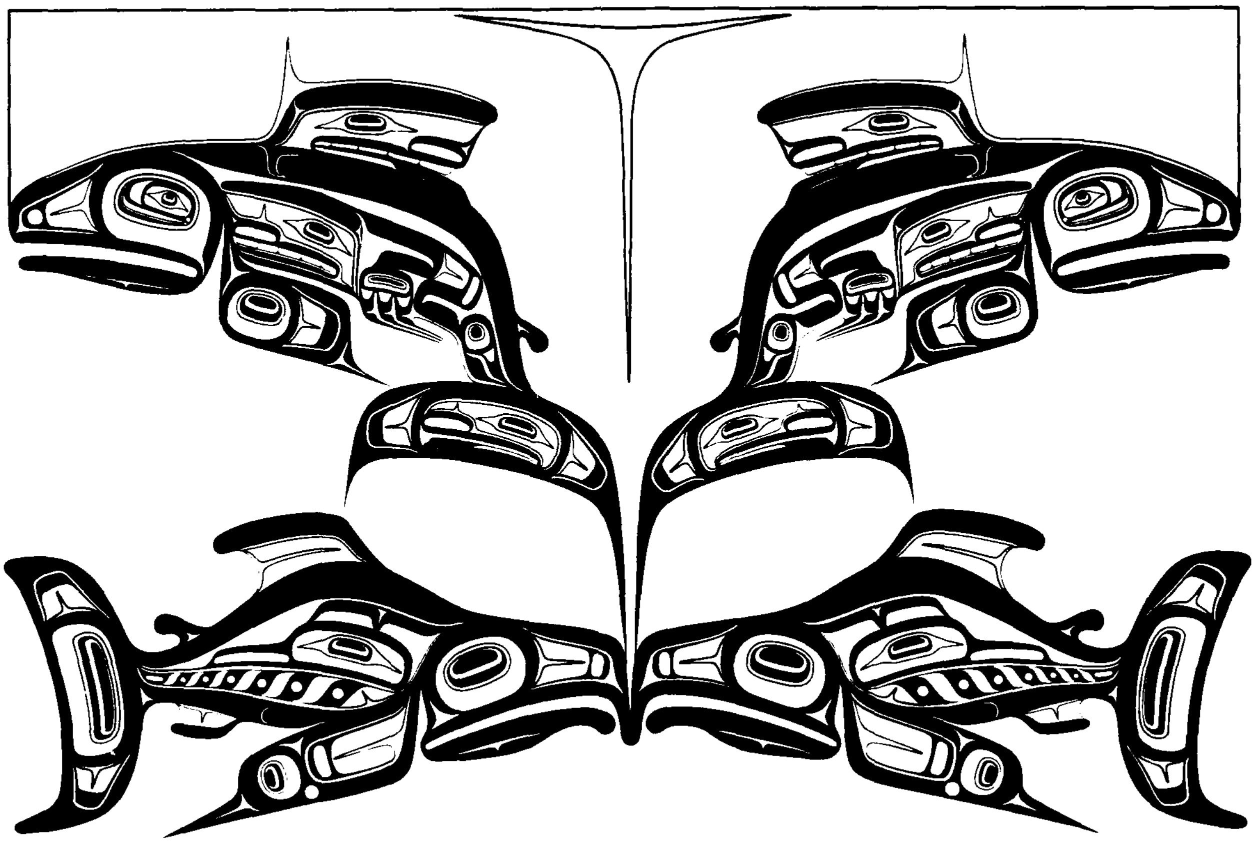
Biological Report 82(11.116)
December 1989

TR EL-82-4

Species Profiles: Life Histories and Environmental Requirements of Coastal Fishes and Invertebrates (Pacific Northwest)

SOCKEYE SALMON



Fish and Wildlife Service
U.S. Department of the Interior

Coastal Ecology Group
Waterways Experiment Station
U.S. Army Corps of Engineers

Cover illustration, "Every Year the Salmon Come Back," by Robert Davidson. A narrative painting originating from personal experience of the Yakun River salmon harvest, Queen Charlotte Islands. A cyclical metaphor: "when the salmon come they generate and influence my life cycle at that time. I'm at the river fishing with everybody else. They come back to give birth and also to die and from death comes new life." Illustration used with permission.

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Species Profiles: Life Histories and Environmental Requirements of Coastal Fishes and Invertebrates (Pacific Northwest)

SOCKEYE SALMON

by

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PREFACE

This species profile is one of a series on coastal aquatic organisms, principally fish, of sport, commercial, or ecological importance. The profiles are designed to provide coastal managers, engineers, and biologists with a brief comprehensive sketch of the biological characteristics and environmental requirements of the species and to describe how populations of the species may be expected to react to environmental changes caused by coastal development. Each profile has sections on taxonomy, life history, ecological role, environmental requirements, and economic importance, if applicable. A three-ring binder is used for this series so that new profiles can be added as they are prepared. This project is jointly planned and financed by the U.S. Army Corps of Engineers and the U.S. Fish and Wildlife Service.

Suggestions or questions regarding this report should be directed to one of the following addresses.

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CONVERSION TABLE

Metric to U.S. Customary

Multiply	*By*	*To Obtain*
millimeters (mm)	0.03937	inches
centimeters (cm)	0.3937	inches
meters (m)	3.281	feet
meters	0.5468	fathoms
kilometers (km)	0.6214	statute miles
kilometers	0.5396	nautical miles
square meters (m^2)	10.76	square feet
square kilometers (km^2)	0.3861	square miles
hectares (ha)	2.471	acres
liters (L)	0.2642	gallons
cubic meters (m^3)	35.31	cubic feet
cubic meters	0.0008110	acre-feet
milligrams (mg)	0.00003527	ounces
grams (g)	0.03527	ounces
kilograms (kg)	2.205	pounds
metric tons (t)	2205.0	pounds
metric tons	1.102	short tons
kilocalories (kcal)	3.968	British thermal units
Celsius degrees (° C)	1.8 (° C) + 32	Fahrenheit degrees

U.S. Customary to Metric

Multiply	*By*	*To Obtain*
inches	25.40	millimeters
inches	2.54	centimeters
feet (ft)	0.3048	meters
fathoms	1.829	meters
statute miles (mi)	1.609	kilometers
nautical miles (nmi)	1.852	kilometers
square feet (ft^2)	0.0929	square meters
square miles (mi^2)	2.590	square kilometers
acres	0.4047	hectares
gallons (gal)	3.785	liters
cubic feet (ft^3)	0.02831	cubic meters
acre-feet	1233.0	cubic meters
ounces (oz)	28350.0	milligrams
ounces	28.35	grams
pounds (lb)	0.4536	kilograms
pounds	0.00045	metric tons
short tons (ton)	0.9072	metric tons
British thermal units (Btu)	0.2520	kilocalories
Fahrenheit degrees (° F)	0.5556 (° F - 32)	Celsius degrees

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FIGURES

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ACKNOWLEDGMENTS

I am grateful to Richard Thorne and Donald Rogers, University of Washington, for their reviews of the manuscript.

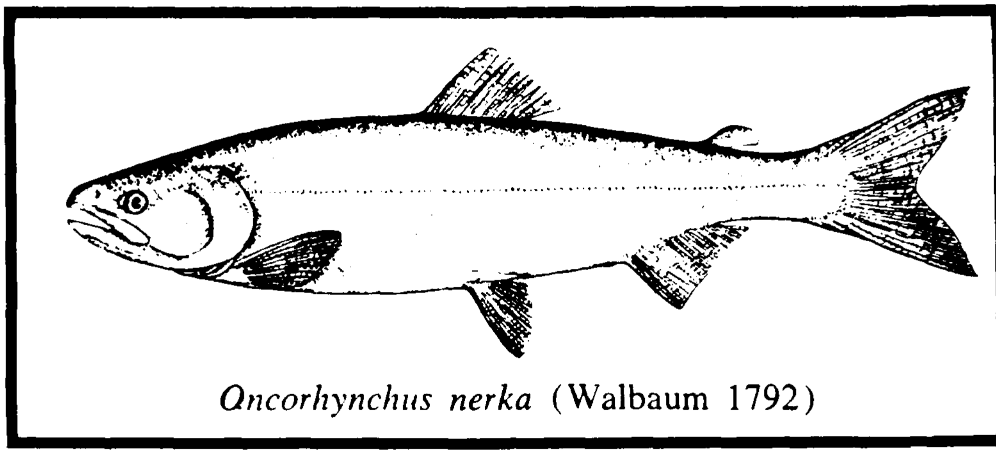

Figure 1. Sockeye salmon (after Hart 1973).

SOCKEYE SALMON

NOMENCLATURE/TAXONOMY/RANGE

Scientific name..............*Oncorhynchus nerka* (Walbaum)
Preferred common name..........................Sockeye salmon (Figure 1)
Other common names.....................Blueback, red salmon, kokanee (Lacustrine stocks only)
Class...Osteichthyes
Order...Salmoniformes
Family...Salmonidae

Geographic range: Found from the Klamath River, California, to the Yukon River, Alaska, but commercially important only from the Columbia River to Bristol Bay. The major Alaskan spawning grounds are in tributaries and lakes of the Kenai, Chignik, Naknek, Kuichak, Wood, and Kodiak Island river systems. In the Pacific Northwest, the major spawning river for sockeye is the Fraser River system in British Columbia, while less important runs exist in the United States in the Baker, Columbia, Cedar, Quinault, and Ozette Rivers in Washington State (Figure 2). The Fraser River (Figure 3) includes a number of important nursery lakes and many tributaries that support the major portion of the sockeye salmon population in the Pacific Northwest. The principle sockeye rearing lakes on the Fraser River are Cultus, Adams, Harrison, Horsefly, Shuswap, and Quesnel Lakes. In eastern Washington, the major nursery lakes for the Columbia River are Lake Wenatchee on the Wenatchee River and Osoyoos Lake on the Okanogan River. There are eight separate geographic stocks of Columbia River sockeye that home to specific rearing lakes (Mullan 1986). In western Washington the major nursery lakes are Quinault Lake on the Quinault River, Ozette Lake on the Ozette River, Baker Lake on the Baker River, and Lake Washington into which the Cedar River flows (Poe and Mathisen 1981). Landlocked populations of sockeye salmon, called kokanee, have been successfully introduced into many western states (Wydoski and Whitney 1979; Wydoski and Bennett 1981).

MORPHOLOGY/IDENTIFICATION AIDS

Dorsal fin (11-16 rays), adipose small, slender and fleshy, anal fin (13-18), pelvic fins (9-11) abdominal in position with a free-tipped fleshy appendage above its insertion, pectoral fins (11-21). Cycloid scales. Gill rakers (29-43) long, rough, slender, and closely set on first gill arch. Body elongate with moderate lateral compression.

Greenish-blue coloration with fine black speckling on the back. No large dark spots. Breeding male with pale

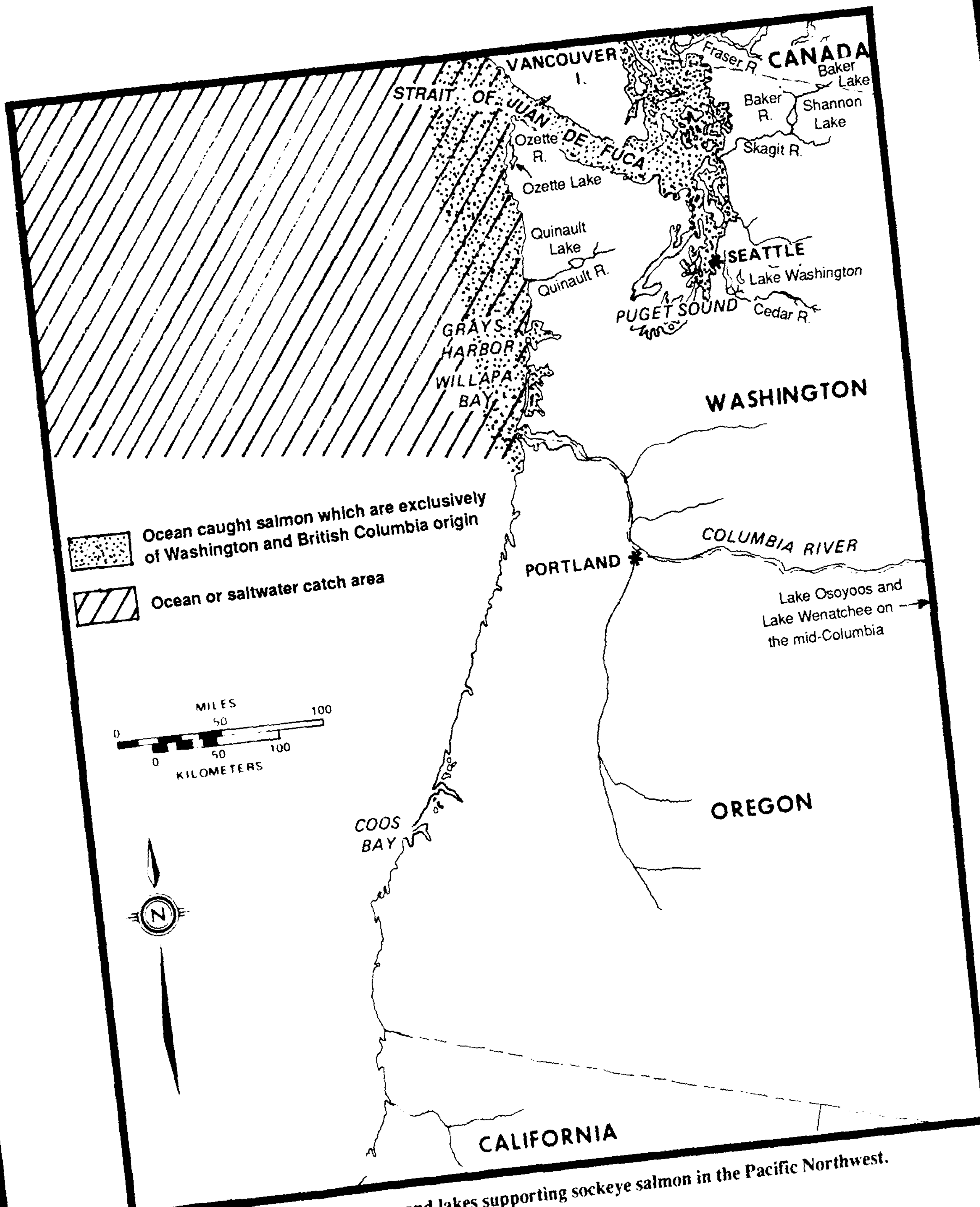

Figure 2. Major rivers and lakes supporting sockeye salmon in the Pacific Northwest.

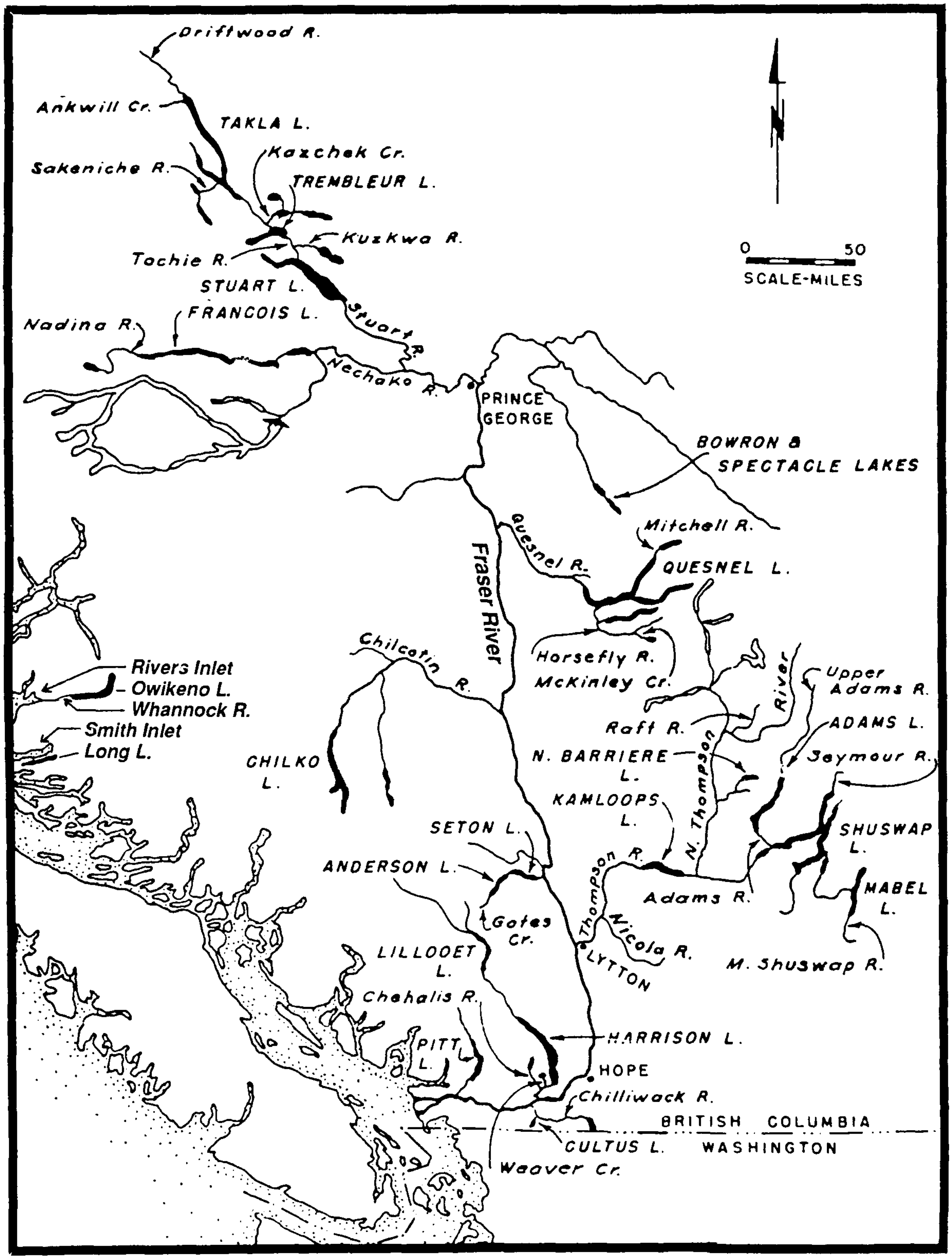

Figure 3. Major sockeye salmon rearing lakes in the Fraser River, Rivers Inlet, and Smith Inlet systems of British Columbia (after Poe and Mathisen 1981).

green head, bright red body, and red fins. Breeding female generally the same with characteristic bright scarlet body. In juveniles the parr marks are shorter than the diameter of eye, oval and usually above lateral line. Hart (1973) and Scott and Crossman (1973) are the source of morphology and identification aids.

REASON FOR INCLUSION IN SERIES

Sockeye salmon are found in commercial quantities along the North American coast from the Columbia River, between Oregon and Washington, to Bristol Bay, Alaska, and are the most valuable commercial fishery in both Alaska and British Columbia. They are extremely important as subsistence and ceremonial fish to the Indians of Alaska, British Columbia, and Washington. The brilliant red flesh of these fish is highly desired by both commercial and sport fishermen.

LIFE HISTORY

Spawning

Sockeye salmon are anadromous, spending 1-4 years in the ocean, usually 2, and 2 years in freshwater. This gives a complex number of life cycle years. With the onset of maturity, sockeye travel from their oceanic feeding areas to their natal streams which are usually associated with lakes. After ascending a river, they spend 1-8 months in the lake before moving to their natal spawning areas. There appears to be a diel migration pattern that operates during migration, and this probably differs between stocks (Manzer et al. 1984). Spawning areas selected by the adults may be (1) in streams flowing into the lake; (2) in the upper sections of the lake's outlet river; or (3) along the shores of the lake where seepage outflows, springs, or wind-induced waves occur (Foerster 1968).

Redds are selected in areas of gravel bottom where there is sufficient waterflow through the gravel to provide the developing eggs and embryos with oxygen and to remove the waste products of metabolism (Foerster 1968). A redd consists of 3-10 nesting pockets, each with an average of 750 eggs (Hart 1973). In general, medium- to small-sized gravel (1.3-10.2 cm according to Reiser and Bjornn 1979) is utilized for redd production. Olsen (1968) has indicated that either sand or gravel may be used by sockeye salmon, depending upon which is available. If small amounts of silt, detritus, or fine sand are mixed with the coarser gravel, they are removed by the fish in the process of excavating the redd (Foerster 1968). The male takes little part in redd building, although he remains near the redd for courtship purposes. The female excavates the redd by vigorous upward and downward motions of her body, causing both the tail and water pressure to move the sand and gravel. When spawning occurs, the female places herself over the pocket, followed by the male a second or two later. Both fish lower their tails to bring their vents close together near the center of the pocket. Eggs and milt are then released while the two fish remain over the pocket for 4-19 seconds. Immediately after spawning, the eggs are buried by the female (Mathisen 1955). Mathisen (1955) observed 198 redds with Bristol Bay sockeye spawning in them at Pick Creek and found egg concentrations 6-9 inches below the gravel surface. Spawning occurs between August and January, depending upon the sockeye stock. Adults die after spawning. Adult spawning escapement can be assessed by several methods including aerial surveys, test fisheries, or hydroacoustics (Thorne 1979; Cousens et al. 1982).

Eggs and Fecundity

The number of eggs per female varies directly with the size of the fish, but there is good evidence that this relationship may vary appreciably between stocks of sockeye (Foerster 1968; Manzer and Miki 1986). Coastal stocks are 18% more fecund than interior stocks in British Columbia. The number of eggs is high compared to other species (averaging about 3,500 per female; Manzer and Miki 1986). However, the size of the eggs (5.29-6.60 mm in diameter) is the smallest among the Pacific salmon (Foerster 1968). High fecundity in sockeye is thought to be related to the long period that they spend in freshwater (Foerster 1968). The fecundity of Pacific Northwest sockeye is reported to vary among females depending upon body size (Table 1; Manzer and Miki 1986) and not age. There is not any relationship of age to fecundity once size is accounted for.

Table 1. Fecundity of sockeye salmon in relation to size, for various areas (adapted from Foerster 1968).

Area	Year	Mean length (cm)	Mean egg content
Babine Lake[a]	1946	60.9	3281
	1947	59.1	3187
	1949	59.7	3353
Lakelse Lake[a]	1939	59.6	3888
	1948	59.0	3860
	1949	58.1	3699
Pick Creek, Wood River[b]	1948	55.3	3968
	1950	53.8	4096
	1951	52.0	3944
	1952	51.7	3952
Kurile Lake, Kamchatka[c]			
River spawners	1929	(57.6)	3790
River spawners	1930	(56.1)	3895
Stream spawners	1932	(58.9)	3600
Lake spawners	1932	(59.0)	4585[d]
Lake Dalnee, Kamchatka[e]	-	(51.2-54.0)	2500-2600
Lake Blizhnee, Kamchatka[e]	-	(49.0-51.0)	2000-2400
Port John, B.C.	1949(18)[f]	51.3	2425
	1950(9)	50.8	2157
	1951(5)	54.3	2632
	1952(7)	52.5	2436
	1953(8)	54.8	2808
	1954(9)	55.2	2711
	1955(15)	52.0	2577
	1956(15)	52.3	2694
	1957(5)	54.2	3101
	1958(14)	53.1	2998
Karluk Lake, Alaska	1938-41(5_3)[g]	58.8	3306
	1938-41(6_3)	60.6	3018
	1938-40-41(6_1)	59.7	3238
	1939, 1941(7_4)	59.7	2968
Cultus Lake, B.C.	1932	58.5	4310
	1933	56.5	3796
	1934	59.0	4282
	1935	59.0	4067
	1937	56.0	3864
	1938	58.5	4246

[a]No segregation according to age. Probably mostly 5_2 fish. According to Foskett (1956), Skeena River sockeye in these years were 70, 82, and 76% 5_2 fish, respectively.
[b]Both 4_2 and 5_2 fish involved.
[c]Egg counts not correlated directly with length of females. Hence, mean length of females, as recorded for the sockeye examined at the mouth of the Ozemaya River, are used. No age separation has been made.
[d]Only four individuals in the sample.
[e]Only ranges in length and egg content available. For lengths, males and females are combined. Neither for length nor egg content is there any segregation according to age. Several year-classes are involved.
[f]Figures in parentheses indicate the number of specimens.
[g]Figures in parentheses indicate the age of the fish on the Gilbert system.

Alevins and Fry

The egg incubation period depends on water temperature (4.4-13.3 °C) and usually lasts 50-140 days (Scott and Crossman 1973). The development rate of sockeye salmon eggs from the fall to spring increases with temperature. They develop normally between 4 and 14 °C (Reiser and Bjornn 1979). After hatching, the young (alevins) remain in the gravel for 3-5 weeks before emerging as free-swimming fry (Hart 1973). The fry emerge in April or May depending on water temperature. Each population exhibits inherent directional and rheotactic preferences that guide them to their nursery lake and disperse them within the lake (Brannon 1982; Quinn 1982a).

They also are extremely light-sensitive and remain at the bottom hiding under stones and debris during daylight hours (Foerster 1968; Stober and Hamalainen 1979). They begin moving about at dusk and rise up into the flowing water at night. This behavior readily facilitates downstream movement into lakes for those sockeye salmon which hatch in streams above lakes. The fry, which must move upstream to nursery lakes, travel during daylight. Clarke and Smith (1972) suggest that light, not temperature, is important in stimulating upstream movement of fry. Quinn (1982b) indicated that sockeye salmon may possess an innate sun orientation mechanism. Migrations of juvenile sockeye salmon are aided by compass directional preferences that are based on a combination of celestial and magnetic guidance mechanisms (Quinn 1982b; Quinn and Brannon 1982).

Observations in British Columbia of the relative lack of upstream movement by sockeye fry at night indicated a need for visual contact with the river bottom (Clarke and Smith 1972). McCart (1967) observed that with upstream migrating fry there is an initial downstream movement, a period of holding, and an eventual return upstream. Upstream movement does not generally begin until the mean daily water temperature exceeds 8 °C (McCart 1967). During the holding period, when fry are concentrated in a narrow strip along the edges of the stream, there is a high mortality due to predation by other fish (McCart 1967).

Lake Residence

Upon entering the nursery lake, sockeye salmon in some lake systems move along the shore for a few weeks, and then move out over deeper water where they concentrate initially at depths of 10 to 20 m (Hart 1973). During the period of lake residence, fry are pelagic schooling fish that subsist mainly on zooplankton. Diel vertical movements include rising into the surface layer at dusk, descending slightly at night, and then at dawn descending to deeper daytime depths (McDonald 1969; Narver 1970; Woodey 1972).

Diel migration in thermally stratified lakes increases the growth rate because of exposure to a 24-hour cycle of variation in temperature. Sockeye fed moderate amounts of food in the laboratory and exposed to daily cyclic temperature change had the highest gross growth efficiency (ration of growth to total food ingested) and growth rate compared to fish exposed to constant high or low temperatures (Biette and Geen 1980a). Constant high temperatures result in slower growth because of energy loss from a high respiration rate, and low temperatures retard growth because they cause a high defecation and excretion rate (Biette and Geen 1980b). However, the migration to greater depths during the day has the disadvantage that the fish are out of the lighted zone where they can visually feed. They may move deeper during the day to avoid predators that hunt visually. However, they feed crepuscularly (at dawn and dusk), perhaps taking advantage of a tradeoff between optimal sunlight conditions for their own feeding on zooplankton and optimal light conditions for predation on the sockeye by larger fish (Clark and Levy 1988).

Young sockeye salmon normally live in the nursery lake for 1 or 2 years, while in some regions of Alaska this is for 3 years, and on rare occasions this residence may last 4 years (Miller and Brannon 1982). In British Columbia this residence is usually only 1 year (Scott and Crossman 1973). This residence time is generally greater the farther north geographically that the nursery area is located. This period is a very crucial stage in sockeye natural production, one in which mortality may be very high due to piscivorus predation (Foerster 1968). Mortality of young fry is size selective, with those that were smallest at the time of emergence having a lower survival (West and Larkin 1986). When surface temperatures in the nursery lakes approach 4 to 7 °C in the spring, most 1-year resident sockeye migrate to sea (Hart 1973). Fish which are larger or that have been in the lake for 2 years tend to migrate earlier. Observations in the Wood River system of Alaska indicated that seaward migration of young sockeye was consistently temperature-related (Burgner 1958). Foerster (1968) observed that cessation of migration seemed to be associated with temperatures of 4.4 to 5.0 °C in the upper waters of Cultus Lake, British Columbia. Rees (1957) found that downstream migrant sockeye smolts in Baker Lake, Washington, clearly occupied the surface layer (water down to 4-5 m), and that fish density decreased with increasing depth with almost no fish observed below 14-15 m. Migration to the sea includes active downstream swimming in quiet river reaches, but is passive and tail first in rapids (Hart 1973). This migration to the sea is rapid (Miller and Brannon 1982).

Saltwater Life

In the Pacific Northwest, sockeye salmon smolts enter the ocean primarily from Puget Sound, the Quinault River on the Olympia Peninsula, the Columbia River in Washington, and the Fraser River in British Columbia (Figure 2). Stocks from the southern locations apparently enter the ocean first, followed by stocks in the more northern and western locations, while the migration in the Strait of Juan de Fuca peaks prior to July (Hartt 1980). Upon entering the marine environment, sockeye salmon proceed immediately to the feeding grounds of the high seas (Eggers 1982). Unlike other Pacific salmon species, young sockeye salmon are not often seen in estuarine and inshore waters after reaching the marine environment (Miller and Brannon 1982). Catches of juveniles originating in the Strait of Juan de Fuca indicate that they migrate along the coastal belt, preceding juvenile chum and pink salmon. It is well known that sockeye salmon travel far during the marine phase of their life, most notably to the northern, nutrient-rich waters of Alaska and the Arctic (Hartt 1980; Brannon 1982). There is evidence of a general intermingling in the Gulf of Alaska region during much of the marine phase. French and McAlister (1970) observed that the distribution of sockeye salmon in various areas of the Northwestern Pacific Ocean seemed to depend on age and maturity rather than on place of origin. For example, stocks from Bristol Bay, which contribute a significant proportion of the North American sockeye fishery, and non-Bristol Bay stocks were found to have a similar distribution in areas of the northeastern Pacific Ocean during the winter (French and McAlister 1970). Sonar observations and gillnet catches show that salmon, rather than forming defined schools, disperse during their feeding periods in the ocean (Burgner 1980). Detailed information on the distribution of sockeye salmon in the north Pacific Ocean obtained from commer‹ ; fleets and research vessels was discussed by French et al. (1976). Sockeye salmon spend a total of 1-4 years as marine residents.

High seas migrations of salmonids and the m chanisms which guide them remain largely unknown. Quinn (1982b) stated that the relative densities of food, predators, and competitors are undoubtedly important, as well as currents, water temperature, and salinity. It was further proposed that salmon navigate using a celestial compass with a backup magnetic compass, the inclination and declination of the earth's magnetic field, and an endogenous circannual rhythm adjusted by the length of the day or photoperiod (Quinn 1982b). Salmon-guiding mechanisms were further discussed by Leggett (1977) and Brannon (1982).

Statistical model predictions have suggested that about 90% of the natural mortality in the ocean occurs during the first 4 months that sockeye salmon are at sea (Furnell and Brett 1986). The marine survival rate varies with smolt size and probably varies with geographic region. Ames (1983) stated that marine survival ranged from 4%-20% with an average of 9.8 adults returning to the Cedar River for each of 100 pre-smolts, a normal range of survival for sockeye salmon stocks. Thorne and Ames (1987) also report marine survival of 4%-20% for Lake Washington sockeye.

GROWTH CHARACTERISTICS

Sockeye salmon growth rates may vary in different parts of the same nursery lake (Pella 1968). In Lake Aleknagik, Alaska, fry in the eastern end of the lake were significantly larger than those in the western end. If salmon fry from both ends of the lake had hatched at the same spawning grounds in the western end, salmon fry which had migrated to the eastern end would be larger because they had hatched earlier and had a longer feeding period during migration to the other end of the lake. Fry at the western end would be smaller because of a more recent hatching and shorter feeding period. Growth rates of sockeye fry varied considerably more in the littoral zone (0.158-0.349 mm per day) than in the limnetic zone (0.233-0.292 mm per day), according to Pella (1968). In the first 12 months of life, the growth of fry has been shown to be related to both the temperature (optimum 15 °C) and the amount of ration available as a percent of dry body weight per day (Brett et al. 1969). As the available ration was decreased from 6% to 1.5% in laboratory experiments, the optimum temperature shifted downward from 15 to 5 °C.

Sockeye fry migrate from their rearing lakes at various sizes (Foerster 1968), with 1-year-old migrants varying from 6.0 to 11.5 cm in length and 2.0 to 15.5 g in weight; 2-year-old migrants varying from 7.6 to 15.6 cm and 18.0 g to 39.1 g; and 3-year-old fish varying from 10.0 to 14.2 cm and 21.0 g to 26.5 g. Although young sockeye salmon will migrate out at all three ages, in Alaska they migrate primarily at age-I or age-II, and in British Columbia they migrate primarily at age-I (Foerster 1968). One-year-old migrant fish in British Columbia have an average length and weight size of about 8 cm and 5 g. Hyatt and Stockney (1985) found 1-year-old smolts weighing less than 2 g in 7 populations of sockeye salmon along the British Columbia coast. The presence of competitor and predator fish as well as the density of the sockeye fry themselves will have an effect on the growth rate (Foerster 1968; Pella 1968; Hyatt and Stockner 1985). Studies on the role of density in regulating growth have generally been between-lake, between-year comparisons. Growth appears to be depressed in areas of heavy sockeye fry density, but Pella (1968) has advanced an alternative hypothesis that the largest of the sockeye fry were the first to leave the crowded rearing areas, thereby leaving only smaller fish. Geography plays an important role in growth: in British Columbia, outer coastal lakes generally produce smaller smolts than do the more productive interior lakes (Stockner and Shortreed 1983).

Hartt (1980) stated that sockeye salmon usually reach a minimum of 10 cm before they are found in the ocean migration routes. Smolts that enter the marine environment are smaller than 10 cm. Addition of nitrogen and phosphorus fertilizer to British Columbia coastal lakes increased production of zooplankton, causing increased in-lake growth of juvenile sockeye salmon and larger outmigrant smolts (Stockner and Hyatt

1984; Hyatt and Stockner 1985). In fertilized lakes, the average weight at migration was 3.8 g, while in unfertilized lakes the average weight at migration was 2.3 g.

The major fingerling growing season includes July, August, and September. Growth in the second season begins prior to or at the time of seaward migration of yearlings. Mean size of first year sockeye caught in marine waters in the northeastern Pacific Ocean ranged from 12 to 20 cm (Hartt 1980). In a study of British Columbia sockeye stocks, Ricker (1982) stated a positive correlation between length of oceanic life and final size.

Smolt-size increases in fertilized lakes will lead to increases in both marine survival and an earlier age of returning adults, thereby increasing the harvestable surplus of sockeye adults (Hyatt and Stockner 1985). Lake fertilization has also been correlated with increased egg-to-juvenile survival of sockeye salmon as well as greatly increased adult returns (Le Brasseur et al. 1978). The fish grow to a maximum reported length of 84 cm in the ocean, but stocks from different river systems have characteristic sizes (Foerster 1968; Hart 1973). According to Foerster (1968), sockeye salmon growth rate during ocean residence is governed by three factors: the amount of food (principally plankton) available; water temperature (growth is generally faster in warmer water); and the degree of competition for food and size of the feeding salmon. However, Ricker (1982) noted that adult sockeye appear to grow larger in years of sub-average marine temperatures. Adult body size and growth rate decrease when sockeye salmon are abundant in the Gulf of Alaska (Peterman 1984). Weight differences can amount to 10%-22% at high abundance of conspecifics. Density-dependent effects arise mainly during early ocean life and are probably due to competition for food (Peterman 1984). Thus, fluctuations in growth are to be expected from year to year which result in different lengths and weights of the fish at maturity.

There are some general consistencies in sockeye growth according to Foerster (1968) which are as follows: (1) the length increment in the second ocean year is appreciably less than in the first and is less in the third ocean season than in the second; (2) among fish of the same freshwater age, those that spend a longer time in the sea have a slower overall growth rate; and (3) sockeye that spend only 1 year and a few months in the sea but that are a total of 3-5 years old have had growth during the second summer in the ocean that is twice that of other fish. Fast growth during the early period of marine life tends to be associated with an earlier age of maturity (Peterman 1985).

THE FISHERY

Forecasting Models

The commonly used linear forecasting method overestimated sockeye runs more often than a nonlinear method for Bristol Bay, Alaska, salmon and the nonlinear method is recommended. Overestimates of returning sockeye may lead to overharvesting and hence reduced long-term yield, and may also result in overinvestment in the fishery by participants (Bocking and Peterman 1988).

Puget Sound Stocks

Commercial catches of sockeye salmon peaked in the late 1930's for both North American and Asian stocks (Figure 4) (French et al. 1976). North American stocks originate primarily from streams and lakes in Alaska and British Columbia; the most important producing area is western Alaska (Figure 5), especially the tributaries of Bristol Bay (French et al. 1976). The Japanese high seas gillnet fishery harvests sockeye salmon of both Asian and North American origin. The Canadian commercial harvest comes from fish originating primarily from British Columbia, while a significant portion of the Washington State commercial catch originates from the Fraser River in southern British Columbia (French et al. 1976). Catches of sockeye salmon in Washington and Oregon have averaged about 1 million fish in recent years (French et al. 1976).

Two sockeye salmon runs originate in the Puget Sound basin (Figure 2)--one in Lake Washington and one in Baker Lake. The larger of the two runs is from Lake Washington, where most of the fish spawn in the Cedar River. This stock was introduced by plantings of fry, fingerlings, and yearlings from Baker Lake, Washington, between 1935 and 1945 (Kolb 1971), and is now the largest sockeye salmon run in the United States outside of Alaska (Stober and Hamalainen 1979). The

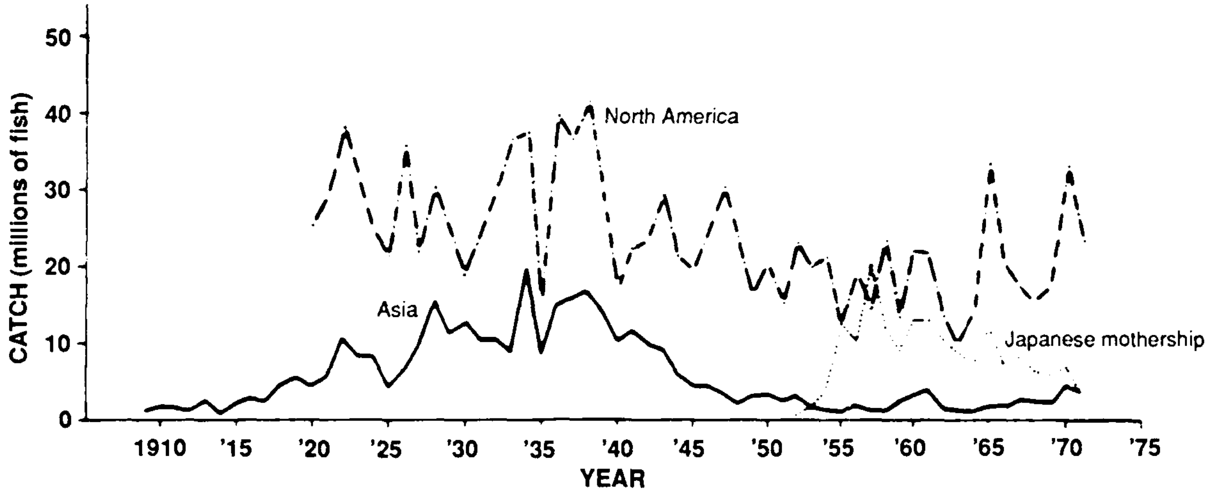

Figure 4. Estimated commercial catch of sockeye salmon in Asia, North America, and the Japanese mothership fishery, 1909-71 (after French et al. 1976).

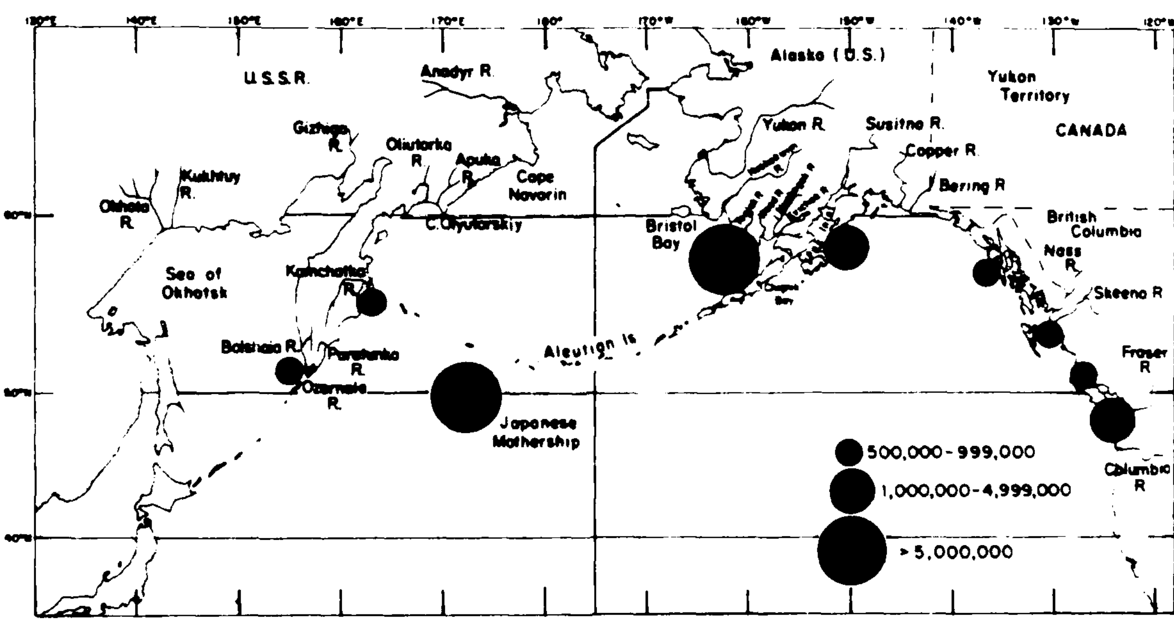

Figure 5. Average annual commercial catch of sockeye salmon in important coastal and high seas fishing areas, 1961-71 (after French et al. 1976).

population is first predicted by presmolt numbers (pre-season forecast), and adult returns are then monitored at the Ballard Locks in June and July to update the earlier estimates. The escapement goal of 350,000 spawners for Lake Washington has been in effect since 1969 (Ames 1983; Puget Sound Tribes et al. 1989). Both escapement and the resulting adult run size have increased between 1968 and 1983 (Table 2; Ames 1983). Three identifiable fisheries exploit the Lake Washington stock: (1) a Puget Sound non-Indian commercial fishery using gillnets and purse seines; 2) an Indian gillnet fishery; and 3) a sport fishery (Bryant 1976). Until the early 1970's, Lake Washington sockeye salmon were managed exclusively for the commercial fishery. In recent years, however, the tribal and sport fisheries have taken the greatest number of fish. The highly successful sport fishery provides an excellent economic return while having little effect on escapement

Table 2. Lake Washington sockeye brood year data (adapted from Puget Sound Tribes et al. 1989).

Brood year	Escapement	Peak Cedar River flow (ft^3/s) Renton	Presmolt population estimate ($X 10^6$)	Resulting adult run size[a]	Jacks	Freshwater survival (pre-smolts per spawner)	Percent marine survival[b]	Return/ spawner
1964	137,500	5,300	-	274,165	-	-	-	1.99
1965	132,000	1,570	-	267,338	-	-	-	2.03
1966	123,000	2,960	-	135,224	-	-	-	1.10
1967	383,000	2,910	7.50	559,074	-	19.6	7.45	1.46
1968	252,000	3,720	3.19	299,461	-	12.7	9.39	1.19
1969	200,000	2,290	3.80	476,191	-	19.0	12.53	2.38
1970	124,000	2,730	2.00	149,649	-	16.1	7.48	1.21
1971	183,000	8,160	1.70	143,578	-	9.3	8.45	0.78
1972	249,000	4,000	3.58	179,915	-	14.4	5.03	0.72
1973	330,000	4,220	4.56[c]	593,148	18,765	13.8	13.01	1.80
1974	126,000	3,520	1.96[c]	311,266	16,015	15.6	15.88	2.47
1975	120,000	8,800	1.14	229,787	2,397	9.5	20.16	1.91
1976	159,000	1,340	3.96	497,322	25,635	24.9	12.56	3.13
1977	275,000[d]	5,670	2.93	119,304	1,848	10.7	4.07	0.43
1978	290,000	1,840	6.80	323,988	5,192	23.4	4.76	1.12
1979	206,000	3,080	3.64	290,401	8,649	17.7	7.98	1.41
1980	361,000	3,020	3.78	477,871	3,832	10.5	12.64	1.32
1981	107,000	5,320	1.14	261,779	2,011	10.7	22.96	2.45
1982	289,000	3,250	2.02	257,542	6,736	7.0	12.75	0.89
1983	227,000	5,540	1.32	222,531	3,329	5.0	16.86	0.99
1984	372,000	1,610	4.99	645,980	4,286	13.4	12.95	1.74
1985	254,000	2,480	0.95	-	1,037	3.0	-	-
1986	249,000	5,070	0.73	-	-	2.9	-	-
1987	207,000	1,820	-	-	-	-	-	-
1988	376,000	-	-	-	-	-	-	-
Average	**229,260**	**3,759**	**3.08**	**319,171**	**7,672**	**12.96**	**9.23**	**1.41**

[a]Includes jacks from next brood year.

[b]These values assume returns are 4-year-old fish only.

[c]Accurate presmolt estimates unavailable. Values used are estimated from the relationship between freshwater survival (presmolt per spawner) and peak floods on the Cedar River.

[d]Actual escapement 435,000 fish. Prespawning mortality reduced effective escapement to 275,000 sockeye.

(Bryant and Mathews 1973). The recent increase in the tribal fishery is due to a 50:50 sharing plan brought about by *United States v. Washington* (Clark 1985). Lake Washington sockeye brood-year data for 1964-79 indicates an average escapement of 212,970 sockeye.

The other run which originates in the Puget Sound basin spawns on beaches of Baker Lake above the hydroelectric reservoir on the Baker River, a tributary of the Skagit River (Figure 2). The sockeye salmon are trapped at facilities near the mouth of the Baker River and trucked upstream to the spawning beaches. Because of the recent average escapements of less than 2,000 sockeye salmon (Table 3), and an escapement goal of 4,500 fish, management recommendations in recent years have called for no targeted Baker River sockeye fishery (Puget Sound Tribes et al. 1989).

Full utilization of the Baker River as a sockeye salmon production area would require improvements to the downstream juvenile passage facilities to ensure that more fish get past the two hydroelectric dams that are present (Puget Sound Tribes et al. 1989). No sport or commercial saltwater fisheries are directed at the Baker River sockeye salmon run. Sockeye fisheries in northern Puget Sound and the Strait of Juan de Fuca take place only when there are harvestable surpluses of British Columbia's Fraser River sockeye salmon available (Puget Sound Tribes et al. 1989). The impact of the mixed stock fishery on the Baker River stock then is minimal.

Table 3. Terminal area catch and escapement for Baker River (Skagit system) sockeye (data adapted from Puget Sound Tribes et al. 1989).

Year	Baker trap escapement	Terminal catch[a]	Terminal run size	Returns/ spawner[b]
1967	4,121	784	4,905	-
1968	3,022	448	3,470	-
1969	1,295	306	1,601	-
1970	821	30	851	-
1971	2,931	1,095	4,026	0.98
1972	10,031	641	10,672	3.53
1973	3,656	1,109	4,765	3.68
1974	3,611	1,069	4,680	5.70
1975	1,303	686	1,989	0.68
1976	1,518	651	2,169	0.22
1977	1,707	387	2,094	0.57
1978	2,716	668	3,384	0.94
1979	865	535	1,400	1.07
1980	499	46	545	0.36
1981	208	264	472	0.28
1982	1,860	287	2,147	0.79
1983	735	172	907	1.05
1984	358	17	375	0.75
1985	92	410	502	2.41
1986	542	39	581	0.31
1987	691	84	775	1.05
1988	818	62	880	2.46

[a]Includes both treaty and non-treaty catches and Skagit Bay and Skagit River.
[b]Brood year = year-4.

Columbia River Stocks

There has been no significant commercial harvest of sockeye salmon on the Columbia River system in recent years (Allen 1977). Historically, the Columbia basin catch which peaked between 1890 and 1900 was highly variable from year to year (Figure 6). The impoundment of the Columbia River for power and irrigation has reduced the river's current velocity and caused a rise in water temperatures, which among other factors, has harmed the native sockeye salmon runs. Declining runs in this river can be correlated with increased number of dams (Mullan 1986). The primary sockeye salmon-producing areas of the Columbia River basin are Lake Osoyoos on the Okanogan River system between Washington and British Columbia and Lake Wenatchee on the Wenatchee River system in Washington (Allen and Meekin 1973; Poe and Mathisen 1981; Mullan 1986). These runs have been partly sustained by stocked fish from the Federal hatchery at Leavenworth, Washington. Approximately 14% of the fish taken in commercial and Indian fisheries in the lower Columbia River originated from this hatchery (Wahle et al. 1979). These two runs are sustained by releasing hatchery fingerlings into the Wenatchee and the Okanogan Rivers (Davidson 1966). Natural reproduction does occur with these two stocks (Peven 1987); however, both returning adults and out-migrating smolts must pass nine dams on the mid-Columbia River (Peven 1987).

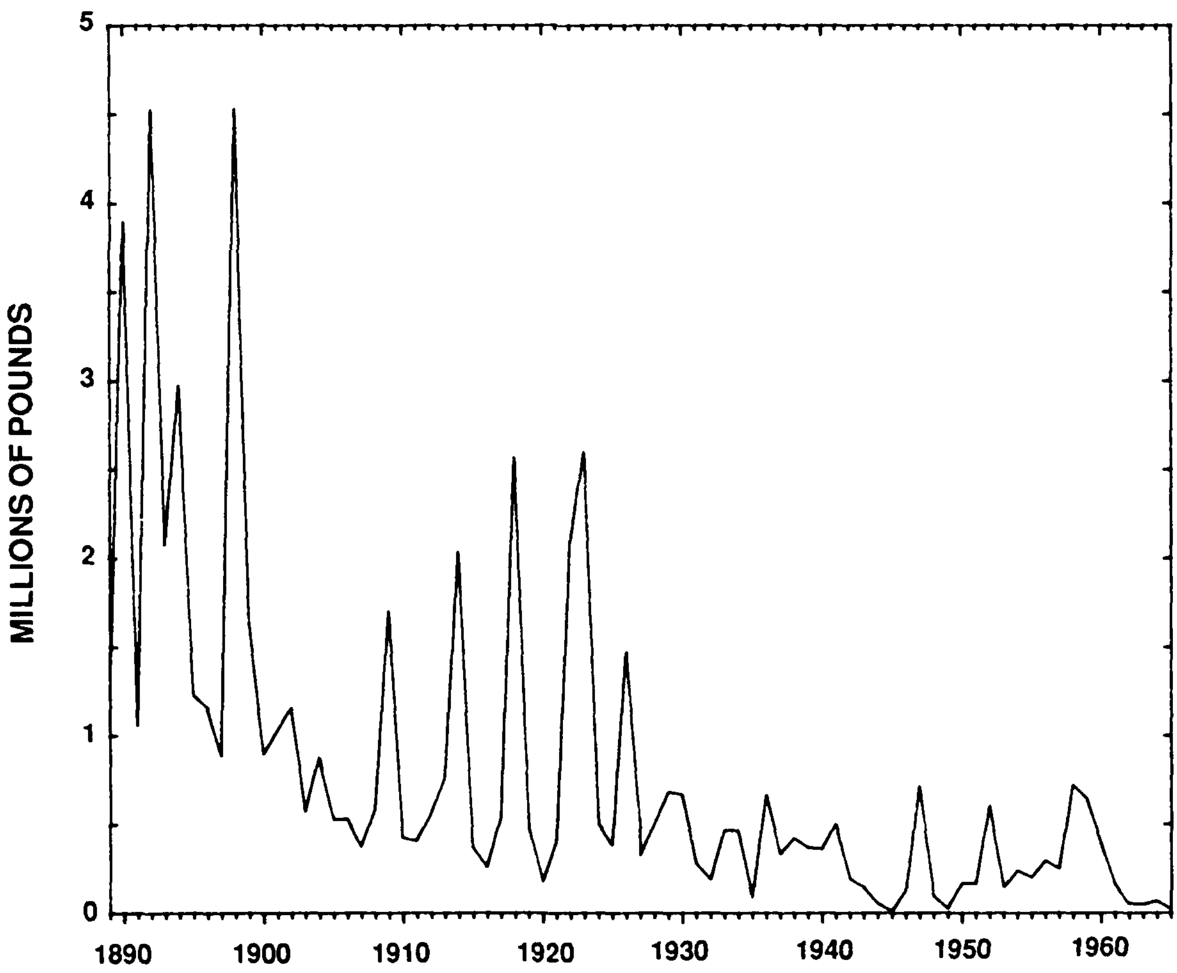

Figure 6. Commercial catches of blueback salmon in the Columbia River 1889 to 1965. Adapted from Craig and Hacker (1940) and Davidson (1966).

North Coastal Stocks

On the North Pacific Coast of Washington State there are two sockeye producing areas: Lake Quinault and Lake Ozette (Poe and Mathisen 1981). The Quinault Indians are the exclusive harvesters of Lake Quinault sockeye salmon in a tribal gill-net fishery that averages 27,500 fish per year, according to the Pacific Fishery Management Council (1983). Lake Ozette was once a moderate producer of sockeye salmon and supported a fishery by the Makah Indian Tribe that yielded over 17,500 fish in 1949 and approximately 15,000 fish in both 1950 and 1951, but subsequently declined to zero in both 1974 and 1975 (Blum 1984). In recent years the Lake Ozette fishery has averaged only about 30 fish per year (Blum 1984). Investigations into the limiting factors that may have caused this spectacular decline were investigated by Dlugokenski et al. (1981) and Blum (1984). Restoration of the Lake Ozette sockeye fishery will be attempted through the use of an introduced sockeye stock that will utilize the lake's tributaries to spawn. The native stock only utilizes the suitable part of the lake shore, which is currently extremely limited in area (Blum 1984).

ECOLOGICAL ROLE

Juvenile sockeye salmon are pelagic, schooling fish and are largely planktivorous. Their primary foods depend on the availability of seasonal zooplankton populations (Foerster 1968; Woodey 1972). Studies in Lake Washington revealed that the primary foods of sockeye salmon were the copepods, *Epischura, Diaptomus, Cyclops*, and the cladoceran, *Diaphanosoma* (Woodey 1972; Eggers 1978). In nursery lakes of British Columbia, common foods of young sockeye salmon include Cladocera (*Bosmina* and *Daphnia*) and copepods (*Cyclops* and *Epischura*) (Foerster 1925, 1968). *Cyclops* constituted the main food item (85%), followed by *Daphnia* (12%) and *Bosmina* (3%), while *Epischura* was encountered only rarely (Foerster 1968). Young sockeye salmon are active and important predators of the planktonic crustaceans, and they may be selective for size and species (Foerster 1968).

Threespine stickleback (*Gasterosteus aculeatus*) and juvenile sockeye salmon in the littoral zone of Great Central Lake exhibited considerable dietary overlap, especially during late spring and summer (Manzer 1976). However, since the salmon and sticklebacks occupy the littoral zone at different times of the year, interspecific competition for food in the lake is probably not serious, especially in years when food is abundant (Rogers 1968; Manzer 1976). In localities where the ratio of fish to food is unfavorable, the growth rate of both species is reduced (Rogers 1968).

Eggers (1977, 1982) believed that three factors governed prey selection by planktivorous fish: (1) differential rates of prey encounter due to differences in prey visibility; (2) differential rates of prey capture efficiency; and (3) optimal foraging where the predator ignores certain small and inferior prey types to increase the time available to search for larger, more valuable prey. Beacham (1986) also indicated that sockeye diet variability may be due to prey abundance and selection by the predator, as well as the possible selectivity of the sampling gear used. Juvenile sockeye salmon may show size-selective predation by shifting their pursuit to the larger zooplankton forms if sufficiently abundant, preferring the larger over the smaller zooplankton forms (Foerster 1968; Eggers 1978, 1982; Beacham 1986).

Daily feeding of young sockeye salmon is heaviest in the afternoon and lightest during the night and early morning (Northcote and Lorz 1966; McCart 1967; Doble and Eggers 1978). Their most intensive feeding period is in August and September, followed by a low in winter, when the stomachs of a considerable number of the fish population empty (Woodey 1972; Doble and Eggers 1978). Feeding rates increase again in February and March (Foerster 1968; Eggers 1978).

Lake Washington juvenile sockeye salmon show consistent seasonal and diel patterns of vertical movement (Eggers 1978). Diel vertical movements have been observed in other sockeye populations (Northcote and Lorz 1966; McDonald 1973). They generally consist of an ascent into surface layers at dusk and a descent to greater depths after dusk, and to even greater depths after dawn (Eggers 1978). In Lake Washington, the mean depth of the population increases progressively deeper from June through February, but the fish again move higher in the water column as smoltification approaches (Eggers 1978).

Throughout the summer to fall growing season, young sockeye in Lake Washington form schools (Woodey 1972) that disperse as dusk approaches and re-form as light increases after dawn (Eggers 1978). During the winter, sockeye do not school, but they resume this behavior during the presmolt growth period before migration (Eggers 1978). Eggers (1978) hypothesized these complex behaviors as a response to avoid predation by such visual predators as the northern squawfish, *Ptychocheilus oregonensis*, and to meet energy requirements. British Columbia sockeye salmon also showed similarly complex feeding and movement behaviors.

The food spectrum of sockeye salmon in the ocean is relatively wide, and substitute organisms are consumed if a favored food item is lacking (Foerster 1968; Beacham 1986). However, the variability of prey items eaten by sockeye salmon is much less than that of either pink salmon, chinook salmon, or coho salmon (Beacham 1986). There was very little difference in the diet of sockeye salmon that are 7 cm or 55 cm in the Strait of Juan de Fuca (Beacham 1986), where the diet was mainly euphausiids with lesser diet components comprised of crab larvae, mysids, the hyperiid amphipod *Parathemisto*, and the Pacific sand lance *Ammodytes hexapterus*. Of the four species of salmon studied by Beacham (1986), sockeye salmon were the least piscivorous. He concluded that morphological differences among the four species (sockeye salmon have the largest number of gill rakers) account for a greater partitioning of the diet than do differences in water depths in which the individual species live. Dell (1963), who examined sockeye salmon stomachs taken off research vessels in the Northeastern Pacific Ocean, south of the Aleutian Islands, observed that euphausiids were the most abundant single food item by volume among immature fish, but were of minor importance in mature fish. More amphipods and fish were eaten by mature sockeye salmon than by immature fish (Dell 1963). Sockeye salmon of all ages feed heavily on euphausiids, hyperiid amphipods, copepods, cladocerans, pteropods, tunicates, and squid during their ocean residence (LeBrasseur 1966; Foerster 1968).

Predators of juvenile sockeye salmon include yearling coho salmon *Oncorhynchus kisutch*, cutthroat trout, *Salmo clarki*; Dolly Varden, *Salvelinus malma*; Arctic char, *Salvelinus alpinus*; prickly sculpin, *Cottus asper*; northern squawfish; and smolts of rainbow trout and steelhead, *Salmo gairdneri* (Foerster and Ricker 1941; Ward and Larkin 1964; Thompson and Tufts 1967; Ginetz and Larkin 1976; Eggers et al. 1978; Ruggerone and Rogers 1984). Studies of Lake Washington fish populations show that northern squawfish are a significant predator of young sockeye (Bartoo 1972; Eggers et al. 1978; Beauchamp 1987). Ward and Larkin (1964) found that rainbow trout preyed heavily upon juvenile sockeye in the western region of Shuswap Lake, British Columbia, and when juvenile sockeye were scarce, the condition of the trout population was relatively poor. Predation mortality of sockeye salmon caused by both rainbow trout and Arctic char decreased during periods of declining light intensities (Ginetz and Larkin 1976; Ruggerone and Rogers 1984). In Lake Washington, 2%-5% of the sockeye smolt production was lost to rainbow trout predation in 1984-85, with longfin smelt *(Spirinchus thaleichthys)* acting as a buffer to higher predation on the young sockeye salmon (Beauchamp 1987). Predation on juveniles appears to be density related because the number of smolts eaten by predators increased as smolt abundance increased (Ruggerone and Rogers 1984).

Qualitative observations of juvenile sockeye salmon at sea showed predator scars caused by lampreys, seals, sea lions, sharks, and predaceous pelagic fishes such as the daggertooth, *Anotopterus pharao*, (Hartt 1980). Predators of adult sockeye salmon include harbor seals *Phoca vitulina*, and killer whales *Orcinus orca*. Adults returning to natal spawning areas are eaten by bears and certain large avian predators (Foerster 1968).

ENVIRONMENTAL REQUIREMENTS

Temperature

According to Reiser and Bjornn (1979), the optimum spawning temperatures of sockeye salmon range between 10.6 and 12.2 °C, while incubation temperatures for successful hatching are between 4.4 and 13.3 °C. Donaldson and Foster (1941) studied the effect of various experimental water temperatures on sockeye fingerlings and found that between 8.9 to 10.0 °C, the growth rate was fastest and mortalities were lowest. Low temperatures of 3.9-7.2 °C as well as high temperatures above 23 °C produced poor growth, low food utilization, and high mortalities (Donaldson and Foster 1941). Brett (1952) observed an upper lethal temperature of 24.4 °C for young sockeye and a preferred range between 12 and 14 °C. In a later paper Brett (1971) indicated that the physiological optimum for sockeye salmon was 15 °C, and even though sockeye salmon will tolerate 24 °C, they are generally limited in the natural environment at temperatures above 18 °C.

Salinity

Young sockeye make the usual physiological changes observed in all migrating salmon going from freshwater to highly saline waters of the marine environment. To withstand this change from freshwater to saltwater, the young fish undergo a process known as smoltification (Wedemeyer et al. 1980). Yearlings retained in freshwater beyond their migration time lost their preference for saltwater (Baggerman 1960). French et al. (1976) found no obvious correlation between sockeye salmon distribution and the ocean salinity, since they occur at various salinities in the North Pacific Ocean and Bering Sea.

Dissolved Oxygen

Sockeye salmon eggs require at least 5.0 mg/L dissolved oxygen for successful incubation (Reiser and Bjornn 1979). Alevins hatched at oxygen concentrations of 3.0 mg/L averaged 16.3 mm in length while those hatched at 11.9 mg/L averaged 19.7 mm in length (Brannon 1965). At temperatures above 15 °C the metabolic rate of young sockeye salmon may be limited by the oxygen available (Brett 1964). At 15 °C, dissolved oxygen levels above 4.2 mg/L do not affect growth of juvenile sockeye, but growth ceases at 2.6 mg/L and below (Brett and Blackburn 1981). Brett (1970) discussed oxygen requirements for fingerling sockeye salmon at 20 °C during various activities and reported that a reduction in oxygen to 50% saturation at high temperatures severely limited energy available for migrating or feeding. Initial distress symptoms may be observed in freshwater salmonid populations at a dissolved oxygen concentration of 6 mg/L at temperatures ranging between 0 and 20 °C, while most fish are adversely affected by lack of oxygen at concentrations below 4.25 mg/L in the same temperature range (Davis 1973).

Substrate

Although adult sockeye salmon utilize many habitats for their benthic spawning sites, such as river, stream, lakeshore, and spring, they generally select sites with medium- to small-sized gravel (Foerster 1968). Reiser and Bjornn (1979) listed gravel from 1.3 to 10.2 cm in diameter as acceptable for sockeye salmon spawning. Excessive amounts of sand and silt in the gravel hindered fry emergence, even though the embryos may hatch and develop normally (Reiser and Bjornn 1979). No substrate preference has been documented for juveniles in rearing lakes or for adults in the marine environment.

Water Depth

The optimum depth for sockeye salmon spawning is 0.3-0.5 m (Reiser and Bjornn 1979). As juveniles, sockeye salmon are within 20 m of the surface in the spring (Mathison and Smith 1982). Rearing juvenile sockeye salmon in lakes commonly display diel vertical migration throughout the growing season (Eggars 1978). Juvenile sockeye salmon in Lake Washington are seldom found near the surface and significant numbers do not venture above 20 m until spring according to Eggars (1978). As smoltification approaches, the young salmon again tend to inhabit the upper part of the water column. More northerly populations may show greater diel vertical migrations. Rees (1957) found that the smolts were near the surface during outmigration.

Water Movement

Sockeye salmon require enough water flow past the developing eggs and embryos to provide oxygen and carry away waste. Sockeye spawning areas usually have water that is moving 21-101 cm^3/s (Reiser and Bjornn 1979). During the incubation period of Lake Washington sockeye salmon in the Cedar River, maximum instantaneous discharges greater than 50 m^3/s have reduced the survival of these fish (Stober and Hamalainen 1979). Velocities of 53-55 cm^3/s have been measured 0.4 ft above the spawning beds of sockeye salmon (Reiser and Bjornn 1979). River flow (peak discharge) during spawning and gravel incubation had a major positive effect on production of presmolts in the Lake Washington stock (Thorne and Ames 1987).

Turbidity

Fine sediments that are suspended or deposited in salmonid rearing areas can adversely affect salmonid populations by clogging fish gills, reducing feeding, and causing fish to avoid some areas (Reiser and Bjornn 1979). Suspended sediments may cause indirect damage by lowering the survival of eggs or alevin and destroying food sources (Tarzwell 1957; Bjornn et al. 1977). Turbid water also absorbs more radiation than clear water and may indirectly result in a thermal barrier to migration of salmon (Reiser and Bjornn 1979).

Streams with silt loads averaging less than 25 mg/L can be expected to support good freshwater fisheries, while silt loads exceeding 4,000 mg/L may stop the upstream migration of adult salmon (Bell 1973).

Oil Spills

The short-term effect of a tanker accident in Bristol Bay, Alaska (releasing 34,000 tons of diesel fuel) on returning adult sockeye salmon was simulated on a computer. Estimated mortalities would be 2%-18% for fish passing through the spill area and 1%-5% of the total stock. From 3% to 7% of the fish traveling through the spill area would probably be tainted with 0.6 ppm or greater levels of hydrocarbons in the flesh. An oil blowout (releasing 3,000 tons/day of crude oil) would cause estimated mortalities of only up to 0.2% of the salmon passing through the blowout area. No tainting with hydrocarbons above 0.6 ppm was predicted (Bax 1987).

REFERENCES

Allen, R.L. 1977. Status of the upper Columbia River salmon and steelhead runs. Pages 84-88 *in* E. Schwiebert, ed. Columbia River salmon and steelhead: proceedings of a symposium. Am. Fish. Soc. Spec. Publ. No. 10.

Allen, R.L., and T.K. Meekin. 1973. Columbia River sockeye salmon study, 1972. Progress report. Washington Department of Fisheries, Olympia. 61 pp.

Ames, J. 1983. Lake Washington sockeye: an example of a low productivity salmon stock. Lake Washington symposium. Trout Unlimited, Mercer Island, Wash. 5 pp.

Baggerman, B. 1960. Salinity preference, thyroid activity and the seaward migration of four species of Pacific Salmon (*Oncorhynchus*). J. Fish. Res. Board. Can. 17(3):295-322.

Bartoo, B. 1972. The vertical and horizontal distributions of northern squawfish (*Ptychocheilus oregonensis*), peamouth (*Mylocheilus caurinus*), yellow perch (*Perca flavescens*), and adult sockeye salmon (*Oncorhynchus nerka*) in Lake Washington. M.S. Thesis, University of Washington, Seattle. 60 pp.

Bax, N.J. 1987. Effects of a tanker accident and an oil blowout in Bristol Bay, Alaska, U.S.A., on returning adult sockeye salmon, (*Oncorhynchus nerka*)--a simulation study. Mar. Environ. Res. 22:177-204.

Beacham, T. D. 1986. Type, quantity, and size of food of Pacific salmon (*Oncorhynchus*) in the Strait of Juan de Fuca, British Columbia. U. S. Natl. Mar. Fish. Serv. Fish. Bull. 84(1): 77-89.

Beauchamp, D.A. 1987. Ecological relationships of hatchery rainbow trout in Lake Washington. Ph.D. Dissertation. University of Washington, Seattle. 236 pp.

Bell, M.C. 1973. Fisheries handbook of engineering requirements and biological criteria. U.S. Army Corps of Engineers, Portland, Oregon. Contract No. DACW57-68-C-0086. 425 pp.

Biette, R M., and G.H. Geen. 1980a. Growth of underyearling sockeye salmon (*Oncorhynchus nerka*) under constant and cyclic temperatures in relation to live zooplankton ration size. Can. J. Fish. Aquat. Sci. 37:203-210.

Biette, R.M., and G.H. Geen. 1980b. The fate of ^{14}C-labeled food ingested by underyearling sockeye salmon, *Oncorhynchus nerka*, in relation to temperature and ration. Can. J. Fish. Aquat. Sci. 37:1184-1192.

Bjornn, T.C., M.A. Brusven, M.P. Molnau, J.H. Milligan, R.A. Klamt, E. Chacho, and C. Schaye. 1977. Transport of granitic sediments in streams and its effects on insects and fish. For. Wildl. Range Exp. Stn., Compl. Rep. Water Resour. Res. Inst. Proj. B-036-IDA. University of Idaho, Moscow. 43 pp.

Blum, J. P. 1984. Management strategies for restoration and rehabilitation of sockeye salmon (*Oncorhynchus nerka*) in Lake Ozette, Washington. Pages 55-62 *in* J.M. Walton and D. B. Houston, eds. Proceedings of the Olympia wild fish conference. Port Angeles, Wash.

Bocking, R.C., and R.M. Peterman. 1988. Preseason forecasts of sockeye salmon (*Oncorhynchus nerka*): comparison of methods and economic considerations. Can. J. Fish. Aquat. Sci. 45:1346-1354.

Brannon, E.L. 1965. The influence of physical factors on the development and weight of sockeye salmon embryos and alevins. Int. Pac. Salmon Fish. Comm. Progr. Rep. No. 12. 26 pp.

Brannon, E.L. 1972. Mechanisms controlling migration of sockeye salmon fry. Int. Pac. Salmon Fish. Comm. Bull. 21:1-86.

Brannon, E.L. 1982. Orientation mechanisms of homing salmonids. Pages 219-227 *in* E.L. Brannon and E.O. Salo, eds. Proceedings of the salmon and trout migratory behavior symposium. University of Washington Press, Seattle.

Brett, J.R. 1952. Temperature tolerance in young Pacific salmon, genus *Oncorhynchus*. J. Fish. Res. Board Can. 9(6):265-323.

Brett, J.R. 1964. The respiratory metabolism and swimming performance of young sockeye salmon. J. Fish. Res. Board Can. 21:1183-1226.

Brett, J.R. 1970. Fish - the energy cost of living. Pages 37-52 *in* W.J. McNeil, ed. Marine Aquaculture. Oregon State University Press, Corvallis.

Brett, J.R. 1971. Energetic responses of salmon to temperature. A study of some thermal relations in the physiology and freshwater ecology of sockeye salmon (*Oncorhynchus nerka*). Am. Zool. 11(1):99-113.

Brett, J.R., and J.M. Blackburn. 1981. Oxygen requirements for growth of young coho (*Oncorhynchus kisutch*) and sockeye (*O. nerka*) salmon at 15 °C. Can. J. Fish. Aquat. Sci. 38:399-404.

Brett, J.R., and D.A. Higgs. 1970. Effect of temperature on the rate of gastric digestion in fingerling sockeye salmon (*Oncorhynchus nerka*). J. Fish. Res. Board Can. 27(7):1967-1979.

Brett, J.R., J.E. Shelbourn, and C.T. Shoop. 1969. Growth rate and body composition of fingerling sockeye salmon, *Oncorhynchus nerka*, in relation to temperature and ration size. J. Fish. Res. Board Can. 26(9):2363-2394.

Bryant, M.D. 1976. Lake Washington sockeye salmon: biological production, and a simulated harvest by three fisheries. Ph.D. Thesis. University of Washington, Seattle. 135 pp.

Bryant, M.D., and S.B. Mathews. 1973. The Lake Washington sockeye salmon sport fishery: catch, fishing effort, and economic evaluation, 1973. Special Report Fisheries Research Institute, University of Washington, Seattle. 18 pp.

Burgner, R.L. 1958. A study of the fluctuations in abundance, growth, and survival in the early life stages of the red salmon (*Oncorhynchus nerka* Walbaum) of the Wood River lakes, Bristol Bay, Alaska. Ph.D. Thesis. University of Washington, Seattle. 200 pp.

Burgner, R.L. 1980. Some features of the ocean migration and timing of Pacific salmon. Pages 153-164 *in* W.J. McNeil and D.C. Himsworth, eds. Symposium on salmonid ecosystems of the North Pacific. Oregon State University Press, Corvallis.

Clark, C.W., and D.A. Levy. 1988. Diel vertical migrations by juvenile sockeye salmon and the antipredation window. Am. Nat. 131:271-290.

Clark, W.G. 1985. Fishing in a sea of court orders: Puget Sound salmon management 10 years after the Boldt Decision. N. Am. J. Fish. Manage. 5:417-434.

Clarke, W.C., and H.D. Smith. 1972. Observations on the migration of sockeye salmon fry (*Oncorhynchus nerka*) in the lower Babine River. J. Fish. Res. Board Can. 29(1):151-159.

Cousens, N.F., G.A. Thomas, G.C. Swan, and M.C. Healey. 1982. A review of salmon escapement estimation techniques. Can. Tech. Rep. Fish. Aquat. Sci. No. 1108. 122 pp.

Davidson, F.A. 1966. Population trends in the blueback and upper Columbia River fall chinook salmon. Public Utility District of Grant County. Ephrata, Wash. 36 pp.

Davis, J.C. 1973. Sublethal effects of bleached Kraft pulpmill effluent on respiration and circulation in sockeye salmon (*Oncorhynchus nerka*). J. Fish. Res. Board Can. 30(2):369-377.

Dell, M.B. 1963. Oceanic feeding habits of the sockeye salmon (*Oncorhynchus nerka* Walbaum), in Aleutian waters. M.A. Thesis. University of Michigan, Ann Arbor. 40 pp.

Dlugokenski, C.E., W.H. Bradshaw, and S.R. Hager. 1981. An investigation into the limiting factors to Lake Ozette sockeye salmon production and a plan for their restoration. U.S. Fish and Wildlife Service Report, Fisheries Assistance Office, Olympia. 51 pp.

Doble, B.D., and D.M. Eggers. 1978. Diel feeding chronology, rate of gastric evacuation, daily ration, and prey selectivity in Lake Washington juvenile sockeye salmon (*Oncorhynchus nerka*). Trans. Am. Fish. Soc. 107(1):36-45.

Donaldson, L.R., and E.J. Foster. 1941. Experimental study of the effect of various water temperatures on the growth, food utilization and mortality rates of fingerling sockeye salmon. Trans. Am. Fish. Soc. 70:339-346.

Eggers, D.M. 1977. The nature of prey selection by planktivorous fish. Ecology 58(1):46-59.

Eggers, D.M. 1978. Limnetic feeding behavior of juvenile sockeye salmon in Lake Washington and predator avoidance. Limnol. Oceanogr. 23(6):1114-1125.

Eggers, D.M. 1982. Planktivore preference by size. Ecology 63:381-390.

Eggers, D.M., N.W. Bartoo, N.A. Rickard, R.E. Nelson, R.C. Wissmar, R.L. Burgner, and A.H. Devol. 1978. The Lake Washington ecosystem: the perspective from the fish community production and for age base. J. Fish. Res. Board Can. 35(5):1553-1571.

Foerster, R.E. 1925. The importance of copepoda in the natural diet of sockeye salmon. Contrib. Can. Biol. 2(16):2009-2016.

Foerster, R.E. 1968. The sockeye salmon, *Oncorhynchus nerka*. Bull. Fish. Res. Board Can. 162. 422 pp.

Foerster, R.E., and W.E. Ricker. 1941. The effect of reduction of predaceous fish on survival of young sockeye salmon at Cultus Lake. J. Fish. Res. Board Can. 5(4):315-336.

Foskett, D.R. 1956. Contributions to the life-history of the sockeye salmon. British Columbia Department of Fisheries Report Number 41.

French, R.R., and W.B. McAlister. 1970. Winter distribution of salmon in relation to currents and water masses in the northeastern Pacific Ocean and migrations of sockeye salmon. Trans. Am. Fish. Soc. 99(4):649-663.

French, R., H. Bilton, M. Osako, and A. Hartt. 1976. Distribution and origin of sockeye salmon (*Oncorhynchus nerka*) in offshore waters of the North Pacific Ocean. Int. North Pac. Fish. Comm. Bull. 34. 113 pp.

Furnell, D. J., and J. R. Brett. 1986. Model of monthly marine growth and natural mortality for Babine Lake sockeye salmon (*Oncorhynchus nerka*). Can. J. Fish. Aquat. Sci. 43(5):999-1004.

Ginetz, R.M., and P.A. Larkin. 1976. Factors affecting rainbow trout (*Salmo gairdneri*) predation on migrant fry of sockeye salmon. J. Fish. Res. Board Can. 33(1):19-24.

Hart, J.L. 1973. Pacific fishes of Canada. Fish. Res. Board Can. Bull. 180. 665 pp.

Hartt, A.C. 1980. Juvenile salmonids in the oceanic ecosystem: the critical first summer. Pages 25-57 *in* W.J. McNeil and D.C. Himsworth, eds. Symposium on salmonid ecosystems of the North Pacific. Oregon State University Press, Corvallis.

Hyatt, K.D., and J.D. Stockner. 1985. Response of sockeye salmon (*Oncorhynchus nerka*) to fertilization of British Columbia coastal lakes. Can. J. Fish. Aquat. Sci. 42(2):320-331.

Kolb, R. 1971. A review of Lake Washington sockeye (*Oncorhynchus nerka*) age and racial characteristics as determined by scale analysis. Wash. Dep. Fish. Suppl. Progr. Rep. 9 pp.

LeBrasseur, R.J. 1966. Stomach contents of salmon and steelhead trout in the northeastern Pacific Ocean. J. Fish. Res. Board Can. 23(1):85-100.

LeBrasseur, R.J., C.D. McAllister, W.E. Barraclough, O.D. Kennedy, J. Manzer, D. Robinson, and K. Stephens. 1978. Enhancement of sockeye salmon (*Oncorhynchus nerka*) by lake fertilization in Great Central Lake: summary report. J. Fish. Res. Board Can. 35:1580-1596.

Leggett, W.C. 1977. The ecology of fish migrations. Annu. Rev. Ecol. Syst. 8:285-308.

Manzer, J.I. 1976. Distribution, food, and feeding of the threespine stickleback, *Gasterosteus aculeatus*, in Great Central Lake, Vancouver Island, with comments on competition for food with juvenile sockeye salmon, *Oncorhynchus nerka*. U.S. Natl. Mar. Fish. Serv. Fish. Bull. 74(3):647-668.

Manzer, J.I., and I. Miki. 1986. Fecundity and egg retention of some sockeye salmon (*Oncorhynchus nerka*) stocks in British Columbia. Can. J. Fish. Aquat. Sci. 43:1643-1655.

Manzer, J.I., M. Wright, I. Miki, and K.D. Hyatt. 1984. Abundance, upstream migration, age-composition and fecundity of Hobiton Lake adult sockeye (*Oncorhynchus nerka*), 1982. Can. Tech. Rep. Fish. Aquat. Sci. 1262. 57 pp

Mathisen, O.A. 1955. Studies on the spawning biology of the red salmon, *Oncorhynchus nerka* Walbaum, in Bristol Bay, Alaska, with special reference to the effect of altered sex ratios. Ph.D. Thesis. University of Washington, Seattle. 285 pp.

Mathisen, O.A., and H.D. Smith. 1982. Hydroacoustic assessment of juvenile sockeye salmon in Babine Lake, British Columbia in 1975. Can. Tech. Rep. Fish. Aquat. Sci. No. 1103. 13 pp.

McCart, P. 1967. Behavior and ecology of sockeye salmon fry in the Babine River. J. Fish. Res. Board Can. 24(2):375-428.

McDonald, J.G. 1969. Distribution, growth, and survival of sockeye fry (*Oncorhynchus nerka*) produced in natural and artificial stream environments. J. Fish. Res. Board Can. 25(2):229-267.

McDonald, J. 1973. Diel vertical movements and feeding habits of underyearling sockeye salmon (*Oncorhynchus nerka*) at Babine Lake, B.C. Fish. Res. Board Can. Tech. Rep. 378. 55 pp.

Miller, R.J., and E.L. Brannon. 1982. The origin and development of life history patterns in Pacific salmonids. Pages 296-309 *in* E.L. Brannon and E. O. Salo, eds. Proceedings of the salmon and trout migratory behavior symposium. University of Washington Press, Seattle.

Mullan, J.W. 1986. Determinants of sockeye salmon abundance in the Columbia River, 1880's-1982: review and synthesis. U.S. Fish Wildl. Serv. Biol. Rep. 86(12). 136 pp.

Narver, D.W. 1970. Diel vertical movements of underyearling sockeye salmon and the limnetic zooplankton in Babine Lake, British Columbia. J. Fish. Res. Board Can. 27(2):281-316.

Northcote, T.G., and H.W. Lorz. 1966. Seasonal and diel changes in food of adult kokanee (*Oncorhynchus nerka*) in Nicola Lake, British Columbia. J. Fish. Res. Board Can. 23(6):1259-1263.

Olsen, J.C. 1968. Physical environment and egg development in a mainland beach area and an island beach area of Iliamna Lake. Univ. Wash. Publ. Fish. New Ser. 3:169-198.

Pacific Fishery Management Council. 1983. Proposed plan for managing the 1983 salmon fisheries off the coasts of California, Oregon, and Washington. Pac. Fish. Manage. Counc., Portland, Oreg. 332 pp.

Pella, J.J. 1968. Distribution and growth of sockeye salmon fry in Lake Aleknagik, Alaska, during the summer of 1962. Univ. Wash. Publ. Fish. New Ser. 3:45-112.

Peterman, R.M. 1984. Density-dependent growth in early ocean life of sockeye salmon (*Oncorhynchus nerka*). Can. J. Fish. Aquat. Sci. 41(12):1825-1829.

Peterman, R.M. 1985. Patterns of interannual variation in age at maturity of sockeye salmon (*Oncorhynchus nerka*) in Alaska and British Columbia. Can. J. Fish. Aquat. Sci. 42(10):1595-1607.

Peven, C.M. 1987. Downstream migration timing of two stocks of sockeye salmon on the mid-Columbia River. Northwest Sci. 61:186-190.

Poe, P.H., and O.A. Mathisen. 1981. Distance from sea and elevation of important sockeye salmon spawning grounds. Fish. Res. Inst. Univ. Wash. Circ. 81-1. 23 pp.

Puget Sound Tribes, Northwest Indian Fisheries Commission, and Washington State Department of Fisheries. 1989. 1989 Puget Sound sockeye salmon forecasts and management recommendations. Joint Report, April 1989. Olympia. 29 pp.

Quinn, T.P. 1982a. Intra-specific differences in sockeye salmon fry compass orientation mechanisms. Pages 79-85 *in* E.L. Brannon and E.O. Salo, eds. Proceedings of the salmon and trout migratory behavior symposium. University of Washington Press, Seattle.

Quinn, T.P. 1982b. A model for salmon navigation on the high seas. Pages 229-237 *in* E.L. Brannon and E.O. Salo, eds. Proceedings of the salmon and trout migratory behavior symposium. University of Washington Press, Seattle.

Quinn, T.P., and E.L. Brannon. 1982. The use of celestial and magnetic cues by orienting sockeye salmon smolts. J. Comp. Physiol. 147:547-552.

Rees, W.H. 1957. The vertical and horizontal distribution of seaward migrant salmon in the forebay of Baker Dam. Wash. Dep. Fish. Fish. Res. Pap. 2(1):5-17.

Reiser, D.W., and T.C. Bjornn. 1979. Habitat requirements of anadromous salmonids. U.S. For. Serv., Pac. Northwest For. Range Exp. Stn. Gen. Tech. Rep. PNW-96. 54 pp.

Ricker, W.D. 1982. Size and age of British Columbia sockeye salmon (*Oncorhynchus nerka*) in relation to environmental factors and the fishery. Can. Tech. Rep. Fish. Aquat. Sci. 1115. 117 pp.

Rogers, D. E. 1968. A comparison of the food of sockeye salmon fry and threespine sticklebacks in the Wood River Lakes. Univ. Wash. Publ. Fish. New Ser. 3:1-44.

Ruggerone, G.T., and D.E. Rogers. 1984. Arctic char predation on sockeye salmon smolts at little Togiak River, Alaska. U.S. Natl. Mar. Fish. Serv. Fish. Bull. 82(2): 401-410.

Scott, W.B., and E.J. Crossman. 1973. Freshwater fishes of Canada. Bull. Fish. Res. Board Can. 184. 966 pp.

Stober, Q.J., and A.H. Hamalainen. 1979. Cedar River sockeye salmon fry emigration. Final report. University of Washington Fisheries Research Institute, Seattle. 52 pp.

Stockner, J.G., and K.D. Hyatt. 1984. Lake fertilization: state of the art after 7 years of application. Can. Tech. Rep. Fish. Aquat. Sci. 1324. 33 pp.

Stockner, J.G., and K.S. Shortreed. 1983. A comparative limnological survey of 19 sockeye salmon (*Oncorhynchus nerka*) nursery lakes in the Fraser River system, British Columbia. Can. Tech. Rep. Fish. Aquat. Sci. 1190. 63 pp.

Tarzwell, C.M. 1957. Water quality criteria for aquatic life. Pages 246-272 *in* Biological problems in water pollution. U.S. Dep. Health Educ. Welfare, R.A. Taft San. Eng. Cent., Cinncinati, Ohio.

Thompson, R. B., and D. F. Tufts. 1967. Predation by Dolly Varden and northern squawfish on hatchery-reared sockeye salmon in Lake Wenatchee, Washington. Trans. Am. Fish. Soc. 96(4): 424-427.

Thorne, R.E. 1979. Hydroacoustic estimates of adult sockeye salmon (*Oncorhynchus nerka*) in Lake Washington, 1972-75. J. Fish. Res. Board Can. 36(9):1145-1149.

Thorne, R.E., and J.J. Ames. 1987. A note on variability of marine survival of sockeye salmon (*Oncorhynchus* *nerka*) and effects of flooding on spawning success. Can. J. Fish. Aquat. Sci. 44:1791-1795.

Wahle, R.J., R.O. Koski, and R.Z. Smith. 1979. Contribution of 1960-63 brood hatchery-reared sockeye salmon, *Oncorhynchus nerka*, to the Columbia River commercial fishery. U.S. Natl. Mar. Fish. Serv. Fish. Bull. 77(1): 229-242.

Ward, F.J., and P.A. Larkin. 1964. Cyclic dominance in Adams River sockeye salmon. Int. Pac. Salmon Fish. Comm. Prog. Rep. No. 11. 113 pp.

Wedemeyer, G.A., R.L. Saunders, and W.C. Clarke. 1980. Environmental factors affecting smoltification and early marine survival of anadromous salmonids. Mar. Fish. Rev. 42(1):1-14.

West, C.J., and P.A. Larkin. 1986. Evidence for size-selective mortality of juvenile sockeye salmon (*Oncorhynchus nerka*) in Babine Lake, British Columbia. Can. J. Fish. Aquat. Sci. 44:712-721.

Woodey, J.C. 1972. Distribution, feeding, and growth of juvenile sockeye salmon in Lake Washington. Ph.D. Thesis. University of Washington, Seattle. 99 pp.

Wydoski, R.S., and D.H. Bennett. 1981. Forage species in lakes and reservoirs of the Western United States. Trans. Am. Fish. Soc. 110(6):764-771.

Wydoski, R.S., and R.R. Whitney. 1979. Inland fishes of Washington. University of Washington Press, Seattle. 168 pp.

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16. Abstract (Limit: 200 words)

Species profiles are literature summaries of the taxonomy, morphology, range, life history, and environmental requirements of coastal aquatic species. They are designed to assist in environmental impact assessment. Sockeye salmon always spawn in a lake associated with a river or in the outlet river. The young fish use the lakes for rearing. The brilliant red flesh is highly prized by commercial and sport fishermen. Washington State and the Columbia River are the southern limit of reproducing populations of sockeye salmon. Sockeye salmon are primarily plankton feeders. They appear to thrive best at temperatures of 10-15 °C. Ocean distribution does not appear to be limited by salinity. Adults require gravel with adequate water circulation for successful spawning and egg hatching.

17. Document Analysis a. Descriptors

Estuaries	Temperature	Oxygen competition
Feeding habits	Suspended sediments	Fisheries
Growth	Salmon	Sediments

b. Identifiers/Open-Ended Terms

Sockeye salmon	Life history	Predators
Oncorhynchus nerka	Competitors	Salinity requirements
Spawning		
Temperature requirements		

c. COSATI Field/Group

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