canadian Journal of Fisheries and Aquatic Sciences* 39: 426-447.
- Bisson, P. A., and J. R. Sedell. 1984. Salmonid populations in streams in clear-cut vs. old-growth forests of western Washington. Pages 121-129 in W. R. Meehan, T. R. Merrell Jr and T. A. Hanley, editors. Fish and wildlife relationships in old-growth forests. American Institute of Fishery Research Biologists, Juneau, Alaska.
- Bisson, P. A., R. E. Bilby, M. D. Bryant, C. A. Dolloff, G. B. Grette, R. A. House, M. L. Murphy, K. V. Koski, and J. R. Sedell. 1987. Large woody debris in forested streams in the Pacific Northwest: past, present, and future. Pages 143-190 in E. O. Salo and T. W. Cundy, editors. Streamside management: forestry and fishery interactions. College of Forest Resources, University of Washington, Seattle. Contribution No. 57.
- Bisson, P. A., J. L. Nielson, and J. W. Ward. 1985. Experimental release of coho salmon (*Oncorhynchus kisutch*) into a stream impacted by Mount Saint Helens volcano. *Proceedings of the Western Association of Fish and Wildlife Agencies* 1984: 422-435.
- 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. 1969. Embryo survival and emergence studies. Salmon and Steelhead Investigation Completion Report, Job 5 Project F-49-R-7. Idaho Department of Fish and Game, Boise.
- Bjornn, T. C., and D. W. Reiser. 1991. Habitat requirements of salmonids in streams. Pages 83-138 in W. R. Meehan, editor. Influences of forest and rangeland management on salmonid fishes and their habitats. American Fisheries Society Special Publication No. 19, Bethesda, Maryland.
- Bottom, D. L., T. E. Nickelson, and S. L. Johnson. 1986. Research and development of Oregon's coastal salmon stocks: coho salmon model. Annual Progress Report AFC-127. Oregon Department of Fish and Wildlife, Portland, Oregon.
- Bowlby, C. E. 1981. Feeding behavior of pinnipeds in the Klamath River, Northern California. Master's thesis. Humboldt State University, Arcata, California.
- 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., M. Hollands, and D. F. Alderdice. 1958. The effect of temperature on the cruising speed of young sockeye and coho salmon. *Journal of the Fisheries Research Board of Canada* 15:587-605.
- Briggs, J. C. 1953. The behavior and reproduction of salmonid fishes in a coastal stream. *Fish Bulletin* 94. California Department of Fish and Game.
- Bodeur, R. D., and W. G. Pearcy. 1990. Trophic relations of juvenile Pacific salmon off the Oregon and Washington coast. *Fishery Bulletin* 88: 617-636.
- Brodeur, R. D. 1991. Ontogenetic variation in the type and size of prey consumed by juvenile coho, *Oncorhynchus kisutch*, and chinook, *O. tshawytscha*, salmon. *Environmental Biology of Fish* 30: 303-316.
- Brodeur, R. D. 1992. Factors related to variability in feeding intensity of juvenile coho salmon and chinook salmon. 104-114. *Transactions of the American Fisheries Society*.



PRELIMINARY DRAFT - COHO SALMON LIFE HISTORY

- Brown, T. G., and G. F. Hartman. 1988. Contributions of seasonally flooded lands and minor tributaries to the production of coho salmon in Carnation Creek, British Columbia. *Transactions of the American Fisheries Society* 117: 546-551.
- 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.
- Brungs, W. A., and B. R. Jones. 1977. Temperature criteria for freshwater fish: protocol and procedures. EPA-600/3-77-061. U. S. Environmental Protection Agency, Duluth, Minnesota.
- Bryant, M. D. 1980. Evolution of large, organic debris after timber harvest: Maybeso Creek, 1949 to 1978. General Technical Report PNW-101. U. S. Forest Service.
- Bryant, M. D. 1982. Organic debris in salmonid habitat in southeast Alaska: measurement and effects. Pages 259-265 in *Acquisition and utilization of aquatic habitat inventory information*. American Fisheries Society, Western Division.
- Bryant, M. D. 1983. The role and management of woody debris in west coast salmonid nursery streams. *North American Journal of Fisheries Management* 3: 322-330.
- Buck, M. K., and R. A. Barnhart. 1986. Trinity River fish habitat studies—an assessment of anadromous fish habitat and related anadromous fish populations below Lewiston Dam in northwestern California. Task I. Evaluation of constructed anadromous salmonid spawning riffles, Trinity River, California. California Cooperative Fishery Research Unit, Humboldt State University, Arcata, California.
- Bugert, R. M. 1985. Microhabitat selection of juvenile salmonids in response to stream cover alteration and predation. Master's thesis. University of Idaho, Moscow.
- Bugert, R. M., and T. C. Bjornn. 1991. Habitat use by steelhead and coho salmon and their responses to predators and cover in laboratory streams. *Transactions of the American Fisheries Society* 120: 486-493.
- Bugert, R. M., T. C. Bjornn, and W. R. Meehan. 1991. Summer habitat use by young salmonids and their responses to cover and predators in a small southeast Alaska stream. *Transactions of the American Fisheries Society* 120: 474-485.
- Burgner, R. L. 1991. Life history of sockeye salmon (*Oncorhynchus nerka*). Pages 3-117 in C. Groot and L. Margolis, editors. *Pacific salmon life histories*. University of British Columbia Press, Vancouver, British Columbia.
- Burner, C. J. 1951. Characteristics of spawning nests of Columbia River salmon. *U. S. Fish and Wildlife Service Fishery Bulletin* 52: 97-110.
- Burns, J. H. 1971. The carrying capacity for juvenile salmonids in some northern California streams. *California Fish and Game* 57: 44-57.
- Burns, J. W. 1972. Some effects of logging and associated road construction on Northern California streams. *Transactions of the American Fisheries Society* 1: 1-17.
- Bustard, D. R., and D. W. Narver. 1975a. 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.
- Bustard, D. R., and D. W. Narver. 1975b. Preferences of juvenile coho salmon (*Oncorhynchus kisutch*) and cutthroat trout (*Salmo clarki*) relative to simulated alteration of winter habitat. *Journal of the Fisheries Research Board of Canada* 32: 681-687.
- Carl, G. C. 1940. Comparison of coho salmon fry from eggs incubated in gravel and in hatchery baskets. *Transactions of the American Fisheries Society* 69: 132-134.
- CDFG (California Department of Fish and Game). 1994. Petition to the Board of Forestry to list coho salmon (*Oncorhynchus kisutch*) as a species. Presented to the California Board of Forestry on January 4, 1994.
- CDFG (California Department of Fish and Game). 1994. California Natural Diversity Data Base. CDFG, Sacramento.
- Cederholm, C. J., D. D. Houston, D. L. Cole, and W. J. Scarlett. 1989. Fate of coho salmon (*Oncorhynchus kisutch*) carcasses in spawning streams. *Canadian Journal of Fisheries and Aquatic Sciences* 46: 1347-1355.
- Cederholm, C. J., and N. P. Peterson. 1989. A summary comparison of two types of winter habitat enhancement for juvenile coho salmon (*Oncorhynchus kisutch*) in the Clearwater River, Washington. Pages 227-233 in B. G. Shepherd, editor. *Proceedings of the 1988 Northeast Pacific chinook and coho salmon workshop*. American Fisheries Society, North Pacific International Chapter.



- Cederholm, C. J., L. M. Reid, and E. O. Salo. 1981. Cumulative effects of logging road sediment on salmonid populations in the Clearwater River, Jefferson County, Washington. Pages 38-74 in Salmon-spawning gravel: A renewable resource in the Pacific Northwest? Report No. 39. State of Washington Water Research Center, Washington State University, Pullman, and the University of Washington, Seattle.
- 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 E. O. Salo, editors. Proceedings of the salmon and trout migratory behavior symposium. School of Fisheries, University of Washington, Seattle.
- Cederholm, C. J., W. J. Scarlett, and N. P. Peterson. 1988. Low-cost enhancement technique for winter habitat of juvenile coho salmon. *North American Journal of Fisheries Management* 8: 438-441.
- 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. 1965. Net production of juvenile coho salmon in three Oregon streams. *Transactions of the American Fisheries Society* 94: 40-52.
- Chapman, D. W. 1966. Food and space as regulators of salmonid populations in streams. *The American Naturalist* 100: 345-357.
- Chapman, D. W. 1988. Critical review of variables used to define effects of fines in redds of large salmonids. *Transactions of the American Fisheries Society* 117: 1-21.
- Chapman, D. W., and E. Knudsen. 1980. Channelization and livestock impacts on salmonid habitat and biomass in western Washington. *Transactions of the American Fisheries Society* 109: 357-363.
- Chilcote, M. W., S. A. Leider, and J. J. Loch. 1986. Differential reproductive success of hatchery and wild summer-run steelhead under natural conditions. *Transactions of the American Fisheries Society* 115: 726-735.
- Clark, J., editor. 1988. Restoring the balance. California Advisory Committee on Salmon and Steelhead Trout, Sausalito, California.
- Clarke, W. C., J. E. Shelbourn, and J. R. Brett. 1978. Growth and adaptation to sea water in "under-yearling" sockeye (*Oncorhynchus nerka*) and coho (*O. kisutch*) salmon subjected to regimes of constant or changing temperature and day length. *Canadian Journal of Zoology* 56: 2413-2421.
- Clarke, W. C., J. E. Shelbourn, and J. R. Brett. 1981. Effect of artificial photoperiod cycles, temperature, and salinity on growth and smolting in underyearling coho (*Oncorhynchus kisutch*), chinook (*O. tshawytscha*), and sockeye (*O. nerka*) salmon. *Aquaculture* 22: 105-116.
- Clarke, W. C., and J. E. Shelbourn. 1981. Growth and smolting of underyearling coho salmon in relation to photoperiod and temperature. Proceedings of the North Pacific aquaculture symposium. Anchorage, Alaska.
- Cloern, J. E. 1976. The survival of coho salmon (*Oncorhynchus kisutch*) eggs in two Wisconsin tributaries of Lake Michigan. *The American Midland Naturalist* 96: 451-461.
- Coble, D. W. 1961. Influence of water exchange and dissolved oxygen in redds on survival of steelhead trout embryos. *Transactions of the American Fisheries Society* 90: 469-474.
- Conte, F. P., H. H. Wagner, J. Fessler, and C. Gnose. 1966. Development of osmotic and ionic regulation in juvenile coho salmon (*Oncorhynchus kisutch*). *Comparative Biochemistry and Physiology* 18: 1-15.
- Cooper, A. C. 1965. The effect of transported stream sediments on the survival of sockeye and pink salmon eggs and alevin. Bulletin 18. International Pacific Salmon Fisheries Commission, New Westminster, British Columbia, Canada.
- Crone, R. A., and C. E. Bond. 1976. Life history of coho salmon, *Oncorhynchus kisutch*, in Sashin Creek, southeastern Alaska. *Fishery Bulletin* 74: 897-923.
- Crouse, M. R., C. A. Callahan, K. W. Malueg, and S. E. Dominguez. 1981. Effects of fine sediments on growth of juvenile coho salmon in laboratory streams. *Transactions of the American Fisheries Society* 110: 281-286.
- Cury, P. 1994. Obstinate nature: an ecology of individuals. Thoughts on reproductive behavior and biodiversity. *Canadian Journal of Fisheries and Aquatic Sciences* 51: 1664-1673.
- Davidson, F. A., and S. J. Hutchinson. 1938. The geographic and environmental limitations of the Pacific salmon (genus *Oncorhynchus*). *Bulletin of the Bureau of Fisheries (U. S.)* 48: 667-692.
- Davis, J. C. 1975. Minimal dissolved oxygen requirements of aquatic life with emphasis on Canadian species: a review. *Journal of the Fisheries Research Board of Canada* 32: 2295-2332.



- Davis, G. E., J. Foster, C. E. Warren, and P. Doudoroff. 1963. The influence of oxygen concentration on the swimming performance of juvenile Pacific salmon at various temperatures. *Transactions of the American Fisheries Society* 92: 111-124.
- Dill, L. M. 1969. The sub-gravel behavior of Pacific salmon larvae. Pages 89-99 in T. G. Northcote, editor. *Symposium on salmon and trout in streams*. H. R. MacMillan Lectures in Fisheries, University of British Columbia, Vancouver.
- Dill, L. M., and T. G. Northcote. 1970. Effects of gravel size, egg depth, and egg density on intra-gravel movement and emergence of coho salmon (*Oncorhynchus kisutch*) alevins. *Journal of the Fisheries Research Board of Canada* 27: 1191-1199.
- Dolloff, C. A. 1983. The relationships of wood debris to juvenile salmonid production and microhabitat selection in small southeast Alaska streams. Doctoral dissertation. Montana State University, Bozeman.
- Dolloff, C. A. 1986. Effects of stream cleaning on juvenile coho salmon and Dolly Varden in southeast Alaska. *Transactions of the American Fisheries Society* 115: 743-755.
- Dolloff, C. A., and G. H. Reeves. 1990. Microhabitat partitioning among stream-dwelling juvenile coho salmon, *Oncorhynchus kisutch*, and Dolly Varden, *Salvelinus malma*. *Canadian Journal of Fisheries and Aquatic Sciences* 47: 2297-2306.
- Druker, B. 1972. Some life history characteristics of coho salmon of the Karluk River system, Kodiak Island, Alaska. *Fisheries Bulletin* 70: 79-94.
- 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.
- Einstein, H. A. 1968. Deposition of suspended particles in a gravel bed. *Journal of the Hydraulics Division, Proceedings of the American Society of Civil Engineers* 94: 1197-1205.
- Elliott, S. T. 1986. Reduction of a Dolly Varden population and macrobenthos after removal of logging debris. *Transactions of the American Fisheries Society* 115: 392-400.
- Ellis, D. V. 1962. Preliminary studies on the visible migrations of adult salmon. *Journal of the Fisheries Research Board of Canada* 19: 137-148.
- Emlen, J. M., R. R. Reisenbichler, A. M. McGie, and T. E. Nickelson. 1990. Density-dependence at sea for coho salmon (*Oncorhynchus kisutch*). *Canadian Journal of Fisheries and Aquatic Sciences* 47: 1765-1772.
- Everest, F. H., and W. R. Meehan. 1981. Forest management and anadromous fish habitat productivity. *Transactions of the North American Wildlife and Natural Resources Conference* 46: 521-530.
- Everest, F. H., G. H. Reeves, J. R. Sedell, J. Wolfe, D. Hohler, and D. A. Heller. 1985. Abundance, behavior, and habitat utilization by coho salmon and steelhead trout in Fish Creek, Oregon, as influenced by habitat enhancement. Annual Report 1985 Project No. 84-11. Prepared by U. S. Forest Service for Bonneville Power Administration, Portland, Oregon.
- Fast, D. E., Q. J. Stober, S. C. Crumley, and E. S. Killebrew. 1982. Survival and movements of chinook and coho salmon alevins in hypoxic environments. Pages 51-60 in E. L. Brannon and E. O. Salo, editors. *Proceedings of the salmon and trout migratory behavior symposium*. School of Fisheries, University of Washington, Seattle.
- 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., and T. G. Northcote. 1992. Large woody debris and salmonid habitat in a small coastal British Columbia stream. *Canadian Journal of Fisheries and Aquatic Sciences* 49: 682-693.
- Fisher, J. P., W. G. Pearcy, and A. W. Chung. 1984. Studies of juvenile salmonids off the Oregon and Washington coast, 1983. *Oceanographic Cruise Report* 84-2. Oregon State University, Corvallis.
- Fleming, I. A., and M. R. Gross. 1990. Latitudinal clines: a trade-off between egg number and size in Pacific salmon. *Ecology* 71: 1-11.
- Foerster, R. E. 1944. Report for 1943 of the Pacific Biological Station, Nanaimo, British Columbia. *Fisheries Research Board of Canada Annual Report for 1943*, Appendix 4, p. 22-27.
- Foerster, R. E., and W. E. Ricker. 1953. The coho salmon of Cultus Lake and Sweltzer Creek. *Journal of the Fisheries Research Board of Canada* 10: 293-319.
- Fraser, F. J., E. A. Perry, and D. T. Lightly. 1983. Big Qualicum River salmon development project. Volume 1: a biological assessment 1959-1972. *Canadian Technical Report of Fisheries*



PRELIMINARY DRAFT - COHO SALMON LIFE HISTORY

- ies and Aquatic Sciences 1189. Department of Fisheries and Oceans, Fisheries Research Branch, Pacific Biological Station, Nanaimo, British Columbia.
- Freeland, H. J. 1990. Sea surface temperatures along the coast of British Columbia: regional evidence for a warming trend. *Canadian Journal of Fisheries and Aquatic Sciences* 47: 346-350.
- Fry, D. H., Jr. 1977. Information on California salmon fisheries and stocks, p. 15-24. *In: Additional information on the exploitation, scientific investigation, and management of salmon stocks on the Pacific coast of the United States in relation to the abstention provisions of the North Pacific Fisheries Convention. International North Pacific Fisheries Commission Bulletin No. 36.*
- Fryer, J. L., and K. S. Pilcher. 1974. Effects of temperature on diseases of salmonid fishes. *Ecological Research Series EPA-660/3-73-020. Environmental Protection Agency.*
- Gangmark, H. A., and R. G. Bakkala. 1960. A comparative study of unstable and stable (artificial channel) spawning streams for incubating king salmon at Mill Creek. *California Fish and Game* 46: 151-164.
- Gerke, R. J. 1973. Salmon spawning habitat improvement study. Project Completion Report, Project Number AFC-59-2. Washington State Department of Fisheries, Olympia and the National Marine Fisheries Service.
- Gerke, R. J. 1974. Salmon spawning habitat improvement study. Project Completion Report 1-93-D. Washington State Department of Fisheries, Olympia.
- 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.
- Godfrey, H. 1965. Coho salmon in offshore waters, p. 1-39. *In: Salmon of the North Pacific Ocean. Part IX. Coho, chinook and masu salmon in offshore waters. International North Pacific Fisheries Commission Bulletin 16.*
- Godin, J.-G. J. 1980. Temporal aspects of juvenile pink salmon (*Oncorhynchus gorbuscha* Walbaum) emergence from a simulated gravel redd. *Canadian Journal of Zoology* 58: 735-744.
- Grant, J. W. A., and D. L. Kramer. 1990. Territory size as a predictor of the upper limit to population density of juvenile salmonids in streams. *Canadian Journal of Fisheries and Aquatic Sciences* 47: 1724-1737.
- Greenley, J. C. 1985. Locations of local and regional salmonid stocks. Pages 153-159 in R. H. Stroud, editor. *Proceedings of the tenth annual marine recreational fisheries symposium. National Coalition for Marine Conservation, Inc., Savannah, Georgia.*
- 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.
- Gribanov, V. I. 1948. The coho salmon (*Oncorhynchus kisutch* Walb.)—a biological sketch. *Izv. Tikhookean. Nauschno-Issled. Inst. Rybn. Khoz. Okeanogr.* 28: 43-101. (Translated from Russian; Fisheries Research Board of Canada Translation Series No. 370).
- Griffiths, J. S., and D. F. Alderdice. 1972. Effects of acclimation and acute temperature experience on the swimming speed of juvenile coho salmon. *Journal of the Fisheries Research Board of Canada* 29: 251-264.
- Groberg, W. J., Jr., R. H. McCoy, K. S. Pilcher, and J. L. Fryer. 1978. Relation of water temperature to infections of coho salmon (*Oncorhynchus kisutch*), chinook salmon (*O. tshawytscha*), and steelhead trout (*Salmo gairdneri*) with *Aeromonas salmonicida* and *A. hydrophila*. *Journal of the Fisheries Research Board of Canada* 35: 1-7.
- Gross, M. R. 1984. Sunfish, salmon, and the evolution of alternative reproductive strategies and tactics in fishes. Pages 55-75 in G. Potts and R. J. Wootton, editors. *Fish reproduction: strategies and tactics. Academic Press, London.*
- Gross, M. R. 1985. Disruptive selection for alternative life histories in salmon. *Nature* 313: 47-48.
- Gross, M. R. 1991. Salmon breeding behavior and life history evolution in changing environments. *Ecology* 72: 1180-1186.
- Hagans, D. K., W. E. Weaver, and M. A. Madej. 1986. Long term on-site and off-site effects of logging and erosion in the Redwood Creek Basin in northern California. Technical Bulletin No. 460. National Council on Air and Streams, New York, New York.
- Hager, R. G., and R. E. Noble. 1976. Relation of size at release of hatchery-reared coho salmon to age, size, and sex composition of returning adults. *The progressive Fish-Culturist* 38: 144-147.
- Hall, J. D., and R. L. Lantz. 1969. Effects of logging on the habitat of coho salmon and cutthroat trout in coastal streams. Pages 355-375 in T. G. Northcote, editor. *Symposium on salmon and trout in streams. H. R. MacMillan Lectures in Fisheries, University of British Columbia, Vancouver.*



PRELIMINARY DRAFT - COHO SALMON LIFE HISTORY

- Hallock, R. J., and D. H. Fry, Jr. 1967. Five species of salmon, *Oncorhynchus*, in the Sacramento River, California. *California Fish and Game* 53: 5-22.
- Harrison, C. W. 1923. Planting eyed salmon and trout eggs. *Transactions of the American Fisheries Society* 52: 191-200.
- Hart, J. L. 1973. Pacific fishes of Canada. *Bulletin of the Fisheries Research Board of Canada* 180: 740 p.
- 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. Andersen, 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 T. G. Brown. 1987. Use of small, temporary, floodplain tributaries by juvenile salmonids in a west coast rain-forest drainage basin, Carnation Creek, British Columbia. *Canadian Journal of Fisheries and Aquatic Sciences* 44: 262-270.
- Hartman, W. L., and R. F. Raleigh. 1964. Tributary homing of sockeye salmon at Brooks and Karluk lakes, Alaska. *Journal of the Fisheries Research Board of Canada* 21: 485-504.
- Hartman, G. F., and J. C. Schrivener. 1990. Impacts of forestry practices on a coastal stream ecosystem, Carnation Creek, British Columbia. *Canadian Bulletin of Fisheries and Aquatic Sciences* 223: 148 pp.
- Hartman, G. F., J. C. Schrivener, L. B. Holtby, and L. Powell. 1987. Some effects of different streamside treatments on physical conditions and fish population processes in Carnation Creek, a coastal rain forest stream in British Columbia. pages 330-372 in E. O. Salo and T. W. Cundy, editors. *Streamside management: forestry and fishery interactions*. College of Forest Resources, University of Washington, Seattle. Contribution No. 57.
- Hasler, A. D., and A. T. Scholz. 1983. *Olfactory imprinting and homing in salmon*. Springer-Verlag, New York.
- Hassler, T. J. 1987. Species profiles: life histories and environmental requirements of coastal fishes and invertebrates (Pacific Southwest)—coho salmon. *Biological Report* 82 (11.70). Prepared by California Cooperative Fishery Research Unit, Humboldt State University, Arcata, California for U. S. Army Corps of Engineers, Coastal Ecology Group, Vicksburg, Mississippi and U. S. Fish and Wildlife Service, National Wetlands Research Center, Washington, D. C.
- Hassler, T. J., C. M. Sullivan, and G. R. Stern. 1991. Distribution of coho salmon in California. Final Report, Contract No. FG7292. Prepared by U. S. Fish and Wildlife Service, California Cooperative Fishery Research Unit, Humboldt State University, Arcata for California Department of Fish and Game.
- Hausle, D. A., and D. W. Coble. 1976. Influence of sand in redds on survival and emergence of brook trout (*Salvelinus fontinalis*). *Transactions of the American Fisheries Society* 105: 57-63.
- Hawkins, C. P., M. L. Murphy, N. H. Anderson, and M. A. Wilzbach. 1983. Density of fish and salamanders in relation to riparian canopy and physical habitat in streams of the northwestern United States. *Canadian Journal of Fisheries and Aquatic Sciences* 40: 1173-1185.
- Hayes, F. R., I. R. Wilmot, and D. A. Livingstone. 1951. The oxygen consumption of the salmon egg in relation to development and activity. *Journal of Experimental Zoology* 116: 377-395.
- Hazzard, A. S. 1932. Some phases of the life history of the eastern brook trout, *Salvelinus fontinalis* Mitchill. *Transactions of the American Fisheries Society* 62: 344-350.
- Heard, W. R. 1991. Life history of pink salmon (*Oncorhynchus gorbuscha*). Pages 121-230 in C. Groot and L. Margolis, editors. *Pacific salmon life histories*. University of British Columbia Press, Vancouver, British Columbia.
- Heifetz, J., M. L. Murphy, and K. V. Koski. 1986. Effects of logging on winter habitat of juvenile salmonids in Alaskan streams. *North American Journal of Fisheries Management* 6: 52-58.
- Heiser, D. W. 1972. Spawning ground improvement—gravel loosening 1971-1972. Progress Report. Washington State Department of Fisheries, Olympia.
- Hicks, B. J., J. D. Hall, P. A. Bisson, and J. R. Sedell. 1991. Responses of salmonids to habitat changes. Pages 483-518 in W. R. Meehan, editor. *Influences of forest and rangeland management on salmonid fishes and their habitats*. American Fisheries Society Special Publication No. 19, Bethesda, Maryland.
- Hindar, K., N. Ryman, and F. Utter. 1991. Genetic effects of cultured fish on natural populations. *Canadian Journal of Fisheries and Aquatic Sciences* 48: 945-957.



PRELIMINARY DRAFT - COHO SALMON LIFE HISTORY

- Hoar, W. S. 1965. The endocrine system as a chemical link between the organism and its environment. Transactions of the Royal Society of Canada Serv. IV 3: 175-200.
- Hobbs, D. F. 1937. Natural reproduction of quinnat salmon, brown trout and rainbow trout in certain New Zealand waters. Fisheries Bulletin 6. New Zealand Marine Department.
- Hobbs, D. F. 1940. Natural reproduction of trout in New Zealand and its relation to density of populations. Fisheries Bulletin 8. New Zealand Marine Department.
- Hofstra, T. D. 1983. Management alternatives for Redwood Creek Estuary. Redwood National Park, Arcata, California.
- Holt, R. A., J. E. Sanders, J. L. Zinn, J. L. Fryer, and K. S. Pilcher. 1975. Relation of water temperature to *Flexibacter columnaris* infection in steelhead trout (*Salmo gairdneri*), coho (*Oncorhynchus kisutch*) and chinook (*O. tshawytscha*) salmon. Journal of the Fisheries Research Board of Canada 32: 1553-1559.
- Holtby, L. B., and M. C. Healey. 1986. Selection for adult size in female coho salmon. Canadian Journal of Fisheries and Aquatic Sciences 43: 1946-1959.
- Holtby, L. B., B. C. Andersen, and R. K. Kadowaki. 1990. Importance of smolt size and early ocean growth to interannual variability in marine survival of coho salmon (*Oncorhynchus kisutch*). Canadian Journal of Fisheries and Aquatic Sciences 47: 2181-2194.
- Holtby, L. B., T. B. McMahon, and J. C. Scrivener. 1989. Stream temperatures and inter-annual variability in the emigration timing of coho salmon (*Oncorhynchus kisutch*) smolts and fry and chum salmon (*O. keta*) fry from Carnation Creek, British Columbia. Canadian Journal of Fisheries and Aquatic Sciences 46: 1396-1405.
- Hope, D. 1993. Petition to list central coast salmon stocks. Submitted to the California State Fish and Game Commission, February 1993, and National Marine Fisheries Service, April 1993. Authorized by Santa Cruz County Fish and Game Advisory Commission and County of Santa Cruz Board of Commissioners, Santa Cruz, California.
- House, R. A., and P. L. Boehne. 1985. Evaluation of instream enhancement structures for salmonid spawning and rearing in a coastal Oregon stream. North American Journal of Fisheries Management 5: 283-295.
- House, R. A., and P. L. Boehne. 1986. Effects of instream structures on salmonid habitat and populations in Tobe Creek, Oregon. North American Journal of Fisheries Management 6: 38-46.
- House, R. A., and P. L. Boehne. 1987. The effect of stream cleaning on salmonid habitat and populations in a coastal Oregon drainage. Western Journal of Applied Forestry 2: 84-87.
- House, R., V. Crispin, and J. M. Suther. 1991. Habitat and channel changes after rehabilitation of two coastal streams in Oregon. American Fisheries Society Symposium 10: 150-159.
- Houston, D. B. 1983. Anadromous fish in Olympic National Park: a status report. Olympic National Park, Port Angeles, Washington.
- Hughes, R. M., and G. E. Davis. 1986. Production of coexisting juvenile coho salmon and steelhead trout in heated model stream communities. ASTM (American Society for Testing and Materials) Special Technical Publications 920: 322-337.
- Hunter, J. G. 1959. Survival and production of pink and chum salmon in a coastal stream. Journal of the Fisheries Research Board of Canada 16: 835-886.
- Hynes, H. B. N. 1975. The stream and its valley. Internationale Vereinigung fuer Theoretische und Angewandte Limnologie Verhandlungen 19: 1-15.
- Ivanov, V. W., and N. L. Andreyev. 1969. Fecundity of the Pacific salmon. Prob. Ichthiol. 9: 59-66.
- Iwamoto, R. N., B. A. Alexander, and W. K. Hershberger. 1983. Salmonid reproduction, 8. School of Fisheries, University of Washington, Seattle.
- Jackson, F. 1975. Big River was dammed. Mendocino, California.
- Johnson, S. L. 1988. The effects of the 1983 El Nino on Oregon's coho (*Oncorhynchus kisutch*) and chinook (*O. tshawytscha*) salmon. Fisheries Research 6: 105-123.
- Judsen, S., and D. F. Ritter. 1964. Rates of regional denudation in the United States. Journal of Geophysical Research 69: 3395-3401.
- Kershner, J. L., H. L. Forsgren, and W. R. Meehan. 1991. Managing salmonid habitats. Pages 599-606 in W. R. Meehan, editor. Influences of forest and rangeland management on salmonid fishes and their habitats. American Fisheries Society Special Publication No. 19, Bethesda, Maryland.
- Kondolf, G. M., M. J. Sale, and M. G. Wolman. 1993. Modification of fluvial gravel size by spawning salmonids. Water Resources Research 29: 2265-2274.



PRELIMINARY DRAFT - COHO SALMON LIFE HISTORY

- Konkel, G. W., and J. D. McIntyre. 1987. Trends in spawning populations of Pacific anadromous salmonids. Technical Report 9. U. S. Fish and Wildlife Service, Washington, D. C.
- 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.
- Koski, K. V. 1975. The survival and fitness of two stocks of chum salmon (*Oncorhynchus keta*) from egg deposition to emergence in a controlled stream environment at Big Beef Creek. Doctoral dissertation. University of Washington, Seattle.
- Koski, K. V., J. Heifetz, S. Johnson, M. Murphy, and J. Thedinga. 1984. Evaluation of buffer strips for protection of salmonid rearing habitat and implications for enhancement. Pages 138-155 in T. J. Hassler, editor. Pacific Northwest stream habitat management workshop. California Cooperative Fisheries Unit, Humboldt State University, Arcata, California.
- Kubicek, P. F. 1977. Summer water temperature conditions in the Eel River system, with reference to trout and salmon. Master's thesis. Humboldt State University, Arcata, California.
- Labelle, M. 1992. Straying patterns of coho salmon (*Oncorhynchus kisutch*) stocks from southeast Vancouver Island, British Columbia. Canadian Journal of fisheries and Aquatic Sciences 49: 1843-1855.
- Larkin, P. A. 1977. Pacific salmon. Pages 156-186 in J. A. Gulland, editor. Fish population dynamics.
- Laufle, J. C., G. B. Pauley, and M. F. Shepard. 1986. Species profiles: life histories and environmental requirements of coastal fishes and invertebrates (Pacific Northwest)—coho salmon. Biological Report 82(11.48), USACE Report No. TR EL-82-4. U. S. Fish and Wildlife Service and U. S. Army Corps of Engineers.
- Lawson, P. W. 1993. Cycles in ocean productivity, trends in habitat quality, and the restoration of salmon runs in Oregon. Fisheries (Bethesda) 18: 6-10.
- Lestelle, L. C., and C. J. Cederholm. 1984. Short-term effects of organic debris removal on resident cutthroat trout. Pages 131-140 in W. R. Meehan, T. R. Merrell, Jr. and T. A. Hanley, editors. Fish and wildlife relationships in old-growth forests. American Institute of Fishery Research Biologists, Juneau, Alaska.
- Lienkaemper, G. W., and F. J. Swanson. 1987. Dynamics of large woody debris in streams in old-growth Douglas-fir forests. Canadian Journal of Forest Research 17: 150-156.
- Lisle, T. E. 1981. Roughness elements: a key resource to improve anadromous fish habitat. Pages 93-98 in T. J. Hassler, editor. Propagation, enhancement, and rehabilitation of anadromous salmonid populations and habitat in the Pacific Northwest symposium. California Cooperative Fishery Research Unit, Humboldt State University, Arcata.
- Lister, D. B., and C. E. Walker. 1966. The effect of flow control on freshwater survival of chum, coho and chinook salmon in the Big Qualicum River. The Canadian Fish Culturist 37: 3-22.
- Lister, D. B., D. E. Marshall, and D. G. Hickey. 1980. Chum salmon survival and production at seven improved groundwater-fed spawning areas. Report No. 1595. Canadian Manuscript Report of Fish and Aquatic Science.
- L-P (Louisiana-Pacific Corporation). 1997. Sustained yield plan for coastal Mendocino County. Calpella, California.
- Lufkin, A., editor. 1991. California's salmon and steelhead. The struggle to restore an imperiled resource. University of California Press, Berkeley.
- MacDonald, J. S., I. K. Birtwell, and G. M. Kruzynski. 1987. Food and habitat utilization by juvenile salmonids in the Campbell River estuary. Canadian Journal of Fisheries and Aquatic Sciences 44: 1233-1246.
- Mace, P. M. 1983. Predator-prey functional responses and predation by staghorn sculpins (*Leptocottus armatus*) on chum salmon fry (*Oncorhynchus keta*). Doctoral dissertation. University of British Columbia, Vancouver.
- Marshall, D. E., and E. W. Britton. 1990. Carrying capacity of coho salmon streams. Canadian Manuscript Report of Fisheries and Aquatic Sciences 2058: 32 p.
- 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. North American Journal of Fisheries Management 6: 1-8.
- Mason, J. E. 1966. The migrant dipper: a trap for downstream-migrating fish. The Progressive Fish-Culturist 28: 96-102.
- Mason, J. C. 1976a. Response of underyearling coho salmon to supplemental feeding in a natural stream. Journal of Wildlife Management 40: 775-788.



PRELIMINARY DRAFT - COHO SALMON LIFE HISTORY

- 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.
- McAllister, T. 1988. Cormorants harassed to save smolts. *The Portland Oregonian*. 15 May.
- McCabe, G. T., Jr., W. D. Muir, R. L. Emmett, and J. T. Durkin. 1983. Interrelationships between juvenile salmonids and nonsalmonid fish in the Columbia River estuary. *Fishery Bulletin* 81: 815-826.
- McCuddin, M. E. 1977. Survival of salmon and trout embryos and fry in gravel-sand mixtures. Master's thesis. University of Idaho, Moscow.
- McFadden, J. T. 1969. Dynamics and regulation of salmonid populations in streams. Pages 313-329 in T. G. Northcote, editor. *Symposium on salmon and trout in streams*. H. R. MacMillan Lectures in Fisheries, University of British Columbia, Vancouver.
- McGie, A. M. 1984. Commentary: evidence for density-dependence among coho salmon stocks in the Oregon Production Index Area. Pages 37-49 in W. G. Pearcy, editor. *The influence of ocean conditions on the production of salmonids in the North Pacific*. Oregon State University Sea Grant Publication, Corvallis.
- McKernan, D. L., D. R. Johnson, and J. I. Hodges. 1950. Some factors influencing the trends of salmon populations in Oregon. *Transactions of the North American Wildlife Conference* 15: 427-449.
- McMahon, T. E. 1983. Habitat suitability index models: coho salmon. Report FWS/OBS-82/10.49. U. S. Fish and Wildlife Service, Western Energy and Land Use Team, Washington, D. C.
- 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. Behavior, habitat use, and movements of coho salmon (*Oncorhynchus kisutch*) smolts during seaward migration. *Canadian Journal of Fisheries and Aquatic Sciences* 49: 1478-1485.
- McMahon, T., and G. Reeves. 1989. Large woody debris and fish. Paper presented at the COPE workshop "Silvicultural management of riparian areas for multiple resources" held at Salishan Lodge, Gleneden Beach, Oregon on 12-13 December 1989. U. S. Forest Service Pacific Northwest Research Station, Portland and Oregon State University College of Forestry, Corvallis.
- McNeil, W. J. 1962a. Variations in the dissolved oxygen content of intragravel water in four spawning streams of southeastern Alaska. Special Scientific Report - Fisheries 402. U. S. Fish and Wildlife Service.
- McNeil, W. J. 1962b. Mortality of pink and chum salmon eggs and larvae in southeast Alaska streams. Doctoral dissertation. University of Washington, Seattle.
- McNeil, W. J. 1966. Effect of spawning bed environment on reproduction of pink and chum salmon. *Fishery Bulletin* 65: 495-523.
- McNeil, W. J., and W. H. Ahnell. 1964. Success of pink salmon spawning relative to size of spawning bed materials. Special Scientific Report - Fisheries 469. U. S. Fish and Wildlife Service.
- Meehan, W. R., and D. B. Siniff. 1962. A study of the downstream migrations of anadromous fishes in the Taku River, Alaska. *Transactions of the American Fisheries Society* 91: 399-407.
- Meehan, W. R., and T. C. Bjornn. 1991. Salmonid distributions and life histories. Pages 47-82 in W. R. Meehan, editor. *Influences of forest and rangeland management on salmonid fishes and their habitats*. American Fisheries Society Special Publication No. 19, Bethesda, Maryland.
- Mih, W. C. 1978. Development of a machine for cleaning salmon spawning streambeds. Fisheries Department Service Contract No. 885, Washington State University Project No. 11W-3815-1657. Prepared by Albrook Hydraulics Laboratory, Washington State University, Pullman for Washington State Department of Fisheries, Olympia.
- Mih, W. C., and G. C. Bailey. 1981. The development of a machine for the restoration of stream gravel for spawning and rearing of salmon. *Fisheries* 6: 16-20.
- Miller, D. J., and R. N. Lea. 1972. Guide to the coastal marine fishes of California. *Fish Bulletin* No. 157. California Department of Fish and Game.
- Miller, W. H., T. C. Coley, H. L. Burge, and T. T. Kisanuki. 1990. Analysis of salmon and steelhead supplementation: emphasis on unpublished reports and present programs. Technical Report, Project 88-100, Part 1. Bonneville Power Administration, Portland, Oregon.
- Miyamoto, J. J. 1979. Homing of pond-reared coho salmon to a small urban stream, Humboldt County, California. Master's thesis. Humboldt State University, Arcata, California.



PRELIMINARY DRAFT - COHO SALMON LIFE HISTORY

- Moring, J. R. 1975. The Alsea watershed study: effects of logging on the aquatic resources of three headwater streams of the Alsea River, Oregon. Part 2—Changes in environmental conditions. Fishery Research Report 9. Oregon Department of Fish and Wildlife, Corvallis.
- Moring, J. R., and R. L. Lantz. 1974. Immediate effects of logging on the freshwater environment of salmonids. Report 58. Oregon Wildlife Commission, Research Division, Portland.
- Moring, J. R., and R. L. Lantz. 1975. The Alsea watershed study: effects of logging on the aquatic resources of three headwater streams of the Alsea River, Oregon. Part I—Biological studies. Fishery Research Report 9. Oregon Department of Fish and Wildlife, Portland, Oregon.
- 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. 1976. Inland fishes of California. First edition. University of California Press, Berkeley.
- Moyle, P. B., J. E. Williams, and E. D. Wikramanayake. 1989. Fish species of special concern of California. Prepared by University of California, Davis for California Department of Fish and Game, Inland Fisheries Division, Rancho Cordova.
- Mundie, J. H., and R. E. Traber. 1983. Carrying capacity of an enhanced side-channel for rearing salmonids. Canadian Journal of Fisheries and Aquatic Sciences 40: 1320-1322.
- Murphy, M. L., J. F. Thedinga, K. V. Koski, and G. B. Grette. 1984. A stream ecosystem in an old-growth forest in southeast 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, editors. Fish and wildlife relationships in old-growth forests. American Institute of Fishery Research Biologists, Juneau, Alaska.
- Murphy, M. L., K. V. Koski, J. Heifetz, S. W. Johnson, D. Kirchhofer, and J. F. Thedinga. 1985. Role of large organic debris as winter habitat for juvenile salmonids in Alaska streams. Proceedings of the Western Association of Fish and Wildlife Agencies 64: 251-262.
- Murphy, M. L., J. Heifetz, S. W. Johnson, K. V. Koski, and J. F. Thedinga. 1986. Effects of clear-cut logging with and without buffer strips on juvenile salmonids in Alaskan streams. Canadian Journal of Fisheries and Aquatic Sciences 43: 1521-1533.
- Myers, K. W., and H. F. Horton. 1982. Temporal use of an Oregon estuary by hatchery and wild juvenile salmon. Pages 377-392 in V. S. Kennedy, editor. Estuarine comparisons. Academic Press, New York.
- Napolitano, M. B. 1996. Sediment transport and storage in North Fork Caspar Creek, Mendocino County, California: water years 1980-1988. Master's thesis. Humboldt State University, Arcata, California.
- Neave, F. 1943. Diurnal fluctuations in the upstream migration of coho and spring salmon. Journal of the Fisheries Research Board of Canada 6: 158-163.
- Neave, F. 1948. Fecundity and mortality in Pacific salmon. Proceedings of the Transactions of the Royal Society of Canada Series 3 42: 99-105.
- Neave, F. 1949. Game fish populations of the Cowichan River. Bulletin of the Fisheries Research Board of Canada 84: 1-32.
- Neave, F., and W. P. Wickett. 1953. Factors affecting the freshwater development of Pacific salmon in British Columbia. Proceedings of the 7th Pacific Science Congress 1949: 548-556.
- Nehlsen, W., J. E. Williams, and J. A. Lichatowich. 1991. Pacific salmon at the crossroads: stocks at risk from California, Oregon, Idaho, and Washington. Fisheries 16: 4-21.
- Nickelson, T. E. 1986. Influences of upwelling, ocean temperature, and smolt abundance on marine survival of coho salmon (*Oncorhynchus kisutch*) in the Oregon Production Area. Canadian Journal of Fisheries and Aquatic Sciences 43: 527-535.
- Nickelson, T. E., W. M. Beidler, M. Willard, and M. J. Willis. 1979. Streamflow requirements of salmonids. Final Report, Federal Air Project, AFS-62. Oregon Department of Fish and Wildlife, Portland.
- Nickelson, T. E., and R. R. Reisenbichler. 1977. Streamflow requirements of salmonids. Research Section Annual Progress Report, Project AFS-62. Oregon Department of Fish and Wildlife, Portland.
- Nickelson, T. E., J. D. Rodgers, S. L. Johnson, and M. F. Solazzi. 1992a. 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.



PRELIMINARY DRAFT - COHO SALMON LIFE HISTORY

- Nickelson, T. E., M. F. Solazzi, S. L. Johnson, and J. D. Rodgers. 1992b. Effectiveness of selected stream improvement techniques to create suitable summer and winter rearing habitat for juvenile coho salmon (*Oncorhynchus kisutch*) in Oregon coastal streams. *Canadian Journal of Fisheries and Aquatic Sciences* 49: 790-794.
- Nielsen, J. L. 1992. Microhabitat-specific foraging behavior, diet, and growth of juvenile coho salmon. *Transactions of the American Fisheries Society* 121: 617-634.
- Nielsen, J. L., M. Maas, and G. Balding. 1991. Anadromous salmonid resources of Mendocino coastal and inland rivers, 1989-1990. An evaluation of rehabilitation efforts based on carcass recovery and spawning activity. Draft Report, Inland Habitat Surveys, Standard Agreement FG9364. California Department of Fish and Game, Sacramento.
- NMFS (National Marine Fisheries Service). 1994. Listing endangered and threatened species and designating critical habitat: petition to list coho salmon throughout its range in Washington, Oregon, Idaho, and California: notice of petition finding and request for information. *Federal Register* 59: 3662-3663.
- NMFS. 1995. Endangered and threatened species; proposed threatened status for three contiguous ESUs of coho salmon ranging from Oregon through central California. *Federal Register* 60: 38011-38030.
- Otto, R. G. 1971. Effects of salinity on the survival and growth of pre-smolt salmon (*Oncorhynchus kisutch*). *Journal of the Fisheries Research Board of Canada* 28: 343-349.
- Pacific Rivers Council, Inc. 1993. Petition to the National Marine Fisheries Service for a rule to list, for designation of critical habitat, and for a status review of coho salmon (*Oncorhynchus kisutch*) throughout its range in Washington, Oregon, Idaho, and California under the Endangered Species Act. Eugene, Oregon.
- Parry, G. 1960. The development of salinity tolerance in the salmon, *Salmo salar* (L.) and some related species. *Journal of Experimental Biology* 37: 425-434.
- Payne, T. R. and Associates. 1989. Lower Klamath River tributary delta study. U. S. Bureau of Indian Affairs, Redding, California.
- Pearcy, W. G., and J. P. Fisher. 1988. Migrations of coho salmon, *Oncorhynchus kisutch*, during their first summer in the ocean. *NOAA Fisheries Bulletin* 86: 173-195.
- Pearcy, W. G. 1992. Ocean ecology of North Pacific salmonids. Washington Sea Grant Program, University of Washington, Seattle, Washington.
- Pearcy, W. G., and 12 coauthors. 1992. Oregon Coastal Natural Coho Review Team report: an assessment of the status of the Oregon Coastal Natural coho stock as required under the definition of overfishing. Pacific Fishery Management Council, Portland, Oregon.
- Peterman, R. M. 1982. Nonlinear relation between smolts and adults in Babine Lake sockeye salmon (*Oncorhynchus nerka*) and implications for other salmon populations. *Canadian Journal of Fisheries and Aquatic Sciences* 39: 904-913.
- Peters, J. C. 1965. The effects of stream sedimentation on trout embryo survival. Pages 275-279 in C. M. Tarzwell, editor. *Transactions of the 3rd seminar on biological problems in water pollution*. Publication No. 999-WP-25. U. S. Public Health Service, Robert Taft Engineering Center, Cincinnati, Ohio.
- Peterson, N. P. 1982a. 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. 1982b. Immigration of juvenile coho salmon (*Oncorhynchus kisutch*) into riverine ponds. *Canadian Journal of Fisheries and Aquatic Sciences* 39: 1308-1310.
- Peterson, N. P., and T. P. Quinn. 1994. Winter survival of coho salmon in Big Beef Creek. Part B. The influence of habitat complexity and fish size on over-winter survival and growth of individually-marked juvenile coho salmon in Big Beef Creek. Pages 62-75 in T. P. Quinn and N. P. Peterson, editors. *The effects of forest practices on fish populations*. Timber/Fish/Wildlife Report No. TFW-F4-94-001. Washington Department of Natural Resources, Olympia.
- Peterson, N. P., and L. M. Reid. 1984. Wall-base channels: their evolution, distribution, and used by juvenile coho salmon in the Clearwater River, Washington, Pages 215-225 in J. M. Walton and D. B. Houston, editors. *Proceedings of the Olympic wild fish conference*. Fisheries Technology Program, Peninsula College, Port Angeles, Washington.
- Phillips, R. W., and H. J. Campbell. 1961. The embryonic survival of coho salmon and steelhead trout as influenced by some environmental conditions in gravel beds. Pages 60-73 in 14th annual report of the Pacific Marine Fisheries Commission. Portland, Oregon.



PRELIMINARY DRAFT - COHO SALMON LIFE HISTORY

- Phillips, R. W., R. L. Lantz, and E. W. Claire. 1973. The entrapment effect of 1-3 mm sand on emergent survival of coho salmon and steelhead trout fry. Unpublished Manuscript. Oregon Game Commission, Division of Wildlife Resources, Corvallis.
- Phillips, R. W., R. L. Lantz, E. W. Claire, and J. R. Moring. 1975. Some effects of gravel mixtures on emergence of coho salmon and steelhead trout fry. *Transactions of the American Fisheries Society* 104: 461-466.
- Platts, W. S., M. A. Shirazi, and D. H. Lewis. 1979. Sediment particle sizes used by salmon for spawning with methods for evaluation. Ecological Research Series EPA-600/3-79-043. U. S. Environmental Protection Agency, Corvallis Environmental Research Laboratory, Corvallis, Oregon.
- Puckett, L. K. 1977. *N/A The Eel River estuary—observations on morphometry, fishes, water quality, and invertebrates. Memorandum Report. California Department of Fish and Game. 52 p.
- Quinn, T. P. 1994. Factors affecting the freshwater and marine growth and survival of coho salmon from Big Beef Creek. Pages 99-115 in T. P. Quinn and N. P. Peterson, editors. The effects of forest practices on fish populations. Timber/Fish/Wildlife Report No. TFW-F4-94-001. Washington Department of Natural Resources, Olympia.
- Quinn, W. H., V. T. Neal, and S. E. Antunez de Mayolo. 1986. Preliminary report on El Nino occurrences over the past four and a half centuries. Reference 86-16, National Science Foundation No. ATM-85 15014. College of Oceanography, Oregon State University, Corvallis.
- 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. General Technical Report PNW-GTR-245. U. S. Forest Service, Pacific Northwest Research Station, Portland, Oregon.
- Reeves, G. H., J. D. Hall, T. D. Roeloffs, T. L. Hickman, and C. O. Baker. 1991. Rehabilitating and modifying stream habitats. Pages 519-557 in W. R. Meehan, editor. Influences of forest and rangeland management on salmonid fishes and their habitats. American Fisheries Society Special Publication No. 19, Bethesda, Maryland.
- Reeves, G. H., and T. D. Roeloffs. 1982. Rehabilitating and enhancing stream habitat: 2. Field applications. Pages 38 p in W. R. Meehan, editor. Influence of forest and rangeland management on anadromous fish habitat in western North America. U. S. Forest Service, Pacific Northwest Forest and Range Experiment Station, Portland, Oregon.
- Reeves, G. H., and J. R. Sedell. 1992. An ecosystem approach to the conservation and management of freshwater habitat for anadromous salmonids in the Pacific Northwest. *Transactions of the North American Wildlife and Natural Resources Conference* 1992: 408-415.
- Reiser, D. W., and T. C. Bjornn. 1979. Habitat requirements of anadromous salmonids. Pages 1-54 in W. R. Meehan, editor. Influence of forest and rangeland management on anadromous fish habitat in western North America. General Technical Report PNW-96. U. S. Forest Service, Pacific Northwest Forest and Range Experiment Station, Portland, Oregon.
- Reiser, D. W., and R. T. Peacock. 1985. A technique for assessing upstream fish passage problems at small-scale hydropower developments. Pages 423-432 in F. W. Olson, R. G. White and R. H. Hamre, editors. Symposium on small hydropower and fisheries. American Fisheries Society, Bethesda, Maryland.
- Ricker, W. E., and A. Robertson. 1935. Observations on the behavior of adult sockeye salmon during the spawning migration. *The Canadian Field-Naturalist* 49: 132-134.
- Ringler, N. H., and J. D. Hall. 1975. Effects of logging on water temperature and dissolved oxygen in spawning beds. *Transactions of the American Fisheries Society* 104: 111-121.
- Robison, E. G., and R. L. Beschta. 1990a. Characteristics of coarse woody debris for several coastal streams of southeast Alaska, USA. *Canadian Journal of Fisheries and Aquatic Sciences* 47: 1684-1693.
- Robison, E. G., and R. L. Beschta. 1990b. Coarse woody debris and channel morphology interactions for undisturbed streams in southeast Alaska, USA. *Earth Surface Processes and Landforms* 15: 149-156.
- Rodgers, J. D. 1986. The winter distribution, movement, and smolt transformation of juvenile coho salmon in an Oregon coastal stream. Master's thesis. Oregon State University, Corvallis.
- Roemmich, D. 1992. Ocean warming and sea level rise along the southwest U. S. coast. *Science* 257: 373-375.
- Ruggles, C. P. 1966. Depth and velocity as a factor in stream rearing and production of juvenile coho salmon. *The Canadian Fish Culturist* 38: 37-53.



PRELIMINARY DRAFT - COHO SALMON LIFE HISTORY

- Salo, E. O., and W. H. Bayliff. 1958. Artificial and natural reproduction of silver salmon at Minter Creek, Washington. Research Bulletin No. 4. Washington Department of Fisheries.
- Sandercock, F. K. 1991. Life history of coho salmon (*Oncorhynchus kisutch*). Pages 397-445 in C. Groot and L. Margolis, editors. Pacific salmon life histories. University of British Columbia Press, Vancouver, B. C.
- Sargent, C. R., P. Taylor, and M. R. Gross. 1987. Parental care and the evolution of egg size in fishes. *American Naturalist* 129: 32-46.
- Scarlett, W. S., and C. J. Cederholm. 1984. Juvenile coho salmon fall-winter utilization of two small tributaries of the Clearwater River, Jefferson County, Washington. Pages 227-242 in J. M. Walton and D. B. Houston, editors. Proceedings of the Olympic Wild Fish Conference. Peninsula College, Port Angeles, Washington.
- Scarnecchia, D. L. 1981. Effects of streamflow and upwelling on yield of wild coho salmon (*Oncorhynchus kisutch*) in Oregon. *Canadian Journal of Fisheries and Aquatic Sciences* 38: 471-475.
- Scott, W. B., and E. J. Crossman. 1973. Freshwater fishes of Canada. Fisheries Research Board of Canada Bulletin 184: 734-740.
- Scrivener, J. C., and B. C. Anderson. 1984. Logging impacts and some mechanisms that determine the size of spring and summer populations of coho salmon fry (*Oncorhynchus kisutch*) in Carnation Creek, British Columbia. *Canadian Journal of Fisheries and Aquatic Sciences* 41: 1097-1105.
- Sedell, J. R. 1984. Habitats and salmonid distribution in pristine, sediment-rich river valley systems: S. Fork Hoh and Queets River, Olympic National Park. Pages 33-46 in W. R. Meehan, T. R. Merrell, Jr. and T. A. Hanley, editors. Fish and wildlife relationships in old-growth forests. American Institute of Fishery Research Biologists, Juneau, Alaska.
- Sedell, J. R., and R. L. Beschta. 1991. Bringing back the "bio" in engineering. *American Fisheries Society Symposium* 10: 160-175.
- Sedell, J. R., F. H. Everest, and F. J. Swanson. 1982. Fish habitat and streamside management: past and present. Pages 249-255 in Proceedings of the Society of American Foresters annual meeting. Society of American Foresters, Bethesda, Maryland.
- Sedell, J. R., and K. J. Luchessa. 1982. Using the historical record as an aid to salmonid habitat enhancement. Pages 210-223 in N. B. Armantrout, editor. Symposium on acquisition and utilization of aquatic habitat inventory information. Western Division, American Fisheries Society, Bethesda, Maryland.
- Sedell, J. R., and F. J. Swanson. 1984. Ecological characteristics of streams in old-growth forests of the Pacific Northwest. Pages 9-16 in W. R. Meehan, T. R. Merrell and T. A. Hanley, editors. Proceedings of the symposium on fish and wildlife relationships in old-growth forests. American Institute of Fishery Biologists, Asheville, North Carolina.
- Sedell, J. R., F. J. Swanson, and S. V. Gregory. 1984. Evaluating fish response to woody debris. Pages 222-245 in Proceedings of the Pacific Northwest stream habitat management workshop.
- Semko, R. S. 1954. The stocks of West Kamchatka salmon and their commercial utilization. Translation Series No. 288. Fisheries Research Board of Canada.
- Shapovalov, L., and W. Berrian. 1940. An experiment in hatching silver salmon (*Oncorhynchus kisutch*) eggs in gravel. *Transactions of the American Fisheries Society* 69: 135-140.
- 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 Waddell Creek, California, and recommendations regarding their management. Fish Bulletin 98. California Department of Fish and Game.
- Shaw, P. A., and J. A. Maga. 1943. The effect of mining silt on yield of fry from salmon spawning beds. *California Fish and Game* 29: 29-41.
- 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.
- Shumway, D. L., C. E. Warren, and P. Doudoroff. 1964. Influence of oxygen concentration and water movement on the growth of steelhead trout and coho salmon embryos. *Transactions of the American Fisheries Society* 93: 342-356.
- Silver, S. J., C. E. Warren, and P. Doudoroff. 1963. Dissolved oxygen requirements of developing steelhead trout and chinook salmon embryos at different velocities. *Transactions of the American Fisheries Society* 92: 327-343.
- Skud, B. E. 1958. Relation of adult pink salmon size to time of migration and freshwater survival. *Copeia* 1958 (3): 170-176.



PRELIMINARY DRAFT - COHO SALMON LIFE HISTORY

- Smith, O. R. 1941. The spawning habits of cutthroat and eastern brook trouts. *Journal of Wildlife Management* 5: 461-471.
- Smith, J. J. 1987. Aquatic habitat and fish utilization of Pescadero, San Gregorio, Waddell, and Pomponio Creek estuary/lagoon systems. Interagency Agreement No. 4-823-6004. Report to California Department of Parks and Recreation. 35 p.
- Smith, A. K. 1973. Development and application of spawning velocity and depth criteria for Oregon salmonids. *Transactions of the American Fisheries Society* 102: 312-316.
- Smith, E. M., B. A. Miller, J. D. Rodgers, and M. A. Buckman. 1985. Outplanting anadromous salmonids: a literature survey. Annual Report Project No. 85-68. Prepared by Oregon Department of Fish and Wildlife for Bonneville Power Administration, Portland, Oregon.
- Smoker, W. A. 1953. Stream flow and silver salmon production in western Washington. Washington Department of Fisheries, Fisheries Research Paper 1: 5-12.
- Smoker, W. A. 1955. Effects of streamflow on silver salmon production in western Washington. Doctoral dissertation. University of Washington, Seattle.
- Solazzi, M.F., S.L. Johnson, and T. E. Nickelson. 1983. The effectiveness of stocking hatchery coho psmolts to increase the rearing density of juvenile coho salmon in Oregon coastal streams. information Report 83-1. Oregon Department of Fish and Wildlife, Portland.
- 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.
- Stauffer, T. M. 1976. Fecundity of coho salmon (*Oncorhynchus kisutch*) from the Great Lakes and a comparison with ocean salmon. *Journal of the Fisheries Research Board of Canada* 33: 1150-1155.
- Stein, R. A., P. E. Reimers, and J. D. Hall. 1972. Social interaction between juvenile coho (*Oncorhynchus kisutch*) and fall chinook salmon (*Oncorhynchus tshawytscha*) in Sixes River, Oregon. *Journal of the Fisheries Research Board of Canada* 29: 1737-1748.
- Steward, C. R., and T. C. Bjornn. 1990. Supplementation of salmon and steelhead stocks with hatchery fish: a synthesis of published literature. Part 2 of Analysis of Salmon and Steelhead Supplementation, Technical Report No. 90-1. Prepared by Idaho Cooperative Fish and Wildlife Research Unit for Bonneville Power Administration, Portland, Oregon.
- Stuart, T. A. 1953. Spawning migration, reproduction and young stages of the loch trout (*S. trutta* L.). *Freshwater and Salmon Fisheries Research Report* 5. Scottish Home Department, Edinburgh.
- Sullivan, K. 1986. Hydraulics and fish habitat in relation to channel morphology. Doctoral dissertation. Johns Hopkins University, Baltimore, Maryland.
- 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.
- Swanson, F. J., G. Lienkaemper, and J. R. Sedell. 1976. History, physical effects, and management implications of large organic debris in western Oregon streams. General Technical Report PNW-56. U. S. Forest Service, Pacific Northwest Forest and Range Experiment Station, Portland, Oregon.
- Tagart, J. V. 1976. The survival from egg deposition to emergence of coho salmon in the Clearwater River, Jefferson County, Washington. Master's thesis. University of Washington, Seattle.
- Tagart, J. V. 1984. Coho salmon survival from egg deposition to emergence. Pages 173-182 in J. M. Walton and D. B. Houston, editors. *Proceedings of the Olympic wild fish conference*. Peninsula College, Fisheries Technology Program.
- Tautz, A. F. 1977. Effects of variability in space and time on the production dynamics of salmonid fishes. Doctoral dissertation. University of British Columbia, Vancouver.
- Taylor, E. B. 1988. Water temperature and velocity as determinants of microhabitats of juvenile chinook and coho salmon in a laboratory stream channel. *Transactions of the American Fisheries Society* 117: 22-28.
- Taylor, E. B. 1991. Behavioural interaction and habitat use in juvenile chinook, *Oncorhynchus tshawytscha*, and coho, *O. kisutch*, salmon. *Animal Behaviour* 42: 729-744.
- Taylor, E. B., and J. D. McPhail. 1985. Variation in body morphology among British Columbia populations of coho salmon, *Oncorhynchus kisutch*. *Canadian Journal of Fisheries and Aquatic Sciences* 42: 2020-2028.



PRELIMINARY DRAFT - COHO SALMON LIFE HISTORY

- Thompson, K. 1972. Determining stream flows for fish life. Pages 31-50 in Proceedings of the instream flow requirement workshop. Pacific Northwest River Basin Commission, Vancouver, Washington.
- Toews, D. A. A., and M. K. Moore. 1982. The effects of three streamside logging treatments on organic debris and channel morphology of Carnation Creek. Pages 129-153 in G. F. Hartman, editor. Proceedings of the Carnation Creek workshop: a ten-year review. Pacific Biological Station, Nanaimo, British Columbia.
- Tripp, D., and P. McCart. 1983. Effects of different coho stocking strategies on coho and cutthroat trout production in isolated headwater streams. Canadian Technical Report of Fisheries and Aquatic Sciences 1212: 176 pp.
- Tschaplinsky, P. J. 1982. Aspects of the population biology of estuary-reared and stream-reared juvenile coho salmon in Carnation Creek: a summary of current research. Pages 289-305 in G. F. Hartman, editor. Proceedings of the Carnation Creek workshop: a ten-year review. Malaspina College, Nanaimo, British Columbia.
- Tschaplinsky, 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.
- Turnpenny, A. W. H., and R. Williams. 1980. Effects of sedimentation on the gravels of an industrial river system. Journal of Fish Biology 17: 681-693.
- van den Berghe, E. P., and M. R. Gross. 1984. Female size and nest depth in coho salmon (*Oncorhynchus kisutch*). Canadian Journal of Fisheries and Aquatic Sciences 41: 204-206.
- van den Berghe, E. P., and M. R. Gross. 1986. Length of breeding life of coho salmon (*Oncorhynchus kisutch*). Canadian Journal of Zoology 64: 1482-1486.
- van den Berghe, E. P., and M. R. Gross. 1989. Natural selection resulting from female breeding competition in a Pacific salmon (coho: *Oncorhynchus kisutch*). Evolution 43: 125-140.
- Vaux, W. G. 1962. Interchange of stream and intragravel water in a salmon spawning riffle. Special Scientific Report - Fisheries 405. U. S. Fish and Wildlife Service.
- Velsen, F. P. J. 1987. Temperature and incubation in Pacific salmon and rainbow trout: compilation of data on mean hatching time, mortality and embryonic staging. Canadian Report of Fisheries and Aquatic Sciences 626.
- Wallis, J. 1968. Recommended time, size, and age for release of hatchery-reared salmon and steelhead trout. Processed Report. Fisheries Commission of Oregon, Clackamas. 61 p.
- Ward, B. R., P. A. Slaney, A. R. Facchin, and R. W. Land. 1989. Size-biased survival in steelhead trout (*Oncorhynchus mykiss*): back-calculated lengths from adults' scales compared to migrating smolts at the Keogh River, British Columbia. Canadian Journal of Fisheries and Aquatic Sciences 46: 1853-1858.
- Ware, D. M., and R. E. Thomson. 1991. Link between long-term variability in upwelling and fish production in the northeast Pacific Ocean. Canadian Journal of Fisheries and Aquatic Sciences 48: 2296-2306.
- Wedemeyer, G. A., R. L. Saunders, and W. C. Clarke. 1980. Environmental factors affecting smoltification and early marine survival of anadromous salmonids. Marine Fisheries Review 42: 1-14.
- West, D. C., J. A. Reeher, and J. A. Hewkin. 1965a. Habitat improvement to enhance anadromous fish production. Closing Report, Tex. Creek Project 10. Oregon State Game Commission, Portland.
- West, D. C., J. A. Reeher, and J. A. Hewkin. 1965b. Habitat improvement to enhance anadromous fish production. Closing Report, Clear Creek Project 11. Oregon State Game Commission, Portland.
- West, J. R. 1984. Enhancement of salmon and steelhead spawning and rearing conditions in the Scott and Salmon rivers, California. Pages 117-127 in T. J. Hassler, editor. Proceedings of the Pacific Northwest stream habitat management workshop. California Cooperative Fishery Research Unit, Humboldt State University, Arcata.
- White, H. C. 1942. Atlantic salmon redds and artificial spawning beds. Journal of the Fisheries Research Board of Canada 6: 37-44.
- Wickett, W. P. 1951. The coho salmon population of Nile Creek. Fisheries Research Board of Canada Progress Report of the Pacific Coast Station 89: 88-89.
- Wickett, W. P. 1954. The oxygen supply to salmon eggs in spawning beds. Journal of the Fisheries Research Board of Canada 11: 933-953.



PRELIMINARY DRAFT - COHO SALMON LIFE HISTORY

- Wickett, W. P. 1958. Review of certain environmental factors affecting the production of pink and chum salmon. *Journal of the Fisheries Research Board of Canada* 15: 1103-1126.
- Wilderness Society, The. 1993. *The living landscape, volume 2. Pacific salmon and federal lands.* Washington, D. C.
- Willis, R. A. 1954. The length of time that silver salmon spent before death on the spawning grounds at Spring Creek, Wilson River, in 1951-52. *Oregon Fish Commission Research Briefs* 5: 27-31.
- Willson, M. F., and K. C. Halupka. 1995. Anadromous fish as keystone species in vertebrate communities. 9: 489-497.
- Wilson, D. A. 1976. Salmonid spawning habitat improvement study. Project Completion Report 1-93-D. Washington State Department of Fisheries and National Marine Fisheries Service.
- Withler, F. C. 1982. Transplanting Pacific salmon. *Canadian Technical Report of Fisheries and Aquatic Sciences* No. 1079. 27 p.
- Woods, P. F. 1980. Dissolved oxygen in intragravel water of three tributaries to Redwood Creek, Humboldt County, California. *Water Resources Bulletin* 16: 105-111.

