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DETERMINANTS OF SOCKEYE SALMON ABUNDANCE IN THE COLUMBIA RIVER, 1880's-1982: A REVIEW AND SYNTHESIS

by

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Carbon and pollen profiles of bottom sediments of Lake Osoyoos indicated that cultural eutrophication of Lake Osoyoos paralleled agricultural development and waste discharge in the Okanogan Valley in the first half of the century. Resulting changes in species of plankton, benthos and fish were first noted in the late 1930's, coincidental with the development of the Coulee Fish-Maintenance Project. Sockeye salmon rehabilitation under the project no doubt initially benefited from nutrient enrichment.

Sockeye production of Lake Osoyoos trended downward in an oscillatory fashion during the post-World War II period, as if controlled by progressive eutrophication; a paralleling phenomenon involving riverine sockeye salmon production was associated with hydroelectric impoundment of the Columbia River. However, the hypothesis that progressive habitat degradation was the main contributor to the decline of Osoyoos sockeye salmon production was not confirmed by correlation, by analogy, or by the process of elimination. Instead, I concluded that Osoyoos was spared excessive biological production and corresponding oxygen exhaustion resulting from critical nutrient loading because water residence time was short. Ecological principles and site-specific information suggested that temporal production of sockeye salmon in mainstem impoundments represented some combination of high food supply (resulting from trophic upsurge and pollution loading) and low density of competitive fish species.

This attempt at holistic interpretation of a vast array of information pertaining to Columbia River sockeye revealed several management implications: (1) natural production potential of remaining nursery lakes was perhaps only moderately less than the goal of 250,000 returning adults; (2) any shortfall might be made up by enhancement of the food supply in Lake Wenatchee; (3) the primary barrier to such enhancement is the societal conflict inherent in simultaneous management for resident and anadromous salmonids; and (4) providing sport fishing opportunity for returning adult sockeye salmon in North Central Washington constitutes strong incentive in alleviating such conflict.

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SUMMARY

Determinants of abundance of sockeye salmon (Oncorhynchus nerka) in the Columbia River are examined with reference to the Grand Coulee Fish-Maintenance Project (1939-1960's), the revival of runs associated with the project (1945-1960's), and the decline in numbers of fish returning to the river that followed (1960's-80's).

Columbia River sockeye salmon are believed to be only rarely caught in the ocean and the fishery has been largely confined to the lower river. Annual catches were 0.25 to 1.3 million fish before 1900, and 50,000 to 730,000 from 1900 to the late 1920's; thereafter they fluctuated widely, but generally were only a fraction of the earlier highs.

Estimates of escapement beyond the fishery become possible after the completion in 1933 of Rock Island Dam, the earliest of the present-day mainstem dams, at River Mile 453. In the 1930's and early 1940's commercial catches remained depressed in relation to annual escapements of 1.6% to 24%. When catch and escapement were brought more nearly into balance beginning in 1945, the runs revived and reasonably high abundance was maintained until about 1960. In subsequent years, sockeye did not maintain themselves even under greatly increased escapement.

Between 1927 and 1982, the sockeye salmon run was lowest in 1945 (10,900 fish) and largest in 1947 (335,300 fish). The large run in 1947 coincided with expected results of the Grand Coulee Fish-Maintenance Project, which featured between 1939 and 1943 intercepting returning adults at Rock Island Dam and either transporting them to two lake systems for natural spawning or to three hatcheries that were constructed. Results of this $3 million mitigation project for blockage of the upper Columbia River by Grand Coulee Dam in 1939 were far-ranging, but not necessarily those surmised from the record run of 1947.

Mark-recovery programs for releases from the 1940-44 and 1960-63 brood years showed that (1) in the historic lowest and highest years of abundance (1945 and 1947), hatchery sockeye salmon made up 10% and 11% of the runs; (2) survival of hatchery juveniles to returning adults averaged 1.62% in the 1940's compared with 0.67% in the 1960's; and (3) adults sacrificed for artificial propagation showed no consistent increased efficiency over natural recruitment in terms of ratios of adults to recruits.

Evidence was examined for possible effects of transfer and introduction of stocks associated with artificial as well as natural propagation. It seems clear that kokanee entrained from the 80,000-acre reservoir (Lake Roosevelt) created by Grand Coulee Dam positively influenced spawner-recruit ratios in the early years of impoundment. This is particularly evident for the 1941 brood year, considering that substantial numbers of kokanee could have become anadromous and returned as "sockeye salmon." The spawner-recruit ratio of 1:98.0 was aberrant, the kokanee population in the new impoundment irrupted, virtually no effective adult sockeye spawning escapement occurred (118 fish), and the 1941 brood produced the record low run of 1945. Although other observations were inconclusive, they seemed to indicate at least some interchange of genetic material between stocks. Seemingly there was no impairment of genetic viability, as judged by a high resiliency of survival in the face of major harvest and genetic and environmental perturbations.

The early post-1900 decline in sockeye salmon abundance can be largely ascribed to losses in habitat due to blockage by dams on tributary streams. Original surface acreage of nursery lakes in the Columbia River Basin was at least 222,850 acres, of which about 4% remained after 1939. For all practical purposes, the remaining viable runs were to Lakes Wenatchee and Osoyoos, located on the Wenatchee and Okanogan rivers. Hydroelectric dams constructed on the mainstem Columbia River from the 1950's to 1967 accounted for the most recent general decline in abundance, due primarily to the loss of smolts in turbines.

Safe limits for water-quality alterations were not being exceeded in the Columbia River in the early 1980's and, with the exception of gas saturation at dams, probably were not exceeded in earlier years. Water temperatures were not greatly different from temperatures recorded in earlier years, when runs were substantial and before hydroelectric development had become extensive, and it is unlikely that temperature and concomitant fish diseases were a primary cause of run declines, except secondarily in the lower Okanogan River. Here, a 44-50% reduction of summertime flows by irrigation diversion, surface discharge of storage lakes, and long distance from cold headwater sources tend to result in elevation of temperatures well above the lethal limits for salmonids and has caused high prespawning mortality of sockeye. Considerations of geology, land use, and the erosion cycle indicated that spawning habitat has been little altered from pristine conditions in the Wenatchee system and may not have been seriously compromised by man's disruptive activities in the Okanaogan. Spawning gravel capacity has not been a factor limiting recent sockeye population size at the abundance levels shown by runs in both rivers.

The environment and species diversity of ultraoligotrophic Lake Wenatchee were little altered from primordial times, and the lake retained a high efficiency in converting a low nutrient base to sockeye production. Lake Osoyoos, by contrast, had a radically altered environment, species diversity, and production capability due to cultural eutrophication and the introduction of exotic fishes. Here the nutrient base was high but efficiency of energy conversion to sockeye salmon production was low.

TABLES

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INTRODUCTION

Grand Coulee Dam barred anadromous salmonids from 1140 miles of the upper Columbia River in 1939. To preserve the runs, the Washington Department of Fisheries (WDF) proposed intercepting returning adults at Rock Island Dam (WDF1938), relocating them to the downstream Wenatchee, Entiat, Methow, and Okanogan rivers, and constructing hatcheries on these streams (Fig. 1).

Sockeye salmon originally spawned and reared in eight tributary-lake systems of the Columbia River (Table 1). After blockage of the upper river by Grand Coulee Dam in 1939, sockeye salmon became almost entirely dependent on Wenatchee and Osoyoos lakes, located on the Wenatchee and Okanogan rivers, for rearing (Fulton 1970). Only a remnant sockeye salmon run to Redfish Lake on the Snake River in Idaho persisted.

Columbia River sockeye salmon are believed to be only rarely caught in the ocean, and the fishery has been largely confined to the lower river. Annual catches ranged from 0.25 to 1.3 million fish before 1900 and were 50,000 to 730,000 through the early 1920's. Catches after the 1920's were generally only a fraction of the earlier highs, but extreme fluctuations in abundance continued (Fig. 2; Fulton 1970; Wahle et al. 1979).

Estimates of escapement beyond the fishery became possible after the completion of Rock Island Dam in 1933 (Fig. 1). Between 2227 and 40,737 sockeye were counted annually until 1941, when only 949 reached the dam. This low escapement resulted from a large catch (150,000 fish) and low flows, aggravated by the filling of Lake Roosevelt behind Grand Coulee Dam, which impeded migration at downstream Celilo Falls (Fish and Hanavan 1948).

Beginning in 1939, and extending to 1943, sockeye salmon were trapped at Rock Island Dam and relocated to Wenatchee and Osoyoos Lakes (Table 2) and to three national fish hatcheries (Leavenworth, Entiat, and Winthrop) that were constructed. Success of this $3 million Grand Coulee Fish-Maintenance Project seemed to be indicated in 1947 when the largest sockeye run recorded between 1927 and 1982 returned--335,300 fish of which 79,800 were counted over Rock Island Dam (Fish and Hanavan 1948). How much of this improvement could be attributed to natural or hatchery propagation was never made clear (Ricker 1972), although the project was deemed to be successful (Gangmark and Fulton 1952; Allen and Meekin 1980). More relevant, perhaps, is the observation that no one has made a thorough study of the factors affecting abundance of the runs, attempted to prove or disprove any of the hypotheses that abound, or demonstrated a probable order of importance of the causes of decline. The development of such an overview is the purpose of the present report, beginning with the life history of sockeye salmon.

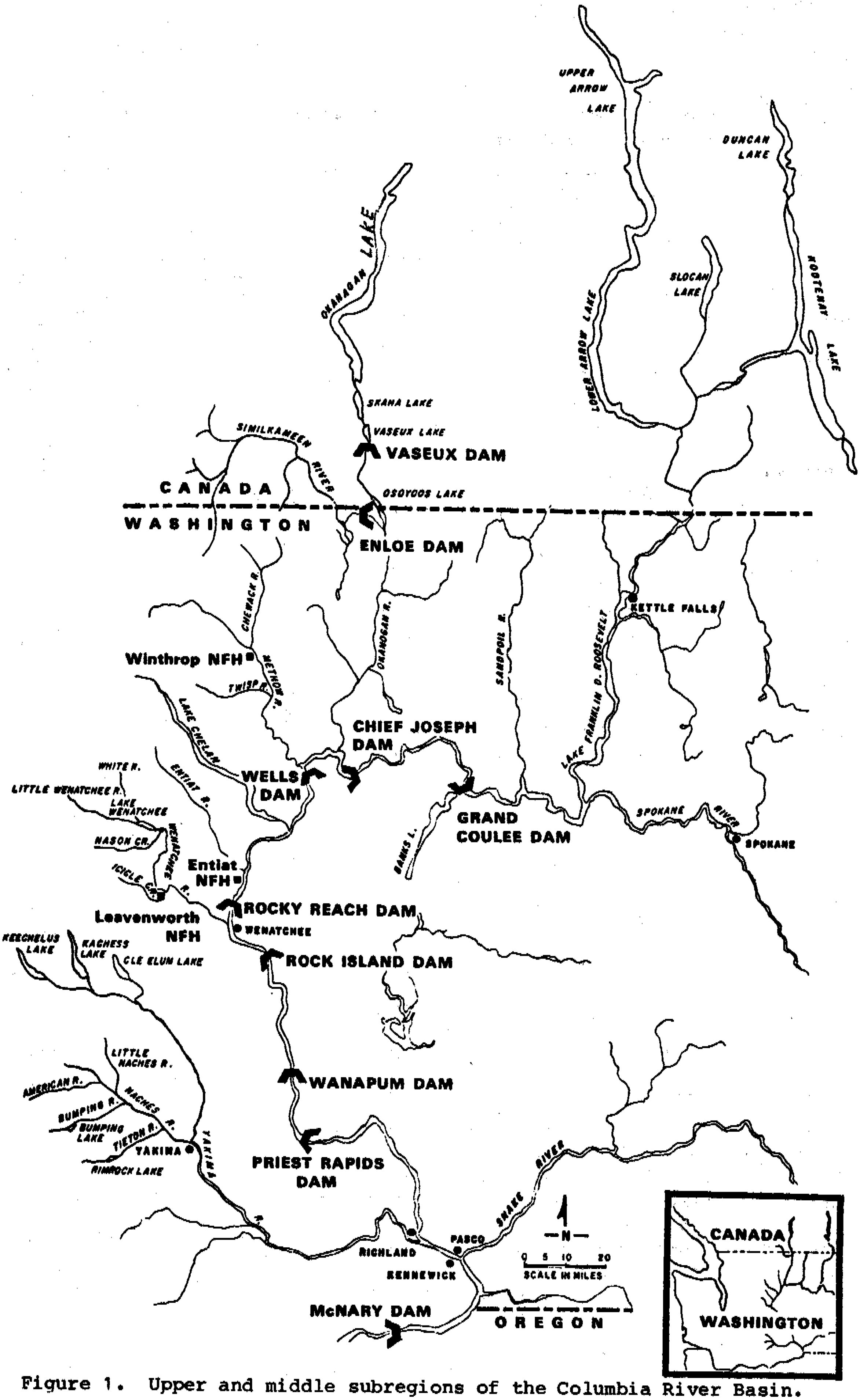

Figure 1. Upper and middle subregions of the Columbia River Basin.

Table 1. Sockeye salmon nursery lakes of the Columbia River Basin, 1910-1982.

River	Lake	Habitat lost		Available in 1982 (surface acres)
		Surface acres	Year(s) passage blocked	
Upper Columbia[a]	Upper Arrow	51,904	1939	
	Lower Arrow	37,504	1939	
	Whatshan	4,004	1939	
	Slocan	16,738	1939	
Okanogan[b]	Osoyoos			5,729
	Skaha	4,967	1921	
	Okanogan	85,990	1915	
Yakima	Bumping	631	1910	
	Cle Elum	1,982	1909-10	
	Kachess	2,744	1904	
	Keechelus	1,240	1904	
Wenatchee	Wenatchee			2,445
Payette	Big Payette	1,000	1914	
	Little Payette	300	1914	
	Upper Payette	200	1914	
Wallowa	Wallowa	1,777	1929	
Salmon[c]	Redfish	1,500	1913-34[d]	1,500
	Alturas	1,200	1913-34	1,200
	Petit	395	1913-34	395
	Stanley	180	1913-34	180
	Yellowbelly	170	1913-34	170
Metolius	Suttle	250	1930	
	Total	214,676		11,619

[a] Presence of kokanee suggests that sockeye salmon once used Kinbasket, Windermere, and Columbia lakes.

[b] Fulton (1970) indicated that Palmer Lake once was used by sockeye. Craig and Suomela (1941) indicated that salmon never ascended above Enloe Falls on the Similkameen River.

[c] Presence of kokanee suggests that sockeye salmon once used Hell Roaring, Little Redfish, and Warm lakes.

[d] Only a remnant sockeye run persisted after passage was restored in 1935.

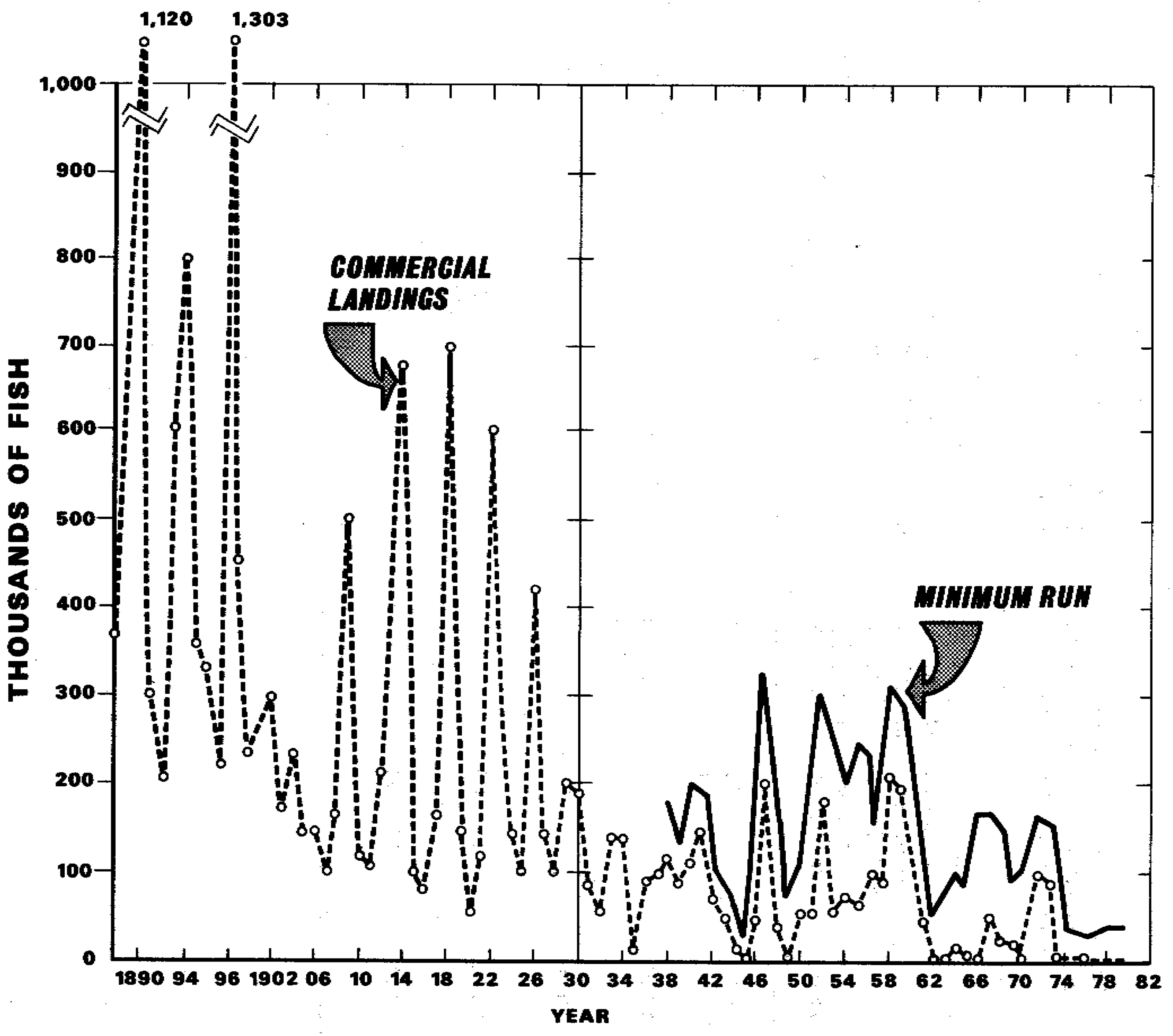

Figure 2. Annual landings and minimum run of Columbia River sockeye salmon.

Table 2. Adult sockeye salmon trapped at Rock Island Dam and relocated for natural or artifical spawning, and percent spawning success (from Fish and Hanavan 1948).

Year	Number of adult sockeye salmon released into lakes and (in parentheses) percent spawned		Number of adult sockeye salmon hauled to hatcheries and (in parentheses) percent spawned		Count at Rock Island Dam (no. of fish)
	Wenatchee	Osoyoos	Leavenworth	Winthrop	
1939	8,148 (92)	10,104 (95)			19,591
1940		9,691 (98)	17,124 (23)		26,894
1941	98 (?)		851 (2)		949
1942	10,884 (92)		4,574 (22)	250 (90)	16,282
1943	13,664 (?)		2,766 (28)	1,503 (53)	17,665

LIFE HISTORY

DESCRIPTION

Sockeye salmon and kokanee, also common in Lakes Wenatchee and Osoyoos, are forms of the same species (Oncorhynchus nerka nerka and O. n. kennerlyi). Usually it is impossible to distinguish between the two forms (Scott and Crossman 1973). Kokanee generally are smaller than sockeye salmon; the usual length is 8-9 inches, although populations consisting of 12- to 15-inch fish, with specimens as large as 21 inches and weighing 4 pounds, have been reported for a few lakes (Ricker and Loftus 1968). A typical 4-year-old Columbia River sockeye is 20 inches long (fork length, used thorughout this report) and weighs 3.7 pounds (Fulton 1970).

DISTRIBUTION

The indigenous distribution of kokanee coincides with the range of sockeye salmon in areas bordering the North Pacific Ocean (Scott and Crossman 1973). Kokanee occur in many inland lakes, in both Asia and North America, to which anadromous salmon no longer have access. Kokanee are currently widely established outside their original range. Scott and Crossman (1973) cautioned that the original distribution may be clouded by the presence of residual populations of sockeye salmon. These fish do not migrate and mature in fresh water at a smaller size than their sea-run parents.

BIOLOGY

Kokanee spawn in fall, either in streams or lakes. Egg number varies with size of female (range, 368-1764; mean, 450). Time to hatching varies from about 140 days at 39.2°F (4°C) to 48 days at 59°F (15°C). (Scott and Crossman 1973).

Columbia River sockeye salmon are also fall spawners and die after spawning. Spawners reach Wenatchee and Osoyoos lakes during July-September. Sockeye salmon may also spawn on gravel shoals of lakes, just as kokanee do, provided there is upwelling or wave action to provide oxygen and remove metabolic wastes from the redds. Only limited shoal spawning of sockeye salmon or kokanee has been noted in Lakes Osoyoos and Wenatchee.

Spawning of sockeye salmon starts in late September and peaks in mid-October in the Okanogan River, and begins in early to late September in the Wenatchee River (Fulton 1970; Table 3). Eggs (1478 to 4446 per female; Major and Craddock 1962) hatch during winter or early spring and the fry emerge from the gravel in early to late spring, apparently at about the same time as kokanee. Most fry move out of the spawning stream to the nursery lake soon after emerging from the gravel. Survivors generally leave the nursery lake the following spring but others remain a year or two longer before migrating to the ocean.

Sockeye salmon usually depend on lake habitat for initial rearing, but fluvial populations are not uncommon, as reported by Foerster (1968):

> In a number of river systems there occur "races" of sockeye which spawn in streams without associated lakes. In some of these cases the fry may drop down directly to the sea. Among returning adult fish there are found individuals with no freshwater period of residence indicated on the scales. Thus, they are termed "oceantype" sockeye. Usually the number of such sockeye are small, due, it is presumed, to a heavy mortality of fry in the sea but in one river of the USSR far east, the Kamchatka River, in one year, 1932, (Krokhin and Krogius, 1937b) 81% of the sockeye were of this type.

It is the nursery lake dependency that is most intriguing in limiting abundance of more prevailing stocks, however, particulary since kokanee and young sockeye salmon commonly inhabit the same areas of a lake and eat identical foods, mainly pelagic plankton (Scott and Crossman 1973).

Table 3. Available hatchery records of dates of first arrival, dates of spawning, number of eggs/female, and survival to hatching for sockeye salmon returning to White and/or Little Wenatchee, Entiat, and Methow rivers, 1944-1963.

	LEAVENWORTH HATCHERY				ENTIAT HATCHERY				WINTHROP HATCHERY		
	White and/or Little Wenatchee Rivers				Entiat River				Methow River		
Year	Date of first arrival	Dates of spawning	No. eggs per female	Survival to hatching (%)	Date of first arrival	Dates of spawning	No. eggs per female	Survival to hatching^a (%)	Dates of spawning	No. eggs per female	Survival to hatching (%)
1944		9/09-09/28	2697	93							
1945		9/05-10/29	2715	91	8/01	?-11/05					
1946		9/04-09/27	2430	95					9/19-10/01	2800	99
1947		8/30-09/22	2655	97					9/02-09/26	2664	92
1948		8/31-09/25	2542	95					9/07-10/04	2063	89
1949		9/02-09/30	2203	96					9/09-10/07	2631	91
1950	9/05	9/06-09/23	2753	96						2549	93
1951	9/04	9/04-10/01	3376	94					9/10-10/01	2614	95
1952	9/01		2674	97					9/10-09/30	2395	95
1953	8/21	9/01-09/16	2689	93	7/15	9/14-10/11	2790	92	9/01-10/09	2699	91
1954		9/08-09/14	3022	97	8/10	9/09-10/06	2751	93	9/08-09/21	2519	92
1955		9/07-09/21	3007^b	95	7/21	8/26-10/09	2906	97		2134	91
1956		8/31-09/15	2825	97	7/23	9/12-10/25	2739	94		2152	97
1957		8/31-09/26	2465^c	94	7/29	9/18-10/14	2672	92		2205	96
1958		9/01-09/16	2750	96	7/09	9/11-10/16	3724	88	8/16-10/03	2253	95^a

Table 3 (continued).

	LEAVENWORTH HATCHERY				ENTIAT HATCHERY				WINTHROP HATCHERY		
	White and/or Little Wenatchee Rivers				Entiat River				Methow River		
Year	Date of first arrival	Dates of spawning	No. eggs per female	Survival to hatching (%)	Date of first arrival	Dates of spawning	No. eggs per female	Survival to hatching[a] (%)	Dates of spawning	No. eggs per female	Survival to hatching (%)
1959	9/09	9/11-09/17	2221[d]	93	7/10	9/14-10/13	2332	94		2139	95[a]
1960	8/26	8/30-09/09	2283[e]	94	7/21	9/09-10/22	2113	94		2222	93[a]
1961	9/01	9/06-09/25	2700[f]				2544			2110	94[a]
1962	8/27	9/03-09/17	2547[g]	95							
1963	8/28	9/05-09/16	3119								
1964			2535	96							
Average no. of eggs per female			2677				2730			2384	

[a] Percent survival to eyed state when the eggs shipped to Leavenworth Hatchery.
[b] Fish reported in very poor condition; 922 died in trap.
[c] Eggs reported as larger than usual.
[d] Run timing two weeks late; held up at Priest Rapids Dam; past ready to spawn.
[e] Fish in poor condition; many net marks; passage problem at Wanapum Dam mentioned.
[f] Condition of fish reported improved over previous year.
[g] Condition of fish reported good with a few females with 3500 eggs per fish.

FACTORS AFFECTING SOCKEYE SALMON ABUNDANCE

Factors affecting the abundance of sockeye can be divided into: (1) commercial harvest, (2) artificial propagation, and (3) environmental influences. Environmental influences describe the complex interplay of climate, habitat, biotic features, and other variables on abundance of sockeye salmon. Following the sections on commercial harvest and artificial propagation, environmental influences are discussed under: (1) habitat loss by dam blockage, (2) habitat alteration, and (3) functional limitations of habitat. Changes in one environmental influence result in an adjustment of the rest--some factors responding more than others, of course, and this would seem particularly true of factors controlling ocean survival, which are not examined.

COMMERCIAL HARVEST

The proportion of a salmon population that can be harvested without jeopardizing the maintenance of the population varies. Some populations produce a large surplus of fish over that needed to perpetuate the population while others do not, as noted by Ricker (1973):

> It is the nature of animals of whatever sort, to penetrate into every habitat where they can eke out a living. Hence it is to be expected that there once existed salmon stocks (even fairly large ones) in marginal situations that needed almost the whole of their recruitment for spawning in order to survive. . . . Such stocks would disappear during the developmental period of the fishery. On the spawning grounds this disappearance would scarcely be noticed amid the general abundance of breeding fish in those days (mostly before 1900), when in any event the information available was poor or lacking. While they lasted, however, such stocks may have contributed importantly to the large runs and easy catches that were then available in the commercial fishing areas.

Marginal situations can be defined as habitat that is precarious due to chronic or recurring restraints that limit species abundance. Major abundance of sockeye salmon centers in lakes generally less than 100 miles from the ocean (Foerster 1968; Burgner et al. 1976; Hartman and Burgner 1972), although there are important exceptions (e.g., Chilko, 690 miles; Babine, 200 miles), including the Columbia River. This distribution can be taken as evidence that survival is highest for coastal stocks, and that the time and distance of their migration ensures most favorable conditions in the different habitats used by different life stages (Thompson 1951). Virtually all Columbia River sockeye runs involved migrations 500 to 1200 miles from the ocean, so it might be suspected that they might have a low tolerance to exploitation.

Beginning in 1938, with the exception of 1941, commercial catches declined, as did the total sockeye salmon run in relation to escapements ranging from 10% to 24% (Table 4). The historic low was in 1945, after which the population increased. The historic high was in 1947, and runs generally were then maintained at reasonably satisfactory levels until 1960, with escapements in the range of 25% to 50%. In 1960-1982 catches generally amounted to much less than escapements, yet the runs have fallen considerably below the average for 1946-60.

Rich (1940a, 1940b) reviewed the sockeye salmon fishery for 1892-1938, and concluded that "the sockeye runs were greatly reduced as long ago as 1900, since which time there has been no marked change in the size of the catch." This statement is at odds with landings (Fig. 2), but it can be assumed that harvest rates were generally high if not excessive (e.g., see Chapman et al. 1982, pp. 1.3-1.11). Rock Island Dam counts in 1933-37 showed only an average of 16% of the runs escaping the fisheries; in 1934, 98.4% of the run was harvested.

Pre-1900 abundance as measured by commercial landings could have reflected, to some degree, one-time harvest of stocks lacking in viability. The ability of surviving stocks to withstand extremes of overharvest in the 1930's and early 1940's, however, reflects amazing tolerance to exploitation. When catch and escapement were brought more nearly into balance beginning in 1945, the runs revived and comparative abundance was maintained until about 1960 (Fig. 2; Table 4). In subsequent years, inability of sockeye salmon to maintain themselves under greatly increased escapement, followed in more recent years by curtailment of all but incidental harvest, did not implicate overharvest as being responsible for the post-1960 decline in abundance.

ARTIFICIAL PROPAGATION

Of the more than 13 billion anadromous salmonids released in waters of Pacific North America before 1929, almost half were sockeye salmon (Wahle and Smith 1979). As it came to be recognized that the benefits from such releases were largely inconsequential in relation to natural production, virtually all sockeye propagation was terminated (Foerster 1968). However, effects of artificial propagation of sockeye salmon in the Columbia River were not inconsequential, as perceived in obscure information.

Returns from Hatchery Releases

Contribution to the fishery of 1961-64 brood releases from Leavenworth Hatchery was not published until the late 1970's (Wahle et al. 1979), and

Table 4. Catch and spawning escapement (thousands) of Columbia River sockeye salmon, 1938-1979.

	A	B		C	D	E			
						Catch by Indians		Escapement	
Year	Total run	Catch zones 1-6	Ratio B/A %	Rock Isl. dam count	Ice Harbor dam count	Colville	Okanogan	C+D-E	%
1938	168.0	125.6	75	17.1				17.1	10
1939	124.8	81.0	65	19.6				19.6	16
1940	196.0	111.9	57	26.9				26.9	14
1941	173.6	150.0	86	0.9				0.9	1
1942	94.5	57.4	61	16.3				16.3	17
1943	73.4	42.9	58	17.7				17.7	24
1944	24.6	16.5	67	4.9				4.9	20
1945	10.9	2.7	25	7.1				7.1	65
1946	101.1	38.3	38	46.6				46.6	46
1947	335.3	211.4	63	79.8		5.0		74.8	22
1948	143.2	29.8	21	84.6		5.0		79.6	56
1949	52.6	7.7	15	18.7		0.5		18.2	35
1950	112.6	50.4	45	50.1		2.5		47.6	42
1951	203.7	46.3	23	102.7		5.0		97.7	48
1952	318.9	165.8	52	113.7		3.0	1.8	108.9	53
1953	260.0	41.0	16	156.0		4.5	1.3	150.2	58
1954	180.0	67.4	37	91.2	1.0[a]	3.9	1.6	86.7	48
1955	245.0	59.7	24	155.8	4.4[a]	4.6	2.5	153.1	63
1956	202.0	81.3	40	92.2	1.3[a]	3.6	1.3	88.6	44
1957	147.8	65.1	44	71.3	0.5[a]	3.6	1.1	67.1	45
1958	313.3	197.2	63	97.9	<0.1[a]	0.5	1.3	96.1	31
1959	270.7	185.0	68	72.3	.03[a]	2.7	1.6	68.3	25
1960	179.1	120.0	67	60.3	<0.1[a]	0.6	1.2	58.5	33

Table 4 (continued).

	A	B		C	D	E			
						Catch by Indians		Escapement	
Year	Total run	Catch zones 1-6	Ratio B/A %	Rock Isl. dam count	Ice Harbor dam count	Colville	Okanogan	C+D-E	%
1961	57.7	40.7	70	19.2	<0.1[a]	0.2	0.4	18.6	32
1962	38.7	14.3	37	29.3	<0.1[a]	0.2	0.7	28.4	73
1963	65.4	14.0	21	64.7	1.1	0.2	1.3	62.1	95
1964	104.9	20.8	20	69.4	1.3	0.2	0.8	67.1	64
1965	55.2	5.9	11	42.4	0.3	0.3	1.2	40.6	74
1966	169.2	4.4	3	164.6	0.3	0.5	1.2	162.6	96
1967	165.4	55.7	34	119.8	0.7	7.5	0.9	110.6	67
1968	134.7	25.3	18	104.8	1.2	2.5	1.9	99.2	74
1969	75.8	27.5	36	38.0	0.7	0.3	0.4	36.6	48
1970	95.3	17.1	18	74.9	0.8	0.8	0.8	72.5	76
1971	150.5	76.2	51	71.4	0.5	1.2	0.7	69.0	46
1972	123.3	77.9	63	43.5	0.4	0.5	0.8	41.8	34
1973	61.3	3.7	6	68.7	0.2	2.0	2.6	63.6	103
1974	43.9	<0.1	<1	33.9	0.2	0.5	0.8	32.4	74
1975	58.2	0.0	0	53.4	0.2	0.5		52.7	90
1976	43.7	0.1	<1	35.4	0.8	0.5		35.7	82
1977	99.8	0.1	<1	90.3	0.6	0.5		89.2	89
1978	18.4	0.0	0	14.7	<0.1	0.5		14.1	77
1979	52.6	0.0	0	50.5	<0.1	0.5		49.9	95

[a] Redfish Creek weir, Snake River (Bjornn et al. 1968).

was primarily a cost-benefit analysis. This report also contained the percentages of hatchery sockeye in the commercial catch for 1964-67, enabling the estimation of returns for the 1961-64 brood releases (Table 5). Another insight consisted of 21 mark-and-recapture experiments involving more than 600,000 sockeye of the 1940-44 brood releases (Table 6) first published by Fulton and Pearson in 1981. Lastly, implementation of the Grand Coulee Fish-Maintenance Project, the WDF plan to preserve salmon runs threatened by Grand Coulee Dam mentioned in the introduction, was reported on in unpublished annual reports of Leavenworth Hatchery by the former U.S. Fish and Wildlife Service branches of Fishery Biology (responsible for biological investigations) and Game Fish and Hatcheries (responsible for fish culture, trapping, and counting of salmon at Rock Island Dam and maintenance of water diversion screens and fishways).

The marked sockeye salmon of Fulton and Pearson (1981) allowed for extrapolation of returns on all hatchery releases, 1940-44 (Table 7). Where there was no direct match between experimental and production fish, recovery values were chosen from experimental groups having the most similarities (i.e., size, time of stocking, etc.). However, the returns of marked fish were modified to include a 39% fin clipping mortality, derived by Weber and Wahle (1969), used by Wahle et al. (1979) in the evaluation of Leavenworth Hatchery sockeye salmon, and reinforced by a 38% loss to fin clipping reported by Foerster (1968).

Extrapolation shows that if all releases of the 1940-44 brood years returned as four-year fish, between 5% and 98% of the 1944-48 sockeye runs consisted of hatchery fish (Table 8). In the historic lowest and highest years of abundance (1945 and 1947), hatchery fish would have made up 10% and 11%, respectively, of the runs. From 5.6 million juveniles released from brood years 1940-44, the return was 91,100 adults, or a survival of 1.62%. Similar calculations for 1960-63 brood releases indicate that 10% to 22% of the runs in 1964-67 consisted of hatchery fish, and that releases of 11.5 million juveniles produced 76,770 adults, or a survival of 0.67% (Table 5).

The above comparison is subject to three biases: (1) Survival for the early years is underestimated. Recovery of marked sockeye that returned to hatcheries and spawning areas in the Fulton and Pearson (1981) study was incomplete, whereas the tally of those captured in the fisheries was virtually complete. The data for later years (1964-67) are assumed to be complete as they represented sampling of a cross section of the runs in the lower river. (2) The use of a four-year run cycle was not exact; small percentages of the runs consisted of other age groups. (3) Returns from fingerlings and yearlings released in spring and fall to lakes and streams were compared with only fingerlings released in fall to Lake Wenatchee in later years. Two of the earlier marking experiments (Table 6, experiments 10 and 13), however, were comparable to fall releases of fingerlings to Lake Wenatchee assessed in the 1960's; returns were 3.32% and 1.03% (vs. 0.67%).

These biases do not alter three conclusions: (1) contribution of hatchery sockeye to run size was substantial in some years; (2) survival of hatchery juveniles to returning adults was about threefold greater in the 1940's

Table 5. Returns for sockeye salmon of brood years 1960-1963 released from Leavenworth Hatchery, based on percentage contribution to commercial catch in 1964-1967 derived by Wahle et al. (1979) from catch sampling.

Brood year	Hatchery releases	Harvest year	Estimated total run	Returns of hatchery fish: Hatchery fish in catch (%)	Returns of hatchery fish: Number in run	Returns of hatchery fish: Estimated survival (%)
1960	2,761,000	1964	104,900	9.8	10,280	0.37
1961	1,777,200	1965	55,200	9.6	5,299	0.30
1962	3,802,500	1966	169,200	21.6	36,547	0.96
1963	3,075,100	1967	165,400	14.9	24,644	0.80
Total or average	11,415,800				76,770	0.67

Table 6. Returns of fin-clipped sockeye and kokanee salmon from 1939-1944 brood releases from Columbia River hatcheries. Data from Fulton and Pearson (1981), but modified to include a 39% marking mortality demonstrated by Weber and Wahle (1969) and Foerster (1968).

Experiment number	Brood year	Marked releases					Recovery (corrected) (%)	Number returned		
		Egg source	Number	Area of release	Date	Size (fish/lb)		Commercial fisheries	Home stream	Strays
Transplantation										
6 a	1941	L Quinault	60,010	Entiat R	5/43	38.0	1.84	670	1	2
7 b	1941	L Quinault	1,945	Icicle Cr	10/43	35.0	0.42	4	--	1
15 c	1943	Bonn Dam	24,990	Spirit L	11/44	229.0	0.03	4	--	--
16 c	1943	Bonn Dam	18,336	Spirit L	4/45	90.0	0.09	10	--	--
17 c	1943	Bonn Dam	19,669	L White Salmon	4/45	?	5.15	578	8	32
18 d	1943	Bonn Dam	10,455	L Cr Metolius R	5/45	?	1.11	54	16	1
19 d	1944	Bonn Dam	25,351	L White Salmon	10/45	130.0	0.22	15	6	13
20 d	1944	Bonn Dam	25,598	L White Salmon	3/46	54.0	1.53	72	134	33
Time and place of liberation										
2 b	1940	Rock Is Dam	50,040	L Osoyoos	11/41	95.0	2.66	798	13	--
3 b	1940	Rock Is Dam	25,000	L Osoyoos	5/42	80.0	0.15	20	4	--
4 b	1940	Rock Is Dam	25,000	L Wenatchee	4/42	?	0.04	6	--	--
5 b	1940	Rock Is Dam	25,000	Icicle Cr	4/42	?	0.18	24	3	--
8 b	1942	Rock Is Dam	31,264	L Osoyoos	3/44	?	0.20	40	--	--
9 b	1942	Rock Is Dam	33,864	L Osoyoos	10/43	117.0	1.87	380	6	--
10 b	1942	Rock Is Dam	35,022	L Wenatchee	10/43	117.0	3.32	686	24	--
11 b	1942	Rock Is Dam	30,186	L Wenatchee	3/44	80.0	0.65	118	3	--
13 b	1943	L Wenatchee	25,183	L Wenatchee	10/44	106.0	1.03	158	1	--
14 b	1943	L Wenatchee	25,051	L Wenatchee	3/45	34.0	1.87	278	8	--
Kokanee--sea run and homing										
12 a	1942	L Chelan	22,341	Entiat R	3/44	49.0	0.01	1	--	--
21 b	1944	L Wenatchee	29,189	Icicle R	3/46	28.0	0.44	47	32	--
22 b	1944	L Wenatchee	60,128	L Wenatchee	9/45	44.0	0.82	268	34	--

Table 6 (continued).

Experiment number	Brood year	Marked releases Egg source	Number	Area of release	Date	Size (fish/lb)	Recovery (corrected) (%)	Number returned Commercial fisheries	Home stream	Strays
<u>Survival of wild fish</u>										
1[e]	1939	Okanogan R	15,932	L Osoyoos	4/28-5/21/41		0.43	36	6	--
Total or average			619,554				1.21	4,268 (91.8%)	299 (6.4%)	81 (1.7%)

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[a]Entiat National Fish Hatchery (NFH), [c]Carson and Big White Salmon NFHs, [d]Little Salmon NFH, [e]wild smolts from Lake Osoyoos.

Table 7. Extrapolation of returns for all releases from Leavenworth, Entiat, and Winthrop hatcheries for sockeye salmon brood years 1940-1944 (based on data from Fulton and Pearson [1981] as modified for marking mortality [Table 6]).

Brood year	RELEASES Hatchery	Number	Area	Date	Size (fish/lb)	Estimated survival (%)	Basis survival estimate[a]	Number adults
1940	Entiat	370,420	L Osoyoos	5/42	87.5	0.15	Exp #3	556
	Leavenworth	25,000	L Osoyoos	5/42	87.5	0.15	Actual #3	24
	Leavenworth	519,256	L Osoyoos	11/41	95.0	2.66	Exp #2	13,812
	Leavenworth	50,040	L Osoyoos	11/41	95.0	2.66	Actual #2	811
	Leavenworth	25,000	Icicle Cr	4/42	?	0.18	Actual #5	27
	Leavenworth	414,016	L Wenatchee	10/41	95.0	2.17	Av #10, #13	8,894
	Sub-total	1,403,732						24,214
1941	Entiat	60,010	Entiat R	5/43	38.0	1.84	Actual #6	673
	Leavenworth	1,945	Icicle Cr	10/43	35.0	0.42	Actual #7	5
	Leavenworth	12,459	L Wenatchee	10/42	?	3.32	Exp #10	414
	Sub-total	74,414						1,092
1942	Entiat	534,204	L Osoyoos	10/43	90.0	1.87	Exp #9	9,990
	Entiat	22,002	L Wenatchee	10/43	76.0	3.32	Exp #10	730
	Entiat	36,400	L Osoyoos	3/44	52.0	0.20	Exp #8	7
	Entiat	7,176	L Wenatchee	3/44	52.0	0.65	Exp #11	47
	Entiat	22,341	Entiat R	3/44	48.0	0.01	Actual #12	1
	Leavenworth	84,456	L Osoyoos	10/43	117.0	1.87	Exp #9	1,579
	Leavenworth	246,273	L Wenatchee	10/43	117.0	3.32	Exp #10	8,176
	Leavenworth	35,022	L Wenatchee	10/43	117.0	3.32	Actual #10	710
	Leavenworth	33,864	L Osoyoos	10/43	117.0	1.87	Actual #9	386
	Leavenworth	31,264	L Osoyoos	3/44	52.0	0.20	Actual #8	40
	Leavenworth	30,186	L Wenatchee	3/44	80.0	0.65	Actual #11	121
	Sub-total	1,083,188						21,787

Table 7 (continued).

Brood year	RELEASES Hatchery	Number	Area	Date	Size (fish/lb)	Estimated survival (%)	Basis survival estimate[a]	Number adults
1943	Winthrop	577,227	L Osoyoos	10/44	90.0	1.87	Exp #9	10,794
	Winthrop	86,788	Methow R	4/45	17.5	1.84[b]	Exp #6	1,597
	Leavenworth	510,911	L Osoyoos	10/44	106.0	1.87	Exp #9	9,554
	Leavenworth	1,453,973	L Wenatchee	10/44	106.0	1.03	Exp #13	14,976
	Leavenworth	25,183	L Wenatchee	10/44	106.0	1.03	Actual #13	259
	Sub-total	2,654,082						37,180
1944	Winthrop	64,939	Methow R	3/46	12.7	1.84[b]	Exp #6	1,195
	Leavenworth	237,428	L Wenatchee	10/45	104.0	2.17	Av #10, #13	5,152
	Leavenworth	15,520	L Wenatchee	11/45	44.0	0.82	Exp #22	127
	Leavenworth	29,129	Icicle Cr	3/46	28.0	0.44	Actual #21	79
	Leavenworth	60,128	L Wenatchee	11/45	44.0	0.82	Actual #22	302
	Sub-total	407,144						6,855
	Grand total	5,622,560						91,128 (1.62%)

[a] The marked sockeye salmon of Fulton and Pearson (1980) allowed for almost complete extrapolation of returns on all hatchery releases in 1940-1944 (Table 6). In those instances where there was no direct match between experimental and production fish, recovery values were chosen from experimental groups having the most similarities (i.e., size, time of stocking, etc.).

[b] Survival 1.84%, as extrapolated from 60,010 marked yearlings (38/lb) released to Entiat River, believed conservative based on 1943-1945 brood year releases of 231,539 unmarked yearlings (12.7-26.0/lb) and subsequent hatchery escapement of 3,906 (1.69%) adult sockeye in years 1946-1949. The Methow River, like the Entiat River, had no previous sockeye run, and even though the 1950 hatchery escapement could have included additional returns (5-year fish) from the 1943-1945 cohort releases, there was no 1946 brood year release which could have contributed to escapement (3-year fish) in 1949. Furthermore, the catch:escapement ratio for years 1946-1949 was about 1:1, suggesting an overall survival of the 1943-1945 brood releases of about 3.0%, which allows for 1949 escapement to have contained some naturally spawned fish (3-year-olds) in 1946.

Table 8. Contribution of Leavenworth, Entiat and Winthrop Hatchery releases (from Table 7) to sockeye salmon runs 1944-1948, based on 4-year cycle return.

Year	Number entering Columbia R.	Hatchery contributions	
		Number	Percent
1944	24,600	24,200	98.0
1945	10,900	1,100	10.1
1946	101,100	21,800	21.6
1947	335,300	37,200	11.1
1948	143,200	6,800	4.7
Total or average	615,100	91,100	14.8

than in the 1960's; and (3) adults sacrificed for artificial propagation (Tables 2 and 9) showed no consistent increased efficiency, in point of returning adults, over natural recruitment based on spawner-recruit ratios (Table 10).

Transfer and Introduction of Stocks

It is reasonable to believe that at least some of the eight geographic stocks of Columbia River sockeye identified (Table 1) contained discrete subpopulations homing to specific lakes, or even to different areas within lakes and streams (Ricker 1972).

(1) Arrow Lake sockeye.--Sockeye salmon used in artificial and natural propagation consisted mostly of the Arrow Lake group (Table 1). Counts from 1935-37 at Rock Island Dam, at Tumwater Dam on the Wenatchee River, and at Zosel Dam on the Okanagon River indicated that about 85% of the Columbia River sockeye run originated above the site of the Grand Coulee Dam (WDF 1938). However, the original distribution of sockeye in the upper Columbia River was never specifically determined (Fish and Hanavan 1947).

H. B. Holmes of the U.S. Bureau of Fisheries suggested in the 1920's that the Okanogan River, from above Osoyoos Lake upstream to Vaseaux Dam, was the principal spawning ground (Craig and Suomela 1936). However, Holmes could account for less than 1000 sockeye spawning in the Okanogan River out of 41,000 counted at Rock Island Dam in 1933, yet could find no evidence from Indian fishermen that the missing fish had proceeded past Kettle Falls. Before inundation by Lake Roosevelt, Kettle Falls (Fig. 1) was the second most important aboriginal fishing area on the Columbia River (Chance 1973).

Ray (1972) reported that the chinook salmon was the primary species harvested at Kettle Falls, and that sockeye salmon did not ascend the Columbia River beyond the Okanogan River. Kennedy (1975), in a study of the utilization of fish by Colville Indians, however, showed that there were runs of sockeye at Kettle Falls, but that they were caught only to vary the diet and supplement the catch of chinook.

Direct evidence that 85% of the Columbia River sockeye salmon originated above Grand Coulee Dam before its construction is limited to the observations of Chapman (1943)[1]. He examined two sockeye caught at Kettle Falls (Indians

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[1] Details of Chapman's attempts to verify the distribution of sockeye in the upper Columbia River, both by direct and indirect means, can be found in WDF (1938), pp. 13 and 14. This account also provides insight as to why Ray (1972) may have been misled into believing that sockeye did not ascend the Columbia River beyond the Okanogan River. The Indians' method of fishing at Kettle Falls was unique. High-back baskets were strung along the edge of the falls. When the fish jumped up over the falls, those that hit the back of the baskets fell into the bottom of the baskets and were captured. Sockeye salmon ascending the falls swam up through the eddies bordering the swift water instead of jumping like the chinook salmon and steelhead trout, making them both hard to observe and hard to catch.

Table 9. Number of sockeye salmon collected from the Little Wenatchee, White, Entiat, and Methow rivers for artifical propagation, 1944-1964.

	Little Wenatchee River			White River			Combined	Entiat River			Methow River		
Year	F	M	Total	F	M	Total	Total	F	M	Total	F	M	Total
1944	79	60	139				139			3			
1945	260	154	414				414			59			
1946	1758	1890	3648				3648			few			99
1947	1371	1387	2758				2758			12			701
1948	2321	1860	4181				4181			17			1644
1949			1108				1108				516	946	1462
1950			1127				1127			45	53	116	169
1951			981			657	1638			6	54	81	135
1952			897			2193	3090	3	3	6	60	101	161
1953				1608	1125	2733	2733	160	167	327	323	531	854
1954	38	19	57	1538	528	2066	2123	106	144	250	20	27	47
1955				1671	557	2228	2228	108	92	200			17
1956				1916	1072	2988	2988	104	91	195			39
1957	1336	705	2041	1033	416	1449	3490	131	89	220	106	128	234
1958							2457	187	195	382	226	199	425
1959	393		393	1131	773	1904	2297	206	232	438			487
1960				1395	837	2232	2232	259	228	487			155
1961	506	193	699	629	259	888	1587	102	90	192			52
1962				1421	847	2268	2268						
1963				1345	738	2083	2083			12			
1964				1345	678	2023	2023						

Table 10. Spawner-recruit ratios for mid-Columbia River sockeye salmon runs (1,000's) for brood years 1938-1975 on a 4-year run cycle.[a]

		Escapement				Spawner:Recruit Ratios		
Year	Total run	A Wild fish[b]	B Hatchery fish[c]	C Wild fish N+4	D Hatchery fish N+4	A:C	B:D	A+B/C+D
1938	168.0	17.1		94.5		1:5.5		
1939	124.8	19.6		73.4		1:3.7		
1940	196.0	9.8	17.1	0.4	24.2	1:0.04	1:1.4	
1941	173.6	0.1	0.85	9.8	1.1	1:98.0	1:1.3	
1942	94.5	12.5	4.8	79.3	21.8	1:6.4	1:4.5	
1943	73.4	13.4	4.3	298.1	37.2	1:22.3	1:8.6	
1944	24.6	4.8	0.14	136.4	6.8	1:28.4	1:48.5	
1945	10.9	6.7	0.47	52.6				1:7.4
1946	101.1	42.9	3.7	112.6				1:2.4
1947	335.3	71.3	3.5	203.7				1:2.7
1948	143.2	73.8	5.8	318.9				1:4.0
1949	52.6	15.7	2.5	260.0				1:14.3
1950	112.6	46.3	1.3	180.0				1:3.8
1951	203.7	95.9	1.8	245.0				1:2.8
1952	318.9	105.6	3.3	202.0				1:1.9
1953	260.0	146.3	3.9	147.8				1:1.0
1954	180.0	84.3	2.4	313.3				1:3.7
1955	245.0	150.7	2.4	270.7				1:1.8
1956	202.0	85.4	3.2	179.1				1:2.1
1957	147.8	63.2	3.9	57.7				1:0.9
1958	313.3	92.8	3.3	38.7				1:0.4
1959	270.7	65.1	3.2	65.4				1:1.0
1960	179.1	54.7	3.8	94.6	10.3	1:1.7	1:2.7	
1961	57.7	16.8	1.8	49.9	5.3	1:2.9	1:2.9	
1962	38.7	26.1	2.3	132.7	36.5	1:5.0	1:15.9	
1963	65.4	60.1	2.1	140.8	24.6	1:2.3	1:11.7	
1964	104.9	65.4	2.0	134.7				1:2.0
1965	55.2	40.6		75.8				1:1.9
1966	169.2	162.6		95.3				1:0.6
1967	165.4	110.6		150.5				1:1.4
1968	134.7	99.2		123.3		1:1.2		
1969	75.8	36.6		61.3		1:1.7		
1970	95.3	72.5		43.9		1:0.6		

Table 10 (continued).

		Escapement						
		A	B	C	D			
Year	Total run	Wild fish[b]	Hatchery fish[c]	Wild fish N+4	Hatchery fish N+4	Spawner:Recruit Ratios A:C	B:D	A+B/C+D
1971	150.5	69.0		58.2		1:0.8		
1972	123.3	41.8		43.7		1:1.0		
1973	61.3	63.6		99.8		1:1.6		
1974	43.9	32.4		18.4		1:0.6		
1975	58.2	52.7		52.6		1:1.0		

[a] A 4-year cycle is not entirely correct; various numbers (usually small) of younger and older sockeye salmon occur.

[b] From Table 4, minus hatchery escapement.

[c] Includes mortality.

reported many more) and observed 12 sockeye in a tributary to Upper Arrow Lake in summer 1938.

(2) Quinault Lake sockeye.--Little mortality of sockeye salmon trapped at Rock Island Dam and released above barriers in Wenatchee and Osoyoos lakes was reported (Fish 1944; Fish and Hanavan 1948). Similar sockeye hauled to hatcheries for egg-taking generally sustained catastrophic losses between time of arrival and the onset of sexual maturation (Table 2). In 1941 all but 20 of 851 sockeye held at Leavenworth Hatchery died. Eggs (211,000) of Lake Quinault sockeye were imported to offset the resulting egg shortage.

In May 1943, 60,010 Quinault yearlings (38 fish/lb) were released into the Entiat River (the rest were released in Lake Osoyoos, Table 11, and Icicle Creek, Table 6). The drainage contains no lake for sockeye rearing, never supported indigenious sockeye (WDF 1938; Craig and Suomela 1941), and was officially stocked with sockeye on only two occasions (Table 11).[2] Both releases were marked (Fulton and Pearson 1981; Table 6, experiments 6 and 12). The second release (March 1944) consisted of kokanee salmon from Lake Chelan, from which only one marked fish was recovered.

Survival of the Quinault sockeye released in 1943 was quite different, 1.84%. One fish was recovered in the Entiat River, three from the Wenatchee River, and 670 from the commercial fisheries. Fulton and Pearson (1981) stated that the Entiat River was fenced and that if more marked fish had returned there, they would have been recovered by hatchery personnel. Various evidence suggests that this was not the case.

No provision for retrieving adult fish to secure a continuing egg supply was made in the original plans for Entiat or Winthrop hatcheries. To remedy this deficiency, small holding ponds were constructed, including various fencing of the rivers. But the emphasis was on chinook salmon and the 2-inch spacing of louvers enabled most sockeye salmon to swim past the weirs. This problem was overcome in the Entiat River by installation of an electrical weir in 1953 (Burrows 1957).

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[2] Allen and Meekin (1980, p. 13) showed that 398 and 41 adult sockeye trapped at Rock Island Dam were relocated to the Entiat River in 1939 and 1940, respectively. Fish and Hanavan (1948), as well as Fish (1944), did not indicate such occurrence, but a "Homing Studies" section (pp. 96, 97) by Hanavan in the 1943 Leavenworth annual report alluded to the fact that 11 sockeye recaptured in the Entiat River after tagging at Rock Island Dam in 1942-43 originated from such introductions. Review of the Annual Project History, Columbia Basin Project, Volume VII-1939, USDI, Bur. Recl., pp. 238-327 and the article "Transplanting the Columbia's Salmon," PFC, USDI, Bur. Fish., Nov-Dec 1939, No. 47, pp. 25-30, does not indicate deviation from the original plan in reserving the Entiat River for only chinook salmon and steelhead trout. Also, comments in original spawning ground surveys of Entiat River relative to origin of sockeye observed do not indicate introductions other than those officially noted (Leavenworth Hatchery biologist Albert Gentry).

Table 11. Stocking history for sockeye salmon produced at Entiat Hatchery.[a]

Brood year	Releases				
	Egg source	Area	Number	Date	Fish/lb
1940	b	L. Osoyoos	395,420	5/42	87.5
1941	L. Quinault	Entiat R.	60,010	5/43	38.0
1942	Leav. NFH	L. Osoyoos	534,204	10/43	90.0
	Leav. NFH	L. Wenatchee	22,002	10/43	76.0
	Leav. NFH	L. Osoyoos	36,400	3/44	52.0
	Leav. NFH	L. Wenatchee	7,176	3/44	52.0
	L. Chelan[c]	Entiat R.	22,341	3/44	49.0
1948	Entiat R.	L. Wenatchee	9,930	10/49	80.0
1950	Little Wen. R.	L. Wenatchee	27,775	4/51	40.0
1951	Leav. NFH	L. Wenatchee	38,269	5/52	38.5
1952	Wenatchee R.	L. Wenatchee	21,652	4/53	34.0
1953	Rock Isl. Dam	L. Wenatchee	23,200	4/54	103.0
1954	Entiat R.	Leav. NFH	175,735	2/55	3993.0
	Entiat R.	Leav. NFH	33,434	5/55	159.0
1955	Rock Isl. Dam	Winthrop NFH	305,526	2/56	3993.0
1956	Rock Isl. Dam	Leav. NFH	119,464	2/57	3993.0
1957	Rock Isl. Dam	L. Wenatchee	161,071	2/58	3993.0
1959	Rock Isl. Dam	Leav. NFH	77,030	2/60	1204.0
Total			1,568,607	(excludes hatchery transfers)	

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[a] Eggs collected from escapement to Entiat River and mostly transferred to Leavenworth NFH not included.

[b] Combination of Lake Quinault eggs (brood year 1941) and eggs from stock trapped at Rock Island dam.

[c] Kokanee (Lake Chelan kokanee originated from Lake Whatcom stock).

The recovery of adult sockeye jumped from six fish in 1952 to 327 in 1953. Even more revealing is that between 192 and 487 adult sockeye were recovered annually through to 1961, when use of the electric weir was abandoned (Table 12).

Only a scattering of adult sockeye were recovered in the years before the electric weir was used. Corroboratively, many of these recoveries coincided with years 1944-46, when release of Quinault sockeye of the 1941 brood could have been expected to return. Fulton and Pearson (1981) reported the percentages of fish taken of the 1941 brood in the commercial catch as three-, four-, and five-year-old fish as being 13, 78, and 9, respectively. A somewhat similar age bracketing of hatchery return was suggested by the recovery of three three-year-old sockeye in 1944, fifty-nine four-year-olds in 1945, plus a "few" observed spawning in the river, and a "few" five-year-olds in 1946, along with 37 observed spawning in the river (Table 12).

There are three other explanations for the origin of the sockeye in the Entiat River, aside from direct releases: (1) inadvertent inclusion of brood stock with chinook or steelhead trapped at Rock Island Dam and relocated to the Entiat River, 1939-40; (2) escape of hatchery juveniles; and (3) straying. The first two possibilities cannot be eliminated. Straying can be eliminated as a mechanism of introduction or, logically, sockeye would have become established historically. Straying as a mechanism of run maintenance can be largely discounted.

In the mark-and-recapture program of Fulton and Pearson (1981), straying was not uncommon, but the numbers of fish involved were small (1.7%). French and Wahle (1964) also demonstrated little straying of adult sockeye tagged at Rock Island Dam. Only 5% were recovered in streams other than the Wenatchee or Okanogan Rivers, and undoubtedly most of the sockeye recovered in Icicle Creek and the Entiat and Methow Rivers had merely returned to their home hatchery streams. A few (19) of the fin-clipped sockeye released from Leavenworth Hatchery in 1962 were recaptured in 1966 below Chief Joseph Dam (R. McConnell, unpublished data). Ricker (1972) described how salmon may "overshoot" the home tributary or "prove" a wrong tributary before reaching the natal stream--behavior subsequently confirmed in electronic tagging studies. Hartman and Raleigh (1964) concluded after observing only a 3% incidence of straying in Alaska that sockeye show a predisposed and tenacious spawning location preference.

The evidence presented for the establishment of Quinault sockeye in the Entiat River is not indisputable. But--as pointed out by Ricker (1972)--in discerning between genetic and environmental influences on salmon, "we should stick to whatever evidence is available, however sketchy it may be."

The significance of the Entiat River run of Quinault sockeye is twofold: (1) 2.4 million progeny were stocked in Lake Wenatchee; and (2) it is an example of a unique sockeye stock adapting to a different environment or being assimilated by the endemic stock.

Table 12. Pertinent observations relating to sockeye salmon runs in the Entiat and Methow rivers.

	Entiat River[a]			Methow River[b]		
Year	Number collected Entiat Hatchery[c]	Number observed spawning in river[d]	Total est. run size[d]	Number collected Winthrop Hatchery[c]	Number observed spawning in river[d]	Total est. run size[d]
1944	3			0		
1945	59	"few"		0		
1946	"few"	37		99		
1947	0			701		
1948	17	25	42	1,644	10	
1949	0	15	15	1,462		2,000
1950	45	35	100	169	1	250
1951	6	135	400	135	0	185
1952	6	193	300	161	0	200
1953	327	0	350	854	9	900
1954	250	32	350	47	22	100
1955	200	85	350	17	91	150
1956	195	0		39	23	
1957	220	0		234	0	
1958	382	0		425	71	
1959	438			487		
1960	487			155		
1961	192			52	0	
1962	0			0	1	
1963	12			0	117	
1964	0			0	102	
1965				0		357[e]
1966				0		1,013[e]
1967				0	2	
1968				0	18	
1969				0	10	
1970				0		
1971		1		0		
1972		3		0		

[a] A total of 60,010 hatchery reared yearlings of the 1941 brood year were released into Entiat River. No hatchery fish were released in other years.

[b] In 1943-1956, 391,985 yearlings and 901,072 fingerlings were released into Methow River. No hatchery fish were released after 1956.

[c] Electric weir was used in diverting run from river to holding ponds in 1953-1961.

[d] Hatchery biologist 1945-1955. Incidental counts since then largely lost but hatchery personnel reported a few sockeye in Methow and 75-150 sockeye in the Entiat 1969-1981.

[e] Electric weir count (Meekin 1967).

Columbia River sockeye make long in-river migrations--currently 500-600 miles and historically much farther. Quinault sockeye spawn only 30-50 miles from salt water and thus expend little energy in migration. On the other hand, Columbia River sockeye salmon are the smallest sockeye known (Ricker 1972) and Quinault sockeye are only slightly larger (3.1-3.7 lbs versus 4.3 lbs average for four- and five-year fish; Fulton and Pearson 1981; Gilbertson 1981).

Columbia sockeye begin their upstream migration in April-May, reach Wenatchee and Osoyoos lakes in July-August, and spawn in tributary streams in September-October. Quinault sockeye first appear in the river en route to Quinault Lake in December-January (Gilbertson 1981). The run peaks (80%-90% of total number) in late May and early June, though some fish run as late as August. They generally do not ascend tributary streams and spawn until November-January, although some spawning has been observed from August to March (Gilbertson 1981).

A sockeye run also became established in the Methow River at about the same time as in the Entiat River. The progenitors were from sockeye intercepted at Rock Island (Table 2) and Bonneville dams. The Methow River also had no history of a sockeye run and lacked a nursery lake (WDF 1938; Craig and Suomela 1941); however, the Methow run was influenced by consistent releases from Winthrop Hatchery (Table 13).

Survival of initial releases (1943-45) apparently was higher (3%) than that of Quinault sockeye (1.8%) introduced into the Entiat River, (Table 7, footnote b). Natural spawning in the Methow River is obscured by hatchery releases, but observations (Table 12) attest that it did occur. The most telling evidence for natural spawning lies in the disclosure, by an electric counting weir, of 359 and 1013 adult sockeye ascending the Methow River in 1965 and 1966 (Meekin 1967), eight and nine years after propagation had ceased at Winthrop Hatchery (Tables 12, 13).

Leavenworth Hatchery is only 2.8 miles upstream from the confluence of Icicle Creek with the Wenatchee River, which in turn is 28.6 miles downstream from Lake Wenatchee. As a consequence, some of the sockeye observed in Icicle Creek could have reflected "proving" of the wrong tributary, or some remaining attraction for the water from that stream in which they had been reared before being released into Lake Wenatchee (Table 14). Nevertheless, sockeye spawned in Icicle Creek (Table 15).

(3) Kokanee.--Discrete stocks of salmon are made possible by the occurrence of homing, a phenomenon described simply as the return of a large majority of the fish hatched in a stream to the same stream to spawn as adults (Ricker 1972). In 1936, 1937, and 1938, observations of numerous adult sockeye below power dams on the Chelan and Similkameen Rivers (Chapman 1941; Bryant and Parkurst 1950) confounded the hypothesis of homing. The dams were built without fishways on falls impassable to salmon since glacial times; however, the dam operators reported the sockeye appeared every year (Chapman 1941). Either the sockeye originated from kokanee in upstream Lake Chelan and Lake Palmer or they were strays from the Columbia or Okanogan rivers.

Table 13. Stocking history for sockeye salmon produced at Winthrop Hatchery.

Brood year	Egg source	Releases			
		Area	Number	Date	Fish/lb
1942	Rock Isl Dam	Leav. NFH	118,000	10/42	eggs
1943	Rock Isl Dam	Leav. NFH	851,000	10/43	eggs
	Leav. NFH	L Osoyoos	577,227	10/44	90.0
	Leav. NFH	Methow R	86,788	4/45	17.5
1944	Carson NFH	Methow R	64,939	3/46	12.7
1945	Methow R				
	Leav. NFH	Methow R	79,812	3/47	26.0
1946	Methow R	L Osoyoos	337,590	4/47	95.0
1947	Methow R	Methow R	310,397[a]	5/48	116.0
	Methow R	Methow R	25,000	9/48	26.5
	Methow R	Methow R	97,000	3/48	23.0
	Methow R	Methow R	2,390	3/49	13.5
1948	Methow R	Methow R	25,000	9/49	45.9
	Methow R	Lake Osoyoos	524,400	9/49	45.9
	Methow R	Methow R	7,240	3/50	22.6
	Methow R	Methow R	21,407	3/50	22.6
1949	Methow R	Methow R	59,413	3/51	18.0
1950	L Whatcom	Methow R	25,006[b]	?/51	320.0
	Methow R	Methow R	1,163	2/52	14.5
1951	Methow R	Methow R	12,000	?/52	35.0
	Methow R	Methow R	32,692	?/53	16.0
1952	L Wenatchee	L Wenatchee	440,960	?/53	159.0
	L Wenatchee	Col R (Pateros)	79,040	?/53	159.0
	Methow R	Methow R	36,142	?/54	29.8
1953	Methow R	Methow R	45,627	?/54	46.0
	L Wenatchee	L Wenatchee	207,508	?/54	335.7
	Methow R	L Wenatchee	138,990	?/54	96.0
	Methow R	Icicle Creek	44,325	?/54	46.0
1954	L Wenatchee	L Wenatchee	100,000	?/55	31.0
	Methow R	L Wenatchee	42,450	?/55	159.0
1955	L Wenatchee	Methow R	190,575	?/56	159.0

Table 13 (continued).

Brood year	Egg source	Releases Area	 Number	 Date	 Fish/lb
1956	L Wenatchee	L Wenatchee	320,400	?/57	44.5
	Methow R	Methow R	24,833	?/57	18.8
1957	L Wenatchee	L Osoyoos	627,460	?/58	32.0
	L Wenatchee	L Osoyoos	466,678	?/58	26.0
Total[c]			5,054,452 (excludes hatchery transfers)		

[a] Inadvertently liberated by flooding.

[b] Kokanee.

[c] Eggs collected from sockeye escapement to Methow River after 1957 shipped to Leavenworth NFH.

Table 14. Stocking history for sockeye salmon produced at Leavenworth Hatchery.

Brood year	Egg source	Releases			
		Area	Number	Date	Fish/lb
1940	Rock Isl Dam	L Osoyoos	569,296	11/41	95.0
	Rock Isl Dam	L Wenatchee	414,016	10/41	95.0
	Rock Isl Dam	Icicle Creek	25,000	4/42	?
1941	L Quinault	Bumping L[a]	25,777	?/43	?
	L Quinault	Icicle Creek	1,945	10/43	35.0
	Rock Isl Dam	L Wenatchee	12,459	10/42	--
1942	Rock Isl Dam	L Osoyoos	84,456	10/43	117.0
	Rock Isl Dam	L Wenatchee	246,273	10/43	117.0
1943	Rock Isl Dam	L Osoyoos	510,911	10/44	106.0
	Rock Isl Dam	L Wenatchee	1,453,973	10/44	106.0
1944	Rock Isl Dam	L Wenatchee	237,428	10/45	104.0
	L Wenatchee	L Wenatchee	85,648[b]	11/45	44.0
	L Wenatchee	Icicle Creek	29,129	3/46	28.0
1945	L Wenatchee	L Wenatchee	601,113	10/46	54.0
	Carson NFH	L Wenatchee	40,533	9/46	129.0
1946	L Wenatchee	L Wenatchee	490,426	4,6/47	1,438.0
	L Wenatchee	L Wenatchee	1,167,000	9,10/47	63.0
1947	L Wenatchee	L Wenatchee	2,338,793	1948	68.0
1948	L Wenatchee	L Wenatchee	4,816,298	1949	121.0
1949	L Wenatchee	L Wenatchee	1,005,959	1950	53.0
	L Whatcom	L Wenatchee	520,599[b]	10/50	253.0
	Methow R	L Wenatchee	395,012	9/50	45.0
1950	L Wenatchee	L Wenatchee	1,260,910	1951	54.0
	Entiat R	Research	41,652	?	--
1951	Entiat R	L Wenatchee	7,118	1952	--
	L Wenatchee	L Wenatchee	112,365	1952	47.0
1952	L Wenatchee	L Wenatchee	342,098	1953	63.0
	Entiat R	L Wenatchee	61,210	1953	63.0

Table 14 (continued).

Brood year	Egg source	Releases			
		Area	Number	Date	Fish/lb
1953	L Wenatchee	L Wenatchee	2,541,733	1954	160.0
	Methow R	L Wenatchee	323,603	1954	159.0
	L Wenatchee	L Chelan	8,912	1954	159.0
	L Wenatchee	Icicle Creek	65,376	1954	159.0
	Methow R	L Chelan	10,952	1954	159.0
	Entiat R	L Wenatchee	202,630	1954	159.0
	Entiat R	L Chelan	31,036	1954	159.0
	L Wenatchee	L Wenatchee	28,949	1955	159.0
1954	L Wenatchee	L Wenatchee	3,148,825	1955	--
	Entiat R	L Wenatchee	291,145	1955	--
1955	L Wenatchee	L Wenatchee	2,883,836	9/56	110.0
	L Wenatchee	Spirit L	200,000	1956	50.0
	L Wenatchee	Lost L (OR)	50,000	1956	--
	Entiat R	L Wenatchee	234,610	1956	--
1956	L Wenatchee	Spirit L	200,304	1957	78.0
	L Wenatchee	Wm Sprg Ind (OR)	50,076	1957	--
	L Wenatchee	L Wenatchee	3,766,288	9/57	133.0
1957	L Wenatchee	L Wenatchee	3,895,030	9/58	96.0
	Entiat R	L Wenatchee	267,663	1958	--
	L Wenatchee	Icicle Creek	4,130	?	32.5
1958	L Wenatchee	L Wenatchee	3,279,992	9/59	67.0
	Methow R	L Wenatchee	394,929	1959	67.0
	Entiat R	L Wenatchee	482,229	1959	67.0
1959	L Wenatchee	L Wenatchee	2,475,762	10/60	40.0
	Methow R	L Wenatchee	295,932	1960	40.0
	Entiat R	L Wenatchee	358,871	1960	40.0
1960	L Wenatchee	L Wenatchee	2,320,784	9/61	38.5
	Methow R	L Wenatchee	79,458	1961	38.5
	Entiat R	L Wenatchee	360,802	1961	38.5
1961	L Wenatchee	L Wenatchee	2,053,936	10/62	51.0
	Methow R	L Wenatchee	5,335	1962	51.0
	Entiat R	L Wenatchee	164,374	1962	51.0
1962	L Wenatchee	L Wenatchee	3,121,000	10/63	46.0
1963	L Wenatchee	L Wenatchee	3,364,000	9/64	57.0
	Skeena R (Canada)	Snake R	477,689	4/65	27.0

Table 14 (continued).

Brood year	Egg source	Releases			
		Area	Number	Date	Fish/lb
1964	L Wenatchee	L Wenatchee	2,826,000	9/65	50.0
1965	Icicle Creek	Icicle Creek	17,000	6/66	24.0
1966	Icicle Creek	Research	175,000	--	--
1967	Icicle Creek	Icicle Creek	1,400	5/69	17.0
1968	Icicle Creek	L Wenatchee	22,000	10/69	38.0
1969	Icicle Creek	Research	41,000	--	--
Total, mid-Columbia River			55,827,425		

[a] Yakima River drainage.
[b] Kokanee.

Table 15. Maximum number (peak count) of sockeye salmon observed in spawning surveys of Wenatchee River Drainage, 1944-1980 (data from hatchery annual reports, surveys of Chelan County PUD and WDF, Allen and Meekin 1973, Craddock 1958, French and Wahle 1965 and 1969, Gangmark and Fulton 1952, Major and Craddock 1962, Major and Mighell 1966).

	Stream or lake						
Year	Icicle Creek	Tumwater Canyon	Lake Wenatchee	Outlet Lake Wenatchee	Nason Creek	White River	Little Wenatchee River
1944	12[a]	--	--	--	--	--	--
1945	45[a]	--	--	--	--	--	--
1946	64[a]	--	--	--	--	--	--
1947	256[a]	--	--	1,082	482	5,587	1,122
1948	50[a]	--	--	1,594	478	7,271	2,701
1949	--	--	--	196	70	924	248
1950	1	--	--	25	--	4,048[b]	(1,127)[c]
1951	20	41	64	230	16	4,537	242
1952	26	46	22	883	167	4,080	677
1953	--	131	64	615	33	1,707	746
1954	55	61	--	218	555	9,604	1,178
1955	47	604	--	24	15	19,079	583
1956	62	17	--	6	--	7,421	4,060
1957	6	0	--	883	2	3,872	5,386
1958	91	0	--	300	0	13,637[d]	2,780
1959	--	several thous.[e]	--	--	--	3,312	778
1960	--	--	--	0	--	13,551[d]	5,298[d]
1961	--	25	--	0	0	1,710[d]	778[d]
1962	486	--	0	--	--	7,729[d]	2,158[d]
1963	4	--	--	95	0	5,400[d]	2,279[d]
1964	955	--	--	37	2	14,481[d]	4,270[d]
1965	157	--	--	202	0	5,094	1,827
1966	3,905[f]	--	--	566	--	21,687	3,526
1967	163[a]	13[g]	--	--	--	2,235	985
1968	344[h]	--	--	--	--	4,124	867
1969	158[i]	--	--	--	--	4,195	1,187
1970	27[a]	--	--	--	--	7,902	1,651
1971	51	--	0	0	0	9,927	1,938
1972	33	1	0	1	0	4,967	1,264
1973	21	--	--	0	--	4,765	2,389
1974	34	--	--	--	--	3,202	1,543
1975	1	--	--	--	--	9,622	4,008

Table 15 (continued).

Year	Stream or lake						
	Icicle Creek	Tumwater Canyon	Lake Wenatchee	Outlet Lake Wenatchee	Nason Creek	White River	Little Wenatchee River
1976	--	--	--	--	--	1,385	245
1977	--	--	--	--	--	21,021	1,670
1978	1	"few"	--	--	--	656	77
1979	1	"few"	--	--	--	3,764	398
1980	1	"few"	--	--	--	2,206	203

[a] Collected at Leavenworth Hatchery trap.

[b] Includes 141 fish artificially spawned.

[c] Entire run was trapped and spawned artificially.

[d] Primarily a weir count.

[e] Road survey estimate; fish possibly delayed by construction at Priest Rapids Dam.

[f] "Sockeye Salmon Tagging Experiment for Population Study in Icicle River, 1966." E.M. Mattzeff. 12/13/66, 4 p. typed.

[g] Many redds but only a few live fish remaining (10/6).

[h] one-hundred fifty fish hauled to Lake Wenatchee and 80 fish artificially spawned at Leavenworth Hatchery.

[i] Hatchery trap accounted for 58 fish.

The egress of kokanee from lakes to the Columbia River was later documented. The most pertinent instance involved a large kill of kokanee of three distict sizes passing through the turbines of Grand Coulee Dam in 1942, the first year of electric generation but the third year of impoundment (Earnest et al. 1966). Dead kokanee were reported to have been so numerous that local residents gathered them for food.

Homing of salmon is now well established, just as is the fact that sockeye salmon can originate from kokanee. Bjornn et al. (1968) showed that more smolts of the 1961 year class were counted from Redfish Lake than the number of eggs available from sea-run sockeye in brood years 1960 and 1961. In retrospect, it is also obvious that not all kokanee that passed through Grand Coulee Dam generators in 1942 were killed.[3] Survivors could have contributed to the aberrant sockeye spawner-recruit ratio of 1:98 for the 1941 brood year (Table 10); the highest spawner-recruit ratio reported by Foerster (1968) was 1:13.

Large losses of kokanee in the tailwater of Grand Coulee Dam were noted for only a few years after 1942 (Earnest et al. 1966), although some losses were noted through to the 1960's (Ray Duff, WDG, personal communication). With one important exception, this observation correlates with reports indicating that kokanee did not maintain their high initial abundance (1942-45) in Lake Roosevelt, despite the stocking of 7.5 million fry, and eventually became a minor component of the fish community (Gangmark and Fulton 1949a; Fulton and Laird, n.d.; Robeck et al. 1954; Earnest et al. 1966; Neilsen 1974; Stober et al. 1976; Harper et al. 1980).

Henderson (1976, not included in Robeck et al. 1954) observed in 1953 that "few kokanee existed" and that "a large loss occurred over Grand Coulee Dam each spring when large volumes of water passed through the reservoir." Snyder (1967), by contrast, indicated that a sizable population of kokanee were present in 1966 and 1967. More than 19,000 kokanee were purse-seined, marked, and released below Chief Joseph Dam (Fig. 1) in spring 1966, but only 18 recoveries were made (at Priest Rapids, McNary, and Bonneville Dams) before the project was abandoned (Snyder 1976). Henderson's "few kokanee" and Snyder's "sizable population" are easily reconciled, considering relative abundance in an 80,000-acre reservoir and selectivity of purse seines in capturing pelagic kokanee concentrations. Most important, the Snyder observations indicated that kokanee numbers in Lake Roosevelt, though evidently much reduced from initial abundance, were still a formidable source of bias in downriver dam counts of sockeye as late as the mid-1960's, particularly considering their apparent susceptibility to entrainment (Stober et al. 1979).

Leavenworth Hatchery annual reports, which included fish-counting activities up to 1958, included notes on large numbers of small kokanee passing

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[3] A corroborative memorandum titled "The downstream migration of kokanee at Grand Coulee Dam, April 1943," by M.G. Hanavan to A.J. Suomela, USFWS, could not be located.

Rock Island Dam in the high flow years of 1946, 1947, and 1950. The 1950 report distinguished three size groups: larger than 16 inches, 13-16 inches, and 7-11 inches. Fish of the smallest size group were sexually mature. About 50,100 sockeye were counted over Rock Island Dam in 1950, of which 5000-6000 were estimated to have been Lake Roosevelt kokanee as indicated by the 7- to 11-inch size range.

Davidson (1965a) reported that 10% (4700 fish) of the 1965 run at Priest Rapids Dam were land-locked kokanee. On the basis of discrepancies in dam counts, Ross (1965) believed these kokanee had migrated from McNary Impoundment over Priest Rapids and Wanapum Dams, but not Rock Island Dam. Davidson noted that this was not the first year that kokanee had been counted at Priest Rapids Dam since counting began in 1960, but that they had not been as abundant in previous years.

Daily fish counting forms and the fish passage report for 1965 (Ross 1965) disclosed only that kokanee were distinguished from sockeye by their "smallness and visible parr marks." Sockeye under 16 inches long were enumerated as "small" at Rock Island Dam during this period (Zimmer et al. 1961), but no reference was made to three distinct size classes as in the case of Earnest et al. (1966) and the annual reports of Leavenworth Hatchery.

In some years, a large portion of the Okanogan River (Lake Osoyoos) sockeye run consists of small (13-18 inches) three-year-old (one-ocean) fish (Craddock 1957; Craddock and Major 1958; Allen and Meekin 1980), and the Rock Island Dam count designation of "small" provided such distinction. The marking experiments of Fulton and Pearson (1981), in contrast, showed that hatchery kokanee released to Lake Wenatchee primarily returned in their fourth year (two-ocean fish; 363) and that three-year (one-ocean) fish were uncommon (6). This time of return was very similar to that of hatchery and naturally spawned sockeye, except that the sockeye were slightly larger than the anadromous kokanee. However, no anadromous kokanee were as short as 7-11 inches.

Sketchy as these observations are, they suggest that kokanee must have influenced sockeye spawner-recruit ratios of the 1940's and 1950's (Table 10), particularly considering that substantial numbers could have become anadromous and returned as "sockeye."

Anadromy in kokanee is suspected of having an environmental basis (Ricker 1972). Kokanee presumably evolved from "residual" anadromous sockeye (Ricker 1959). Conditions unfavorable to the anadromous type would favor the evolution of a non-anadromous type (Seeley and McCammon 1966). The release of large juvenile kokanee directly into streams accordingly might be suspected of overriding lacustrine programming. Nevertheless, in the Fulton and Pearson (1981) experiments involving kokanee released as large yearlings into the Entiat River and Icicle Creek, returns were 0.01% and 0.44% in spring and fall, respectively, compared with 0.82% for fingerlings released into Lake Wenatchee in fall. Even in Lake Wenatchee, however, genetic and environmental cause and effect are confounded, as described by Ricker (1972):

> It seems possible that these kokanee [Lake Wenatchee] may have evolved from the lake's anadromous sockeye stock rather recently (over the past 60 years or so) as the Wenatchee River became increasingly difficult for salmon to ascend by reason of water diversions and high temperatures. This is suggested partly by their dull colour. More important is the fact that their progeny, planted in the lake after being reared to the autumn fingerling stage, produced a respectable number (0.5%) [corrected for fin clipping loss] of anadromous sockeye of normal appearance, though somewhat smaller than the progeny of anadromous sockeye from the same lake. [This is Fulton and Pearson's (1981) experiment No. 22, which does not depict how many, if any, kokanee were produced as well.] Thus there may still be a very incomplete separation of kokanee from sockeye at this lake.

Kokanee were first introduced into Lake Chelan (Campbell 1977) and other lakes of north-central Washington, possibly including Wenatchee and Palmer Lakes, in 1917. Records of the Washington Department of Game (WDG), which go back only to the time of the Department's creation in 1933, show that 22.5 million kokanee were stocked in Lake Wenatchee between 1934 and 1966. The major, if not single, progenitor source for these fish, as well as for the 7.5 million kokanee introduced into Lake Roosevelt, was Lake Whatcom, in northwest coastal Washington. Kokanee of the Whatcom strain typically have the dull color described by Ricker (1972) for Lake Wenatchee kokanee and, although adults do not have parr marks (mentioned by Ross (1965) as distinguishing between kokanee and sockeye at Priest Rapids Dam), they are often "mottled" (L. Brown, WDG, personal communication).

Evidence of Genetic Alteration

Sockeye salmon are not a generic, homogeneous species, and this fact was not fully appreciated at the time of the Grand Coulee Fish-Maintenance Project. It is now known that there is an incredible amount of diversity in the species in regard to timing of spawning runs, time of spawning, and place of spawning. These differences have a hereditary basis and are adaptations that have evolved for optimum survival in each river system.

Available evidence of genetic alteration of Columbia River sockeye salmon resulting from translocation of stocks is examined under the following headings: (1) run timing; (2) small size of Okanogan River sockeye; (3) inlet-outlet spawning of Wenatchee river sockeye; (4) biochemical genetic variation; and (5) sockeye salmon and kokanee relationships.

(1) Run timing.--Fulton and Pearson (1981) suggested that early run timing of Quinault sockeye, as documented by recovery of fin-clipped fish in the lower Columbia River, may have persisted for at least a few fish of the second generation, as perceived through early and late migrants at Bonneville Dam. Corroboratively, counts at Rock Island Dam in 1933-47 (Fish and Hanavan 1943) depicted higher-than-average numbers of sockeye passing through the

Table 16. Fish counts for 1933-1947 showing higher-than-average numbers of sockeye salmon passing Rock Island Dam May-June 1944-1946 (Fish and Hanavan 1948) when the 1941 brood introduction of early-running Quinault sockeye could have been expected to return.

Ending date of 7-day period		Mean 1933-1943	Year[a]			
			1944	1945	1946	1947
May	7	0	0	3	0	1
	14	0	0	0	0	0
	21	2	0	2	1	0
	28	1	1	1	4	0
June	4	0.3	0	43	15	0
	11	0.7	0	85	6	0
	18	1.3	3	77	13	0
	25	7.1	8	119	11	4
July	2	95	24	243	26	130
	9	406	570	425	165	2,982
	16	1,643	1,644	723	1,540	25,362
	23	3,676	1,916	1,672	10,829	25,267
	30	4,261	576	1,386	22,256	15,777
Aug	6	4,488	97	1,400	7,860	6,182
	13	1,986	48	623	1,829	2,570
	20	1,120	27	222	829	1,209
	27	314	8	79	126	246
Sept	3	201	4	18	22	54
	10	38	5	15	10	19
	17	18	1	2	16	20
	24	17	0	0	3	6
Oct	1	9	0	1	1	1
	8	3	0	0	0	1
Total		18,287.4	4,932	7,139	46,563	79,834

[a] Historic low and high runs entering Columbia River (1933-1980) were in 1945 (10,900) and 1947 (335,300), respectively.

ladders in May and June 1945-46 (Table 16). The 1941 brood of Quinault sockeye released to the Entiat River would have been expected to return 1945-46.

Even though some Quinault sockeye return from the sea to Lake Quinault early (December-March), most (80-90%) return at about the same time as endemic sockeye return to the Columbia River (May-June). Davidson (1967), who compared the mean dates of occurrence of sockeye runs at Bonneville and Rock Island Dams from 1944-1966, found that beginning in 1944, the runs at Rock Island Dam occurred later, at the rate of 0.0208 day per year, whereas the runs at Bonneville Dam occurred earlier, at the rate of 0.2619 day per year. The trend of retardation in timing at the upstream Rock Island Dam, which in 1966 amounted to 6.2 days, occurred coincidentally with development of impoundments on the river (Table 17). These symptoms suggest a possible influence from Quinault sockeye, which hold in Quinault Lake for from three to ten months before proceeding to spawning tributaries (Gilbertson 1981).

Survival (return to the commercial fisheries) of the 1941 hatchery brood of Quinault sockeye was an exceptional 1.8%. The effect of Quinault sockeye on the gene pool could also have been high. In 1945 when most (78%) of the harvest of Quinault fish occurred as four-year-olds, total run size was at the record low of 10,900 fish. The fisheries accounted for 2700 fish, of which 523 (19%) were fin-clipped Quinault stock. Similar representation for Quinault fish in the escapement of 7100 sockeye over Rock Island Dam is therefore likely and is reinforced by atypical numbers of early migrants passing the dam in 1945 (Table 16), as well as by the establishment of a sockeye population in the Entiat River during the same general period.

Evidence for effects of Quinault stock on sockeye runs to Lake Wenatchee is intertwined with problems of fish passage at two turn-of-the-century dams on the Wenatchee River. The Dryden Power and Irrigation Diversion Dam is 17.6 miles above the mouth of the Wenatchee River. Before abandonment of hydroelectric generation in 1957, the eight-foot dam diverted virtually the entire flow in late July through early October from a 1.3-mile section of the river channel between the dam and the tailrace of the power house, a drop of 50 feet in elevation (Fig. 3). Early-run sockeye were a possible biological solution to the low flow passage problem in summer and represented the reason for selecting Quinault stock in overcoming the egg shortage in 1941 (USFWS 1944). Fifteen-foot Tumwater Dam and Diversion are 15 miles above Dryden Dam. The drop in elevation from the dam spillway to the mouth of Tumwater Canyon, 3.7 miles downstream, is 287 feet (Fig. 4). Flows before abandonment of hydroelectric generation in 1957 in the 2.2-mile diversion section of the boulder-bedrock channel ranged from torrent to trickle, potentially posing a barrier to fish migration during both high- and low-water stages.

Fish migrating upstream were counted at Tumwater Dam in 15 years between 1935 and 1973. The widely differing numbers (Table 18) show that in high-flow years sockeye salmon passage was delayed between Rock Island and Tumwater Dams, but with notable exceptions (Fig. 5). In 1957, mean peak dates of the run at Rock Island (July 19) and Tumwater (July 26) were the earliest for the

Table 17. Chronology of hydroelectric power dam construction on the Columbia River.

Years of construction	Name	Location (river mile)	Reservoir length (miles)	Surface area (acres) Reservoir	Surface area (acres) Natural river
1930-33	Rock Island	453	21	3,458	2,781
1933-38	Bonneville	145.5	46.2	20,400	15,000
1933-41	Grand Coulee	597	150	80,000	18,100
1947-54	McNary	292	61	38,100	23,138
1950-55	Chief Joseph	545	52	7,800	4,601
1952-57	The Dalles	191.7	23.9	10,500	6,016
1956-59	Priest Rapids	397	18	7,000	4,315
1956-61	Rocky Reach	474	42	9,200	4,710
1958-68	John Day	215.6	76.4	50,000	27,570
1959-63	Wanapum	415	38	13,800	6,950
1963-67	Wells	515.8	29.2	10,700	4,162

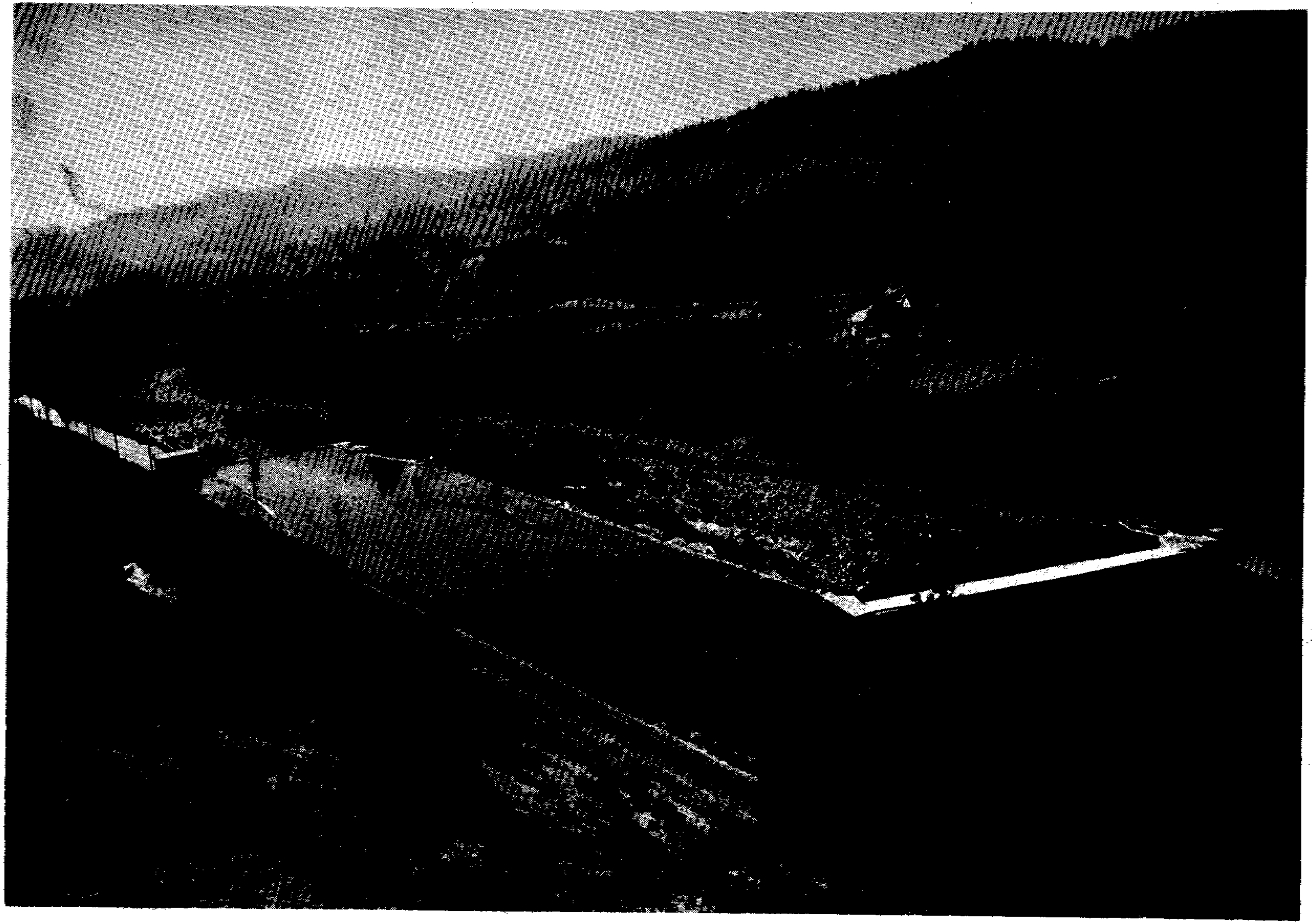

Figure 3. Dryden Power and Irrigation Diversion Dam, Wenatchee River, in the early 1940's during August. Fish ladder at upper horizontal section at right end of dam. Flow below island is approximately 40 cfs. Power and irrigation diversion at lower horizontal section at left end of dam.

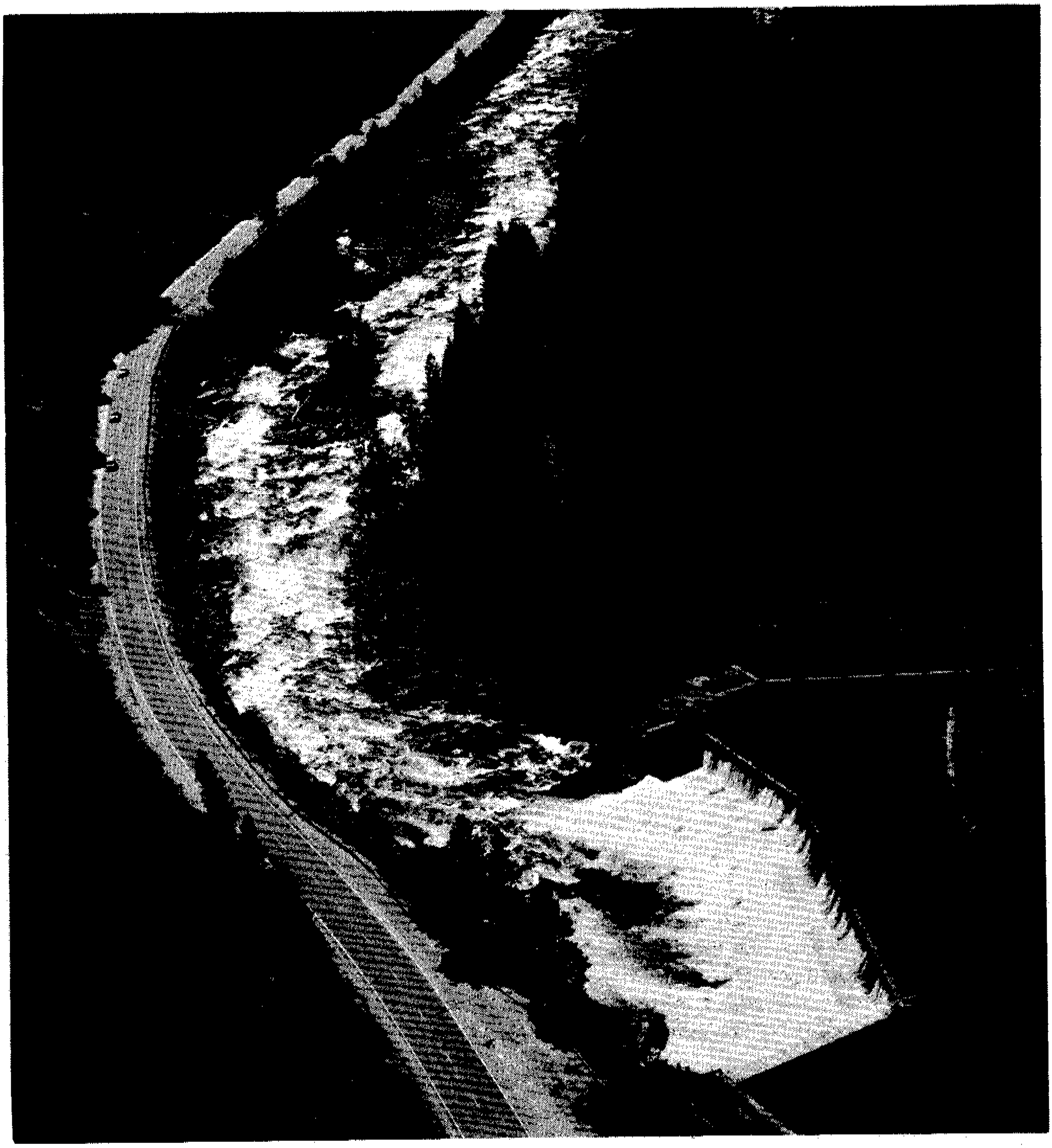

Figure 4. Tumwater Dam, Wenatchee River (low water stage), 1980. High water hydraulic block to sockeye salmon migrating upstream located downstream from area in photograph. Fish ladder located at left end of dam.

Table 18. Mean passage dates for sockeye salmon at Rock Island and Tumwater dams in relation to Wenatchee River flows.

Year	Mean passage date		Days en route	Run size	Wenatchee River mean flow (cfs)[b]	
	Rock Island	Tumwater[a]			July	Aug
1935	Jul 23-30	Aug 29	33	889	4,945	1,447
1936	Jul 23-30	Aug 4	8	29	2,257	790
1937	Jul 16-23	Sep 2	44	65	4,481	1,071
1953	Jul 23	Aug 5	13	13,069	6,888	1,967
1954	Jul 26	Aug 12	17	25,652	10,350	4,003
1955	Jul 26	Aug 10	15	51,820	7,695	2,420
1956	Jul 23	Aug 6	14	25,518	8,358	2,149
1957	Aug 1	Jul 28	9	28,231	2,577	1,069
1959	Aug 1	Aug 17	16	13,005	7,076	1,840
1964	Jul 26	Aug 5	20	26,811	7,866	2,492
1965	Jul 22	Aug 1	10	11,988	4,491	1,600
1966	Jul 21	Jul 30	9	38,925	4,027	1,258
1967	Jul 23	Aug 5	13	12,468	5,455	1,467
1972	Jul 25[c]	Aug 14	20	8,102[d]	9,455	3,719
1973	Jul 16	Jul 26	10	10,888	2,482	952

[a] French and Wahle (1959) noted it appears characteristic of the sockeye escapement at Tumwater to rise to a peak in daily counts soon after the first arrivals appeared at the dam. In the present study, differences between mean and peak passage dates at either dam varied only between 1 to 3 days, and days en route would not have been materially altered by using peak passage dates.

[b] USGS gauge at the town of Peshastin; 22-year average - 3,750 cfs July and 1,190 cfs August.

[c] Priest Rapids Dam mean passage date plus 5 days travel time.

[d] Count incomplete.

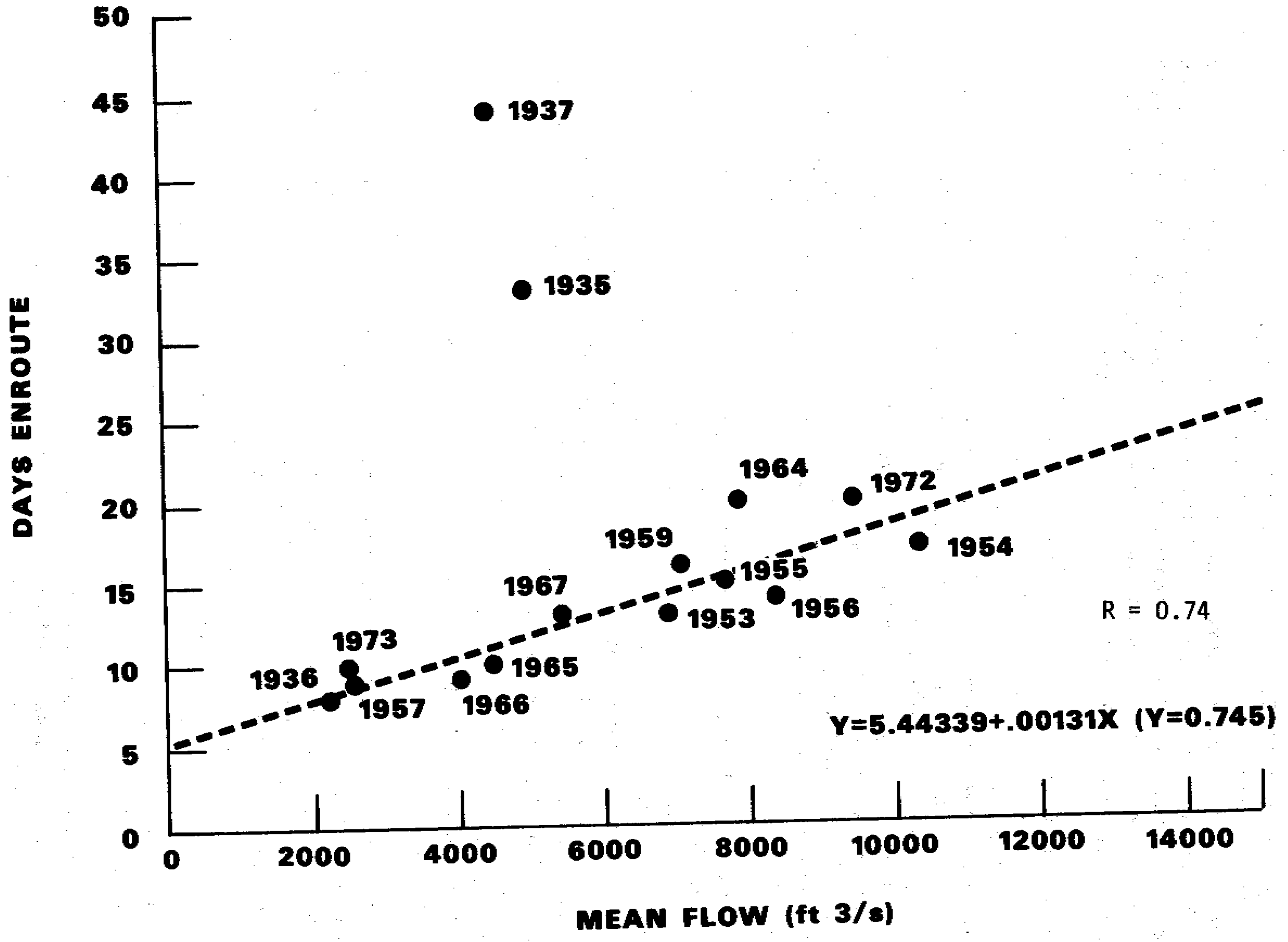

Figure 5. Flow in Wenatchee River in July and the number of days en route for sockeye salmon migrating between Rock Island and Tumwater dams, 1953-73. (Data for 1935-37 are plotted but were not used in the regression analysis.)

15 years of records, despite slightly below-average flows in July and August (Table 18). Earliest passage and shortest time en route between the two dams in 1957 also correlate with the first major release of Quinault sockeye (202,630 fingerlings in 1953). In all other years (1955, 1956, 1964), with one exception (1965), when the progeny of Quinault sockeye released in Lake Wenatchee could have been expected to return, abnormally high average July flows of 7000 cfs or better may have delayed passage, masking the influence of early run timing. In 1965, Wenatchee river flows were more moderate, although above average, and mean passage time of sockeye between Rock Island and Tumwater Dams required only one more day than in 1957 (Table 18).

Entiat River Quinault sockeye stock never exceeded 15% of the annual releases to Lake Wenatchee and amounted to only 7% of the 1953 total brood release correlated with earliest run timing in 1957 (Table 19). However, daily counts at Tumwater Dam in 1957 suggested that the run consisted of fish having both early and normal run timing (Fig. 6). Furthermore, a few Entiat River Quinault sockeye were released into Lake Wenatchee as early as 1948 and the spawn-taking in tributary streams, which was the source of most of the sockeye released back into the lake, was highly selective for early-run fish. Invariably the hatchery quota of 3 to 4 million eggs was filled by the earliest migrants, and fish arriving later passed the weirs and spawned naturally (Table 3).

The observation that the sockeye count at Tumwater Dam was not as markedly reduced in 1935 (889) as in 1936 (29) and 1937 (65) provides another dimension to the problem of possible genetic alteration (Table 18). Mean July and August flows of the Wenatchee River were moderately above average, but not in the range that inhibited passage, yet passage time between Rock Island and Tumwater Dams was 33 days later than average (Fig. 5). Mean date of run at Rock Island was estimated to have occurred on July 27, or about average, whereas the mean date of the run at Tumwater Dam was August 29, the latest date on record. Barring extreme distortion of the run by selective harvest in the lower Columbia River, the native sockeye salmon of the Wenatchee River seemingly ran much later because of the hydraulic block in Tumwater Canyon in spring and early summer.

One of the tenets of homing is that salmon stocks having the longest migration migrate earliest (Thompson 1951; Ricker 1972). The predominance of Arrow Lake sockeye in the Rock Island Dam count of the 1930's might have masked any any remnant stock having a slightly later run and a shorter travel distance. Affidavits collected by Craig and Suomela (1941) from eight old-time Wenatchee River area residents seem to confirm this speculation. They reported that before construction of the Leavenworth Mill Dam in 1904 or 1905, the fall run of salmon appeared in the upper Wenatchee River in August-September and was much larger than the spring run, and was composed of chinook, coho, and sockeye salmon and steelhead trout.

(2) Small size of Okanogan River sockeye.--The varying number of three-year sockeye in the Okanogan (Table 20) versus primarily four-year sockeye in the Wenatchee cannot be explained by selective harvest (Bilton 1970; Hirose 1973) because the results would be seen in runs to both rivers.

Table 19. Numbers and sources of sockeye and kokanee salmon stocked in Lake Wenatchee, 1940-1968.

	Strain and source of fish released				
	Sockeye salmon				Kokanee
Brood year	L Wenatchee[a]	Entiat R[b]	Methow R[c]	Carson NFH[d]	Lake Whatcom
1940	414,016				274,730
1941	12,459				449,975
1942	246,273				864,000
1943	1,453,973				1,212,000
1944	237,428				1,306,000
1945	601,113			40,533	1,700,000
1946	1,657,426				1,970,000
1947	2,338,793				910,277
1948	4,816,298	9,930			2,331,750
1949	1,005,959				1,520,599
1950	1,288,685				
1951	150,634	7,118			
1952	363,750	61,210	440,960		
1953	2,801,390	202,630	462,593		1,000,000
1954	3,248,825	291,145	42,450		500,000
1955	2,883,836	234,610			980,000
1956	4,086,688				1,303,000
1957	4,056,101	267,663			
1958	3,279,992	482,229	394,929		418,000
1959	2,475,762	358,871	295,932		504,600
1960	2,320,784	360,802	79,458		500,000
1961	2,053,936	164,374	5,335		137,000
1962	3,121,000				499,700
1963	3,364,000				506,150
1964	2,826,000				359,000
1965					379,000
1966					373,780
1968	22,000				
Totals	51,127,121	2,440,582	1,721,657		18,999,561

[a] Original spawners trapped at Rock Island Dam.
[b] Original spawners from Quinault Lake stock.
[c] Original spawners from Rock Island and Bonneville dams.
[d] Spawners trapped at Bonneville dam.

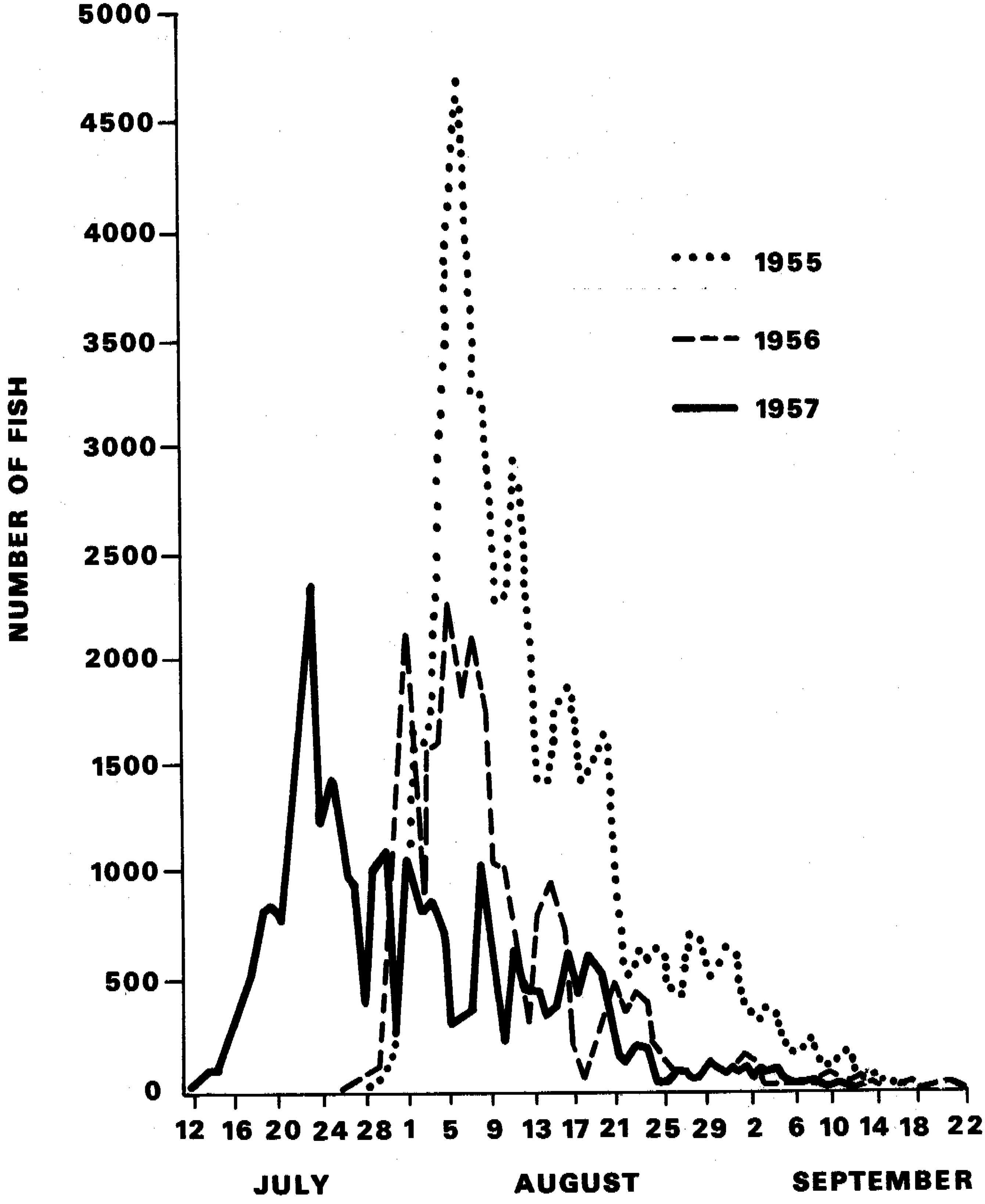

Figure 6. Timing of spawning runs of sockeye salmon passing Tumwater Dam, 1955-57 (French and Wahle 1959).

Table 20. Percentage of 3-year-old sockeye salmon in runs in the Okanogan River and in total runs in the Columbia River, 1945-1974 (data from Craddock 1957, Tufts and Craddock 1963, Allen and Meekin 1980).

Year	Okanogan River		Total run Columbia River percent
	Sample size	Three-year-olds percent	
1945			32.0
1946			14.0
1947			13.0
1948			6.0
1949			8.0
1950			22.0
1951			5.9
1952			3.0
1953		86.6	20.1
1954		20.9	8.1
1955	1,221	12.7	3.9
1956	929	24.9	8.8
1957	695	30.0	5.1
1958	208	84.1	5.8
1959	326	15.0	3.1
1960	140	33.0	3.6
1961	38	78.9	5.1
1962	73	58.8	9.7
1966	259	47.9	
1967	421	48.7	
1968	480	13.8	
1969	137	18.3	
1970	867	93.2	
1971	626	5.6	
1972	453	51.2	
1973	479	24.8	
1974	78	39.7	

Major and Craddock (1962) discounted genetic influence because of (1) the lack of correlation between one-year ocean sockeye of year N and those of year N+3; (2) the scarcity of three-year fish in the Wenatchee; and (3) the same source of progenitors. They speculated that the absence of one-year ocean sockeye in the Wenatchee River could mean that conditions simply did not lend themselves to the production of such fish.

Lake Wenatchee qualifies as classic sockeye-rearing habitat in being cold and well oxygenated but infertile. Lake Osoyoos, on the other hand, poses the environmental hazards of hypolimnic oxygen depletion, lethal epilimnic heating, and predation and competition by warmwater fish (discussed later). But for the sockeye that survive such perils, or in years when such perils are less acute or non-existent due to climatic variability, the lake offers relatively abundant food. Consequently Lake Osoyoos in some years produces some of the largest sockeye smolts reported in the literature, whereas those from Lake Wenatchee are average (Tables 21, 22).

Accelerated rearing of smolts to a large size before release characteristically increases the number of one-year ocean salmon and steelhead. Bilton (1978, 1980) demonstrated that atypically large coho salmon smolts released into a stream on Vancouver Island, British Columbia, returned relatively more as jacks than did corresponding typical (smaller) smolts. Stockner (1979) reported that since fertilization of Great Central Lake, also on Vancouver Island, the proportion of jacks in sockeye runs progressively increased over pre-enrichment levels.

(3) Inlet-outlet spawning.--As alluded to earlier, Arrow Lake sockeye undoubtedly represented a mixture of subpopulations that were uniquely adapted to specific environments. The most remarkable fjord-like lakes of North America are in British Columbia, and Upper and Lower Arrow are outstanding examples (Hutchinson 1957). The steep-sided morphology of such basins is not conducive to terminal tributaries suitable for sockeye spawning, because of their high gradient, lack of gravel, or inaccessibility due to cascades (Bryant and Parkhurst 1950). This was verified by Pinsent et al. (1974) for Okanogan Lake, another fjord-like basin (Hutchinson 1957). Accordingly, we might expect some sockeye subpopulations to have become dependent on the interconnecting river between lakes for spawning--an expectation that was met in the Okanogan River.

Gangmark and Fulton (1952) first called attention to sockeye spawning in a half mile of the outlet of Lake Wenatchee and the adjacent lower two miles of Nason Creek. Over the years this population dwindled to only an occasional spawner, but about 1600 sockeye were counted in the first survey in 1947, and the highest number--2100 spawners--in 1948 (Table 15). Scale samples revealed a freshwater life history no different from that of fish spawning in the Little Wenatchee and White Rivers and it was assumed that the fry moved upstream to the lake for rearing (Gangmark and Fulton 1952). Biologist Albert Gentry recorded the following contrary observations in the 1948 annual report of the Leavenworth Hatchery:

Table 21. Average lengths and weights of seaward-migrating yearling sockeye from selected lakes (modified from Foerster 1968).

Region and lake	Average size Length (cm)	 Weight (g)	Number of years' data	Reference[a]
Fraser system				
Cultus	8.5	6.3	11	1
Harrison	9.5	9.2	2	2
Lillooet	7.7	4.5	1	2
Shuswap	6.3	2.3	2	2
Chilko	7.6	4.3	5	2
Francois	10.5	12.0	1	2
Stuart	9.5	8.4	1	2
Vancouver Island				
Great Central[b]	6.4-7.8	2.5-4.2	8	3
Skeena system				
Lakelse	8.2	5.5	1	4
Babine	8.3	5.7	4	5
Central B.C. coast				
Owikeno	6.1	2.0		6
Port John	8.4	6.2		7
Alaska				
Karluk	11.1	-	6	8
Little Kitoi	6.2	2.0	1	9
Ruth[c]	11.2	13.6	1	9
Midarm	7.2	2.7	1	9
Kamchatka				
Dalnee	11.5	15.5		10
Azaback	10.0	9.3		10
Columbia system				
Osoyoos[d]	9.6-12.8	13.0	10	11
Wenatchee	7.5-11.2	6.0	11	11
Redfish	4.4-13.2		11	12
Lake Washington[d]	12.7	18.5	5	13

[a] References are numbered as follows: 1--Foerster 1944; 2--Clutter and Whitsel 1959; 3--LeBrasseur et al. 1978; 4--Foerster 1952; 5--Dombroski 1954; 6--Foskett 1958; 7--Foerster 1968; 8--Barnaby 1944; 9--Meehan 1966; 10--Kroquis 1961; 11--Table 22, present report; 12--Bjornn et al. 1968; 13--Eggers 1978.

[b] Includes prefertilization, fertilization, and post-fertilization.

[c] Treated with rotenone before sockeye fry were stocked.

[d] Culturally eutrophic lakes.

Table 22. Lengths of yearling sockeye smolts from Wenatchee and Osoyoos Lakes, 1957-1982.

Lake and year	No. fish sampled	Length (cm) Average	Length (cm) Range	Reference
Osoyoos				
1957	365	9.6	7.5-14.4	Allen and Meekin 1980[a]
1958	407	10.3	7.5-13.9	Allen and Meekin 1980[a]
1972	122	10.6	8.5-12.4	Allen and Meekin 1980
1973	360	11.2	9.0-13.4	Allen and Meekin 1980
1974	22	11.1	10.0-12.4	Allen and Meekin 1980
1977	174	11.5	9.0-14.8	Unpublished[b]
1977	269	11.7	10.0-15.0	Unpublished[b]
1978	45	10.9	8.6-12.5	Unpublished[b]
1981	1,385	12.8	8.4-15.1	Weitkamp and Neuner 1981
1982	3,418	11.0	7.6-14.7	Unpublished[b]
Wenatchee				
1955	744	8.6	5.0-11.0	French and Wahle 1959
1956	411	7.5	5.5-9.7	French and Wahle 1959
1958	312	9.6	7.5-13.8	Unpublished[a]
1961	--	9.3		Unpublished[a]
1967	562	11.2	7.0-14.9	Allen and Meekin 1980
1972	81	8.4	6.5-14.9	Allen and Meekin 1980
1973	132	8.1	6.5-11.4	Allen and Meekin 1980
1974	23	9.1	7.0-12.4	Allen and Meekin 1980
1959-63	--	--	7.5-9.5	Allen and Meekin 1973[a]

[a] Unpublished data from D.R. Craddock (personal communication).

[b] Data from Steve Hays and James McGee, Chalan and Douglas County PUDs: 1977--tow-net samples, Rocky Reach Impoundments; 1977--purse seine samples Rocky Reach Impoundment; 1978--purse seine samples, Wells Impoundment; 1982--inclined-plane trap, Okaogan River.

> During the fall of 1947 several hundred blue-black salmon adults spawned in the area just below Lake Wenatchee. The resulting fry emerged from the gravel nests and proceeded to move seaward. Samples of these fish were obtained 30 miles downstream from the spawning area.

In the annual report for 1949 he again reported:

> It was found that blueback salmon fry resulting from natural spawn deposits in the Wenatchee River (1948), immediately below Lake Wenatchee, were moving seaward rather than moving up into the lake to remain until yearlings before migrating to the sea. Several samples of these fry were collected at Tumwater Dam, some 15 miles below point of incubation.

We know now only that the hatchery biologist monitored the emigration of sockeye fry to Lake Wenatchee and the smolt outmigration from the lake with fyke traps for a number of years (Table 23), and that he marked sockeye redds in the lake outlet in fall 1947 and observed the redds until emergence of fry the following spring.

Inlet fry lost from Lake Wenatchee, not unlike the newly stocked fingerlings reported by Wahle et al. (1979) or outlet fry too weak to swim upstream into the lake (Clark and Smith 1972), might be suspected of having influenced the hatchery biologist's observations. Only four fry (34-45mm long) were observed among 36,679 juvenile sockeye migrants sampled 66 miles below Lake Osoyoos on the Okanogan River in 1981-82 (Weitkamp and Neuner 1981; 1982 data furnished by James McGee, Douglas County Public Utility District (PUD)). Only 34 fry (35 mm long) were observed out of 51,533 juvenile sockeye migrants sampled at Tumwater Dam on the Wenatchee River in 1955-56 (French and Wahle 1959). The fry at Tumwater Dam could have originated in the Lake Wenatchee outlet or Nason Creek; at least 773 and 39 sockeye spawned in these areas in the parental years of 1954 and 1955, respectively (Table 15). In limited sampling at the Dryden diversion in June 1980, 157 sockeye fry (35-40 mm long) were captured (Chelan County PUD 1980). These fry could be accounted for by spawning in Tumwater Canyon, which has persisted over the years (Table 15). The possibility of fry swimming upstream into Lake Wenatchee from this location seems remote, considering the steep gradient and the hydraulic block to adults described earlier.

No sockeye fry were sampled from the Dryden diversion in 1937, before introduction of Arrow Lake sockeye to the Wenatchee River system, but about 500 older juveniles were collected (WDF 1938). It was here that the Leavenworth Hatchery biologist reported sampling fry in 1948 that originated in the outlet of Lake Wenatchee.

The spawning of sockeye salmon downstream from nursery lakes and the movement of fry upstream into the lake are common (Burgner et al. 1969; Clarke and Smith 1972; Van Cleve and Bevan 1973; Ellis 1974) and genetically programmed (Raleigh 1967, 1971). After emergence, fry are displaced downstream

Table 23. Timing of sockeye salmon downstream migration, Wenatchee River system (data from Leavenworth Hatchery annual reports unless otherwise noted).

Year	Dates of run Start	 Peak	 End	Size range (mm)
Fry emigration to Lake Weantchee from Little Wenatchee and White rivers				
1947	Mar 24		Apr 22	26-30
1948			Apr 25	
1949	Apr 7			
1972[a]				26-30
Smolt outmigration from Lake Wenatchee (Tumwater Dam trapping)				
1946	Apr 14			
1947	Apr 23		May 15	
1948	Apr 12	5/9-15	May 25	64-127
1949[b]	Apr 7	4/27	May 10	89-152
1950[b]	Apr 12	5/1-5	May 19	
1951	Apr 13	4/27-5/3	May 21	
1952	Mar 26	4/29	May 21	
1953	Apr 15	4/28	May 15	
1954	Apr 8	4/28	May 14	
1955[c]	Apr	5/1-3	May 18	50-110
1956[c]	Apr	5/1-6	May 10	55-97

[a] Allen and Meekin 1980; May sampling only.
[b] Several thousand yearlings remained in lake in 1949 and 1950.
[c] French and Wahle 1959.

and accumulate in areas of low velocity. Eventually they move upstream in slack current along stream margins, and have been described as "creating something of a spectacle, if abundant" (Van Cleve and Bevan 1973). Despite extensive smolt trapping activities in the outlet of Lake Wenatchee in 1958-63, no upstream movement of fry was reported.

Anas and Gauley (1956), who examined 8145 juvenile sockeye passing Bonneville Dam on the Columbia River in 1949-53, found that only 1.6% consisted of young-of-the-year and that most were of smolt size and passed the dam during summer (Table 24). The appreciable (but declining) sockeye spawning from 1947 through to the mid-1960's was not associated with Lake Wenatchee but consisted of returning adults with scales exhibiting a typical one-year freshwater residency. This sequence of observations led to the question of where the initial rearing occurred. Fluvial rearing is a possibility. Considering the relatively large numbers of sockeye spawning downstream of Lake Wenatchee (Table 15), as well as those spawning in the Entiat and Methow Rivers (Table 12); however, the information points to rearing in Columbia River impoundments.

(4) Biochemical genetic variation.--A significant difference in the gene frequencies between salmon populations, as determined by electrophoretic methodology, is considered positive evidence that the populations are genetically different (Utter et al. 1980). May and Utter (1974) reported that variants occurred at a low frequency for two enzyme systems, MDH and PHI (PGI), indicating that Wenatchee sockeye (N = 58) and Okanogan sockeye (N = 59) were genetically distinct from one another. Although most fish of both populations had identical forms of both enzymes, four Okanogan fish contained a variant for PHI (PGI) that was not observed in any of the Wenatchee fish. Different variant forms for MDH were found in the two populations; one variant type was found in two Wenatchee fish and a different variant type was seen in six Okanogan fish.

Heterogeneity was further suggested between sockeye of these two rivers by Utter in 1981. The GPT-C allele was found at a frequency of 11% in an Okanogan sample (72) but was lacking in a Wenatchee sample (52). Allelic frequencies of Lake Quinault sockeye and Lake Whatcom kokanee are typical of those of other populations sampled southward through the Fraser River drainage into Washington. Wenatchee and Okanogan river samples differ from this major population grouping in the frequency of PGM variants and the presence of PGI variants. Thus available information suggests the hypothesis that gene pools other than those of Quinault sockeye and Whatcom kokanee predominate in Columbia sockeye, and that current populations have descended from native runs that are ancestrally distinct from populations found in the Fraser River drainage into coastal Washington (Utter et al. 1980; F.M. Utter, personal communication).

(5) Sockeye-kokanee relationships.--Electrophoretic studies of sockeye and kokanee simultaneously spawning in a tributary to Lake Washington have shown that spawning occurred without significant gene flow between the two forms (Utter et al. 1980). Seemingly this lack of gene flow does not exclude the possibility of hybridization, which has been reported elsewhere (Ricker

Table 24. Age and length of sockeye smolts at Bonneville Dam, 1949-1953 (data from Anas and Gauley 1956).

Length group (mm)	Age 1[a] (0's)	2 (yearlings)	3 (2 yr olds)	4 (3 yr olds)	5 (4 yr olds)
31-40	2				
41-50	15				
51-60	15				
61-70	20	22			
71-80	42	197			
81-90	22	567			
91-100	8	1561			
101-110	4	2557			
111-120	1	1407			
121-130		443			
131-140		298			
141-150		243			
151-160		137			
161-170		64	5		
171-180		45	15		
181-190		13	31		
191-200		31	20		
201-210		5	25		
211-220		5	38		
221-230			51		
231-240		2	98		
241-250		1	43		
251-260			58		
261-270			6		
271-280			15		
281-290			1	2	1
291-300			1	1	
301-310			1	5	
Total	129	7,598	409	8	1
Percent	1.6	93.3	5.0	0.1	0.01

[a] Most migrated summer; all other ages mostly spring (April-May).

1972). Generally, it is believed that the two forms are segregated at spawning as a result of differences in spawning habitat or time, but such differences have not been obvious in the Wenatchee and Okanogan Rivers.

Studies of kokanee from Lake Okanogan by Eric Parkinson, University of British Columbia, and from Lake Roosevelt by Kenneth Johnson and William Hershberger, University of Washington, do not indicate significant gene flow between Columbia River sockeye and kokanee (F. Utter, NMFS, personal communication). Their findings showed allelic frequencies typical of those in populations in the Fraser River drainage into coastal Washington. These southern fish have previously been described as distinct from Columbia River sockeye (population grouping 2 versus grouping 3 for Columbia River; Utter et al. 1980).

(6) Conclusions.--With evidence so inconclusive, what hypothesis is possible? Ricker (1972) provides many examples of how stock diversity and close adaptation can be maintained, even with appreciable interchange of genetic material between stocks. Although the long-term significance of the co-mingling of stocks reported in this paper is unknown, genetic viability has seemingly not been impaired. Sockeye runs to the Columbia River have persisted in the face of major genetic, environmental, and harvest perturbations and the resiliency of survival, particularly at threshold population levels, has been amazingly high.

Disease

Sockeye salmon production at the Leavenworth hatcheries was abandoned in the 1960's because of low benefits to costs (Wahle et al. 1979) and catastrophic losses from infectious hematopoietic necrosis (IHN; Rucker et al. 1953). Gould and Wedemeyer (1981) emphasized that fish diseases are not so much a problem of pathogens alone, but rather of a combination of host susceptibility, infectious agent pathogenicity, and environmental stress. For example, many fish diseases (including IHN) are serious problems only in hatcheries, due to abnormal densities, water temperatures, diets, or some combination of such factors.

The virulent nature of the epizootics recorded at the Leavenworth hatcheries casts doubt on the quality of the juvenile sockeye released. The ability of an animal to cope with disease, as already indicated, involves many variables. For instance, immune response may be favorably affected as temperature rises to a certain point, but higher water temperatures then adversely affect the animal's immune system, making it susceptible to an infectious agent of even low pathogenicity. This detail does not apply to IHN, in which pathogenicity is lost at temperatures above the optimum (62°F). Sometimes a normal, healthy animal may acquire an immunity to a disease agent even though the exposure is insufficient to elicit infection. Later, if conditions change, the animal can easily withstand an otherwise lethal exposure (Gould and Wedemeyer 1981).

The facts suggest that some immunization of sockeye that had either been exposed to or had survived IHN at the Leavenworth hatcheries did occur. In the extensive mark-and-recapture studies of Fulton and Pearson (1981) involving sockeye, chinook and coho salmon, and steelhead trout in the early 1940's, returns of sockeye were at least comparable to, and in many instances superior to, those of the other salmonids released. Although this period was several years before IHN was first reported, there is little question that it was present from the inception of these hatcheries (Rucker et al. 1953; Watson et al. 1954).

HABITAT LOSS BY DAM BLOCKAGE

The original surface acreage of sockeye nursery lakes in the Columbia Basin was at least 222,850 acres (Table 1). For practical purposes the remaining viable runs are to Lakes Wenatchee and Osoyoos, which together make up an area of 8174 acres, or about 4.0% of the original nursery lake habitat.

There is no written record of the contribution that Lakes Wenatchee and Osoyoos might have made to sockeye salmon runs of the Columbia River in the pre-settlement era. Contributions of adult sockeye per unit of nursery lake before 1900 can be compared with those in 1951-60 and 1971-79, however, assuming that commercial catches represented 50% to 75% of total run size before 1900. Lakes Wenatchee and Osoyoos have produced an above-average number of adult sockeye per unit of area 1951-1960 and 1971-1979 compared to Columbia River nursery lakes prior to 1900 (Table 25). This is also reflected in a 96% reduction in nursery lakes area accompanied by a 94.5%-91.7% reduction in production of adults between the 19th and 20th centuries.

HABITAT ALTERATION

Sockeye salmon habitat may also be degraded or destroyed by man-related disturbances involving laddered dams and reservoirs, irrigation diversion, watershed alteration, and agricultural, industrial, and residential pollution. Impacts from these sources are examined under the following topics: (1) dams; (2) flow regimes and irrigation withdrawal; (3) water quality; (4) water temperatures; and (5) erosion and sedimentation.

Dams

Hydroelectric dams constructed on the Columbia and Snake Rivers have created conditions that have proved devastating to salmon and steelhead trout. Dam-induced nitrogen supersaturation has been cited as the cause of mortalities ranging from 40% to 95% of all juvenile salmon and steelhead that emigrated from the Snake River Basin during high flow years in 1965-75 (Ebel et al. 1975; Ebel and Raymond 1976). Meekin and Allen (1974) reported similar mortality of adult sockeye and chinook salmon on the mid-Columbia

Table 25. Estimated average number of adult sockeye salmon produced per acre of available nursery lake in 1889-1899, 1951-1960, and 1971-1979, Columbia River Basin (data from Fulton 1970 and Tables 1 and 4 of this report).

Years	Average size of run	Surface acreage of nursery lakes	Average number of adult sockeye salmon produced per acre
1889-1899	1,306,000[a] 871,000[b]	222,850	5.9[a] 3.9[b]
1951-1960	231,900	8,174[c]	28.4
1971-1979	72,400	8,174[c]	8.9

[a] If harvest represented 50% of run size.
[b] If harvest represented 75% of run size.
[c] Lakes Wenatchee and Osoyoos.

River in the late 1960's. However, the problem of gas-bubble disease in high-flow years was alleviated by the expansion of generating capacity at existing dams, completion of upstream storage reservoirs (allowing greater regulation of flows), and installation of spillway deflectors at some Snake River dams.

In low-flow years, when little or no water is spilled, all downstream migrants must pass through turbines, where many are killed and others are injured and left vulnerable to predation. This turbine-and-predator-related mortality has been reported to range from 15% to 30% per dam, or a cumulative loss approaching nearly total destruction of out-migrants passing a series of dams in low-water years (Schoeneman et al. 1961; Oligher et al. 1966; Raymond 1976, 1978).

Within this context, the decline of sockeye salmon from the high abundance soon after World War II requires little further explanation. However, impacts of environment on species are not independent or equal in effect. For example, the nearly equal counts of adult sockeye obtained at all Columbia River dams indicate that this species, in contrast to chinook and steelhead, suffers little mortality between dams (Fredd 1966).

Flow Regime and Irrigation Withdrawal in Wenatchee and Okanagon Rivers

(1) Wenatchee River.--The Wenatchee River originates in Lake Wenatchee and is a high-gradient, snow-fed stream whose tributaries rise at elevations of 5500-7500 feet in the Cascade Mountains. Base flow is 3100 cfs.

Lake Wenatchee is fed primarily by the Little Wenatchee River (15% average contribution to Wenatchee River flow) and the White River (25%). Principal tributaries below Lake Wenatchee are Nason Creek (18%), Chiwawa River (15%), and Icicle Creek (20%). Icicle Creek enters at River Mile 26 at Leavenworth. Upstream of Leavenworth (70% of the basin) the topography is mountainous and used largely for timber harvest and recreation; downstream, the river enters a broader, U-shaped valley that is fully used for irrigated fruit-growing--a status achieved by 1923.

The estimated annual depletion in river discharge from irrigation corresponds to a reduction in stream flow of 350 cfs for five months (annual application of 4 acre-feet/acre x 26,000 acres x 0.5042 ÷ 150 days = 350 cfs). Assuming, however, a consumptive use of only 2.0 acre-feet/acre (Sylvester 1959), this diversion would result in a return flow, prorated over 12 months, of 72 cfs, or a net reduction in stream flow during the irrigation season of 278 cfs. This amounts to 17%, 32%, and 23% of the mean annual potential flow (1930-1979) for August, September, and October, as measured at the USGS gauging station at River Mile 21.5, below which most irrigation diversion occurs.

(2) Okanogan River.--This river originates in Canada's Okanogan Lake, flows through Osoyoos Lake, which extends across the international boundary,

and continues southward to the Columbia River--a distance of 124 miles (Fig. 1). In the 82 miles within the United States, the river falls only 165 feet. The basin is about six-fold larger than the Wenatchee River Basin (8340 vs. 1310 square miles). Where the Okanogan's major tributary, the Similkameen River, enters (just below Osoyoos Lake), the two streams have almost the same drainage area (3580 and 3210 square miles, respectively), but the average annual flow of the Similkameen is almost four times that of the Okanogan (2132 cfs and 640 cfs, respectively). This divergence in flow between the two basins occurs because mountain ranges shield the upper Okanogan from coastal precipitation and because the Similkameen has much broader headwaters at generally high elevations (Osborn and Sood 1973). By way of comparison, average values of runoff per square mile of drainage area are (in cfs per square mile): Similkameen River at Nighthawk, 0.65; Okanogan River at Oroville, 0.20; Wenatchee River at Peshastin, 2.9.

Aside from the lower gradient and appreciably lower runoff per square mile of drainage area, the Okanogan River also differs from the Wenatchee River in being regulated by natural lakes that have been raised by low-head dams (Wood, 2298 acres; Kalamalka, 6400 acres; Okanogan, 85,990 acres; Skaha, 4967 acres; Vaseux, 680 acres; and Osoyoos, 5729 acres).

Irrigation use in British Columbia corresponds to 612 cfs flow of the Okanogan River (annual application of 4 acre-feet acre x 45,580 acres irrigated x 0.5042 ÷ 150-day irrigation season = 612 cfs). Only 1.5 acre-feet/acre returns to streams and ground aquifers (Simons 1953). Return flow, prorated over 12 months, amounts to 101 cfs for Canadian abstraction or a net daily reduction in stream flow during the five-month irrigation season of 511 cfs. This amounted to 49%, 50%, and 44% of the mean annual potential flow for August, September, and October in 1943-50 at Oroville, Washington, in the absense of upstream diversion (USGS 1955).

Irrigation withdrawal in the State of Washington (annual application of 4 acre-feet/acre x 22,500 acres irrigated by stream flow x 0.5042 ÷ 150-day irrigation season), corrected for nonconsumptive use and delayed return flow, amounts to 252 cfs of river flow, or a cumulative total loss of 763 cfs. This amounts to 40%, 40%, and 46% of the mean annual potential flow for August, September, and October, 1929-50, at Tonasket, Washington (USGS 1955). Tonasket (River Mile 57) is below the Okanogan River's junction with the Similkameen and below major irrigation diversions.

Although these analyses are not highly refined, they illustrate that flows during the late summer in the Okanogan River are strongly influenced by irrigation diversion. Even with the tremendous storage in its lakes, low flow of the Okanogan River at Oroville, Washington, drops to only 129 cfs once in about 20 years as a result of withdrawals for irrigation and lack of precipitation (Osborn and Sood 1973).

Water Quality

Water in the Wenatchee River system, despite a 40% increase in mineral constituents since 1910 (Sylvester 1959), is generally soft, high in dissolved oxygen and low in total dissolved solids (Table 26). Water in the Okanogan River is more highly mineralized, primarily because agriculture is more extensive, the land more arid, and the concentration of natural solute greater (Walters 1974). Here, too, average levels of dissolved oxygen have remained high ($\geq$ 10 mg/l; Table 26) and those of biogenous nitrogen and phosphate have generally remained low.

Gould and Wedemeyer (1981) observed that existing information on current toxic contaminant levels in Columbia River waters and on the biological impacts the contaminants are having was surprisingly incomplete. It is known that the salmon populations now carry small body burdens of PCB's and chlorinated hydrocarbon pesticides, presumably because of widespread irrigated agriculture. However, with due deference to the possibilities of chronic sublethal water pollution, Gould and Wedemeyer (1981) concluded that safe limits for water-quality alterations are not now being exceeded in the Columbia River and (except for gas supersaturation) probably were not exceeded in the past.

Water Temperatures

Gould and Wedemeyer (1981) also examined water temperatures as a factor in predisposing salmonids to disease, which in turn might have contributed to recent population declines. Their findings reinforce the earlier ones of Bell et al. (1976) that main-stream Columbia River temperatures are not greatly different from temperatures recorded in earlier years, when runs were substantial and before extensive hydroelectric development of the river. Gould and Wedemeyer (1981) concluded that it is highly unlikely that temperature and concomitant fish diseases were a primary cause of recent declines of runs of anadromous salmonids in the Columbia River. However, they pointed out that the high prespawning mortality of sockeye salmon in some years on the Okanogan River is a possible exception.

Thermal impediments to the return of adult sockeye to the Okanogan River have been well documented (Major and Mighell 1965; Allen and Meekin 1980). Short-term maximum for survival of juvenile and adult sockeye salmon has been reported as 22°C (72°F) by the U.S. Environmental Protection Agency (1976), and the upper lethal temperature has been reported as 24.4°C (75.9°F) by Scott and Crossman (1973). Optimum temperature range is 10°C-15°C or 50°F-60°F (Bouck et al. 1975; Bouck 1977), and preferred temperatures are 12°C-14°C (53.6°F-57.2°F) according to Scott and Crossman (1973). Reduction of summertime flows by about one half by irrigation diversion, surface discharge of storage lakes (Ward and Stanford 1981), and long distances from cold headwater sources tend to elevate temperatures of the lower Okanogan River, well above lethal limits for salmonids (28°C or 80°F)--particularly in drought years. Water temperatures in other tributaries to the Columbia River in north-central Washington do not attain such elevated maxima (Table

Table 26. Average (upper number) and range (in parentheses) for certain water quality characteristics of Wenatchee, Okanogan, Similkameen, Entiat, and Methow rivers at different locations (river miles in parentheses following name; data from Pacific Northwest River Basins Commission 1971).

Dissolved oxygen (mg/l)	Temp. (C)	pH	Total dissolved solids (mg/l)	Ortho PO_4 (mg/l)	NO_3-N (mg/l)
Wenatchee (35.5)					
10.9	8.1	7.1	28	0.01	0.04
(4.2-13.6)	(0.1-22.2)	(5.8-7.4)	(20-37)	(0.00-0.03)	(0.00-0.20)
Wenatchee (1.1)					
11.9	9.5	7.4	42	0.02	0.09
(9.1-16.4)	(0.0-25.3)	(6.8-8.8)	(23-66)	(0.00-0.20)	(0.02-0.18)
Okanogan (81.9)					
11.0	11.5	8.0	168	0.02	0.05
(8.4-13.2)	(1.2-26.0)	(7.4-8.5)	(149-178)	(0.00-0.04)	(0.02-0.11)
Similkameen (5.6)					
11.0	11.7	7.7	100	0.02	0.03
(8.2-14.5)	(0.8-23.0)	(7.1-8.1)	(52-132)	(0.01-0.09)	(0.00-0.09)
Okanogan (1.4)					
10.9	11.5	7.8	137	0.05	0.05
(5.8-15.4)	(0.0-28.1)	(7.1-8.4)	(59-205)	(0.00-0.16)	(0.00-0.18)
Entiat (6.2)					
11.8	8.4	7.5	55	0.02	0.05
(8.9-14.2)	(0.0-19.6)	(6.8-8.0)	(30-79)	(0.00-0.07)	(0.00-0.16)
Methow (0.5)					
11.5	9.1	7.8	96	0.02	0.13
(9.3-14.2)	(0.0-20.5)	(6.9-8.4)	(45-130)	(0.00-0.20)	(0.00-0.32)

26). Maxima are of shorter duration as well, and usually of diel occurrence (Sylvester 1959) rather than lasting up to 2 to 3 weeks as in the Okanogan (Allen and Meekin 1980).

Erosion and Sedimentation

Poor land-use practices associated with farming, grazing, logging, mining, or construction are recognized as the principal causes of accelerated erosion. Occasional contributors to accelerated erosion are natural events such as the large fires that swept the Entiat River drainage in 1970 and resulted in extensive sedimentation of stream courses (Helvey 1980). Aside from modification of channel habitat by bed loading, it is generally agreed that the production of salmonids is lowered under high sedimentation primarily through the effects on embryos and fry before and during emergence from the gravel, and of lowered aquatic food production due to changes in the substrate composition (Cedarholm et al. 1980).

(1) Wenatchee River.--Accelerated land erosion has not been a problem for sockeye salmon on spawning grounds of the Wenatchee River based on the history of land use. In 1931 irrigators petitioned the U.S. Forest Service (USFS) for protection from logging and grazing in the Little Wenatchee River watershed (63,350 acres). Findings were equally applicable to the paralleling White River watershed (96,000 acres) where sockeye salmon also spawn.

Putnam (1936) demonstrated that the marked diminution in summer flow of the Wenatchee River beginning in 1922 occurred not as a result of impaired ground storage or runoff resulting from fire, overgrazing, or logging, but from decreases in precipitation. This was part of a reoccurring pattern of drought over much of the West in the "dust bowl" years of the 1920's and 1930's. Putnam (1936) wrote as follows:

> When the Forest Service took charge of the Little Wenatchee watershed in 1908, there were about 3200 acres of burns. These burns contain the only denuded areas and essentially all materially accelerated erosion. . . . Since 1908 the area burned over in the Little Wenatchee River watershed has been held at 740 acres. This is about 1% of the total area of the watershed [0.04% annually], and could not be expected even at worst to have perceptible effects on streamflow.
>
> Accelerated erosion is highly localized because the coarse soils of the watershed absorb water very rapidly even when barren, and large volumes of water are ordinarily deposited on the soil slowly by melting snow instead of rapidly by torrential rains. Because the soils are very shallow and incapable of supporting true water tables except in the valley fills or perhaps in pockets on side slopes in localized areas, soil storage capacity is very limited. Whenever (as during spring thaws) large volumes of water are deposited on the soil the storage capacity of the watershed is overburdened, and the rivers rise very rapidly, but the runoff takes place not over the surface but along

> the steeply sloping bedrock beneath the soil. This subsurface runoff is facilitated by the soil's extreme permeability.
>
> Domestic stock [3400 sheep for two months] under regulation have overgrazed 205 [of 6890] acres or less than 1% of the total area of the watershed. These areas are similar to the recently burned areas in being too small [and widely dispersed at high elevations] to affect streamflow perceptibly under any conditions.
>
> Upon the average range areas erosion is not accelerated. Even in burns at low elevation (below about 3500 feet) no damage is done by grazing because weeds, brush, and reproduction come in rapidly after fire and resume control of the area. The conditions most conducive to accelerated erosion are found along sheep driveways [these unique effects of sheep grazing were only recently confirmed in Idaho by Platts (1981)] in old burns at high elevation (above about 3500 feet) where the fires were apparently unusually hot and destructive and where growing conditions are unfavorable. In such places grazing tends to delay recovery, but the original and by far the most damage was caused by fire.

At the time of Putnam's report, logging had been limited to the floodplain of the Little Wenatchee River in the early 1900's (USFS 1972). Logging resumed in 1941 (57 acres) but did not increase substantially until 1952. Between 1952 and 1979, 4113 acres were logged. Area impacted amounted to 6.5% of the drainage or 0.002% annually. On the White River drainage 1334 acres were logged in 1952-79, affecting 1.4% of the drainage or 0.0005% annually (raw data furnished by Gran Rhodus, USFS).

Due to the steep and dissected topography of the drainages, logging is concentrated along stream courses or on adjacent sideslopes, involving no more than 20% of the total watershed areas. Although such a factor would increase the area affected annually by logging fivefold, the percentage would still remain below 1% and would remain below that percentage even if the annual area of logging impact were increased another fivefold to allow for a five-year period of vegetation recovery.

Investigations throughout the Northwest have shown that logging roads are a principal contributor of sediments to streams. When the percentage of road area in the Clearwater River, Washington, basin exceeded 2%, or two miles of road per square mile of basin, sediment began to accumulate in the spawning gravels (Cedarholm et al. 1980). The Clearwater drainage has a geology characterized by shales, siltstone, sandstone, and graywacke subject to crumbling under the heavy weights typically hauled on logging roads. The basins of the Little Wenatchee and White rivers have only 0.6 mile of road per square mile of basin; 19 of the total 150 miles of road are paved, and the geology is characterized by hard rocks that are not easily pulverized by logging trucks. Again, the comparison is distorted because of the concentration of roads in valley bottoms.

Rainy Creek is a major tributary drainage (10,733 acres) of the Little Wenatchee River. Between 1953 and 1976, 13.4% of the watershed (vs. 6.5% for the entire drainage) was logged, or 0.006% annually (vs. 0.002% for the entire drainage). There are 10.3 miles of logging roads or an average of 0.61 mile of road per square mile of basin, of which 80% closely parallels the creek. No effects on the benthic macroinvertebrates in the Rainy Creek watershed could be detected from logging and logging roads in 1975-76 (Wood 1977). More than 25% of the 1.3-square-mile study area had recently been clearcut and contained slightly more than 2.0 miles of logging road per square mile of basin.

Lack of impact was attributed to the small area of clearcuts (average, 26 acres; range, 1-125), the yarding of felled timber away from the water course, the use of riparian buffer strips, and the high flushing rate of the streams. Not mentioned as a contributing factor was that the soils in such U-shaped valleys and sideslopes are coarse and resistant to erosion (Table 27, landforms 30, 25, 34), as Putnam (1936) noted.

Extent of fires in the Little Wenatchee and White River drainages since Putnam's report in 1936 has been less than the 0.04% he documented (Gran Rhodus, USFS, personal communication). Grazing by sheep has been reduced by about one half (3400 for two months to 1000-1500 for one and one-half months), and methods of trailing sheep to pasture have been improved, with some even trucked to clearcuts to control the rank vegetation established after timber harvest (Dennis McMillan, USFS, personal communication).

(2) Okanogan River.--Areas estimated as being in need of erosion control in the lower Okanogan River Valley included 5% of the forest land (50 square miles), 60% of the rangeland (646 square miles), and 80% of the dry cropland (107 square miles). Irrigated cropland makes up only 2% of the basin total but tends to be near the river and discharge silt-laden return flow into it. In addition, the river banks have been overgrazed and trampled by livestock in many areas, resulting in destabilization and sloughing (Pacific Northwest River Basins Commission 1977). Similar conditions prevail upstream in Canada (Stockner and Northcote 1974).

Inundation of the narrow U-shaped valley bottom in Canada during heavy runoff is usually prolonged compared to that in an unregulated floodplain. In 1957 all except 1.2 miles of the sockeye spawning habitat below Vaseaux Dam was channelized to hasten natural drainage (Barnaby 1950; Gangmark and Fulton 1952).

The Canada Fisheries Service (1973) reported that siltation has not been a problem to sockeye salmon egg survival in the Okanogan River below Vaseaux Dam. Allen and Meekin (1980) reported that intragravel survival of sockeye eggs and fry was significantly higher in the Wenatchee (91%) than in the Okanogan (73%). However, much of the sampling in the Okanogan was in the channelized section. Here the substrate was reported as "comprised mostly of loose sandy materials, certainly not ideal for sockeye spawning."

Table 27. Erosion and hydrologic interpretations of principal landforms along streams from Lake Wenatchee to headwater areas (data from McColly 1976).

Dominant landforms[a]	Erosion hazard	Stability		Sedimentation yield potential
		Natural state	Expected from road building	
Confluence with lake (3)	Low	Very high	Unchanged	High
Upstream canyon bottoms (13)	Very high; sensitive to channel cutting	Very high	Unchanged	High
Above foregoing canyon bottoms, L. Wenatchee R (11)	High; sensitive to channel cutting	Very high	Unchanged	High
Above (13) canyon bottom, White River (12)[b]	Very high; sensitive to channel cutting	Very high	Unchanged	High
Nearly level to steep glaciated sideslopes, White River (38)	Moderate to high	Moderate	Increased	Moderate
Sideslopes, U-shaped valleys, L. Wenatchee R (30)	Moderate to high	Moderate	Increased	Moderate
U-shaped valleys & valley bottoms (25) (both drainages)	Low	Very high	--	Moderate
Highly dissected sideslopes (34)	High	Moderate	Increased	Moderate

[a] There is considerable intermingling of types; number in parentheses represents dominant mapping type.

[b] Principal areas of sockeye salmon spawning.

Nasmith (1962 as reported in Booth 1969) described the alluvium of the Okanogan floodplain as primarily consisting of glacial drift ranging from fine sand to coarse gravel. Logically, the sand in the channelized section was originally largely armored with gravel due to hydrologic sorting (Simons 1979). Evidence for this is seen in the natural channel remaining below Vaseaux Dam. It is not likely then that the less-than-ideal sockeye spawning substrate of the channelized section rests with events of accelerated erosion and sedimentation from outside the channel but is instead an inherent problem of bed-load movement and alteration.

Turbidity is low in the Okanogan River, as well as in the Wenatchee, except during periods of high runoff. High runoff generally corresponds to spring-summer snowmelt and not fall-winter spawning and incubation of sockeye eggs (Pacific Northwest River Basins Commission 1971). A partial exception to this was the flood of June 1948. The Okanogan River more than doubled its flow and stayed at almost that same volume into October, whereas its principal tributary, the Similkameen, typical of other unregulated rivers in north-central Washington, experienced similar flooding but quickly subsided (Osborn and Sood 1973). Observations of H. A. Gangmark (1949) reveal the difficulties encountered in fall 1948 in counting spawning sockeye salmon due to the high and silty water: "Salmon were observed in practically all sections of the river, but it was impossible to count them with any degree of accuracy." Gangmark also noted sockeye spawning in gravel that would normally be on dry ground. The total run of sockeye in the Columbia River four years later (1952) was the second highest on record (318,900); runs three (1951) and five (1953) years later were also well above normal (203,700 and 260,000, respectively; Table 4).

FUNCTIONAL LIMITATIONS OF HABITAT

Ecological integrity of an aquatic ecosystem has been defined as the maintenance of structural and functional characteristics of that locale (Cairns 1977). Structure based on counts of community components reflects how the basic building blocks of aquatic communities (i.e. species) are arrayed. An abnormal change in one or more structural characteristics is generally accepted as reflecting change(s) in habitat. Nevertheless, any ecosystem has some capability to adjust to impacts of stress and still retain its structure and function, barring extremes of ecological incompleteness (e.g. blockage of anadromous fish by dams).

Functional attributes of an aquatic community center on nutrient or energy transfer. Food gathering, and the morphological-behavioral adaptations that form its basis, is therefore considered the paramount animal function in aquatic ecosystems, including the general strategy of animals to restrict energy-costing locomotion in feeding (Cummins 1972).

Much of the fluctuation common in sockeye salmon production has been ascribed to variations in survival of the young in fresh water during either the egg or fry stage or during the period of lake residence (Foerster 1968). Variations in survival relate to changes in energy transfer or function, either in a short-term cyclic norm or in a long-term disconformity inevitably involving changes in structure and habitat as well.

Spawning Habitat

Allen and Meekin (1980) estimated optimum spawners at 36,080 and 6720 sockeye for the White and Little Wenatchee Rivers, respectively, based on available spawning gravel (89,800 m^2). There is additional spawning gravel (51,800 m^2, Gangmark and Fulton 1952; 11,700 m^2, Allen and Meekin 1980) in lower Nason Creek and in the outlet of Lake Wenatchee, but there has been no appreciable sockeye spawning in these areas since the mid-1960's (Table 15).

The Canada Fisheries Service and WDF (1973) estimated that spawning gravel (108,860 m^2) in the natural channel of the Okanogan River immediately below Vaseaux Dam (2 km) will accommodate a minimum of 35,000 sockeye spawners at a flow of 325 cfs. Under a more optimal flow of 470 cfs, available spawning gravel would be increased (155,515 m^2) and accommodate 50,000 sockeye spawners. Some sockeye also spawn in the channelized reach of the Okanogan River (15 km), as well as in Lake Osoyoos, but the amount of spawning gravel in these areas has not been defined.

Relating spawning escapement to quantity and quality of gravel is difficult. Spawning counts are frequently little more than a crude index of escapement from year to year. Water clarity, experience of the observer, weather, and timing of counts with respect to peak spawning are but some of the factors influencing reliability and consistency of escapement estimates (Gangmark and Fulton 1952; Allen and Meekin 1980; Neilson and Geen 1981). Problems in quantifying suitable spawning substrate are also large (Burner 1951; Canada Fisheries Service and WDF 1973; Allen and Meekin 1980). Less than ideal substrate may be used for spawning at times with considerable success (Allen and Meekin 1980). Space used by a spawning female sockeye may be large when escapements are low and small when they are high (Burgner et al. 1969). Within such uncertainty it is reasonable that spawning gravel capacity has not been a limiting factor of recent sockeye population size at the abundance levels displayed by runs.

Rearing Habitat

It is generally recognized that optimum fry recruitment will vary among lakes depending on morphometric, edaphic (pertaining to nutrient availability), and climatic interrelationships.

(1) Trophic status and primary production.--Ryder (1965), by selecting lakes so as to exclude most of the variability due to climate, derived a highly significant multiple regression for fish yield on mean depth (as an index of morphometry) and total dissolved solids (TDS) (as an index of edaphic conditions: (log "morphoedaphic index" (MEI)--TDS (ppm) divided by mean depth (feet)--vs. annual sport and commercial harvest in pounds/acre). Pinsent et al. (1974) concluded that the MEI, although useful as a general indicator

of trophic conditions, was too imprecise to reflect the cultural eutrophication (accelerated increase of nitrogen, phosphorus, and other nutrients resulting from man's activities) of Okanogan Valley lakes without modification. Sockeye lakes generally lack sufficient fishing effort (Hartman and Burgner 1972) to qualify for MEI yield treatment as well--limitations recognized in the original application of the index (Ryder 1965). Nevertheless it is important to appreciate that while the meanings of TDS and mean depth in the index are imprecise, they do depict critical interrelationships in an ecosystem (Ryder et al. 1974).

Ratios of TDS and mean depth show sockeye lakes as typically oligotrophic (characterized by abundant oxygen in deep water as a consequence of small nutrient supply and low productivity of organic material), with values of around 1.0 or less (Table 28). Ryder (1965) concluded that an MEI of about 2.0 separated oligotrophic from eutrophic lakes (lakes characterized by paucity or absence of oxygen in bottom waters as a consequence of high nutrient content and high primary production). Lake Wenatchee has an MEI of 0.17, whereas Osoyoos has a value of 3.32 (Table 28).

Phosphorus supply is considered to be the main determinant of primary production in most temperate-zone lakes (Williams et al. 1977; Lambou et al. 1976; Schindler 1974; Dillon and Rigler 1974; Bachmann and Jones 1974; Edmondson 1970). Although all oligotrophic lakes have low ambient total phosphorus concentrations, incorporation of phosphorus into phytoplankton varies from lake to lake (Hern et al. 1981). The efficiency of utilization of phosphorus is largely dependent upon the availability of light, a sufficient supply of nitrogen and other macro- and micronutrients, and biological availability of the various phosphorus species (Hern et al. 1981).

Using the method of Dillon and Rigler (1975), it is possible to estimate the phosphorus exported per unit of watershed (13.3 $mg/m^{-2}/yr^{-1}$), which, combined with the drainage area (709,120,000 m^2), provides an estimate of the terrestrial phosphorus exported to Lake Wenatchee (9427 kg/yr^{-1}). Phosphorus in precipitation falling on the lake (58 $mg/m^{-2}/yr^{-1}$; Tiedemann et al. 1980) and lake size (9,780,000 m^2) allows calculation of the aerial phosphorus load to the lake (567 kg/yr). Input of phosphorus from humans (one half of the 520,300 visitor-days estimated for the Lake Wenatchee Ranger District [USFS 1979] converted to man-years [713] x 0.80 kg phosphorus per man-year [Dillon and Rigler 1975]) and from sockeye carcasses (average run of 15,000 fish x 3.7 pounds each with a 0.003364% wet weight phosphorus content [Foerster 1968]) amounts to 570 kg and 84 kg, respectively. Total loading can then be combined with the lake's morphometry and water budget (flushing rate, as determined by 19 years of gauging records [USGS 1955], and phosphorus retention coefficient, dependent on both morphometry and water budget) to predict a total phosphorus concentration that is related to the average summer chlorophyll a concentration. Chlorophyll a is a simple estimator of phytoplankton standing crop. Summer chlorophyll a concentration, spring phosphorus concentration, and summer Secchi-disc transparency, except in dystrophic (brown) water, are significant correlates of lake trophic status (Dillon and Rigler 1974, 1975; Carlson 1977).

Table 28. Morphoedaphic index (MEI) and sockeye salmon production characteristics of selected lakes.

Location and lake	Morpho-edaphic index	Adult escapement (number/acre), average	Smolt production (pounds/acre)		Egg to smolt survival (%)		Smolt to adult survival (%)		Adult production (number/acre)	
			Range	Average	Range	Average	Range	Average	Historical av/max	Average
Columbia River										
Osoyoos	3.32	9	2.6-24.7	12.4	2.4-38.0	12.0	0.6-6.6	3.0	2	9
Wenatchee	0.17	8	2.0-11.6	6.3	1.7-12.3	5.5	0.7-5.6	2.9	28	9
Red Fish[a]	0.17	0.5	0.03-0.51	0.2	0.6-143.8		0.1-1.8			
Vancouver Island										
Great Central[b]	0.04	4		1.8		3.0	0.7-2.7	1.7		5
		5	2.1-8.1	5.4	9.8-11.1	10.3	5.1-8.7	7.4		32
			3.2-9.7	6.5	3.3-6.7	5.2				
Fraser River										
Chilko[c]	0.15	4	0.4-5.0	1.9	2.6-6.7	4.2				18
Cultus[c]	1.06	22	1.5-26.7	9.8	0.9-7.8	2.0		9.9		107
Skeena River										
Lakelse[c]	1.20	6	1.1-5.5	2.0	0.4-8.4	1.5				10
Babine[c]	0.25	4	0.3-4.8	1.8	0.5-6.1	3.0				8
King Island										
Port John[c]	0.48	4	0.6-2.8	1.3	0.5-8.0	3.0				
Alaska										
Midarm[d]	2.86			1.3		3.6				
Ruth[d]	3.55		8.2-32.8	16.5	7.3-46.9	16.1				
Little Kotoi[d]	1.71	14	0.4-8.2	2.3	2.0-8.5	4.0				
Chignik[e]	0.66	55							200	100
Black[e]	7.04	18							64	32
Iliamna[e]	0.18	6								10
Karluk[c]	0.27	28	21.3-79.3	43.6	0.5-0.9	<1.0		21.4	293	49

Table 28 (continued).

Location and lake	Morpho-edaphic index	Adult escapement (number/acre), average	Smolt production (pounds/acre)		Egg to smolt survival (%)		Smolt to adult survival (%)		Adult production (number/acre)	
			Range	Average	Range	Average	Range	Average	Historical av/max	Average
Aleknagik[f]	0.19	9							39	19
Nerka[f]	0.18	10								
Beverly[f]	0.13	9								
Kulik[f]	0.10	8								
Asia										
Danee[c]	0.95	176	16.9-48.1	20.5	<0.1-1.1	0.3		31.4		
Kurile[c]		203		49.9		2.9				

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[a] Bjornn et al. 1968; MEI estimated as similar to Wenatchee.

[b] LeBrasseur et al. 1978.

[c] Foerster 1968.

[d] Meehan 1966.

[e] Burgner et al. 1969.

[f] Burgner 1964.

According to these calculations the annual phosphorus budget (10,600 kg) is similar to that used in primary production (9800 kg), and the contribution of phosphorus from sockeye carcasses and humans is negligible (0.008% and 5.4%, respectively). The largest possible error involves the choice of the phosphorus (P) land-export figure based on nearby watersheds in the Entiat River drainage. Since the glacial period, much of the area has been covered by volcanic pumice and ash deposits, the primary source of phosphorus in these drainages (Tiedemann et al. 1978). High phosphorus content of volcanic ash and pumice is relatively immobile (Nimlow 1980), but fire is suspected of increasing mobility (Tiedemann et al. 1978). The Entiat River subdrainages were heavily burned (Helvey 1980) prior to determination of an average phosphorus export of 40.0 $mg/m^{-2}/yr^{-1}$ (Tiedemann et al. 1978). The Lake Wenatchee phosphorus supply was estimated as one-third of this value based on phosphorus levels of streams from three burned subwatersheds that were two or three times greater than in a stream from an adjacent unburned subwatershed.

Phosphorus used in primary production was estimated using the method of Dillon and Rigler (1975) based on an average summer chlorophyll a concentration of 1.6 mg/m^{-3}, which in turn was a theoretical correlate of a spring phosphorus concentration of 8.4 mg/m^{-3}. While confirmed by field determinations (chlorophyll a in July and September of 1.2 and 1.9 mg/m^{-3}, mean phosphorus in April and May of 8.3 mg/m^{-3}; USGS 1974), confirmation is spurious because of replacement of the lake volume with snowmelt between sampling periods. In an average year the volume of Lake Wenatchee is replaced 2.2 times, but with a minimum of one exchange occurring at the time of snowmelt in late May through early July.

Rapid lake flushing at the beginning of the growing season delays the utilization and incorporation of phosphorus into phytoplankton as evidenced in Lake Wenatchee by late summer-early fall abundance of zooplankton (Fig. 5). However, insufficiency of the nitrogen supply could also affect plankton production.

Dillon and Rigler (1975) developed their relationship for estimating average summer chlorophyll a concentration in lakes with spring N:P ratios (total phosphorus to total Kjeldahl nitrogen) of 12 or more as a conservative estimate of the lower limit for proportionate uptake. An N:P ratio of 16 in Lake Wenatchee during April-May 1974 satisfied this criterion while an N:P ratio of 8 on 18 July, following spring flushing, did not (USGS 1974). Moreover, inadequate N:P ratios of about 3 have been determined in the downstream Wenatchee River at Leavenworth in four other late spring-early summer periods (USGS 1964, 1965, 1978, 1979).

The source of practically all nitrogen compounds is fixation of atmospheric nitrogen. Fixation may occur electrically or photochemically in the atmosphere or by bacterial fixation in water, but bacterial fixation in soils is of most quantitative significance (Hutchinson 1957). More than 90% of the soils of the Lake Wenatchee Basin have been shown to be deficient in nitrogen but not in phosphorus (McColley 1976). These soils commonly deficient in adequate levels of nitrogen, moreover, have been reported as generally responding

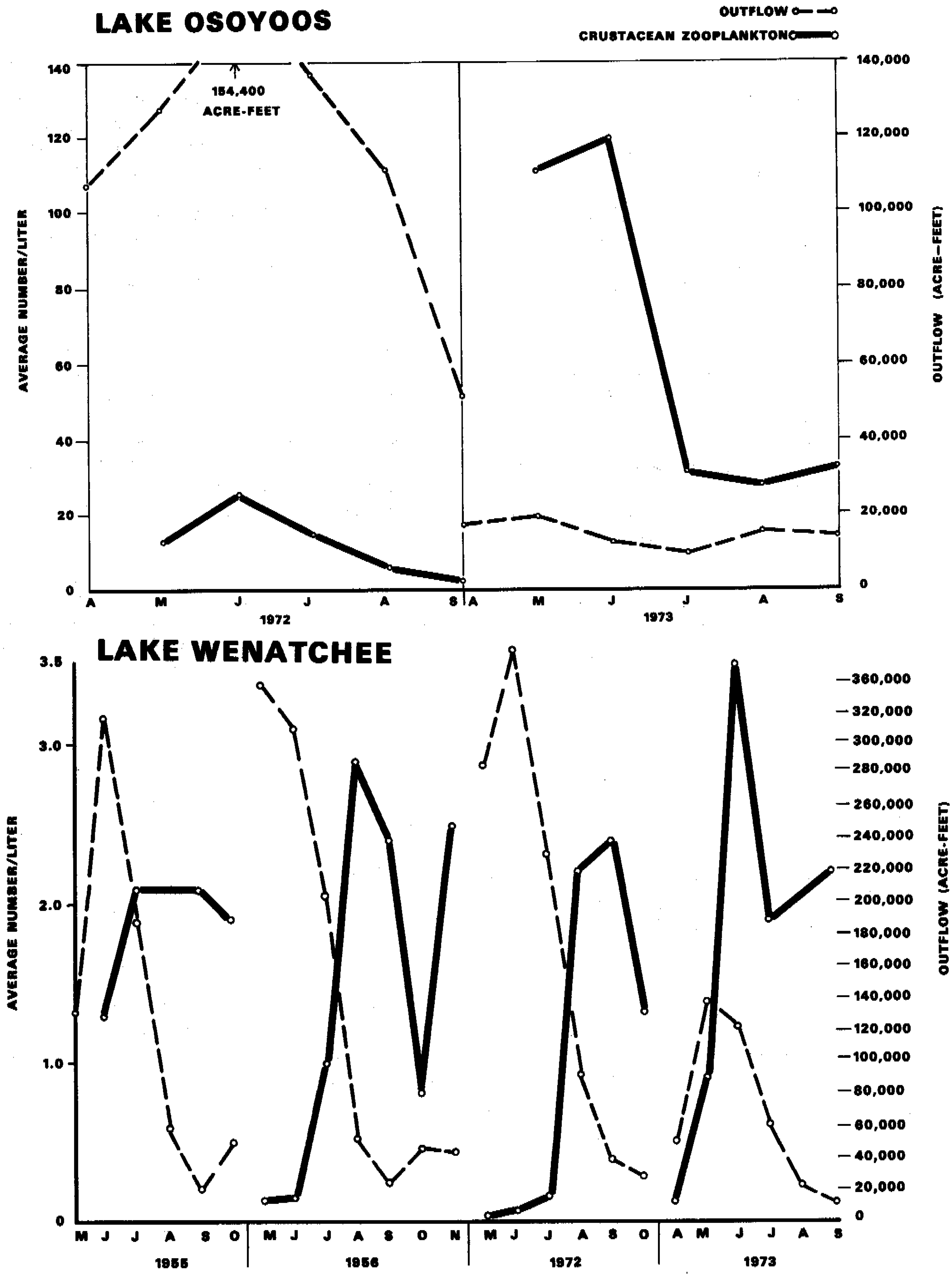

Figure 7. Seasonal abundance of zooplankton and discharge, Lakes Osoyoos and Wenatchee.

favorably to application of nitrogen (McColley 1976). Accordingly, it is reasonable to assume that Lake Wenatchee is indeed nitrogen-limited and that the limited nitrogen received in precipitation and fixed by bacterial action in surface water is of more than minor importance.

Fixation of atmospheric nitrogen proceeds most rapidly in open water during winter (Hutchinson 1957). Lake Wenatchee freezes about every other year, but not before about mid-January, with ice cover lasting only to late March-early April. This could allow an overwinter accumulation of nitrogen and account for the favorable N:P ratio of 16 reported for spring 1974. More salient, perhaps, are the observations surrounding nitrogen cycling in soils and stream flow of the Entiat River drainage that were independent of the effects of fire (Tiedemann et al. 1978).

Maximum monthly NO_3-N levels in stream flow generally increased sharply in winter and early spring, reaching peak values just prior to or during peak spring runoff with a subsequent rapid decline in early summer. The rise in NO_3-N levels in winter and early spring prior to peak flows in 1971, 1972, and 1974 indicated that moisture migrated from the snowpack into the soil mantle prior to the major snowmelt period in late spring. Such movement was verified. This moisture transported NO_3-N from the upper soil layers to the shallow ground aquifers, described by Putnam (1936), and eventually to the streams. Sharply reduced concentration showed that the moisture flux from snowpack to ground water exhausted soil NO_3-N in excess of that retained by an ion exchange (Tiedemann et al. 1978).

Liebig's Law of the Minimum is that some nutrient, least available relative to the growth requirements of a given organism, imposes primary limitations on the growth of that organism. Temperature is also important to freshwater algae in determining geographical distribution and controlling rates of anabolic and catabolic fluxes as well as rates of the nutrient reflux, and could affect productivity by accelerating or retarding physiological processes (Smith 1950; Mortimer 1969). The extremely low water temperatures (maximum 16°C) of Lake Wenatchee therefore might be suspected of overshadowing nutrient limitations, except that temperature has not been demonstrated as an important factor influencing primary production over the range of 2.6-43.2°C (Hern et al. 1981). Low water temperatures, however, are conducive to maximum fixation of atmospheric nitrogen and virtually preclude denitrification that occurs at high water temperatues (Hutchinson 1957).

Compensatory function of an ecosystem operates within the range of tolerance not only of primary producers but of primary and secondary consumers as well, and is further restricted by an optimal point within the overall range of tolerance of all the species in the food chain. MEI, Secchi-disk transparency, chlorophyll a, and phosphorus concentration rank primary production in Lake Wenatchee with the lowest reported in the literature (Dillon and Rigler 1974; Carson 1977; Stockner and Shortreed 1979). Within such constraint, characteristic of ultraoligotrophic lakes, the range of ecosystem compensatory function would seem small.

Morphoedaphic features and compensatory function of Lake Osoyoos contrast sharply with those of Lake Wenatchee (Table 29). Osoyoos consists of three largely independent basins, with upstream basins sufficiently large to influence nutrient content in downstream basins. Instead of being terminal to a small, largely unaltered mountainous watershed (277 square miles), Osoyoos is the final catchement of a large, lake-regulated drainage (3210 square miles) receiving nutrients from population centers, industries, and agriculture along its course (Booth 1969; Stockner and Northcote 1974). Increased nutrient loading over several decades, symptomized by nuisance algal growths, has led to appreciable hypolimnetic oxygen deficit, decreased water clarity, and changes in algal species composition (Booth 1969).

The estimated annual phosphorus budget of Lake Osoyoos is only a little more than two times greater than Lake Wenatchee (22,000 vs. 10,600 kg; Stockner and Northcote 1974), but Osoyoos has a lesser volume of water (290,330 vs. 440,100 acre-feet) and greater area (5729 vs. 2445 acres; Table 29). Shallower Osoyoos has more shoal area for the growth and attachment of photosynthetic organisms, with a resulting greater biomass of grazing and (ultimately) predator species. Shallower depths also contribute to an overall warmer temperature regime, allowing for more rapid growth and consequently production of warm-water benthos organisms and fishes. A larger proportion of the water mass is in the euphotic zone, allowing for relatively greater mixing and higher efficiency of primary production averaged over any water column of constant cross-sectional area. By contrast, the larger area of profundal zone in Wenatchee may act as a "nutrient sink," a zone in which phosphorus may accumulate and not be available, at least for parts of the year, to plankton inhabiting the euphotic zone. Perhaps for these reasons, Osoyoos has a much higher chlorophyll a content and lower transparency due to a higher efficiency of utilization of phosphorus compared to Wenatchee (Table 29). However, it has been suggested by Stockner and Northcote (1974) that Osoyoos may also be nitrogen-limited.

Average water exchange of Lake Osoyoos is not dissimilar to that of Lake Wenatchee (1.6 vs. 2.2 times yearly), but the time required for one exchange at the start of the two-fold-longer growing season is about 180 days for Osoyoos vs. 42 days for Wenatchee (Table 29). Inasmuch as nitrogen is readily lost in the effluent from lakes and phosphorus is not, flushing rate could outweigh the effect of phosphorus content in Osoyoos, at least for part of the growing season as suggested for Wenatchee.

The high flushing rates of Lakes Wenatchee and Osoyoos would appear to be somewhat characteristic of sockeye lakes. Water residence time of 13 sockeye lakes reported by Stockner and Shortreed (1979) ranged from 0.2 to 4.6 and averaged 1.7 exchanges per year. Sockeye lakes commonly share the feature of glacial formation as depressions in rivers (Burgner et al. 1969; Hartman and Burgner 1972). Depending on storage ratio, the edaphic influence of rapid flushing could be large, placing them in the somewhat ambiguous category of a reservoir--neither lake nor stream, but somewhere in between (Ryder et al. 1974).

Table 29. Biochemphysical features of Wenatchee and Osoyoos lakes (Osoyoos data from USGS 1955, Booth 1969, Stockner and Northcote 1974, Allen and Meekin 1980; Wenatchee data from references cited in text).

Feature	Lake Wenatchee	Lake Osoyoos Northern Basin[a]	Lake Osoyoos Middle Basin	Lake Osoyoos Southern Basin
Area (acres)	2,445	2,477	532	2,720
Mean depth (feet)	180	68	19.5	41
Volume (acre feet)	440,100		--- 290,330 ---	
Total dissolved solids (mg/l)	28	168	168	168
Morphoedaphic index	0.17	2.47	8.62	410
Summer Secchi disc transparency (ft)	20.7	8.3	8.9	10.5
Chlorophyll a (ug/l)	1.6	23.0	--	--
Mean total nitrogen (mg/l)	0.083	0.065	0.135	0.154
(range)	(.03-.19)	(.001-.179)	(.001-.801)	--
Mean total phosphorus (mg/l)	.005	.022	.025	.027
(range)	(.00-.030)	(.002-.048)	(.001-.052)	--
Spring N:P ratio	16	4-18	8	--
Total phosphorus load (kg/yr^{-1})	10,600	22,000	--	--
Growing season	75 days		--- 162 days ---	
Water exchanges per year	2.2		--- 1.6 ---	
Time required for one water exchange at start of growing season	42 days		--- 180 days ---	
N:P ratio after spring water exchange	3-8		--- not applicable ---	
August water strata (feet)	1-300	22-60	10-20	1-20
$\geq$ 5.0 mg/l oxygen and $\leq$ 70°F temperature	(1939)		--- (1968) ---	
(year)	(1957)	33-99	40-50	20-36
	(1972)		--- (1972) ---	

---

[a] Booth (1969) indicated that the northern basin acted as a nutrient trap and has proceeded further toward ultimate eutrophication than the downstream basin. Numbers and volume of mesotrophic plankton (e.g., Anabaena spp., Fragilaria crotonensis) were far greater in the northern basin than predominant oligotrophic species (e.g., Dinoorya, Melosera, Asterichella formosa) in the middle basin. Saether (1970) categorized the northern basin as moderately eutrophic and the central basin as strongly eutrophic, based on benthos composition.

(2) Zooplankton food supply (secondary production).--WDF (1938) collected several thousand plankton organisms per tow in Osoyoos compared to only a few organisms in Wenatchee in 1938. Gangmark and Fulton (1952) reported plankton was more than twice as abundant in Osoyoos than in Wenatchee during September and October 1939-1940. Ruggles (1958) reported Wenatchee as having very little phytoplankton and a low standing crop of zooplankton in 1955-1956. Rotifers, relatively unimportant as food for sockeye (Ricker 1937; LeBrasseur and Kennedy 1972), were most abundant. Copepods and cladocerans, of primary importance to sockeye as food in most lakes (Foerster 1968), including Wenatchee (Chapman and Quistorff 1938) and Osoyoos (Allen and Meekin 1980), followed next in abundance. Highest zooplankton standing crop occurred in late summer-early fall, with seasonal abundance inversely correlated with water residence time (Fig. 7).

Allen and Meekin (1980) sampled zooplankton in Lake Wenatchee in 1972-1973. Their findings were similar to those reported by Ruggles (Fig. 7). They also found zooplankton in Lake Osoyoos to greatly exceed that in Wenatchee but with peak abundance occurring in spring. Lake Osoyoos may be one of the most, and Lake Wenatchee one of the least, productive sockeye lakes with respect to crustacean zooplankton. When ranked according to number of crustacean zooplankton per liter for lakes reported by Foerster (1968), the relative order is Osoyoos (21.4), Cultus (16.4), Karluk (15.0), Dalnee (13.4), Lakelse (5.7), Wenatchee (1.0), and Port John (0.7). Lack of zooplankton data on a weight or volume basis for Wenatchee and Osoyoos precludes more decisive comparison.

In endeavoring to use zooplankton abundance as an index to fish production, it is necessary to keep in mind other peculiarities of such information. Standing crop or biomass represents only those zooplankters present in the lake at time of sampling. Production includes all biomass elaboration involving several generations of organisms over an annual cycle, including those that die natural deaths, those that emigrate or are flushed from the lake, and those that are eaten.

In simple food chains of oligotrophic lakes (i.e. phytoplankton-zooplankton-sockeye), increases in the biomass of sockeye lead to decreases in the density of the zooplankton, and decreases in the density of the zooplankton lead to decreases in the growth rate and biomass of sockeye (Warren 1971). If decreases in food resulting from low production or high consumption of zooplankton cause the growth rate of sockeye to approach zero, then sockeye biomass will tend to decrease, because of weight loss or mortality. But the decrease in sockeye biomass will permit the biomass of the zooplankton organisms to increase, and this will tend to increase sockeye growth rate (Warren 1971). If such density-dependent, dynamic equilibria did not occur, sockeye would overgraze their food supply and high zooplankton density would not be associated with the high smolt production, which the comparisons of Foerster (1968) broadly depict.

Natural predator-prey equilibria owe their stability to a long-shared evolutionary history. Prey species have evolved sufficient defense mechanisms for some individuals to survive in each generation, while predator species have evolved characteristics that assure some individuals in each generation an adequate harvest of prey (Murdock and Oaten 1975). Elimination or reduction of the larger species of zooplankton in Connecticut lakes by alewife (Alosa pseudoharengus) and near extinction of lake trout (Salvelinus namaycush) in the Great Lakes by sea lamprey (Petromyzon marinus) are well-documented examples of prey species lacking in defense mechanisms for avoiding overharvest by exotic predators (Brooks and Dodson 1965; Murdock and Oaten 1975).

In food chains of culturally eutrophic lakes, usually involving more diverse assemblages of fish species and food organisms, equilibria between species and their food supply are destabilized due to increases in nutrients and changes in trophic pathways (Li and Moyle 1981). Some species are declining or becoming extinct while others are expanding, but because of time lags in the response of predator populations to prey densities, production of individual species may be highly erratic for an indeterminate number of years. This is in sharp contrast to oligotrophic lakes, like Lake Wenatchee, that have evolved stable species communities over long periods of time narrowly adjusted to low nutrient content (Li and Moyle 1981). Lake Osoyoos, having a higher nutrient content for phytoplankton production in comparison to Lake Wenatchee, should nevertheless maintain a higher zooplankton standing crop and a higher sockeye growth rate at higher sockeye biomasses so long as food is the resource primarily limiting growth and production.

(3) Smolt production.--Biomass or production of sockeye has been directly measured by counting and weighing out-migrants from a number of lakes (Table 28). Although absolute reliance cannot be placed on all the indirect estimates developed for Lakes Wenatchee and Osoyoos (Table 30), these data seem sufficient to indicate about a two-fold greater production of sockeye smolts in Lake Osoyoos (mean, 12.4; range, 2.6-24.7 lbs/acre) than in Lake Wenatchee (mean, 6.3; range, 2.0-11.6 lbs/acre).

When ranked according to the production of sockeye smolts from other lakes, Lake Wenatchee fits into the category of least productive lakes (≤ 10 lbs/acre), typified by Chilko, Cultus, Lakelse, Babine, and Port John, which is consistent with gross similarity in morphoedaphic features (Table 28). Osoyoos, on the other hand, falls short of the production of the most productive lakes (≥ 20 lbs/acre), such as Karluk, Dalnee, and Kurile, despite more positive morphoedaphic features.

(4) Environmental and competitive interactions.--The difference between potential and realized smolt production in Lake Osoyoos seems to be largely a matter of interactions between species, assuming adequate seeding. Fisheries Service Canada and WDF (1973) estimated that Osoyoos Lake, based on the International Pacific Salmon Fish Commission plankton index and adjusted for the progeny of 37,000 kokanee, could accommodate the progeny of 280,300 adult sockeye, or 75 spawners per acre. A striking feature of the actual escapement is that the average number of spawning sockeye per unit lake area has never come close to such a maximum (Table 28 and 31). The average number of spawning sockeye per unit lake area (8.9/acre) likely bears some relationship to innate production capability (Burgner 1964).

Table 30. Estimates of sockeye salmon smolt production, Wenatchee and Osoyoos Lakes.

Year	Origin	Smolt abundance (millions)	Average length (cm)	Average weight (g)	Pounds/ acre
Lake Wenatchee (2,445 acres)					
1960[a]	Hatchery and wild	0.8	8.1	5.0	3.6
1961[a]	Hatchery and wild	0.76	9.5	8.5	5.8
1962[a]	Hatchery	1.06	8.6	6.1	5.8
1962[a]	Wild	0.96	8.8	6.6	5.8
1962[a]	Total	2.02	--	--	11.6
1963[a]	Hatchery	0.93	9.5	9.2	3.1
1963[a]	Wild	0.37	8.5	6.0	2.0
1963[a]	Total	1.3	--	--	5.1
1965[b]	Hatchery and wild	0.33	11.2[c]	13.6	4.0
1966[b]	Hatchery and wild	0.68	11.2[c]	13.6	8.3
1967[b]	Hatchery and wild	0.61	11.2[c]	13.6	7.5
1973[d]	Wild	1.7	8.1[e]	5.2	8.0
1974[d]	Wild	0.5	9.1[e]	7.3	3.3
1976[b]	Wild	1.09	8.5[c]	6.0	5.6
Lake Osoyoos (5,729 acres)					
1965[b]	Wild	4.6	11.3[c]	13.9	24.7
1966[b]	Wild	6.1	9.6[c]	8.6	20.2
1967[b]	Wild	0.94	12.8[c]	20.3	7.3

Table 30 (continued).

Year	Origin	Smolt abundance (millions)	Average length (cm)	Average weight (g)	Pounds/ acre
1973[d]	Wild	2.1	11.2[e]	13.6	11.0
1974[d]	Wild	0.5	11.1[e]	13.3	2.6
1976[b]	Wild	1.55	11.5[c]	14.7	8.8

[a] Unpublished data of D.R. Craddock, NMFS, who trapped smolts at outlet, 1958-1963.

[b] Priest Rapids Dam population estimates (Sims and Miller 1976, Park and Bently 1968) apportioned back to Lake Wenatchee and Lake Osoyoos based on subsequent adult count differences (4-year cycle) at Rock Island and Rocky Reach dams and corrected for an average 15% mortality, as shown, at each dam prior to enumeration at Priest Rapids Dam.

[c] Average lengths estimated from Table 22 so as to reflect an inverse relationship between growth and population density.

[d] Acoustic estimate (Dawson et al. 1973, Dawson and Thorne 1974).

[e] Allen and Meekin 1980.

Table 31. Maximum number (peak count) of sockeye salmon observed in spawning surveys of Okanogan River Drainage, 1947-1980 (data from same sources as Table 15).

Year	Similkameen R. below Enloe Dam	Zosel Dam count	Lake Osoyoos	Okanogan River above Osoyoos		
				Above DS-13	DS-1 to DS-13	Total
1947	--	--	--	6,027[a]		6,027
1948	--	--	"few"[b]	7,175[c]		7,175
1949	--	--	--	133		133
1950	10	--	--	500		500
1951	--	--	--	5,602		5,602
1952	--	3,217	--	10,360		10,360
1953	--	67,542	--	15,165		15,165
1954	0	3,780	--	5,673		7,233
1955	0	4,130	--	19,320		19,320
1956	40	668	--	16,067	--	16,067
1957	23	2,019	--	8,533	"few"	8,533
1958	[d]	--	--	10,628	"few"	10,628
1959	--	--	--	20,205	642[e]	20,847
1960	--	--	0	3,421	"few"	3,421
1961	--	--	--	691	0	691
1962	--	944	--	1,969	--	1,969
1963	--	16,033	--	--	--	--
1964	--	--	--	6,286	--	6,286
1965	--	--	--	5,408	54	5,462
1966	--	--	--	44,865	--	44,865
1967	--	--	--	16,786	--	16,786
1968	--	--	--	7,440	--	7,440
1969	--	--	--	2,815	3,420[e]	6,235
1970	--	--	--	13,580	4,230[e]	17,810
1971	--	--	1,200[e]	21,767	3,761	26,728
1972	--	--	--	9,441	5,355[e]	14,796
1973	--	--	--	6,328	--	6,328
1974	--	--	--	3,080	--	3,080
1975	--	--	--	6,684	--	6,684
1976	--	--	--	8,535	--	8,535
1977	--	--	--	4,870	--	4,870
1978	--	--	--	420	--	420
1979	--	--	--	839	--	839
1980	--	--	--	5,000	--	5,000

[a] The 1947-1955 counts are for entire river, diversion dam to Lake Osoyoos.
[b] Noted by Burner 1951.
[c] Estimated on 1947 count.
[d] Several hundred sockeye noted August 6, 1958 (incl. 200-300 mortalities).
[e] Projected on 3 fish/redd.

Sockeye salmon and the indistinguishable kokanee are one species in a community of 21 species that depend upon the food and space resources available in Osoyoos Lake (Table 32). Similarities in environmental requirements and behaviors of sockeye and rainbow trout can be expected to produce an intense struggle for survival. The numeorus and fine gillrakers of sockeye are much more highly adapted to feeding on zooplankton than are the gillrakers of trout. Numerical and weight ratios between sockeye/kokanee and rainbow trout were 4:1 and 7:1 in sport catches and 26:1 and 4:1 in gillnet catches in 1971 (Pinsent et al. 1974). Other fish species gillnetted outnumbered and outweighed sockeye about 4:1 and 10:1, reflecting no competitive advantage. Based on a reservoir data base (Jenkins 1982), not available to Pinsent et al. (1974) in morphoedaphic indexing of Lake Osoyoos, MEI suggests standing fish crops in Lakes Osoyoos and Wenatchee of about 250 and 27 lbs/acre (Robert Jenkins, USFWS, personal communication). Estimates of annual sockeye smolt production (Table 30) account for 5% (range, 0.4%-10%) in Osoyoos and 23% (range, 7.4%-43%) in Wenatchee of the estimated fish biomass.

If either rainbow trout or sockeye existed as the sole species in Osoyoos, they would occupy a relatively wider range of microhabitats, an expression of their potential niche. With coexistence, available and suitable microhabitats are partitioned between the two species, an expression of the realized niche. The contraction of the potential niche into the realized niche is an adaptive evolutionary strategy to avoid direct competition between species. It forces a change from generalist to specialist in regard to habitat selection and feeding preferences (Behnke, in press).

An important outcome of niche theory is that the sum of two or more realized niches is greater than the sum of one potential niche, although realization of the one niche provides more biomass of an individual species (Behnke, in press). For example, numbers and biomass of rainbow or brown trout were consistently depressed in ponds where other fishes were removed but that contained abundant young-of-the-year planktivorous alewives provided as forage (McCaig 1980).

Severity of the interaction between species is regulated by how well a habitat favors a species. Each species is genetically programmed to perform within certain limits of heat and cold, water content of salts and gases, and habitat structure, as well as being influenced by competition for resources and the effects of predators.

Interconnected Chignik and Black Lakes are two of the most productive sockeye salmon lakes in Alaska (Burgner et al. 1969; Hartman and Burgner 1972). Black is shallow (mean depth, 3 m). Chignik has less area than Black but has six times the volume. These characteristics are reflected in MEI's of 7.94 for Black and 0.66 for Chignik (Table 28). Threespine and ninespine sticklebacks and pond smelt are much more abundant in Black than in Chignik, but Chignik has about a three-fold greater escapement and production of adult sockeye than Black (Table 28). Hartman and Burgner (1972) detailed how it was not clear to what extent interspecific competition for food influenced sockeye production. Diets of sockeye, sticklebacks, and smelt overlapped in Black but also differed in substantial ways--i.e. the

Table 32. The fishes of selected sockeye salmon lakes of North America and Asia (from Hartman and Burgner 1972 with Lakes Wenatchee and Osoyoos added).

Common name	Scientific name	Osoyoos	Wenat- chee	Cultus	Babine	Ili- amna	Alek- nagik	Karluk	Chig- nik	Dalnee
Arctic lamprey	*Lampetra japonica*					X	X			
Pacific lamprey	*Entosphenus tridentatus*					X	X			
Least cisco	*Coregonus sardinella*					X				
Arctic cisco	*Coregonus autumnalis*					X				
Humpback whitefish	*Coregonus pidschian*					X	X			
Lake whitefish	*Coregonus clupeaformis*	X			X					
Pink salmon	*Oncorhynchus gorbuscha*					X	X	X	X	
Chum salmon	*Oncorhynchus keta*					X	X	X	X	
Coho salmon	*Oncorhynchus kistuch*					X	X	X	X	X
Sockeye salmon[a]	*Oncorhynchus nerka*	X	X	X	X	X	X	X	X	X
Chinook salmon	*Oncorhynchus tshawytscha*		X			X	X	X	X	
Mountain whitefish	*Prosopium williamsoni*	X	X	X	X					
Pygmy whitefish	*Prosopium coulteri*	X				X	X		X	
Round whitefish	*Prosopium cylindraceum*					X	X			
Cutthroat trout	*Salmo clarki*		X	X						
Rainbow trout	*Salmo gairdneri*	X	X		X	X	X	X	X	
Arctic char	*Salvelinus alpinus*					X	X	X		
Dolly Varden	*Salvelinus malma*		X	X		X	X	X	X	X
Lake trout	*Salvelinus namaycush*				X	X				
Arctic grayling	*Thymallus arcticus*					X	X			
Pond smelt	*Hypomesus olidus*					X	X		X	
Rainbow smelt	*Osmerus mordax*					X	X			
Eulachon	*Thaleichthys pacificus*					X				
Alaska blackfish	*Dallia pectoralis*					X	X		X	
Northern pike	*Esox lucius*					X	X			

Table 32 (continued).

Common name	Scientific name	Osoyoos	Wenat-chee	Cultus	Babine	Ili-amna	Alek-nagik	Karluk	Chig-nik	Dalnee
Redside shiner	Richardsonius balteatus	X	X							
Chiselmouth	Acrocheilus alutaceus	X								
Lake chub	Couesius plumbeus				X					
Common carp	Cyprinus carpio									
Tench	Tinca tinca	X								
		X								
Peamouth	Mylocheilus caurinus	X								
Northern squawfish	Ptychocheilus oregonensis	X	X	X	X					
Longnose dace	Rhinichthys cataractae		X		X					
Largescale sucker	Catostomus macrocheilus	X	X	X						
White sucker	Catostomus commersoni				X					
Bridgelip sucker	Catostomus columbianus	X								
Longnose sucker	Catostomus catostomus	X			X	X				
Black bullhead	Ictalurus melas	X								
Burbot	Lota lota				X	X	X			
Threespine stickleback	Gasterosteus aculeatus			X		X	X	X	X	X
Ninespine stickleback	Pungitius pungitius					X	X	X	X	X
Pumpkinseed	Lepomis gibbosus	X								
Smallmouth bass	Micropterus dolomieui	X								
Largemouth bass	Micropterus salmoides	X								
Black crappie	Pomoxis nigromaculatus	X								
Yellow perch	Perca falvescens	X								
Prickly sculpin	Cottus asper	X	X	X	X					
Coastrange sculpin	Cottus aleuticus				X		X		X	X
Slimy sculpin	Cottus cognatus						X	X		

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[a] Lacustrine stocks of sockeye salmon are known as kokanee.

sticklebacks depended heavily on aquatic insect larvae, the pond smelt on zooplankton, and the sockeye primarily on adult insects, to a lesser extent on zooplankton, and to a minor extent on insect larvae. From what was discussed previously, it is not unexpected to find partitioning of food resources between the fishes of Black Lake, particularly considering the uniform shallow habitat. A common error in not discerning between cause and effect of interspecific competition is illustrated by long-term studies of Paul Lake, British Columbia.

The introduction of redside shiner into Paul Lake resulted in a severe decline in growth and production of trout. At densities of 5000-100,000 per acre, the redside shiner monopolized the main food supply (Gammarus) of the trout. The shiner proved more successful than the trout in feeding in beds of vegetation, and the warmer surface water and good protective cover afforded by the weed beds effectively removed the shiner from trout predation for most of the year (Crossman 1959; Johannes and Larkin 1961). Had food studies been limited to the period after redside shiners had become abundant and gammarids largely eliminated, virtually no indication of interspecific competition between shiners and trout for a common food resource would have been found (Crossman and Larkin 1959).

In contrast to the situation in Paul Lake, redside shiners became established in Yellowstone Lake, Wyoming, many years ago, but the deep morphometry and cold temperatures of the lake are not favorable for the species and no negatve impact on the trout population has been apparent (Behnke, in press). The role of indigenous redside shiners is evidently similarly restricted in Lake Wenatchee. In warmer, shallower Lake Osoyoos, the native redside shiner is common to abundant, but impact is masked by the diverse assemblage of fishes. Common carp, tench, black bullhead, pumpkinseed, smallmouth bass, largemouth bass, black crappie, and yellow perch are exotic warm- or cool-water fish species (Scott and Crossman 1973) whose establishment in Osoyoos required the usurpation of native fish production (Table 32). Pinsent et al. (1974) observed that the ability of the Okanogan Valley lakes to produce salmonids varied inversely with the abundance of other fish species present and the degree of eutrophication.

The outstanding results generally achieved in chemically renovating marginal but highly fertile lakes constitute conclusive proof that competitive interactions severely, if not critically, inhibit production of salmonids (Lennon et al. 1971; Klingbiel 1975; Trimberger 1975). Many reclaimed lakes in eastern Washington, characterized by high summer water temperatures and low oxygen content, consistently produce as high as 150 pounds of trout per acre (McLeod 1958), but only so long as density of competitive fishes is low or nonexistent.

A seven-fold increase in sockeye salmon production was documented for Ruth Lake, Alaska, following removal of resident fishes with rotenone (Meeham 1966; Table 28). Equally illuminating is the atypical high survival (i.e. to 46.9% in Ruth; 20%-30% not unusual in trout lakes) of fry and fingerling salmonids restocked in reclaimed lakes. This shows that it is survival and not some ultimate largess of egg deposition that most counts in salmonid production, a truism reflected in the huge variability in reproductive success of sockeye (Foerster 1968).

The population irruption of kokanee in Lake Roosevelt during initial impoundment was mentioned earlier. A subsequent irruption of kokanee in Banks Lake (27,200 acres) also occurred when this offstream re-regulating irrigation reservoir to Lake Roosevelt (Fig. 1) began filling in 1951 and before stocking began in 1956 (personal communications from R. Duff, WDG; R. Rennie, WDG (retired); and R. McKown, Bureau of Reclamation; Duff 1973; Stober 1976a). It, too, evidently represented some combination of high food supply resulting from trophic upsurge (Baranov 1961), low density of competitive species, and high reproductive success of kokanee entrained from Lake Roosevelt.

CONCLUSIONS

The evolution of Pacific salmon rests with a high degree of spatiotemporal organization of behavior permitting an array of species-stock life-history patterns (Miller and Brannon 1982). Sockeye salmon have evolved specialized adaptive features in behavior and physiology for initial rearing in oligotrophic lakes of low but stable nutritive bases that are not unlike reservoirs in having high but variable flushing rates.

Oligotrophic lakes are most sensitive to disturbances (Colby et al. 1972; Li and Moyle 1981), but the environment and species diversity of ultraoligotrophic Lake Wenatchee are little altered from primordial times, and the lake retains a high efficiency in converting a low nutrient base to sockeye production. Lake Osoyoos, by contrast, has a radically altered environment, species diversity, and production capability due to cultural eutrophication and the introduction of exotic fishes. Here the nutrient base is high and efficiency of energy conversion to sockeye production is low.

Culturally eutrophic lakes are those in the process of rapid change. They are unlike naturally eutrophic lakes, which have evolved from oligotrophic status slowly over long periods of time, allowing relative stability of biological interactions (Li and Moyle 1981). Carbon and pollen profiles of bottom sediments indicate that cultural eutrophication of Lake Osoyoos paralleled agricultural development and waste discharge in the Okanogan Valley in the first half of the century (Stockner and Northcote 1974). Resulting changes in species of plankton, benthos, fish, and possibly atypical numbers of one-ocean sockeye were first noted in the late 1930's coincidental with the development of the Grand Coulee Fish-Maintenance Project (WDF 1938; Stockner and Northcote 1974). Sockeye salmon rehabilitation under the project no doubt initially benefited from nutrient enrichment.

The addition of nitrogen and phosphorus to Great Central Lake, Vancouver Island, British Columbia, in 1970-1973 increased phytoplankton and zooplankton by several-fold and the survival of juvenile sockeye salmon by 2.6 times. Returning adults, however, increased from an average of less than 52,000 in prefertilization years to more than 373,000 in the year-classes produced during feritlization (LeBrasseur et al. 1978).

Increased nutrients and increased organic production lead to oxygen depletion in the deeper, cooler water of lakes, as well as precipitating changes among the plankton, benthos, fishes, and macrophytes. Thus, while salmonids dependent on the deeper, colder water for summer survival may respond to initial eutrophication with increased growth and survival, production may eventually be inhibited or curtailed depending on the degree of ultimate oxygen deficit (Colby et al. 1972).

Effects on fish production in Okanogan lakes are most detailed for Skaha Lake upstream of Lake Osoyoos with the addition of sewage beginning in 1948. Here the contribution of salmonids in gill net catches fell from 15% to less than 5% over more than two decades (Northcote et al. 1975). Skaha, as well as downstream Vaseaux and Osyoos Lakes, however, were spared excessive biological production and corresponding oxygen exhaustion resulting from critical nutrient loading because of limited water residence time (Stockner and Northcote 1973).

Lake Washington is one of the most studied culturally eutrophic lakes in North America and has the largest run of sockeye salmon in the contiguous 48 states. Enrichment occurred over a 30-year period by sewage discharged by the City of Seattle. Peak primary production occurred in the early 1960's, but since waste diversion in the late 1960's production has fallen steadily, attaining pre-1930 conditions in 1975. Zooplankton production, although not increased in proportion to increases in primary production, has not decreased with de-eutrophication, but Daphnia, a preferred food item of sockeye, has reappeared (Woody 1972; Edmondson 1977b; Eggers et al. 1978).

Lake Washington sockeye have shown a good correlation with noncritical levels of eutrophication, despite severe periodic winter flooding on spawning tributaries (Doble and Eggers 1978; Stockner 1979; Stober and Hamalainen 1980). Returns of adult sockeye salmon increased from less than 50,000 in 1960 to 536,000 in 1971 (Bryant 1976). Nevertheless, the fish community of this large, deep lake is dominated by benthos-consuming fish species (e.g. prickly sculpin, peamouth, northern squawfish, yellow perch, and largescale sucker; Eggers et al. 1978), which are similar to those in Osoyoos (e.g. yellow perch, lake whitefish, largescale sucker, longnose sucker, common carp, northern squawfish, peamouth, chiselmount, prickly sculpin; Pinsent et al. 1974).

In Lake Washington, fish production through the benthos detrital food chain is substantially greater than fish production through the equally appreciable plankton food chain because of interactions of competition and predation between species (Eggers et al. 1978). For example, squawfish feed heavily on sockeye when sockeye are abundant and switch to sculpin when sockeye abundance is low. Antipredation behavior (e.g. limiting time spent in feeding and feeding in regions of low light intensity that are removed from regions of high zooplankton abundance) has also been shown to be a factor in lack of sockeye exploitation of food resources (Eggers et al. 1978). One could expect even more inhibition to sockeye exploitation of food resources in shallower Lake Osoyoos with progressive decreases in hypolimnic oxygen concentration.

It is possible to estimate the relative contribution of Wenatchee and Osoyoos Lakes to sockeye runs in the Columbia River beginning in 1947 (Table 33 and 34; Fig. 8) so as to assess the effect of progressive eutrophication

Table 33. Distribution of sockeye salmon escapements (thousands) to Columbia River, 1947-1981 (data sources and methodology described in text).

Year	Rock Island and Ice Harbor dam counts	Wenatchee River escapement				Okanogan River escapement				Snake River lake escapement	
		Lake		River		Lake		River			
		No.	%	No.	%	No.	%	No.	%	No.	%
1947	79.8	30.8	38.6	7.8	9.8	41.1	51.5	0.1	0.1	--	--
1948	84.6	33.3	39.4	7.1	8.4	42.2	50.7	2.0	1.5	--	--
1949	18.7	3.6	19.3	0.6	3.2	12.5	66.8	2.0	10.7	--	--
1950	50.1	--	--	0.1	--	--	--	2.9	--	--	--
1951	102.7	18.4	17.9	1.2	1.2	82.5	80.3	0.6	0.6	--	--
1952	113.7	19.7	17.3	5.3	4.7	88.2	77.6	0.5	0.4	--	--
1953	156.0	9.2	5.9	3.9	2.5	141.7	90.8	1.2	0.8	--	--
1954	92.2	21.3	23.1	4.4	4.8	65.0	70.5	0.5	0.5	1.0	1.0
1955	160.2	48.3	30.1	3.5	2.2	103.5	64.6	0.5	0.3	4.4	2.8
1956	93.5	25.1	26.8	0.4	0.4	66.4	71.0	0.3	0.3	1.3	1.4
1957	71.8	23.7	33.0	4.5	6.3	42.6	59.3	0.5	0.7	0.5	0.7
1958	98.0	32.8	33.5	2.0	2.0	61.3	62.6	1.8	1.8	0.1	0.1
1959	72.6	8.0	11.0	5.0	6.8	58.3	80.3	1.0	1.4	0.3	0.4
1960	60.4	30.9	51.2	--	--	28.7	47.5	0.7	1.6	0.1	0.2
1961	19.3	6.4	33.2	0.1	0.5	12.3	63.7	0.4	2.1	0.1	0.5
1962	29.4	17.0	57.8	2.4	8.2	9.7	33.0	0.2	0.7	0.1	0.3
1963	65.8	27.2	41.3	0.5	0.8	36.7	55.8	0.3	0.5	1.1	1.6
1964	70.7	32.2	45.5	5.0	7.1	32.0	45.3	0.2	0.3	1.3	1.8
1965	42.7	8.9	20.8	1.8	4.2	31.2	73.0	0.5	1.2	0.3	0.7
1966	164.9	29.4	17.8	5.6	3.4	128.6	78.0	1.0	0.6	0.3	0.2
1967	120.5	9.5	7.9	0.9	0.7	109.3	90.7	0.1	0.1	0.7	0.6
1968	106.0	11.7	11.0	1.7	1.6	91.3	86.1	0.1	0.1	1.2	1.1
1969	38.7	16.8	43.4	0.8	2.1	20.3	52.5	0.1	1.3	0.7	1.8
1970	75.7	17.5	23.1	0.1	0.1	57.2	75.6	0.1	0.1	0.8	1.1
1971	71.9	21.3	29.6	0.3	0.4	49.7	69.1	0.1	0.1	0.5	0.7

Table 33 (continued.)

Year	Rock Island and Ice Harbor dam counts	Wenatchee River escapement				Okanogan River escapement				Snake River lake escapement	
		Lake		River		Lake		River			
		No.	%	No.	%	No.	%	No.	%	No.	%
1972	43.9	16.3	37.1	0.2	0.5	26.9	61.3	0.1	0.2	0.4	0.9
1973	68.9	19.7	28.6	0.1	0.2	48.8	70.8	0.1	0.2	0.2	0.2
1974	34.1	12.7	37.2	0.2	0.6	20.9	61.3	0.1	0.3	0.2	0.6
1975	53.6	26.3	49.1	0.1	0.2	26.9	50.2	0.1	0.2	0.2	0.3
1976	36.2	8.2	22.7	0.1	0.2	27.2	75.1	0.1	0.2	0.8	2.2
1977	90.9	64.5	71.0	0.1	0.1	25.6	28.2	0.1	0.1	0.6	0.6
1978	14.8	6.4	43.2	0.1	0.7	8.1	54.7	0.1	0.7	0.1	0.7
1979	50.6	21.6	42.7	0.1	0.2	28.7	56.7	0.1	0.2	0.1	0.2
1980	52.8	22.7	43.0	0.1	0.2	29.9	56.6	0.1	0.1	0.1	0.1
1981	47.1	16.4	34.8	0.1	0.1	30.6	64.9	0.1	0.1	0.1	0.1

Table 34. Estimated origin of total sockeye salmon run (thousands) entering the Columbia River, based on Table 33.

Year	Total run	Lake Wenatchee	Lake Osoyoos	Redfish Lake	Total riverine
1947	335.3	129.4	172.7		33.2
1948	143.2	56.4	72.6		14.2
1949	52.6	10.2	35.1		7.3
1950	112.6				6.8
1951	203.7	36.5	163.6		3.6
1952	318.9	55.2	247.5		16.2
1953	260.0	15.3	236.1		8.6
1954	180.0	41.6	126.9	2.0	9.5
1955	245.0	73.7	158.2	6.9	6.2
1956	202.0	54.1	143.4	2.8	1.4
1957	147.8	48.8	87.6	1.0	10.3
1958	313.3	105.0	196.1	0.3	11.9
1959	270.7	29.8	217.4	1.2	22.3
1960	179.1	91.7	85.0	0.4	8.0
1961	57.7	19.2	36.8	0.3	1.4
1962	38.7	22.4	12.8	0.1	3.4
1963	65.4	27.0	36.5	1.0	0.9
1964	104.9	47.7	47.5	1.9	7.8
1965	55.2	11.5	40.3	0.4	3.0
1966	169.2	30.1	132.0	0.3	6.8
1967	165.4	13.1	150.0	1.0	1.3
1968	134.7	14.8	116.0	1.5	2.3
1969	75.8	32.8	39.8	1.4	1.8
1970	95.3	22.0	72.0	1.0	0.3
1971	150.5	44.5	104.1	1.0	0.8
1972	123.3	45.7	75.6	1.1	0.9
1973	61.3	17.5	43.4	0.1	0.3
1974	43.9	16.4	26.8	0.3	0.4
1975	58.2	28.6	29.2	0.2	0.2
1976	43.7	9.9	32.9	0.7	0.2
1977	99.8	70.9	28.1	0.6	0.2
1978	18.4	7.9	10.1	0.2	0.2
1979	52.6	22.5	29.8	0.1	0.2
1980	58.9	29.0	29.9	0.1	0.2
1981	47.1	16.4	30.6	0.1	0.1

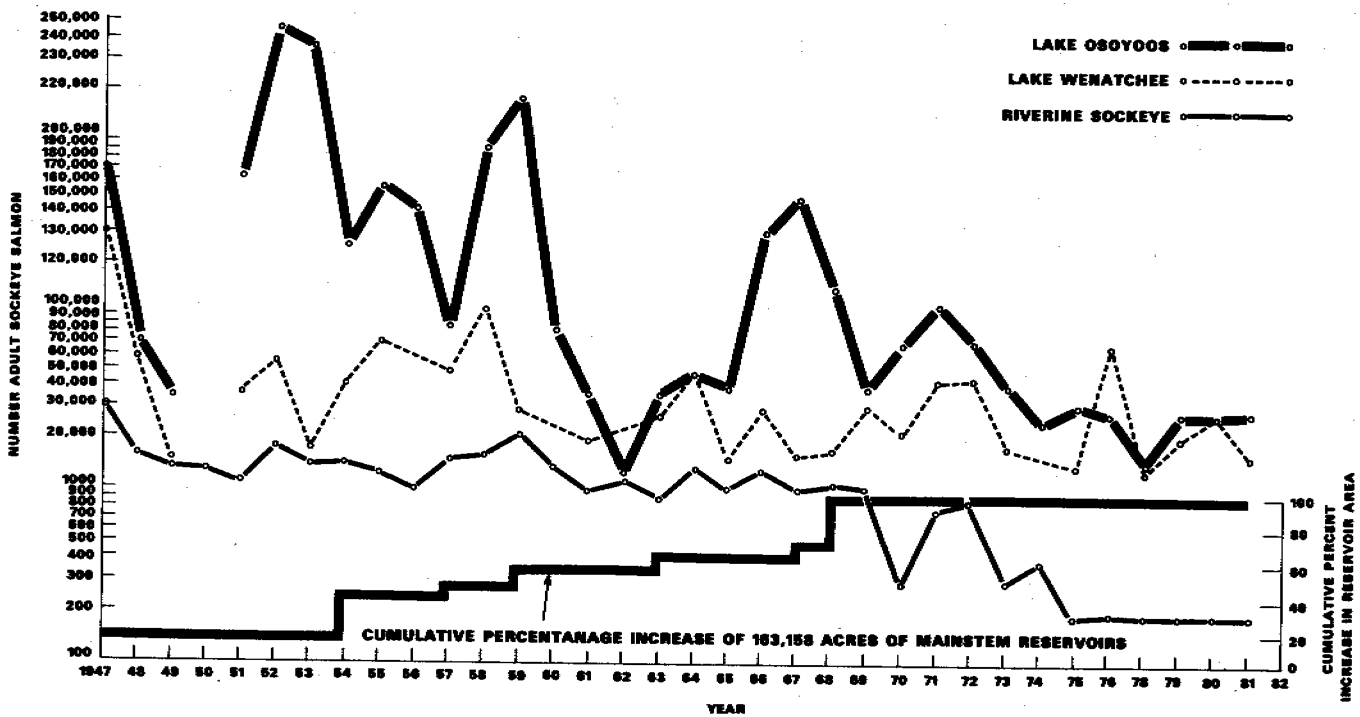

Figure 8. Annual estimates of origin of mid-Columbia River adult sockeye salmon and cumulative percentage increase of mainstem reservoir area.

on Osoyoos sockeye production. Escapements to the Wenatchee River through 1961 were taken from the published reports of Gangmark and Fulton (1952) and Craddock (1958) and the unpublished reports of Silliman (1947), Gangmark and Fulton (1948, 1949b), Fulton (1952), Craddock (1954, 1955, 1956, 1957a, 1957b), Craddock and Major (1958, 1959, 1960), Craddock and Parks (1961), and Tufts and Craddock (1962). After 1961, sockeye passing Rock Island Dam could either proceed up the Columbia River over Rocky Reach Dam or enter the Wenatchee River (Fig. 1, 9, and 10) and escapement was the difference between the two dam counts.

Escapement to Lake Osoyoos was the Rock Island Dam count, minus the escapement to the Wenatchee River, minus the escapement to the Entiat, Methow, and Similkameen Rivers as noted in hatchery returns and spawning ground counts. Earlier I described sockeye spawning in the Wenatchee River and Nason and Icicle Creeks in which the fry were not associated with Lake Wenatchee (Table 15). I also described instances of sockeye rearing in mainstem Columbia River impoundments, suggesting recruitment from the foregoing sockeye as well as sockeye spawning in the Entiat, Methow, and Similkameen rivers lacking nursery lakes (Tables 12 and 31). These sockeye were designated riverine, and spawning counts after 1962 were enumerated for population size utilizing the "Factor 5" method of Gangmark and Fulton (1952) as had been applied to counts not subjected to enumeration by weir up until 1962. Riverine escapements were then subtracted from the Okanogan and Wenatchee Rivers escapements, with the difference representing the production of Lake Osoyoos and Lake Wenatchee (Tables 33 and 34). Lastly, the percentage composition by escapement components (e.g. Lakes Wenatchee, Osoyoos, Redfish, and riverine, Tables 33 and 34) was applied to total run size entering the Columbia River.

Results show that sockeye production of Lake Osoyoos trended downward in an oscillatory fashion during the post-World War II period, as if controlled by a progressive eutrophication (Fig. 8). A paralleling phenomenon involving riverine sockeye production was associated with hydroelectric development of the Columbia River.

Rock Island, Bonneville, and Grand Coulee Dams began operation in 1933, 1938, and 1941, respectively. By 1967, most of the Columbia River had been turned into a series of impoundments of which 163,158 acres were accessible to sockeye salmon--an increase over original river area of 68,516 surface acres (Table 17).

The relatively small volumes and high flushing rates (1-6 days) of mainstem Columbia River reservoirs place them in a riverine category; mid-Columbia reservoirs actually qualify as a tailwater to Lake Roosevelt. Production at the primary level is dependent for the most part on allochthonous detritus, sessile algae, and macrophytes (Hynes 1970). Primary consumers are largely represented by dipterans, although amphipods, oligochaetes, isopods, mollusks, turbellarians, and crayfish may be locally abundant (Robeck et al. 1954; Becker 1971; Page and Neitzel 1976a, 1976b; Gray and Dauble 1976a, 1976b, 1977, 1978; Wolf 1976; Walberg et al. 1981). Since water retention time is several times shorter than the life cycle of crustacean zooplanktoners (i.e.

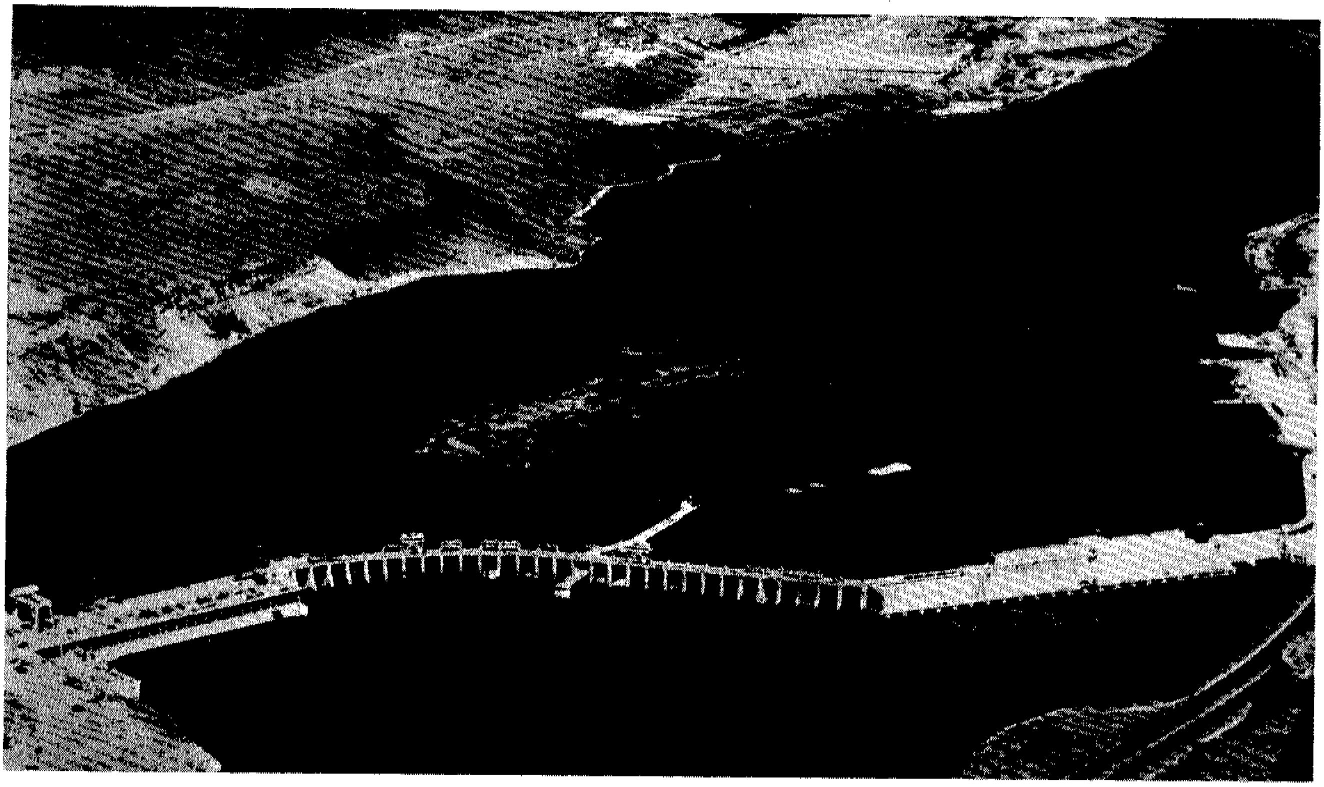

Figure 9. Rock Island Dam (River Mile 453), Columbia River, 1982. Old power house (1933) on right, new power house (1980) on left of photo.

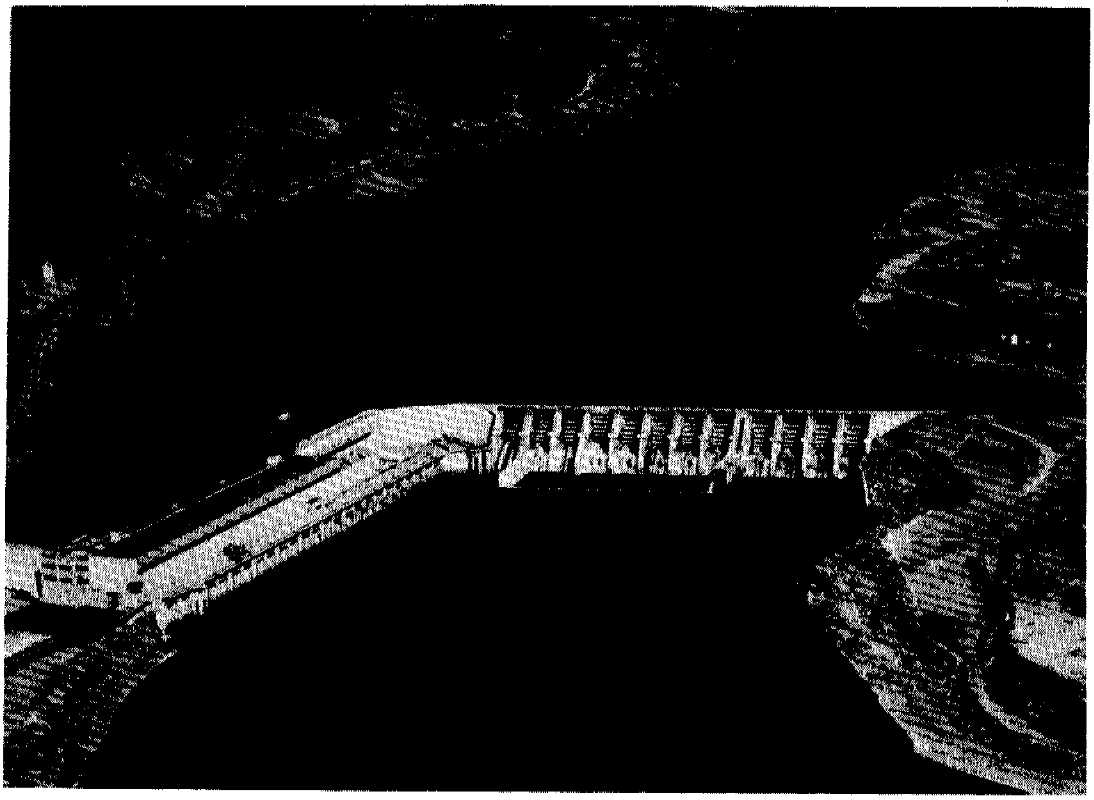

Figure 10. Rocky Reach Dam (River Mile 474), Columbia River, 1982.

copepods and daphnid cladocerons), they are virtually absent from flow-through reservoirs except for sloughs or backwaters (Hynes 1970; Page and Neitzel 1976a; Erickson et al. 1977; Walburg et al. 1981). Only Lake Roosevelt, at least above McNary Reservoir on the Columbia River, contains sufficient storage volume allowing reduced water exchange so as to permit significant development of crustacean zooplankton (Stober et al. 1981).

Initial impoundment, with corresponding changes in nutrient concentration, is an unstable period abiologically (e.g. Baranov 1961), and this instability is reflected biologically through the various species transformations with aging of reservoirs (e.g. Ryder et al. 1974). Initial response of sockeye (kokanee) salmon to such transition in Lake Roosevelt and in the off-stream, re-regulating Banks Lake impoundment took the form of population irruption. Like response of sockeye in flow-through reservoirs of the Columbia River would seem precluded considering apparent obligate dependency on crustacean zooplankton as food. Minimal fish species diversity, density, and interaction immediately following impoundment, however, no doubt allowed feeding on a wide range of organisms not normally of major importance in sockeye diets.

Young sockeye are not random but selective feeders, actively sorting and pursuing their prey (Foerster 1968)--learned rather than congenital behavior (Vinyard 1981). Eggers (1980) demonstrates many behavioral repertoires of sockeye salmon in Lake Washington in response to dynamic environmental constraints or opportunities. Chapman and Quistorff (1938) show that while the food of young sockeye in Lake Wenatchee was almost entirely of zooplankton origin, upon entering the Wenatchee River as smolts they fed on water boatmen, beetle larvae, and dipteran larvae. Meehan (1966) reported sockeye from Ruth Lake, which had been reclaimed to eliminate competition from other fishes, as primarily having fed on dipteran larvae and oligochaetes.

Hartman and Burgner (1972) reported similar preferences for sockeye in Black Lake, Alaska, another shallow, naturally eutrophic lake (Table 28). Food habit studies of young sockeye in typical oligotrophic lakes (e.g. Aleknagik, Karluk, Great Central, etc.; Table 28), furthermore, while reflecting a near-total dependency on crustacean zooplankton, also demonstrate the species' ability to ingest other kinds of organisms, particularly dipteran larvae that predominate in flow-through reservoirs (Ricker 1937; Rogers 1968; Hartmand and Burgner 1972; LeBrasseur et al. 1978).

Major deviations in sockeye salmon dietary norms are most closely associated with shifts from typical oligotrophic lakes. Naturally eutrophic lakes, such as Ruth (before reclamation), Midarm, Little Kitoe, and Black (Table 28), biologically had evolved stable fish species assemblages geared to perpetuation of community structure. Lake Washington, by contrast, has a fish species assemblage exhibiting dynamic transformation in response to the destabilizing effects of cultural eutrophication and de-eutrophication (Eggers et al. 1978). Initial impoundment of the Columbia River also had to have involved fish assemblages undergoing transformations in response to changes in physical habitat as well as changes in nutrient content.

Trophic upsurge of new impoundments is well documented (Baranov 1961). Less clear are the biological impacts from untreated wastes formerly discharged to flow-through reservoirs of the Columbia River. One reason for this is that although there has been a dramatic decrease in untreated municipal and industrial wastes entering the Columbia River since 1945, there was no overall accounting until after 1977, when most pollution abatement facilities were operational as mandated in the Federal Clean Water Act of 1972.

In 1971 it was estimated that municipalities and industries produced organic wastes equivalent to those from a population of 2.04 million people, with only the equivalent of the wastes of 68,500 people actually reaching waterways in the mid-Columbia subregion. This did not include wastes from rural populations, irrigated farming, livestock, and other non-point sources suspected of contributing high nitrate-nitrogen concentrations in some reaches of the Columbia River (Pacific Northwest River Basins Commission 1971). Within this perspective it is reasonable to estimate a waste effluent to the mid-Columbia during the 1950's that was the equivalent of the domestic sewage from one million people. Figuring 3.3 pounds per capita-year phosphorus supply (Johnson and Owen 1971, as reported in Dillon and Rigler 1975; this is a higher value than that used in calculating the Lake Wenatchee phosphorus budget but is applicable because legislation to reduce the phosphorus content of laundry detergents had not occurred in the 1950's), I estimate that 3.3 million pounds of phosphorus entered the mid-Columbia annually.

By way of reference, this is 500 times the elemental phosphorus used in the annual fertilization (33 tons elemental nitrogren and phosphorus with an atomic ratio of 10:1) of Great Central Lake that so spectacularly increased sockeye salmon production (LeBrasseur et al. 1978). Proportional increase in sockeye production could not be expected in impoundments of the Columbia River due to tremendous discharge and short water retention time (De Anglis 1980) and especially considering that Great Central Lake has a water retention time of 34 years (Costella et al. 1979). Still, considering the magnitude of phosphorus and inferred nitrogen enrichment, only a small portion need have been sequestered and cycled in food webs over 365 linear miles of impoundments to have had biological impact. Adding to probable impact was that hydroelectric generation was more sporadic in early years, allowing nutrients, especially in summer and early fall, greater transit time.

The effects of noncritical nutrient enrichment of salmonid streams have not been widely documented. However, in the AuSable River, Michigan, the trout population dropped from an average of about 150 lb/acre to about 110 lb/acre after sewage discharge from a city and a fish hatchery was terminated (Alexander et al. 1979). Intensive installation of instream habitat improvement devices failed to reverse the downward trend in growth and biomass of the trout population, pinpointing food limitations as the cause of the decline.

Little is known about long-term species transformations of the Columbia River, except that salmon, steelhead, and sturgeon were once more abundant than at present, and that various exotic fishes have become established. Nevertheless, it can be assumed that optimum rearing opportunity for sockeye in flow-through impoundments was transitory. Space and food resources logically were rather quickly dominated by such species as the ubiquitous northern squawfish, peamouth, and largescale sucker described for Chief Joseph Reservoir by Erickson et al. (1977). While sockeye could revert from specialist to generalist in exploiting the initial population vacuum created by impoundment, a reverse shift could not occur in the same habitat filled with competitive species. Avoiding competition and predation by occupying pelagic areas and feeding on zooplankton, as in typical sockeye lakes, was not an option.

This is not to imply that new impoundments quickly achieved static equilibrium, and that no sockeye could have been reared thereafter. The resulting species composition, abstracted from the original species pool and augmented by introductions, with some species declining and others increasing, coupled with sequential impoundment and variable pollution loading, argues for a lengthy state of flux. Furthermore, even though problems of gas-bubble disease were not noted until the end of the dam-building era, selective effects of gas supersaturation on sockeye salmon, competitive fishes, or both cannot be ruled out in earlier years (Weitkamp and Katz 1980; Bouck 1980; Crunkilton et al. 1980; Montgomery and Becker 1980). Chief Joseph Dam was most responsible for gas supersaturation problems on the mid-Columbia beginning in 1955.

It is impossible to precisely quantify the interactive, integrative, and emergent properties of an ecosystem as large and dynamic as the Columbia River. Of overriding usefulness is sound, if imprecise, explanation of gross deviations in spatio-temporal yield patterns of sockeye, explainable in events and confirmed by ecological principle or specific example. Within this framework, what has happened to Columbia River sockeye fits reasonably well with the available facts with but one exception. Only Lake Wenatchee sockeye reflect a negative trend, from about 45,000-55,000 to about 25,000-35,000 fish, that is not confounded by other influences and could be ascribed to increased dam turbine mortality of smolts in recent years (Fig. 8).

That turbine mortality has become a major limiting factor to sockeye production is suggested by several observations: (1) the decline in hatchery sockeye survival from 1.62% for releases from 1940-1944 to 0.67% for releases from 1960-1963 (Tables 5 and 6); (2) average egg-to-smolt survival, but apparently below-average smolt-to-adult survival (Tables 28 to 35); and (3) the overall decline in spawner:recruit ratios in 1938-1975, even after speculative adjustment for artifacts noted (Table 10; Beiningan 1976). The case for deterioration of smolt passage is strengthened by looking at the relationship between mid-Columbia River discharge and sockeye abundance, which has been most associated with upstream nursery lakes (Table 1) over the past 65 years (Fig. 11).

Generally, when discharge increased, sockeye decreased and vice versa until the late 1950's, except for 1940-1941, when the relationship was voided by lack of egg deposition. In 1941, only 949 adult sockeye reached Rock Island Dam, of which 98 were relocated to Lake Wenatchee to spawn naturally and 851 were hauled to the Leavenworth Hatchery, where all but

Table 35. Estimates of sockeye salmon egg-to-smolt and smolt-to-adult survival, Wenatchee and Osoyoos lakes, based on a four-year run cycle.

Year	Smolt abundance (millions) and origin[a]		Egg deposition two years before[b] (millions)	Egg to smolt survival	Run of adults two years later[c] (thousands)	Smolt to adult survival
			Lake Wenatchee			
1960	0.8	hw	26.5	3.0	22.4	2.8
1961	0.76	hw	10.4	7.3	27.0	3.6
1962	1.06	h	3.2	33.1	10.3[d]	1.0
1962	0.96	w	31.7	3.0	37.4	3.9
1963	0.93	h	3.0	31.0	5.3[d]	0.06
1963	0.37	w	3.0	12.3	6.2	1.7
1965	0.33[e]	hw	19.6	1.7	14.1	4.2
1966	0.68[e]	hw	40.9	1.7	16.3	2.4
1967	0.61[e]	hw	18.2	5.5	34.2	5.6
1973	1.7	w	28.5	6.0	28.6	1.7
1974	0.5	w	16.2	3.0	9.9	2.0
1976	1.09	w	13.4	8.1	7.9	0.7
			Lake Osoyoos			
1965	4.6	w	12.0	38.0	150.0	3.3
1966	6.1	w	88.4	6.9	116.0	1.9
1967	0.94	w	23.7	4.0	39.8	4.2
1973	2.1	w	57.6	3.6	29.2	1.4
1974	0.5	w	20.1	2.4	32.9	6.6
1976	1.55	w	9.0	17.2	10.1	0.6

[a] From Table 30. Abbreviations: h--hatchery fish; w--wild fish.

[b] From state and federal spawning ground surveys summarized largely by Allen and Meekin 1980.

[c] From Table 34.

[d] From Table 5.

[e] Overestimate; does not distinguish between limited numbers of riverine smolts and lacustrine smolts (Tables 33 and 34).

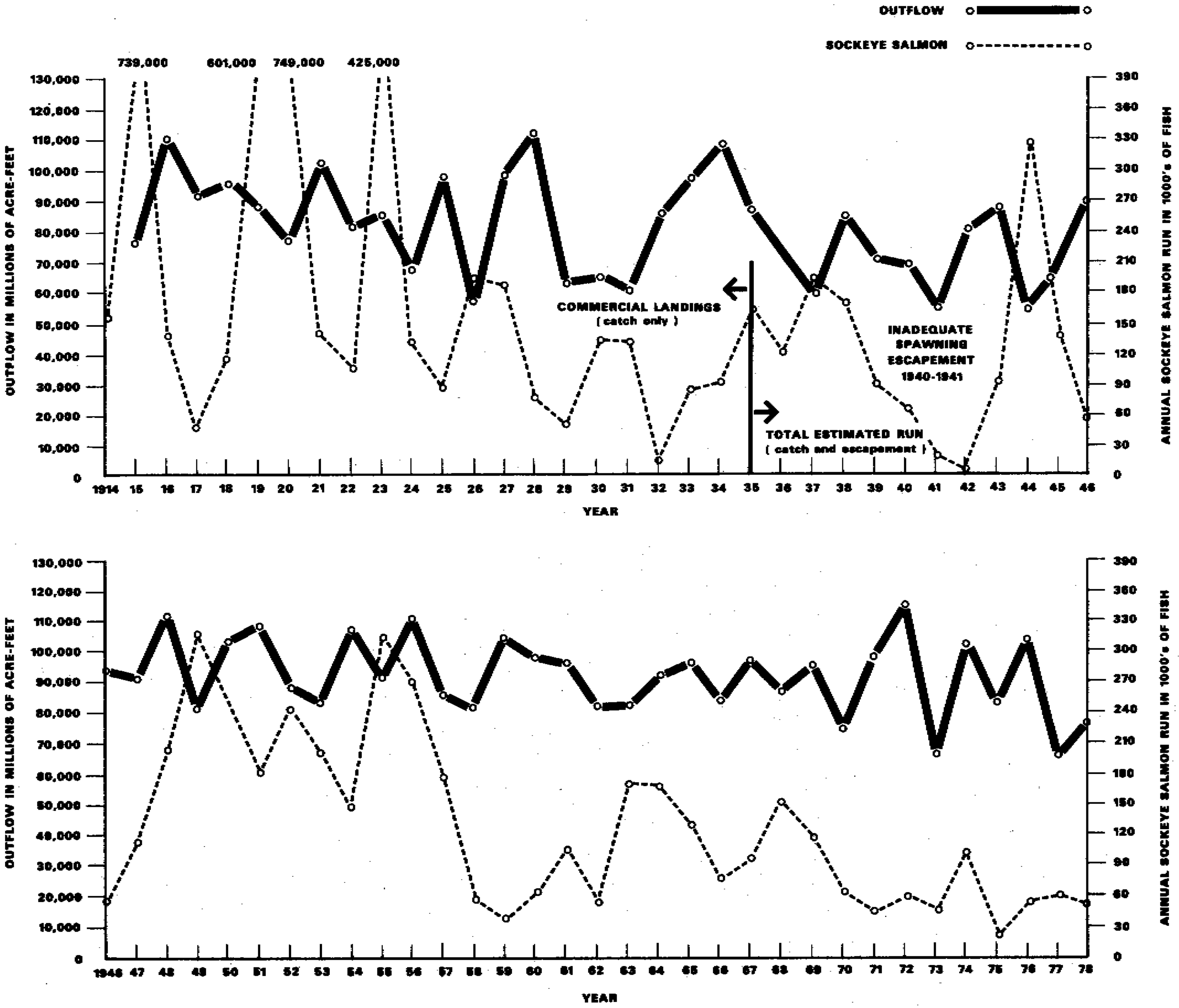

Figure 11. Relationship between Columbia River discharge at Rock Island Dam and annual sockeye salmon run (set back 3 years to correspond with year of juvenile lake residency).

20 died before spawning (Table 2). Not surprisingly, the 1941 brood year produced the record low run of 10,900 sockeye in 1945, which consisted of 10.1% hatchery fish (Table 8) and suspected large numbers of anadromous kokanee originating from Lake Roosevelt. About one-half of the 1940 Rock Island Dam escapement died prior to spawning after relocation to the Leavenworth Hatchery, leaving 3971 spawned at the hatchery and 9691 hauled to Lake Osoyoos. The 1944 run resulting from the 1940 brood amounted to 24,600 fish, of which 98% were calculated as having been of hatchery origin (Table 7 and 8).

Catastrophic mortality of sockeye salmon awaiting sexual maturation in the Icicle Creek bypass of Leavenworth Hatchery occurred in drought years when water temperatures rose into the low to mid-70's (°F). High prespawning mortality of sockeye in the Okanogan River has also been associated with drought years, but with water temperatures reaching 80°F. It is likely then that the 9691 spawners relocated to Osoyoos in the record drought of 1940 suffered an even greater mortality than those hauled to Leavenworth Hatchery, a deduction given further weight by recovery of only 627 (6.5%) carcasses from the lower end of the lake where released (Fish and Hanavan 1948). While 98% of the carcasses were noted as spawned-out (Table 2), reflecting inlake spawning, this too was anomalous in that only limited lake spawning has been noted over the years.

The relationship between higher sockeye abundance and lower discharge can be explained by greater nutrient retention and greater food abundance in nursery lakes during years of low water exchange (Fig. 7). There is no confounding high incidence of devastating winter flooding of spawning grounds, because discharge within the upper-Columbia subregions is principally late spring snowmelt (Pacific Northwest River Basin Commission 1971).

Although such analysis is necessarily qualitative due to lack of total run size and suspected insufficient escapement in pre-1938 years (e.g. only 2227 sockeye reached Rock Island Dam in 1934), the dichotomy indicated is that food abundance, as regulated by nursery-lake water exchange, accounted for a significant share of the variability in annual sockeye production up until about the late 1950's. In later years, turbine mortality of smolts apparently increasingly curtailed the increase in adults that should have accrued form greater smolt production in years of low water exchange (Fig. 12).

There has been about a 50% reduction of adult sockeye from Lake Wenatchee since 1947-1957 that can be ascribed to the effects of turbine mortality involving seven mainstem hydroelectric projects (Fig. 8). Corresponding decline of Osoyoos adult sockeye due to turbine mortality in the same time period logically was of the same magnitude, plus the additional mortality associated with two additional mainstem dams, or about 64% (50% plus 7% for each additional dam). Actual decline in average run size has been about 70% (Fig. 8). Accordingly, I deduce that progressive habitat degradation resulting from cultural eutrophication has been pretty much held in check by high water exchange, as suggested by Stockner and Northcote (1973).

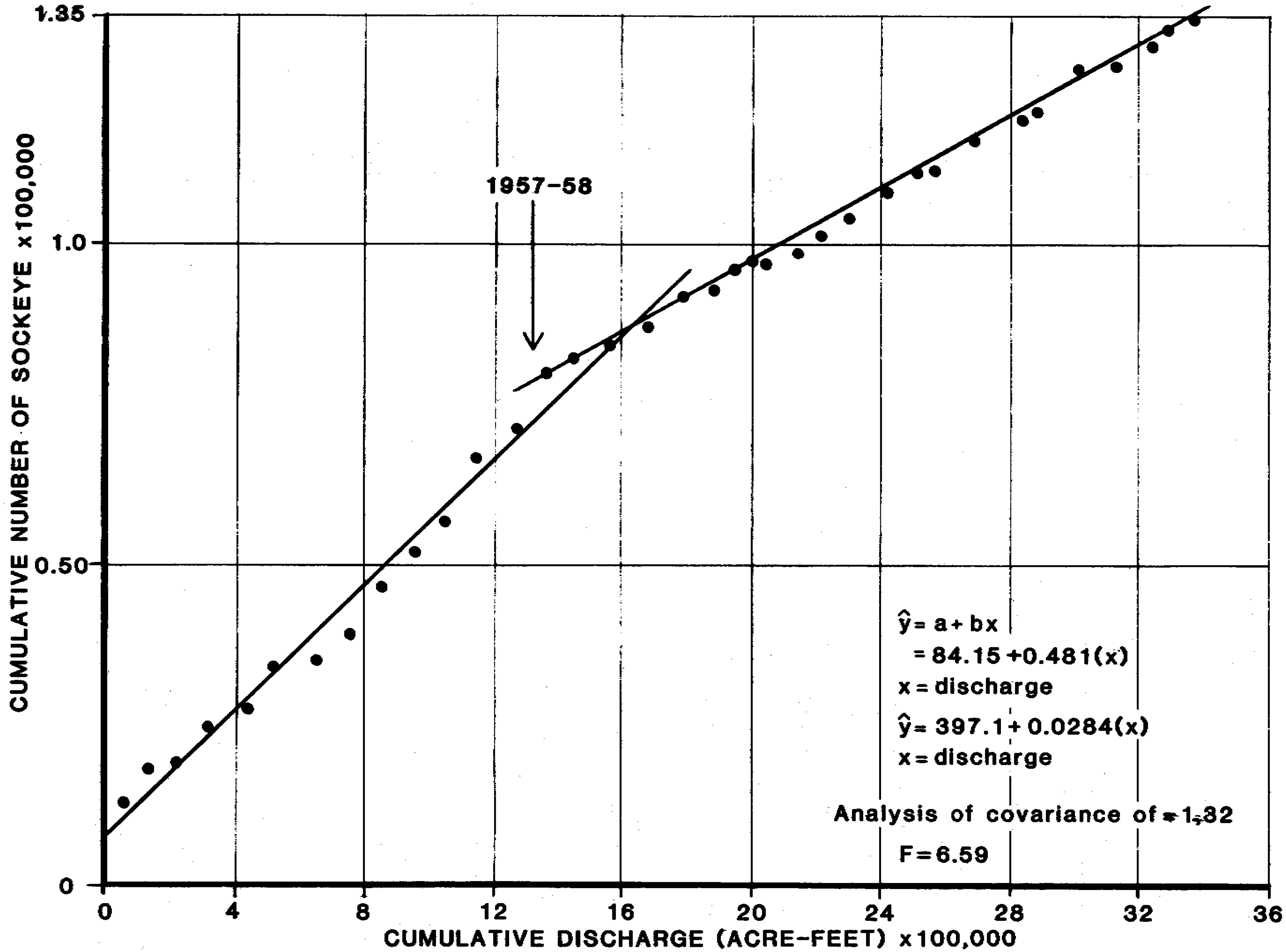

Figure 12. Double-mass curve of discharge (acre-feet) and sockeye production (catch and escapement set back three years to reflect lake residency) for Lake Wenatchee showing a decided change (significant at the 95% confidence level) between 1944 and 1957 and between 1958 and 1978.

MANAGEMENT GOALS, CONFLICTS, AND OPTIONS

If management is to be effective, it is essential to identify the component limiting the resource and any problems associated with a corrective strategy.

GOALS

The overwhelming need, of course, is to reduce smolt mortality at dam turbines. Safe smolt passage is beyond the scope of this report. The Columbia River Basin Salmon and Steelhead Management Framework Plan (Chaney and Holubetz 1981) projected 250,000 adult sockeye returning to the Columbia River as realistically achievable with improved smolt passage and hatchery production. Hatchery production would account for 175,000 of these fish.

Lack of technology in controlling IHN (infectious hematopoietic necrosis) presently precludes effective hatchery propagation of sockeye salmon. Fortunately, the potential for natural production in remaining nursery lakes is perhaps only moderately less than the long-range management goal, and any shortfall might be made up by enhancement of the food supply in Lake Wenatchee.

CONFLICTS

Local residents and the Washington Department of Game (WDG) in 1952 alleged that sockeye salmon management in Lake Wenatchee had been intensified to the point that it was impossible for trout and kokanee to successfully compete with sockeye. WDG requested that the stocking of sockeye be reduced by half and that escapements back to the lake be curbed (letter of John A. Biggs, Director, WDG, May 22, 1952). The U.S. Fish and Wildlife Service replied that excessive harvest, loss to predator fishes, and the record flood of June 1948 were the causative factors in the decline of the sport fisheries (letter of Leo L. Laythe, Regional Director, June 24, 1952).

Undoubtedly, the struggle for survival between kokanee and sockeye was initially masked in the sockeye rehabilitation program for Lake Wenatchee. In four of five years between 1940 and 1945, water exchange of the lake was below average and theoretically there was more food available to ameliorate competitive interaction (Fig. 13). Moreover, in 1941 and 1942, density of rearing sockeye was minimal because only 98 spawners were relocated to the lake (Table 2) and releases of hatchery fish were limited (Table 19).

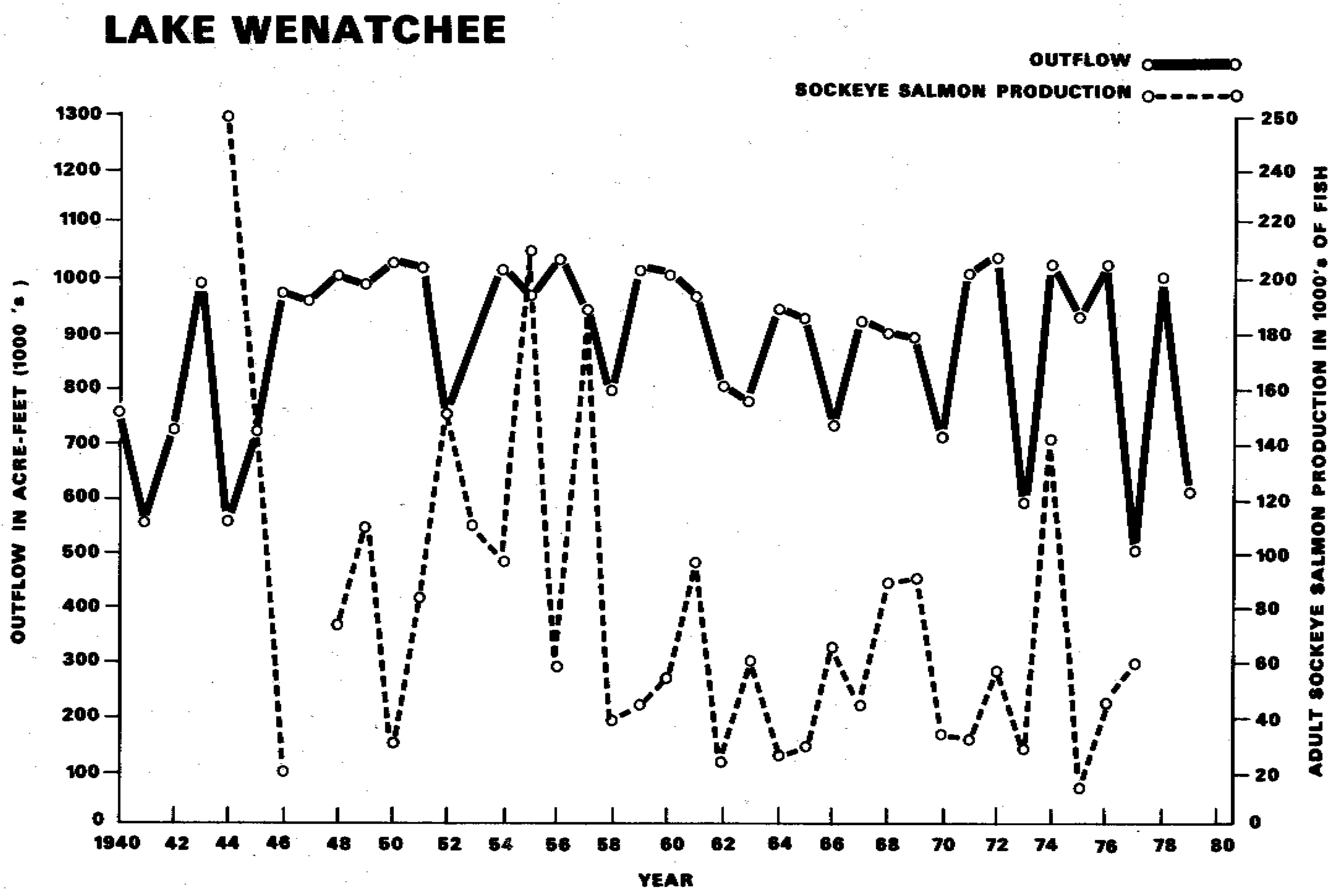

Figure 13. Lake Wenatchee sockeye salmon production (catch and escapement, year N) comparing year of lake residency (year N-3) with discharge.

Peak density of rearing sockeye, as reflected in adult returns three years later (1947 run of 129,400, Table 34), is suggested to have occurred in 1944, a year of very low water exchange (Fig. 13). Recruitment was from 13,664 relocated adults (Table 2) and 1.4 million hatchery fingerlings (Table 19).

From 1946 through 1951, water exchange of Lake Wenatchee was above normal and sockeye production declined (Fig. 13). Water exchange declined in 1952 and there was an upsurge in sockeye production. Kokanee responded similarly, projecting a time-lag of sport-harvested fish two to four years after a given water and brood year.

Following the crash in kokanee numbers associated with the record flood of June 1948, very few kokanee were caught 1949-1950, and these were reported as thin fish 3.0-6.0 inches in length (Table 36). The catch increased to 2000 fish averaging 7.0 inches long in 1951. In 1952, 9055 kokanee were estimated harvested and the first spawners (2500) since 1946 were observed at the Leavenworth Hatchery weir on the White River. The harvest increased again in 1953 to 18,000 kokanee, with average and maximum sizes of 8.75 and 11.0 inches. Peak harvest of 60,000 kokanee was estimated in 1954, followed by a decline to 40,000 fish in 1955 and a still further unknown decline in 1956 (Table 36).

There were no creel censuses on Lake Wenatchee in 1957-1959, but it was about this time that the inverse relationship between low water exchange and high sockeye abundance reversed itself due to suspected turbine mortality of smolts (Fig. 11). Accordingly, one would not expect sockeye abundance, as reflected in return of adults three years later, to corroborate low water exchange.

The year 1958 was below average for water exchange and was followed by three years (1959-1961) of higher-than-average water exchange (Fig. 13). Remnants of the theoretically strong year-class of kokanee resulting from low water exchange in 1958 had a catch rate of 7.5 fish per angler in 1960. In 1961-1962, the catch rate declined to about 4.0 fish per angler. Following below-average lake water exchange in 1962 and 1963, the catch rate increased to 6.2 and 7.4 kokanee per angler in 1963 and 1964. Total catch also increased from 17,408 to 31,549 kokanee from 1963 to 1964 (Table 36).

Kokanee harvest ranged from less than 1.0 to 3.0 pounds per acre in Lake Wenatchee. Homogeneous small size of up to five year-classes in the population suggests, however, that actual standing crop of kokanee conceivably rivaled that of juvenile sockeye (Table 30). For example, large numbers of kokanee (4382 and 8764) were released as being under the minimum 6.0-inch size limit in 1963 and 1964 (Table 36).

Table 36. Surviving observations of kokanee, Lake Wenatchee (Leavenworth Hatchery biologist* coordinated voluntary creel census and interviewed anglers weekends and holidays 1949-1956; Washington Department of Game (WDG) creel check 1960-1962; U.S. Bureau Commercial Fisheries (BCF) creel census 1962-1964).

Year(s)	Observations
1920*	Kokanee fishing popular since 1920 (parallels record for nearby Lake Chelan where kokanee introduced 1917; Campbell 1977).
1930s	Kokanee overpopulated; 5.0" spanwers common (WDF 1938).
1940-48*	300 anglers/day common to record flood of June 1948, when kokanee all but disappeared. Av. size - 7.0". 650 females and 600 males spawned from L. Wenatchee and White rivers 1944; av. 7.5". Larger in 1945; 400 eggs/female vs. 308 eggs/female in 1944.
1949-50*	Few caught; av. size 3.0-4.0" (6.0" max.); thin.
1951*	2,000 harvest, size - 7.0". 205 spawned from tributaries, 5.0"-6.0". Av. size 1949-51 - 5.0" (Gangmark and Fulton 1952).
1952*	9,055 harvest; 2,500 spawners in tributaries, first observed since 1946.
1953*	18,000 harvest (14,216 recorded). Av. size - 8-3/4"; max. - 11.0". Scale readings: 27%, 3-year-olds; 36%, 4-year-olds; 37%, 5-year-olds. 1,820 spawners counted in White River, est. total - 5,500.
1954*	60,000 harvest (56,635 recorded). Peak catch May 10-30 (5,075 fish May 16). 1,000 spawners in White River, but water too high for good observations.
1955*	40,000 harvest (34,312 recorded). Large schools of spawners in White River, but water too high for accurate counts.
1956*	Fishing not as good as in 1955, but still excellent.
1957-59	No creel census maintained.
1960	WDG creel check - 1,141 anglers; 8,584 kokanee (7.5/angler).
1961	WDG creel check - 1,392 anglers; 5,442 kokanee (3.9/angler).
1962	WDG creel check - 520 anglers; 2,103 kokanee (4.0/angler). Sub-legal (<6.0") creel census (BCF) catch - 7,013.

Table 36 (continued).

Year(s)	Observations
1963	17,408 harvest (6.2/angler). Sub-legal (<6.0") catch - 4,382.
1964	31,549 harvest (7.4/angler). Sub-legal (<6.0") catch - 8,764.

See also Appendix 1.

OPTIONS

Sport Fishing Allocation

Sockeye salmon are not generally recognized as sport fish because of their purported lack of catchability in freshwater. Anglers pioneered methods of fishing sockeye salmon in Lake Washington in the 1970's. In high-abundance years anglers now take about 10% of runs or 30,000-40,000 sockeye salmon by hook-and-line (James Aimes, WDF, personal communication). Similar fishing opportunity is possible in North Central Washington in equitably redistributing the rent from the sockeye resource.

Predator Control

Control of salmon predators has had a mixed history, with far more failures than successes (Meachum and Clark 1979). Larkin (1979) cautioned not to expect long-term benefits to the prey from predator control. He pointed out, however, that where predators are exerting depensatory mortality (Neave 1952) the best way of giving the prey a chance to increase is to provide respite from predation.

Compensatory predation as described by Eggers et al. (1978) for Lake Washington, similarly disrupted by man, more than likely is the prevailing mode of predation on sockeye juveniles in Lake Osoyoos. Omnivorous northern squawfish are facultative predators in both lakes. Wahle et al. (1978) concluded that the disappearance of two million hatchery sockeye in Lake Wenatchee in each of 1962 and 1963 (Table 35) was largely caused by predation. Thompson and Tufts (1967) documented heavy predation by bull charr[4] and squawfish during the period of hatchery release to the lake. The predilection of predators for prey that are conspicuously different from other prey of the same kind (Parson et al. 1970, quoted in Larkin 1979) applies to hatchery fish before acclimation to wild existence. Thompson (1959) examined the stomach contents of 3546 squawfish from the Columbia River and found that most of the salmon eaten consisted of recent hatchery releases.

Thompson and Tufts (1967) also examined 94 bull charr and 280 squawfish prior to and after hatchery releases in fall and found that 19% of the charr and less than 1% of the squawfish had eaten 43 sockeye. Twenty-seven of 75 bull charr caught by anglers during spring-summer contained 61 sockeye; none of 54 squawfish examined contained sockeye (unpublished data of Roy Wahle, NMFS). The remains of 12 sockeye were found in stomachs of 113 squawfish and the remains of 26 sockeye in the stomachs of 39 bull charr in the summers of 1949-1951 by Gangmark and Fulton (1952). These data do not demonstrate depensatory predation, nor do they implicate northern squawfish as a major predator of fingerling-size sockeye in Lake Wenatchee. However, predation by squawfish on newly-emerged sockeye fry or in unusual circumstances could

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[4] *Salvelinus confluentus* and not *S. malmo*, Dolly Varden charr (see caption of Fig. 14 for explanation).

be severe (e.g. below dams during smolt outmigration or in a supplemental feeding program discussed next).

Regier et al. (1979) marshals a convincing case that in "virgin" ecosystems, a large fraction (50%) of the total biomass of fish consisted of large, old individuals that fed on organisms two or more trophic steps removed from phytoplankton. The early abundance and large size of bull charr in Lake Wenatachee can only be interpreted as reflecting such phenomena (Fig. 14). Bull charr live 10-20 years, reach a size of up to 30 pounds, are mainly piscivorous when given the opportunity, and are easily caught (Behnke 1980). In fact, hook-and-line predation by man on large bull charr amounts to depensatory mortality, and it can be concluded that predation by bull charr on sockeye in Lake Wenatchee is less now than historically.

With change in habitat, harvest, or both, virgin ecosystems inevitably change (Larkin 1979). The evidence shows that such stresses tend to deform a fish community toward dominance by small-to-medium-sized trophic generalists (cyprinids, percids, clupeids, and osmerids) and away from large piscivores and specialist benthivores (Regier and Loftus 1972; Spangler et al. 1977; Regier et al. 1979). With Lake Wenatchee dominated by similar trophic generalists, large bull charr may have qualified originally as a "keystone predator" (Paine 1966), by reducing competitive interactions at lower trophic levels (Meachum and Clark 1979). Such a niche role would be appropriate today.

Wild salmonids are a declining resource, while fishing demand is insatiable. Once angling pressure reaches a certain point, and this point can vary enormously between species, recycling the catch is the most viable management option to maintain older, larger fish in the population. For bull charr in Lake Wenatchee, as little as ten hours per acre of angling may result in over-exploitation of larger fish (Larry Brown, WDG, personal communication).

Fertilization--Supplemental Feeding

In 1975, WDF proposed fertilizing Lake Wenatchee to increase sockeye production. The proposal died due to a lack of interest on the part of local residents.

It is not at all clear whether fertilization would significantly increase the food supply for the target species in Lake Wenatchee. Why this is so is found in the results from lake fertilization projects reviewed by Stockner (1979):

1. Nutrient enrichment leads to increased autotrophic production, which in most cases has led to increased zooplankton biomass.
2. For some (not all) lakes, zooplankton biomass increases and changes in species diversity have enhanced the nursery capacity of the lake(s) for resident and anadromous salmonid populations, as shown by faster growth and/or higher survival rates.

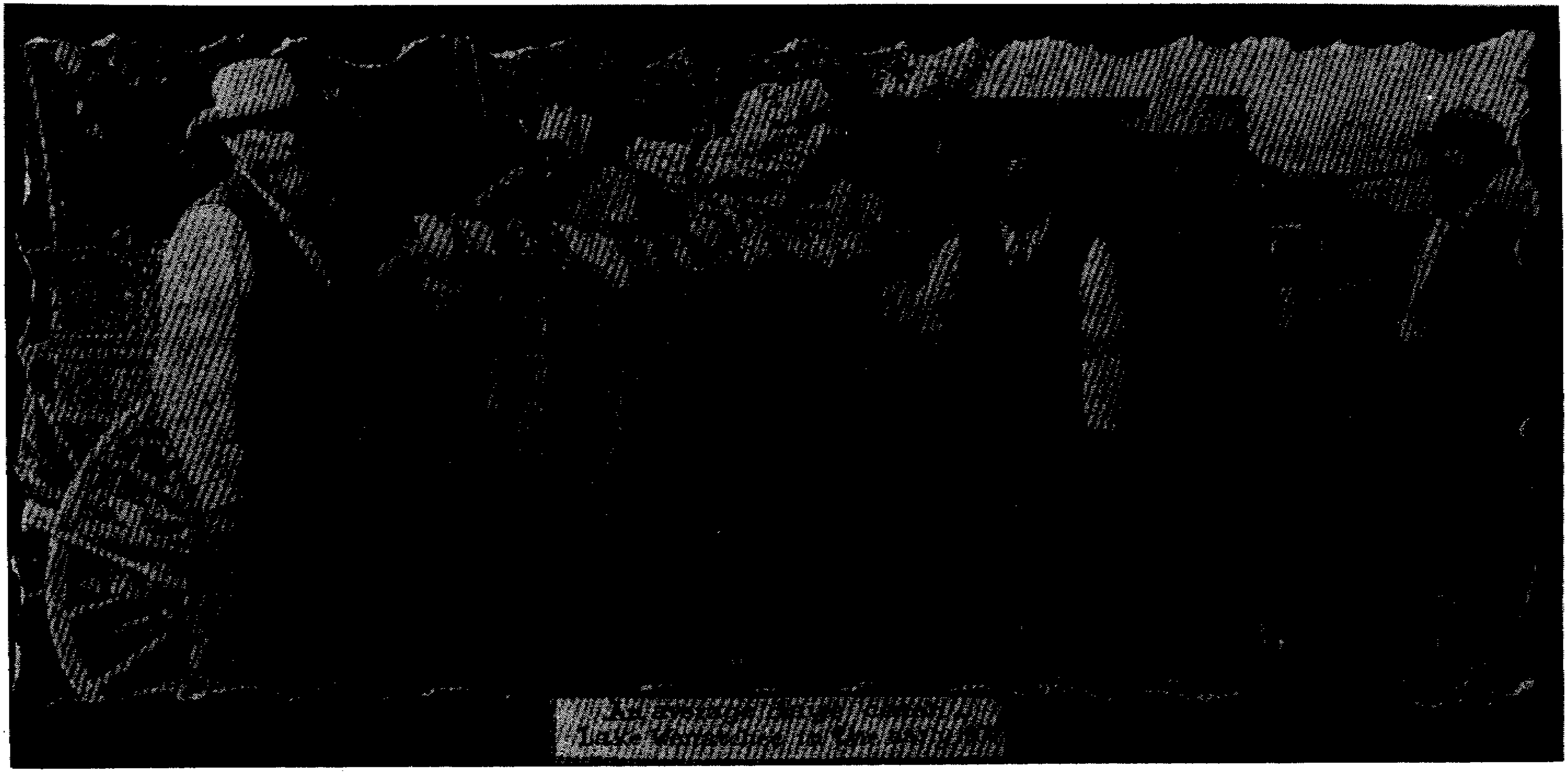

Figure 14. An average day's catch, Lake Wenatchee in the early 1900's. Lack of sufficient detail precludes rigorous identification, but massive heads and jaws, relative blunt snouts, eyes near tips of heads, etc. (i.e., Cavender 1978) indicate fish shown as bull charr (personal communication, Robert Behnke, Co. St. Un.). For years the bull charr and the Dolly Varden charr have been combined under Salvelinus malma. The latter name is correctly applied to the form which is generally anadromous and not highly piscivorous in freshwater. The bull charr or bull trout, S. confluentus, a name inspired by its large, broad head, is highly piscivorous and commonly associated with inland waters of the Columbia River Basin (Armstrong and Morrow 1980, Behnke 1980, Cavender 1980).

3. For a variety of reasons (many as yet unexplainable), treated lakes have responded differently to fertilization, suggesting that extrapolation of results from one to another, treated to untreated, could be erroneous and/or dangerous.

4. Lake recovery can be relatively fast (within a year or two) following cessation of enrichment.

Of primary concern in Lake Wenatchee is the high water exchange. Crustacean zooplankton used as food by sockeye salmon usually attain a spring maximum in abundance and sometimes a less-well-defined fall maximum in most lakes (Pennak 1953). Appreciable abundance of zooplankton in Lake Wenatchee is delayed until late summer-early fall. It seems clear that this displacement in the seasonal occurrence of zooplankton is governed by variable water exchange (Fig. 7). Small zooplankton species may reach reproductive age in about ten days and the larger species in about twenty days. These generation times are a minimum of one-half to one-fifth of the average water retention time during snowmelt, and do not allow substantial biomass development during this period of rapid water exchange. Primary production is also limited at this time, due to rapid flushing of nitrogen. The discrepancy between necessary time for reproduction of zooplankton and/or buildup of nitrogen content and flushing rate of the lake becomes even more exacerbated in years of above-normal runoff. In the record flood of June 1948, associated with the crash in the kokanee population, one complete water exchange occurred in a 20-day period; and in 1946 associated with an extreme low in sockeye abundance (Fig. 13), average yearly exchange (2.2) occurred in May and June alone.

If important food items are not available for initial growth of sockeye, survival will be poor (Foerster 1968). Egg-to-smolt survival of 1961 and 1962 brood year sockeye in Lake Wenatchee was estimated at 3.0% and 12.4%. Sockeye not subjected to low food abundance during spring-early summer, due to hatchery existence from time of parental spawning until release back to the lake the following fall, had egg-to-smolt survival rates of 33.1% and 31.0% (Table 35, years 1962 and 1963).

How availability of food affects survival is also evidenced in the introduction of opossum shrimp (*Mysis relicta*) on kokanee in a number of western lakes. In deep lakes, where *Mysis* escape major predation by settling on the bottom during the day and as a consequence attain high abundance, they may virtually eliminate zooplankton, as in Lake Tahoe, California (Cordone 1980), or alter species composition and temporal distribution, as in Lake Pend Oreille, Idaho (Bowler and Rieman 1980).

Bowler and Rieman (1980) documented the severe decline of kokanee in Lake Pend Oreille after *Mysis* became established. Rieman and Falter (1981) showed how crustacean zooplankton only appeared and increased in abundance as the mysids became seasonally isolated from near-surface strata by increasing thermal stratification and transparency. Displacement in kokanee food availability during spring-early fall in Lake Pend Oreille corresponds to to the prevailing seasonal occurrence of zooplankton in Lake Wenatchee, resulting from high water exchange at the time of spring snowmelt (Fig. 7).

Sockeye fry emerge from the gravel of the Little Wenatchee and White Rivers and emigrate to Lake Wenatchee during late March-early May (Table 23). Juvenile sockeye are opportunistic trophic generalists, with a demonstrated capability of searching out and selecting desired foods. It would seem that the fry might be trained to use hatchery feed dispensed from automatic or demand feeders located in the inflow area of the lake. Whether one would continue to feed throughout the entire growing season or switch to fertilization (with ammonium sulfate[5]) during the period when water retention is sufficient to allow substantial development of zooplankton is problematical. It is possible, however, that direct feeding prior to and during the period of rapid water exchange might be sufficient in attaining a large increase in survival of fry that would not subsequently overtax food and space resources. During the first 2.5 months, mortality of fry was 65.4% in Cultus Lake, then was linearly related to period of lake residence between months 3.5 and 9.5 (Foerster 1938). As the year advanced and sockeye increased in size, mortality dropped off, a phenomenon reflected in the appreciable (one-third) overwinter carryover of hatchery sockeye in Lake Wenatchee, but with little or no growth between time of fall release and outmigration the following spring.

The record flood of June 1948, which evidently severely depressed kokanee and sockeye survival in Lake Wenatchee, was associated with an above-average run (163,600) of sockeye from Lake Osoyoos in 1951 (Table 34). Water exchange of Osoyoos in March-May prior to June 1948 flooding was well below normal. This combined with earlier emergence of fry (Allen and Meekin 1980), due to warmer water temperatures, and greater food abundance, even during record-year (1972) water exchange (Fig. 5), could have allowed fry to have reached some threshold size critical to high survival.

Whatever the answers to these questions, they can only be gained through an assessment of essential factors, followed by a prototype plan of action. Stockner (1979) provides guidelines in arriving at and evaluating such a program.

There are also a number of other areas where new knowledge could provide benefits. Especially intriguing is the sevenfold increase in adult sockeye runs, compared to only a 2.6 increase in smolts, resulting from fertilization of Great Central Lake (Le Brasseur et al. 1978). Even in this well-documented project, however, many of the links in the sockeye salmon food chain remained obscure, including the mechanisms responsible for the surprisingly large increase in adult returns. In this respect it should not be overlooked that despite the high egg-to-smolt survival for hatchery sockeye noted for Lake Wenatchee, wild smolts produced four to five times as many returning adults as hatchery smolts (Table 35, years 1962 and 1963).

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[5] Sulfur, as well as nitrogen, is severely limited in watershed soils (Klock et al. 1971).

Length of lake residence among sockeye is at least partially dependent upon growth. The physiological minimum limit for adequate hypoosmoregulatory capacity is near 4.0 g (Clarke et al. 1978), which corresponds roughly to the weights and lengths of small smolts (Table 21). Growth in turn is inversely related to population density (Johnson 1956, 1958; Ward and Larkin 1964; Ruggles 1965; Bjornn et al. 1968). Bjornn et al. (1968) proposed the following relationships among size of juveniles and duration of lake residence: (1) if density is low and growth good (85-110 mm), smolts migrate at age one; (2) if density is low and growth unusually good (≥ 100 mm), migration tends to be delayed another year; (3) if densities are high and growth rates low (≤ 85 mm), juveniles tend to hold over one more year. These density-growth-migration relationships are not in full agreement with the rather extensive literature on the subject. The conclusions are drawn from another Columbia River sockeye ecosystem (Red Fish Lake) similar to Lake Wenatchee, however, and represent the prevailing view that migration is induced by some combination of size and density of young, as noted by Rounsefell (1958); at a high density the fish leave at an earlier age because of population pressure, but only if they have attained a threshold size. Population pressure had to have been a major factor for the respectable number of anadromous kokanee resulting from the kokanee released to Lake Wenatchee in 1945 (Table 6, experiment 22) elaborated on by Ricker (1972) earlier.

Smolt production, then, is theoretically optimized by a biomass made up of juveniles that are large enough to smolt after one year of lake residence, but not so large as to create carryovers, residual sockeye or kokanee that will compete for food with the next year-class of developing juveniles. Lake Wenatchee sockeye grow to a threshold migration size of about 75-85 mm (range 50-124 mm) in one year (Table 22). At this size, the energy expenditure used to capture food organisms, apparently, increasingly leaves little energy available for growth. This is reflected in small size of kokanee with longevity of up to five years. The same trophodynamics is exhibited by rainbow trout in reservoirs where the major component of the diet is zooplankton and growth all but stops at about 12.0 inches (Behnke, in press).

Energy used in maintenance of carryover and residual sockeye/kokanee is energy dissipated from production of yearling sockeye smolts. How a population of older, larger bull charr in Lake Wenatchee would benefit anadromous sockeye is illustrated by the preference of predators for devouring foods of the largest possible size, with morphological features imposing a limiting and optimum size of the principally utilized prey (Ivlev 1961). This trophic principle does not exclude ingestion of smaller prey, but decreases utilization below the optimum size. As a result, large bull charr could be expected to primarily consume residual sockeye/kokanee.

Habitat Preservation

Although better than 95% of the Wenatchee and White River watersheds are in National Forest ownership, ironically much of the stream area used by sockeye salmon for spawning is on private land. The stability of these areas in their natural state is very high, but development for any purpose makes them extremely sensitive to channel cutting (Table 27). These critical areas should be preserved in their natural state.

Water Quality

Short water retention time appears to have temporarily saved Lake Osoyoos from the more serious effects of cultural eutrophication. Stockner and Northcote (1974) noted that much of the pollution to Osoyoos was from uncontrollable diffuse sources and a substantial reduction in load was possible only by attitudinal or institutional change. Water quality deterioration, together with increased water demands by agriculture, industry, and a growing population, has been a matter of particular concern to the public on both sides of the international border. This is best reflected with costly programs to control Eurasian water milfoil (*Myriophyllum spicatum*; Newroth 1977; U.S. Army Corps of Engineers 1979), which has spread dramatically throughout the Okanogan drainage since 1971 (Pacific Northwest River Basins Commission 1977).

Nuisance growths of water milfoil are stimulated and sustained by favorable environmental factors, not the least of which is an abundance of nutrients. Mechanical or chemical control treats symptoms rather than causes and is, therefore, of little long-term benefit in solving the problem.

The interplay between man and nature has often in the past and can in the future create environments that are ecologically stable, economically profitable, esthetically rewarding, and favorable to the continued growth of civilization (Dubos 1973). Pollution of the environment has been defined as a misplaced resource in a world of diminishing resources. Capitalizing on such a resource by design requires better understanding of nutrient cycling in the Columbia River. Although the level of waste treatment has increased over the years to a minimum of secondary, it must be borne in mind that secondary treatment does not remove nutrients, but actually changes them to a more available form for plants and animals.

Management of Mainstem Reservoirs

If mainstem Columbia River reservoirs once served as nursery-lake habitat for sockeye salmon, presumably some fraction of this existing habitat (163,158 acres) could be made to function similarly in the future. Korn and Smith (1971) demonstrated that Columbia River basin reservoirs do have management potential for anadromous salmonids, but they dealt with off-stream storage reservoirs, in which the problems are different than in flow-through reservoirs.

Restoration of Extirpated Runs

Bumping, Cle Elum, Kachess and Keechelus Lakes in the Yakima River drainage originally contained 6597 surface acres (Table 1). Davidson (1965*b*) believed that a large share of Columbia River sockeye originated in these lakes prior to isolation by crib dams in the early 1900's. Today these natural lakes are unladdered irrigation reservoirs subject to severe annual drawdown and do not offer much prospect for sockeye restoration.

There are six lakes comprising 3445 acres on the Salmon River, Idaho accessible to sockeye salmon, with a remnant run persisting to Redfish Lake and effort under way to restore a run to Stanley Lake. Observations and discussions with local residents led Evermann in 1894 to believe that these lakes were very important rearing areas for Columbia River sockeye (Bjornn et al. 1968). On the other hand, Fulton (1970) indicated that Salmon River ecosystems were never large producers of sockeye.

By far the greatest potential for restoration of sockeye salmon in the Columbia Basin are Lakes Skaha and Okanogan, upstream of Lake Osoyoos on the Okanogan River. Although early abundance is unclear, the two lakes have a combined area of close to 91,000 acres (Table 1), and only two small fish ladders would be needed to make them accessible to sockeye salmon. However, such a proposal has not been acceptable to Canadian authorities in the past (Barnaby 1950; Gangmark and Fulton 1952).

Okanogan and Skaha Lakes provide a sport fishery of considerable value, dominated by kokanee (8-14 inches in length) followed by rainbow trout (Pinsent et al. 1974). This is similar to downstream Lake Osoyoos, although smallmouth bass are increasingly important in the fisheries (Ken Williams, WDG, personal communication).

Sport-fish benefits from sockeye restoration in Okanogan and Skaha lakes might prove illusory. Limited tributary spawning areas already limit resident sport-fish potential in the lakes (Pinsent et al. 1974). Then there is the high incidence of prespawning mortality of sockeye associated with high water temperatures in the Okanogan River. Returning adults would also have a longer migration through smaller channels in reaching the upper drainage and be more vulnerable to high water temperatures as well as poaching, which continues from that described by Gangmark and Fulton (1952).

REFERENCES

Alexander, G.R., W.J. Buc, and G.T. Schnicke. 1979. Trends in angling and trout populations in the main Au Sable and North Branch Au Sable rivers from 1959-79. Mich. Dep. Nat. Resources, Fish. Res. Rep. 1865. 59 p.

Allen, R.L. and T.K. Meekin. 1973. Columbia River sockeye salmon study. 1972 prog. rep. Wash. Dep. of Fish., Olympia, Wa. 60 p.

Allen, R.L. and T.K. Meekin. 1980. Columbia River sockeye salmon study, 1971 - 1974. Prog. rep. No. 120, Wa. Dep. Fish., Olympia, Wa. 75 p.

Anas, R.E. and J.R. Gauley. 1956. Blueback salmon, Oncorhynchus nerka, age and length at seaward migration past Bonneville Dam. USFWS, Spec. Sci. Rep. Fish. 185, Wa., D.C. 46 p.

Armstrong, R.H. and J.E. Morrow. 1980. The dolly varden charr, Salvelinus malma. In: Charrs, salmonid fishes of the genus Salvelinus. (E.K. Balon ed.). Dr. W. Junk, The Hague, Netherlands, 99-140.

Bachmann, R.W. and J. R. Jones. 1974. Phosphorus inputs and algal blooms in lakes. Iowa St. Jour. Res., 49(2):155-160.

Baranov, I.V. 1961. Biohydrochemical classification of reservoirs in the European USSR. Pages 139-183 in P.V. Tyurin, editor. The storage lakes of the USSR and their importance for fishery. Bulletin of the State Scientific Research Institute of Lake and River Fisheries, Volume 50. (Translated from Russian), International Program for Scientific Translations, Catalog No. 1638-50. U.S. Dept. of Comm., Wa., D.C.

Barnaby, J.T. 1950. Interim report of Okanogan flood control project. Processed rep. USFWS, Seattle, Wa. 5 p.

Barrachlough, W.E. and D. Robinson. 1977. The fertilization of Great Central Lake. III. Effect on juvenile sockeye salmon. U.S. Nat. Mar. Fish. Serv. Fish Bull. 70:37-48.

Becker, C.D. 1971. Response of Columbia River invertebrates to thermal stress. Battelle, Pac. Northwest Lab., Richland, Wa. No. 1550, Vol. 1, Part 2, p. 217-219.

Behnke, R.J. 1980. A systematic review of the genus Salvelinus. In: Charrs, salmonid fishes of the genus Salvelinus (E.K. Balon ed.) Dr. W. Junk Publishers, Hague, Netherlands, 441-480.

Behnke, R.J. (in press). The native trouts of western North America. USFWS.

Beiningen, K.T. 1976. Columbia River Fisheries Project: Fish runs. In: Investigative reports of Columbia River fisheries project. Pacific Northwest Regional Commission, Vancouver, Or. E 65.

Bell, M.C., Z.E. Parkhurst, R.G. Porter, and M. Stevens. 1976. Effects of power peaking on survival of juvenile fish at lower Columbia and Snake River dams. U.S. Army Corps of Eng. (DACW57-75-C-0173). 35 p. and appendices.

Bilton, H.T. 1970. Comparison of the fecundity of sockeye salmon in the Skeena River catch with the fecundity of those in the escapement. Fish. Res. Bd. of Can. MS Rep. 1096: 1-8.

Bilton, H.T. 1978. Returns of adult coho salmon in relation to mean size and time at release of juveniles. Can. Fish. Mar. Ser. Tech. Rep. 832, 73 p.

Bilton, H.T. 1980. Return of adult coho salmon in relation to mean size and time at release of juveniles to the catch and the escapement. Can. Fish. Mar. Ser. Tech. Rep. 941, 41 p.

Bjornn, T.C., D.R. Craddock, and D.R. Corley. 1968. Migration and survival of Redfish Lake, Idaho, sockeye salmon, Oncorhynchus nerka. Trans. Amer. Fish. Soc. 97(4): 360-373.

Booth, D.M. 1969. Water quality studies in Osoyoos Lake, B.C. MS Thesis Un. of British Columbia, Dep. of Agricultural Mechanics. 180 p.

Bouck, G.R. 1977. The importance of water quality to Columbia River salmon and steelhead. Trans. Amer. Fish. Soc., Spec. Publ. #10, p. 149-154.

Bouck, G.R. 1980. Etiology of gas bubble disease. Trans. Amer. Fish. Soc. 109(6): 703-707.

Bouck, G.R. and G.A. Chapman, P.W. Schneider, D.G. Stevens. 1975. Effects of holding temperatures on reproductive development in adult sockeye salmon (Oncorhynchus nerka). Proceedings 26th Annual Northwest Fish Culture Conference, p. 24-40.

Bowler, B. and B. Reiman. 1980. Status of kokanee stocks in Priest, Pend Oreille and Coeur d'Alene Lakes, Idaho. Proc. West. Assoc. St. Game and Fish Comm., Kalispell, Mt. 494-495.

Brooks, J.L. and S.I. Dodson. 1965. Predation, body size and composition of plankton. Science 150: 28-35.

Bryant, F.G. and Z.E. Parkhurst. 1950. Survey of the Columbia River and its tributaries; area III, Washington streams from the Klickitat and Snake Rivers to Grand Coulee Dam, with notes on the Columbia and its tributaries above Grand Coulee Dam. USFWS, Spec. Sci. Rep. 37, 108 pp.

Bryant, M.D. 1976. Lake Washington sockeye salmon: Biological production, and a simulated harvest by three fisheries. Ph.D. thesis. Un. of Wa. Seattle. 159 p.

Burgner, R.L. 1964. Factors influencing production of sockeye salmon (Oncorhynchus nerka) in lakes of southwestern Alaska. Verh. Internat. Verein Liminol. Stuttgart, XV: 594-513.

Burgner, R.L., C.J. Di Costanzo, F.J. Ellis, G.Y. Harry, Jr., W.L. Hartman, O.E. Kerns, Jr., O.A. Mathisen, and W.F. Royce. 1969. Biological studies and estimates of optimum escapements of sockeye salmon in the major river systems in southwestern Alaska. USFWS, Fish. Bull. 67(2): 405-459.

Burner, C.J. 1951. Characteristics of spawning nests of Columbia River salmon. USFWS, Fish. Bull. 61(52): 97-110.

Burrows, R.E. 1957. Diversion of adult salmon by an electrical field. USFWS, Spec. Sci. Rep. 246, 11 p.

Cairns, J. 1977. Aquatic ecosystem assimilative capacity. Fish. Bull. Amer. Fish. Soc. 2(2): 5-7.

Calkins, R.D., W.F. Durand, and W.H. Rich. 1939. Report of the board of consultants on the fish problems of the upper Columbia River, Section II. Stanford Un., Calif., 127 p.

Campbell, D. 1977. Lake Chelan historical: Interview of Harry Buckner, old-time resident, Stehekin, Washington, 1974. L. C. History Notes, Vol. V No. 1.

Canada Fisheries Service and Wa. Dep. Fish. 1973. Pacific salmon: Population and habitat management requirements. Okanogan Study Committee, Preliminary Rep. #16, 45 p.

Carlson, R.E. 1977. A trophic state index for lakes. Limnol. Oceanogr., 22: 361-369.

Cavender, T.M. 1980. Systematics of Salvelinus from the North Pacific Basin. In: Charrs, salmonid fishes of the genus Salvelinus (E.K. Balon ed). Dr. W. Junk Publishers, Hague, Netherlands, 295-322.

Cedarholm, C., E. Salo, B. Edie, J. Togart, D. Martin, C. Noggle, and L. Reid. 1980. The Clearwater River effects of logging road caused sediment on salmonids study. Nat. Council of the Paper Industry for Air and Stream Improvement, Inc., Portland, Ore. 16 p.

Chance, D.H. 1973. Influence of the Hudson's Bay Company on the native cultures of the Colville District. Northwest Anthropological Res. Notes, Vol. 7, No. 1, Part 1, 114 p.

Chaney, E. 1978. A question of balance; water/energy - salmon and steelhead production in the upper Columbia River basin. Pac. Northwest Res. Info. Center, Inc., Eagle, Ida., 29 p.

Chaney, E. and T. Holubetz. 1981. Columbia River Basin salmon and steelhead management framework plan. Columbia River Fisheries Council, Portland, Or. 38 p. plus appendix.

Chapman, D.J., M. Van Hyning, and D.H. McKenzie. 1982. Alternative approaches to base run and compensation goals for Columbia River salmon and steelhead resources. Battelle, Pac. Northwest Lab., Richland, Wa. 56 p.

Chapman, W.M. 1941. Observations on the migration of salmonid fishes in the Upper Columbia River. Copeia, No. 4, 240-242.

Chapman, W.M. 1943. The spawning of chinook salmon in the main Columbia River. Copeia 1943: 168-170.

Chapman, W.M. and E. Quistorff. 1938. The food of certain fishes of north central Columbia River drainage, in particular, young chinook salmon and steelhead trout. Wa. Dep. Fish., Biol. Rep. 37A, 14 p.

Chelan County PUD. 1980. Draft environmental impact statement. Dryden hydroelectric project. FERC no. 2843. 174 p. and appendices.

Clarke, W.C. and H.D. Smith. 1972. Observations on the migration of sockeye salmon fry in the lower Babine River. Jour. Fish. Res. Bd. Can. 29(2): 151-159.

Clarke, W.C., J.E. Shelbourn and J.R. Brett. 1978. Growth and adaptation to seawater in underyearling sockeye and coho salmon subjected to regimes of constant or changing temperature and daylight. Can. Jour. Zool., 56: 2413-2421.

Colby, P.J., G.R. Spangler, D.A. Hurley, and A.M. McCombie. 1972. Effects of eutrophication on salmonid communities in oligotrophic lakes. Jour. Fish. Res. Bd. Can. 29(6): 975-983.

Cordone, A. 1980. The kokanee salmon in Lake Tahoe, California/Nevada. Proc. West. Assoc. State Game and Fish Comm., Kalispell, Mt. 496-497.

Costella, A.C., K.S. Shortreed, and J.G. Stockner. 1979. Phytoplankton fractionation studies in Great Central Lake, British Columbia: A nutrient enriched sockeye salmon (Oncorhynchus nerka) nursery lake. Fish & Mar. Serv. Tech. Rep. 880, B.C., Can. 27 p.

Craddock, D.R. 1954. Estimation of spawning population in the Okanogan River, 1954. USFWS typed rep., Seattle, Wa., 5 p.

Craddock, D.R. 1956. A report on the blueback salmon spawning migration of the Okanogan River, 1955. USFWS processed rep., Seattle, Wa. 13 p.

Craddock, D.R. 1957*a*. A report on the blueback salmon spawning population, Okanogan River, 1956. USFWS processed rep., Seattle, Wa., 9 p.

Craddock, D.R. 1957*b*. Spawning escapement of Okanogan River blueback salmon (*O. nerka*) 1957. USFWS processed rep., Seattle Wa. 7 p.

Craddock, D.R. 1958. Spawning escapement of Okanogan River blueback salmon (*Oncorhynchus nerka*), 1957, Spec. Sci. Rep.: Fish. No. 175, 7 p.

Craddock, D.R., R.L. Major. 1958*a*. The spawning escapement of Columbia River blueback salmon (*O. nerka*) 1958. U.S. Bur. of Comm. Fish., Seattle, Wa., 9 p.

Craddock, D.R. and R.L. Major. 1958*b*. The spawning escapement of Columbia River blueback salmon (*O. nerka*) 1958. USFWS processed rep., Seattle, Wa., 11 p.

Craddock, D.R. and R.L. Major. 1959. The spawning escapement of Columbia River blueback salmon (*O. nerka*). USFWS processed rep., Seattle, Wa., 13 p.

Craddock, D.R. and R.L. Major. 1960. Spawning escapement of Columbia River blueback (*O. nerka*). USFWS processed rep., Seattle, Wa., 16 p.

Craddock, D.R. and N.B. Parks. 1962. Spawning escapement of Columbia River blueback salmon (*O. nerka*), 1961. USFWS processed rept., Seattle, Wa., 17 p.

Craig, J.A. and A.J. Suomela. 1936. The migrations of salmon and steelhead trout in the upper Columbia River. Unpub. MS, U.S. Bur. of Fish., 16 p.

Craig, J.A. and A.J. Suomela. 1941. Time of appearance of the runs of salmon and steelhead trout native to the Wenatchee, Entiat, Methow and Okanogan rivers. Unpub. MS, USFWS. 35 p. plus 18 affadavits and accompanying letters of corroboration.

Crossman, E.J. 1959. Distribution and movements of a predator, the rainbow trout, and its prey, the redside shiner, in Paul Lake, British Columbia, Jour. Fish. Res. Bd. Can. 16(3): 247-267.

Crossman, E.J. and P.A. Larkin. 1959. Yearling liberations and changes of food affecting rainbow trout yield in Paul Lake, British Columbia. Trans. Amer. Fish. Soc. 88(1): 36-44.

Crunkilton, R.L., J.M. Czarneski, and L. Trial. 1980. Severe gas bubble disease in a warmwater fishery in the midwestern United States. Trans. Amer. Fish. Soc. 109(6) 725-733.

Cummins, K.W. 1972. What is a river?--zoological description. In: R.T. Oglesby (ed.), River ecology and man. Academic Press, N.Y., 33-52.

Davidson, F.A. 1965a. The survival of the downstream migrant salmon at the power dams and its effect on the migratory fish populations in the river. PUD Grant Co., Ephrata, Wa., 14 p.

Davidson, F.A. 1965b. The development of irrigation in the Yakima River Basin and its effect on the migratory fish populations in the river. PUD Grant Co., Ephrata, Wa., 14 p.

Davidson, F.A. 1967. The effect of a succession of dams on the Columbia River on the upstream movement of the blueback salmon runs. PUD Grant Co., Ephrata, Wa. 35 p.

Dawson, J., R. Thorne, and J. Traynor. 1973. Acoustic surveys of Lake Wenatchee and Lake Osoyoos in 1973. Un. of Wa. FRI Rep. No. 7315, 18 p.

DeAngelis, D.L. 1980. Energy flow, nutrient cycling, and ecosystem resilience. Ecology 61(4): 764-771.

Dillon, P.J. and F.H. Rigler. 1974. The phosphorus-chlorophyll relationship in lakes. Limnol. Oceanogr. 19: 767-773.

Dillon, P.J. and F. J. Rigler. 1975. A simple method for predicting the capacity of a lake for development based on lake trophic status. Jour. Fish. Res. Bd. Can., 32(9): 1519-1531.

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. Amer. Fish. Soc. 107(1): 36-45.

Dubos, R. 1973. Humanizing the earth. Science 179(4075): 769-772.

Duff, R.L. 1963. 1971-72 Banks Lake creel census. Wa. Dep. Game, Olympia, Wa. 39 p.

Earnest, D.E., M.H. Spence, R.W. Kiser, and W.D. Brunson. 1966. A survey of the fish populations, zooplankton, bottom fauna and some physical characteristics of Roosevelt Lake. WDG, Olympia, Wa. 44 p.

Ebel, W.J. Effects of atmospheric gas supersaturation on survival of fish and evaluation of proposed solutions. In U.S. Army Corps of Eng. 5th prog. rep. on fish. eng. res. program 1973-1978, Portland, Or.

Ebel, W.J. and H.L. Raymond. 1976. Effect of atomospheric gas supersaturation on salmon and steelhead trout of the Snake and Columbia rivers. NMFS, Mar. Fish. Rev. 7: 1-14.

Ebel, W.J., H.L. Raymond, G E. Monan, W.E. Fan, and G.K. Tanonaka. 1975. Effect of atmospheric gas supersaturation caused by dams on salmon and steelhead trout of the Snake and Columbia rivers. NMFS, Northwest Fish. Center, Seattle, Wa.

Edmondson, W.T. 1970. Phosphorus, nitrogen and algae in Lake Washington after diversion of sewage. Sciece, 169: 690-691.

Edmondson, W.T. 1977<u>a</u>. Trophic equilibrium of Lake Washington. EPA-600/3-77-087. Ecological Res. Series, Corvallis, Or. 36 p.

Edmondson, W.T. 1977<u>b</u>. Lake Washington, North American Project: A Study of U.S. Water Bodies. EPA-600/3-77-086 Ecological Res. Series, 288-300.

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. 1980. Feeding ecology of Lake Washington juvenile sockeye salmon and the salmon enhancement problem. <u>In</u>: Salmonid ecosystems of the North Pacific, W.J. McNeil and D.C. Himsworth (eds), Or. St. Un. Press, Corvallis, Or., 165-170.

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 forage base. Jour. Fish. Res. Bd. Can. 35(12): 1553-1571.

Erickson, A.W., I.J. Stober, J.J. Brueggeman, and R.L. Knight. 1977. An assessment of the impact on the wildlife and fisheries resource of Rufus Woods Reservoir expected fom the raising of Chief Joseph Dam from 946 to 956 m.s.l., Un. of Wa., 444 p.

Fish, F.F. 1944. The retention of adult salmon with particular reference to the Grand Coulee Fish-Salvage Program. USFWS, Spec. Sci. Rep. 27, 29 p.

Fish, F.F. and M.G. Hanavan. 1948. A report on the Grand Coulee Fish Maintenance Project 1939-1947. USFWS, Spec. Sci. Rep. 55. 63 p.

Foerster, R.E. 1968. The sockeye salmon, <u>Oncorhynchus</u> <u>nerka</u>. Fish. Res. Bd. Can. Bull. #162. 422 p.

Fredd, L.C. 1966. Analysis of differences in fish counts at Columbia River Dams. U.S. Army Corps of Eng. DA-35-026, CIVENG-65-44, Fish. Comm. Or., Portland, Or. 50 p.

French, R.R. and R.J. Wahle. 1959. Biology of chinook and blueback salmon and steelhead in the Wenatchee River system. USFWS, Spec. Sci. Rep.: No. 304, 17 p.

French, R.R. and R.J. Wahle. 1964. Study of loss and delay of salmon passing Rock Island Dam, Columbia River, 1954-56. USFWS, Bur. Comm. Fish., Fish. Bull., Vol. 65, No. 2, p. 339-368.

French, R.R. and R.J. Wahle. 1965. Salmon escapements above Rock Island Dam 1954-60. USFWS, Spec. Sci. Rep.: Fish. No. 493, 18 p.

Fulton, L.A. 1950. Lake Wenatchee study, 1949-50. USFWS typed rep., Seattle, Wa., 7 p.

Fulton, L.A. 1952. Okanogan River blueback salmon surveys. 1952. USFWS typed rep., Seattle, Wa., 8 p.

Fulton, L.A. and M.C. Laird. No date. A cursory survey of tributaries to Roosevelt Lake with reference to spawning potential for salmon, 1965-66. Draft of unpublished mimeo rep. NOAA, NMFS, Seattle, Wa., 100 p.

Fulton, L.A. and R.E. Pearson. 1981. Transplantation and homing experiments on salmon, Oncorhynchus spp., and steelhead trout, Salmo gairdneri, in the Columbia River system: Fish of the 1939-44 broods. NOAA. Tech. memo. NMFS, NWC-12. 97 p.

Gangmark, H.A. 1949. Blueback salmon studies Columbia River 1948. USFWS typed Rep., Seattle, Wa., 20 p.

Gangmark, H.A. and L.A. Fulton. 1949a. Preliminary surveys of Roosevelt Lake in relation to game fishes. USFWS, Spec. Sci. Rep. Fish. No. 5. 39 p.

Gangmark, H.A. and L.A. Fulton. 1949b. Blueback salmon studies Columbia River 1949. USFWS typed rep., Seattle, Wa., 14 p.

Gangmark, H.A. and L.A. Fulton. 1952. Status of Columbia River blueback salmon runs, 1951. USFWS, Spec. Sci. Rep.: Fish. No. 74, 29 p.

Gilbertson, L. 1981. Preseason management report for spring and summer fisheries on the Quinault and Queets Rivers - Quinault Indian Nation, Taholah, Wa., 82 p.

Gould, R.W. and G.A. Wedemeyer. 1981. The role of fish disease in the decline of Columbia River anadromous salmonid populations. USFWS/NMFS Col. R Endangered Species Project, Nat. Fish. Res. Center, Seattle, Wa. 81 p.

Gray, R.H. and D.D. Dauble. 1976a. Synecology of the fish community near Hanford Generating Project and assessment of plant operational impacts. WPPSS Columbia River Ecology Studies, Vol. 1, Battelle, Pac. Northwest Lab., Richland, Wa., p. 5.1-5.55.

Gray, R.H. and D.D. Dauble. 1976b. Synecology of the fish community near WNP 1, 2, and 4, and assessment of suitability of plant area for salmonid spawning. WPSS Columbia River Ecology Studies, Vol. 2, Battelle, Pac. Northwest Lab., Richland, Wa., p. 5.1-5.71.

Gray, R.H. and D.D. Dauble. 1977. Fish community studies near WNP 1, 2 and 4, October 1975 through December 1976. WPPSS Columbia River Ecology Studies, Vol. 3, Battelle, Pac. Northwest Lab., Richland, Wa., p. 5.1-5.46.

Gray, R.H. and D.D. Dauble. 1978. Fish studies near WNP 1, 2, and 4: March through December 1976. WPPSS Columbia River Ecology Studies, Vol. 4, Battelle, Pac. Northwest Lab., Richland, Wa., p. 5.1-5.74.

Harper, R.J., K.M. McMaster, L.G. Beckman and W.R. Nelson. 1980. Annual rep.; Assessment of fish stocks in Lake F.D Roosevelt, prepared for U.S. Bur. Recl. by USFWS, Contract WPRS-0-07-10-X0216, 74 p.

Hartman, W.L. and R.F. Raleigh. 1964. Tributary homing of sockeye salmon at Brooks and Karluk Lakes, Alaska. Jour. Fish. Res. Bd. Can., 21(3): 485-504.

Hartman, W.L. and R.L. Burgner. 1972. Limnology and fish ecology of sockeye salmon nursery lakes of the world. Jour. Fish. Res. Bd. Can., 29(6): 699-715.

Helvey, J.D. 1980. Effects of a North Central Washington wildfire on runoff and sediment production. Water Res. Bd., Amer. Water Res. Assoc., Vol. 16(4), p. 627-634.

Henderson, C. 1976. In: Final environmental statement, Columbia Basin Project, Washington. USDI, Bur. Recl., Vol. 1, Ephrata, Wa.

Hern, S.C., V.W Lambou, L.R. Williams, and W.D. Taylor. 1981. Modifications of models predicting trophic state of lakes: adjustment of models to account for the biological manifestations of nutrients. EPA-600/31-81-001, Las Vegas, Nev. 38 p.

Hirose, P.S. 1973. Results of the sockeye salmon fishing in the Columbia River, 1970-73. Information Rep. 73-4. Fish Comm., Or. 21 p. processed.

Hutchinson, G.E. 1957. A treatise on limnology. Vol. 1, Geography, Physics and Chemistry. John Wiley & Sons, Inc., N.Y., 1015 p.

Hutton, S.E. 1940. The new salmon hatchery at Leavenworth. Prog. Fish. Cult. No. 52, p. 24-30.

Hynes, H.B.N. 1970. The ecology of running waters. Univ. of Toronto Press, Toronto, Can. 555 p.

Ivlev, V.S. 1961. Experimental ecology of the feeding of fishes. Translated from Russian by Douglas Scott. Yale Univ. Press, New Haven, Ct. 302 p.

Jenkins, R.M. 1982. The morphoedaphic index and reservoir fish production. Trans. Amer. Fish. Soc. 111: 133-140.

Johannes, R.E. and P.A. Larkin. 1961. Competition for food between redside shiners (Richardsonius balteatus) and rainbow trout (Salmo gairdneri) in two British Columbia lakes. Jour. Fish. Res. Bd. Can. 18(2): 203-220.

Johnson, W.E. 1956. On the distribution of young sockeye salmon in Babine and Nilkitkwa Lakes, British Columbia. Jour. Fish. Res. Bd. Can., 13(5): 695-708.

Johnson, W.E. 1958. Density and distribution of young sockeye salmon throughout a multibasin lake system. Jour. Fish. Res. Bd. Can., 15: 961-982.

Kennedy, D.I. 1975. Utilization of fish by the Colville Okanogan Indian people. Unpub. Ms., B.C. Indian Language Project, Victoria, Can., 77 p.

Klingbiel, J.H. 1975. Use of fish toxicants in Wisconsin, 1941-73. In: Rehabilitation of fish populations with toxicants: a symposium, P.H. Eschmeyer (ed.), North Cent. Div., Amer. Fish. Soc., Spec. Publ. #4, p. 54-59.

Klock, G.O., J.M Geist, and A.R. Tiedemann. 1971. Erosion control fertilization - from pot study to field testing. Sulphur Inst. Jour. 7(3): 7-10.

Korn, L. and E.M. Smith. 1971. Rearing juvenile salmon in Columbia River Basin storage reservoirs. In: Reservoir fisheries and limnology, G.E. Hall (ed.), Amer. Fish. Soc. Spec. Publ. 8, p. 287-298.

Lambou, V.W., L.R. Williams, S.C. Hern, R.W. Thomas, and J.D. Bliss. 1976. Prediction of phytoplankton productivity in lakes. In: Environmental monitoring and simulation, W.R. Ott (ed.). EPA-600/9-76-016, Wa., D.C. pp. 696-700.

Larkin, P.A. 1979. Predator-prey relations in fishes, an overview of the theory. In: Predator-Prey Systems in Fisheries Management, H. Clepper (ed.), 12-22, SFI, Wa., D.C.

LeBrasseur, R J. and O D. Kennedy. 1972. The fertilization of Great Central Lake II. Zooplankton standing stock. Nat. Mar. Fish. Serv., Fish. Bull. 70(1): 25-36.

LeBrasseur, R.J., C.D. McAllister, W.E. Barraclough, O.D. Kennedy, J. Manzer, D. Robinson, and K. Stephens. 1978. Enhancement of sockeye salmon in Great Central Lake: Summary report. Jour. Fish. Res. Bd. Can. 35:1586-1596.

Lennon, R.E., R.A. Schmick, and R.M. Burress. 1971. Reclamation of ponds, lakes, and streams with fish toxicants; a review. FAO Fish. Tech. Paper 100, USFWS, 99 p.

Li, H.W. and P.B. Moyle. 1981. Ecological analysis of species introductions into aquatic systems. Trans. Amer. Fish. Soc. 110(6):772-782.

Manzer, J.T. 1976. Distribution, food and feeding of the 3-spine stickleback in Great Central Lake, Vancouver Island, with comments on competition for food with juvenile sockeye salmon. Fish. Bull. 74(3):647-668.

May, B. and F.M. Utter. 1974. Biochemical genetic variation of the genus Oncorhynchus in Pacific Northwest populations: A progress report and program summary. Report of contractual work by NMFS for WDF, 12 p.

Major, R.L. and D.R. Craddock. 1962. Influence of early maturing females on reproduction potential of Columbia River blueback salmon (Oncorhynchus nerka). USFWS, Bur. Comm. Fish., Fish. Bull. 61, p. 429-437.

Major, R.L. and J.L. Mighell. 1966. Influence of Rocky Reach Dam and the temperature of the Okanogan River on the upstream migration of sockeye salmon. USFWS, Bur. Comm. Fish., Fish. Bull. 66(1), p. 131-147.

McCaig, R.S. 1980. Effect of sea-run alewives on rainbow trout and brown trout in reclaimed ponds. Prog. Fish. Cult. 42(1): 59-63.

McColley, P.D. 1976. Soil resource inventory Wenatchee National Forest. USDA, USFS, Northwest Region, 318 p.

McLeod, K. 1958. Fertilization of water. In: Fish farming and fisheries management. Wa. Dep. of Fish., p. 71-78.

Meachum, C.P. and J.H. Clark. 1979. Management to increase anadromous salmon production. In: Predator-prey systems in fisheries management, H. Clepper (ed.), 377-386. SFI, Wa., D.C.

Meehan, W.R. 1966. Growth and survival of sockeye salmon introduced into Ruth Lake after removal of resident fish population. USFWS, Spec. Sci. Rep., Fish No. 532, Wa., D.C., 18 p.

Meekin, T.K. 1967. Report on the 1966 Wells Dam chinook tagging study. Wa. Dep. Fish., Olympia, Wa., 41 p.

Meekin, T.K. and R.L. Allan. 1976. Summer chinook and sockeye salmon mortality in the upper Columbia River and its relationship to nitrogen supersaturation. WDF, Tech. Rep. 12, p. 127-143.

Miller, R.J. and E.L. Brannon. 1982. The origin and development of life history patterns in Pacific salmonids. In: Proceedings of the salmon and trout migratory behavior symposium, E.L. Brannon and E.O. Salo (eds.), Un. of Wa., 296-309.

Montgomery, J.C. and C.D. Becker. 1980. Gas bubble disease in smallmouth bass and northern squawfish from the Snake and Columbia Rivers. Trans. Amer. Fish. Soc. 198(6):734-736.

Mortimer, C.H. 1969. Physical factors with bearing on entrophication in lakes in general and in large lakes in particular. In: Eutrophication: causes, consequences and correctives. Nat. Acad. Sci., Wa., D.C., p. 340-368.

Murdoch, W.W. and A. Oaten. 1975. Predation and population stability. Adv. Ecol. Res. 9:1-131.

Neave, F. 1952. "Even-year" and "odd-year" pink salmon populations. Trans. Royal Soc. Canada (V), Sec. 3, 46:55-70.

Neilson, J.D. and G.H. Geen. 1981. Enumeration of spawning salmon from spawner residence time and aerial counts. Trans. Amer. Fish. Soc. 110(4):554-556.

Newroth, P.R. 1977. Aquatic plant management programme. Government of British Columbia, Ministry of the Environment, Victoria, Can. 6 p.

Nielsen, J.R. 1974. Investigation of the walleye fishing in Franklin D. Roosevelt Lake, p. 20-26. In: A survey and evaluation of sport fisheries in Region One with special emphasis on the walleye fishing. Prog. Rep. Wa. Dep. Game Project No. F-64-R, Job No. 2, Olympia, Wa.

Nimlos, T.O. 1980. Volcanic ash soils. Western Wildland 6(3):22-24.

Northcote, T.G., T.G. Halser, and S.J. MacDonald. 1975. Fish as indicators of water quality in the Okanogan Basin lakes, British Columbia. Okan. Basin Study Comm. Prelim. Rep. 22, 79 p.

Oligher, R. and I.J. Donaldson. 1966. Fish passage through turbines tests at Big Cliff Hydroelectric Plant. U.S. Army Corps of Eng. Prog. Rep. No. 6.

Oregon Fish Commission and Washington Department of Fisheries. 1971. Status report: Columbia River fish runs and commercial fisheries, 1938-70. Joint Invest. Rep., Vol. 1, No. 1, 87 p.

Oregon Department of Fish and Wildlife and Washington Department of Fisheries. 1979. Columbia River fish runs and fisheries, 1957-1978. Vol. 2, No. 2, 68 p.

Orsborn, J.F. and M.N. Good. 1973. Technical supplement to the hydrographic atlas, Okanogan-Methow River Basins study area. R.L. Albrook Hydraulic Lab., Wa. St. Un., Pullman, 85 p.

Pacific Northwest River Basins Commission. 1971. Water quality and pollution control. Appendix XII, Columbia Pacific Region, Comprehensive Framework Study. PNRB Comm., Vancouver, Wa. 136 p.

Pacific Northwest River Basins Commission. 1977. The Okanogan River Basin Level B. Study of the water and related land resources (revised). PNRB Comm., Vancouver, Wa., 100 p.

Page, T.L. and D.A. Neitzel. 1976<u>a</u>. Zooplankton: seasonal distribution, relative abundance and entrainment effects. <u>In</u>: Final rep. on aquatic ecological studies conducted at the Hanford generating project, 1973-74. WPPSS Columbia River Ecology Studies Vol. 1, by Battelle, Pac. Northwest Lab., Richland, Wa.

Page, T.L. and D.A. Neitzel. 1976<u>b</u>. Seasonal and relative abundance of Columbia River macrobenthos near WNP 1, 2, and 4 from September 1974 to September 1975. <u>In</u>: Aquatic ecological studies near WNP 1, 2, and 4, September 1974 thorugh September 1975. WPPSS Columbia River Ecology Studies Vol. 2, by Battelle, Pac. Northwest Lab., Richland, Wa.

Paine, R.T. 1966. Food web complexity and species diversity. Am. Naturalist 100:65-75.

Park D.L. and W.W. Bentley. 1968. A summary of the 1967 outmigration of juvenile salmonids in the Columbia Basin. Prog. Rep., U.S. Bur. Commer. Fish., Seattle, Wa. 14 p.

Pennak, R.W. 1953. Cladocera. Pages 350-382. <u>In</u>: Fresh-water invertebrates of the United States. Ronald Press, N.Y., N.Y.

Pinsent, M.E. and G.D. Koshinsky T.J. Willcocks, J. O'Riordan. 1974. Fisheries and sport fish potentials of the Okanogan Basin. Okanogan Study Committee, Tech. Supplement IX(A), 249 p.

Platts, W.S. 1981. Effects of sheep grazing on a riparian-stream environment. USDA, USFS Intermountain Forest and Range Stations, Res. Note INT-307, 6 p.

Putnam, R.W. 1936. The Little Wenatchee River watershed, its resources and their management. USDA, U.S. Forest Service, Wenatchee, Wa., 79 pages plus figures, plates, and tables.

Raleigh, R.J. 1967. Genetic control in the lakeward migrations of sockeye salmon fry. Jour. Fish. Res. Bd. Can. 24(12):2613-2622.

Raleigh, R.J. 1971. Innate control of migrations of salmon and trout fry from natal gravels to rearing areas. Ecology 52(2):291-297.

Ray, V.F. 1972. Fisheries of the confederated tribes of the Colville Reservation. Wa., D.C. 54 p.

Raymond, H.L. 1976. Effect of dams and river regulation on runs of anadromous fish at the Mid-Columbia and Snake Rivers. Proc. Instream Flow Needs Symp. and Spec. Conf., AFS and ASCE, Boise, Id., p. 444-465.

Raymond, H.L. 1978. Effects of dams and impoundments on migrations of juvenile chinook salmon and steelhead trout from the Snake River, 1966 to 1975. Unpubl. ms., NMFS, Seattle, Wa.

Regier, H.A. 1973. The sequence of exploitation of stocks in multi-species fisheries in the Laurentian Great Lakes. jour. Fish. Res. Bd. Can. 30:1992-1999.

Regier, H.A. and K.H. Loftus. 1972. Effects of fisheries exploration on salmonid communities in oligotrophic lakes. Jour. Fish. Res. Bd. Can. 29:959-968.

Regier, H.A., J.E. Paloheimo, and V.F. Gallucci. 1979. Factors that influence the abundance of large piscivorous fish. In: Predator-prey systems in fisheries management, H. Clipper (ed.), p. 333-341. SFI, Wa., D.C.

Rich, W.H. 1940a. The present state of the Columbia River salmon resource. Proc. 6th Pac. Sci. Cong. 3:425-430.

Rich, W.H. 1940b. The future of the Columbia River salmon fisheries. Standford Ichthyological Bull. 2(2):37-47.

Ricker, W.E. 1937. The food and food supply of sockeye salmon (Oncorhynchus nerka Walbaum) in Cultus Lake, British Columbia. Jour. Biol. Bd. Can. 3(5):450-468.

Ricker, W.E. 1940. On the origin of kokanee, a fresh-water type of sockeye salmon. Trans. Roy. Soc. Can., Sect. V, Ser. 3, 34:121-135.

Ricker, W.E. 1950. Additional observations concerning residual sockeye and kokanee (Oncorhynchus nerka). Jour. Fish. Res. Bd. Can. 16(6):897-902.

Ricker, W.E. 1972. Hereditary and environmental factors affecting certain salmonid populations. Fish. Res. Bd. Can., 160 p.

Ricker, W.E. and K.H. Loftus. 1968. Pacific salmon move east. Annual Review, Fisheries Council Canada rep., 3 p.

Rieman, B.E. and C.M. Falter. 1981. Effects of the establishment of Mysis relicta on the macrozooplankton of a large lake. Trans. Amer. Fish. Soc. 100:613-620.

Robeck, G.G., C. Henderson, R.C. Palange. 1954. Water quality studies on the Columbia River. U.S. Dept. Health, Education, and Welfare. Robert A. Taft Sanitary Engineering Center, Cincinnati, Ohio, 99 p. plus appendices.

Robinson, D.G.and W.E. Barraclough. 1978. Population estimates of sockeye salmon in a fertilized oligotrophic lake. Jour. Fish. Res. Bd. Can. 35(6):851-860.

Rogers, D.E. 1968. A comparison of the food of sockeye salmon fry and threespine sticklebacks in the Wood River Lakes. In: Further studies of Alaska sockeye salmon, R.L. Burgner (ed.). Un. of Wa., Vol. III, p. 3-43.

Rounsefell, G.A. 1958. Factors causing decline in sockeye salmon of Karluk River, Alaska, USFWS, Fish. Bull. 58:83-169.

Ross, P.L. 1965. Fish passage report 1965, Priest Rapids and Wanapum Dams, Columbia River System, Washington. PUD No. 2 Grant Co., Ephrata, Wa., 69 p.

Rucker, R.R., W.V. Whipple, S.R. Parvin, and C.A. Evans. 1953. A contagious disease of salmon possibly of virus origin. USFWS, Fish. Bull. 76(54): 35-46.

Ruggles, C.P. 1958. Biological studies of Lake Wenatchee. USFWS Process. Rep., 50 p.

Ruggles, C.P. 1965. Juvenile sockeye studies in Owikeno Lake, British Columbia. Can. Fish. Cult. 36:3-21.

Ryder, R.A. 1965. A method for estimating the potential fish production of North-temperate lakes. Trans. Amer. Fish. Soc. 94(3):214-218.

Ryder, R.A., S.R. Kerr, K H. Loftus, and H.A. Regier. 1974. The morphoedaphic index, a fish yield estimator - review and evaluation. Fish. Res. Bd. Can. 31(5):663-688.

Saether, O.A. 1970. A survey of the bottom fauna in lakes of the Okanogan Valley, British Columbia. Fish. Res. Bd. Can., Tech. Rep. 196:1-26.

Schindler, D.W. 1974. Entrophication and recovery of experimental lakes: implications for lake management. Science 84:897-899.

Schoeneman, D., R. Pressey, and C. Junge. 1961. Mortalities of downstream migrant salmon at McNary Dam. Trans. Amer. Fish. Soc. 90(1):58-72.

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

Seely, C.M. and G.W. McCammon. 1966. Kokanee. In: Inland fisheries management, A. Calhoun (ed.). Ca. Dep. F. and G.:274-294.

Silliman, R.P. 1947. The 1947 blueback salmon runs in the Columbia River. USFWS typed rep., Seattle, Wa., 7 p.

Simons, D.B. 1979. Effects of stream regulation on channel morphology. In: The ecology of regulated streams, J.V. Ward and J.A. Standford (eds.). Plenum Press, New York and London:95-111.

Simons, W.D. 1953. Irrigation and streamflow depletion in Columbia River Basin above The Dalles, Or. USGS water supply paper 1220.

Sims, C.W. and D.R. Miller 1976. Migrational characteristics of juvenile salmonids in the mid-Columbia during 1976. Rep. by NMFS for mid-Columbia PUDs, Seattle, Wa., 18 p.

Smith, G.M. 1950. The fresh-water algae of the United States. McGraw-Hill, N.Y. 719 p.

Snyder, G.R. 1967. Unpublished data of fish samplings in Lake Roosevelt. NOAA, NMFS, Seattle, Wa.

Snyder, G.R. 1976. In: Final environmental statement, Columbia Basin Project, Washington. USDI, Bur. Recl., Vol. 1, Ephrata, Wa.

Spangler, G.R., N.R. Payne, J.E. Thorpe, J.M. Bryne, H.A. Regier, and W.J. Christie. 1977. Responses of percoids to exploration. Jour. Fish. Res. Bd. Can., 34:1938-1988.

Stockner, J.G. and T.G. Northcote. 1974. Recent limnological studies of Okanogan Basin lakes and their contribution to comprehensive water resource planning. Jour. Fish. Res. Bd. Can. 31(5):955-976.

Stockner, J.G. 1979. Lake fertilization as a means of enhancing sockeye salmon populations: The state of the art in the Pacific Northwest. Rep. 740, Fish. and Mar. Ser., B.C., Can. 14 p.

Stockner, J.G. and K.S. Shortreed. 1979. Limnological studies of 13 sockeye salmon (Oncorhynchus nerka) nursery lakes in British Columbia, Canada. Fish. and Mar. Ser. Tech. Rep. 865, Dep. Fish and Oceans, Resour. Ser. Branch, Pac-Environment Inst., B.C. 125 p.

Stober, Q.V. and A.H. Hamalainene. 1980. Cedar River sockeye salmon production. FRI, Un. of Wa., 59 p.

Stober, Q.V., M.E. Kopache, and T.H. Jagielo. 1981. The limnology of Lake Roosevelt, 1980. Final Rep. to USFWS, contract 14-16-0009-80-004 by FRI, Un. of Wa., 116 p.

Stober, Q.J., R.W. Tyler, G.L. Thomas, L. Jensen, J.A. Knutzen, D.L. Smith, and R.E. Nakatani. 1976a. Operational effects of irrigation and pumped storage on the ecology of Banks Lake, Washington. 3rd Annual Prog. Rep. Bur. Recl., Contract 14-06-100-7794 by FRI, Un. of Wa., 313 p.

Stober, Q.J., R.W. Tyler, C. Petrosky, and D. Gaudit. 1976b. A survey of fisheries resources in the forebay of FDR reservoir. Periodic Rep. No. 3, FRI, Un. of Wa., 50 p.

Stober, Q.V., R.W. Tyler, C.E. Petrosky, K.R. Johnson, C.F. Cowman, Jr., J. Wilcock, and R.E. Nakatani. 1979. Development and evaluation of a net barrier to reduce entrainment loss of kokanee from Banks Lake. Final Rep. Bur. Recl. Contract 7-07-10-S0023, by FRI, Un. of Wa., 246 p.

Sylvester, R.O. 1959. Water quality study of Wenatchee and Middle Columbia Rivers before dam construction. USFWS Spec. Sci. Rep., Fish. 290, 116 p.

Thompson, R.B. 1959. Food of the squawfish (Ptychocheilus oregonensis), of the lower Columbia River. USFWS Bull. 158, Vol. 60:43-58.

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. Amer. Fish. Soc. 96(4):424-427.

Thompson, W.F. 1951. An outline for salmon research in Alaska. A talk prepared for the Meeting of the International Council for the Exploration of the Sea at Amsterdam, Oct. 1-9, 1951. FRI, Un. of Wa., 49 p.

Tiedemann, A.R., J.D. Helvey, and T.D. Anderson. 1978. Stream chemistry and watershed nutrient economy following wildfire and fertilization in Eastern Washington. Jour. Environ. Quality, Vol. 7(4):580-588.

Tiedemann, A.R., J.D. Helvey, and T.D. Anderson. 1980. Effects of chemical defoliation of an Abies grandis habitat on amounts and chemistry of throughfall and stemflow. Jour. Environ. Quality, Vol. 9(2):320-328.

Trimberger, J.E. 1975. Evaluation of angler-use benefits from chemical reclamation of lakes and streams in Michigan. In: Rehabilitation of fish populations with toxicants: a symposium, P.H. Eschmeyer (ed.). North Cent. Div., Amer. Fish. Soc., Spec. Publ. #4, p. 60-65.

Tufts, D.F. and D.R. Craddock. 1963. Spawning escapement of Columbia River sockeye salmon (O. nerka), 1962. USFWS processed rep., Seattle, Wa., 17 p.

U.S. Army Corps of Engineers. 1979. Eurasian watermilfoil. Seattle District, Wa. 4 p.

U.S. Department of Interior. 1939. Transplanting the Columbia's salmon. Prog. Fish. Cult. No. 47, p. 25-30.

U.S. Fish & Wildlife Service. 1944. Program of biological investigations in connection with the Grand Coulee Fish Salvage Program for the fiscal year of 1944. 7 p.

U.S. Forest Service. 1972. Little Wenatchee River stream survey. Wenatchee Nat. For., Wenatchee, Wa., 15 p. plus maps, photos, raw survey data.

U.S. Forest Service. 1979. Administrative unit summary, Wenatchee Nat. For., Lake Wenatchee R.D. district.

U.S. Geological Survey. 1955. Compilation of records of surface waters of the United States through September 1950. Part 12. Pacific Slope Basins in Washington and Upper Columbia River Basin. Water Supply Paper 1316, Wa., D.C. 592 p.

U.S. Geological Survey water data reports for years designated.

Utter, F.M., D. Compton, S. Grant, G. Milner, J. Seeb, and L. Wishard. 1980. Population structures of indigenous salmonid species of the Pacific Northwest. In: Salmonid ecosystems of the North Pacific, W.J. McNeil and C.D. Himsworth (eds.), Or. St. Un. Press, Corvallis, 165-170.

Van Cleve, R. and D.E. Bevan. 1973. Evaluation of causes for the decline of the Karluk sockeye salmon runs and recommendations for rehabilitation. USFWS Fish Bull., Vol. 71(3):627-649.

Vinyard, G.L. 1982. Feeding success of hatchery-reared kokanee salmon when presented with zooplankton prey. Prog. Fish. Cult. 44(1):37-39.

Walters, K.L. 1974. Water in the Okanogan River Basin, Wa. St. Dep. of Ecology. Water Supply Bull. 34, 136 p.

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. Fish. Bull. 77(1):229-242.

Wahle, R.J. and R.Z. Smith. 1979. A historical and descriptive account of Pacific Coast anadromous salmonid rearing facilities and a summary of their releases by region, 1960-76. NOAA Tech. Rep. NMFS SSRF-736, 40 p.

Ward, F.J. and P.A. Larkin. 1964. Cyclic dominance in Adams River sockeye salmon. Int. Pac. Salmon Fish Comm. Prog. Rep. 11.

Ward, J.V. and J.A. Stanford (eds.). 1979. The ecology of regulated streams. Plenum Press, New York and London, 398 p.

Warren, C.E. 1971. Biology and water pollution control. Saunders, Philadelphia, Pa. 434 p.

Washington Department of Fisheries. 1938. A report on the preliminary investigations into the possible methods of preserving the Columbia River salmon and steelhead at the Grand Coulee Dam. WDF, Olympia, Wa. 121 p.

Watson, S.W., R.W. Guenther, and R.R. Rucker. 1954. A virus disease of sockeye salmon: Interim report. USFWS, Spec. Sci. Rep.: Fish. 138, 36 p.

Weber, D., and R.J. Wahle. 1969. Effect of finclipping on survival of sockeye salmon (Oncorhynchus nerka). Jour. Fish. Res. Bd. Can. 26: 1263-1271.

Weitkamp, D.E. and M. Katz. 1980. A review of dissolved gas supersaturation literature. Trans. Amer. Fish. Soc. 109(6):659-702.

Weitkamp, D.E. and J. Neuner. 1981. 1981 juvenile salmonid monitoring Methow River, Okanogan River and Wells Dam forebay. Douglas Co. PUD, by Parametrix, Inc., Bellevue, Wa. 56 p.

Williams, L.R., V.W. Lambou, S.C. Hern, and R. W. Thomas. 1977. Relationships of productivity and problem conditions to ambient nutrients: National eutrophication survey findings for 418 eastern lakes. Working Paper No. 725. Las Vegas, Nev. 20 p.

Wolf, E.G. 1976. Characterization of the benthos community. In: Final rep. on aquatic ecological studies conducted at the Hanford Generating Project, 1973-74. WPSS Columbia River Ecology Studies Vol. 1, by Battelle, Pac. Northwest Lab., Richland Wa. 205 p.

Woodey, J.C. 1972. Distribution, feeding, and growth of juvenile sockeye salmon in Lake Washington. Ph.D. thesis, Un. of Wa. 169 p.

Wood, J.R. 1977. The aqutic insects of Rainy Creek, with special reference to caddisflies (Trichoptera). M.S. thesis, Central Wa. St. College, Ellensburg, 71 p.

Zimmer, P.D., C.C. Davidson, and F.S. Anders. 1961. Annual fish passage report, Rock Island Dam, Columbia River, Washington, 1959. USFWS, Spec. Sci. Rep., Fish. No. 394, 14 p.

'Silvers' prompt some golden memories

A little item in the "40 Years Ago" column last week noting that "Several limit catches of silvers have been made recently at Lake Wenatchee . . ." must have started many old timers' memories back-pedaling. Because in those long gone years it was around Memorial Day that one of the unique fishing experiences of this area began.

Silver trout fishing at Lake Wenatchee had to be seen to be believed. During the short period that the silvers (now known as kokanee) "ran," the delectable trout were pulled in by impatient fishermen, literally hand over hand, two or three on a single line. The fishing was fabulous.

I first experienced it a couple of years after the above item appeared. My fishing companion shall be nameless because he is now one of the most respected fly fishing purists in the area, and if it were known he once went after silvers with salmon eggs and worms he might be drummed out of the fraternity.

We started our first quest for silvers trolling. That required a heavy Jack Lloyd to attract the trout, with the leader attached by a rubber band, necessitated because the trout's mouth was reputed to be so "soft." Trolling up lake we picked up a fish or two, but the fishing was nothing to justify the tales we'd heard.

An Editor's Notebook

by Bob Woods
Executive Editor

Then rounding the point near the head of the lake we came upon the real silver fishing scene. At the mouth of the Little Wenatchee some logs were anchored to the bottom, probably remnants of an ancient fish trap. There from those logs on either side of the stream extended two lines of boats, a couple of dozen in each line, each boat tied to the one in front, and each occupied by fishermen literally hauling in their catches hand over hand.

The fishing wasn't just at that spot, of course. Each dock near Telma was lined by fishermen resting comfortably in chairs and hauling in the silvers almost as rapidly as their counterparts in the boats. Every year one of the big Game Department trout plants in this area was of silvers in Lake Wenatchee. Although the silvers could be caught there in limited numbers most of the season. the real run only lasted a few weeks and it usually occurred around Memorial Day.

They still fish for silvers in Lake Wenatchee, although the Game Department long since quit planting them there. The log anchors at the Little Wenatchee are long gone, but catches are still made from the same docks near Telma. But both in numbers and size they are only a small imitation of what used to be, and the reason is as much a phenomenon of nature as was the old run itself. Here's the story:

When Grand Coulee Dam shut off the salmon-spawning area of the upper Columbia, an effort was made to transfer some of the runs to other streams, and to augment them from salmon hatcheries. The sockeye (also called blueback) salmon were assigned to Lake Wenatchee. The lake was considered ideal for that, because the sockeyes spawn in a stream above the lake, then spend 18 months in the lake before heading out to sea. They return to spawn as 4-year-olds.

In 1940 returning sockeyes were trapped at Rock Island Dam, trucked to the new Leavenworth hatchery, spawned artificially, and when the eggs were hatched the tiny fish were released into Lake Wenatchee. There they grew until instinct directed them to swim down the Wenatchee River to the Columbia and on out to sea. The trapping, hatching and release program continued for three more years to provide a complete cycle.

But would the salmon return to the lake in which they had been planted? Even as they trapped, spawned, and planted, the biologists couldn't know until it was time for their freshman class to come home. And come home they did, almost 5,000 of them in 1944. The run has had its ups and downs since, but today most of the sockeye salmon that go to sea via the Columbia River are progeny from those hand-raised fish that found a new home at Lake Wenatchee.

What does that have to do with the silver trout run? Simply this: silver trout are just sockeye salmon that haven't gone to sea. Over the years they've become landlocked. When those sea-going sockeye started to mingle with their landlocked brethren, their sea-going instinct prevailed, and the silver trout followed them out to the ocean. Only a few at first; then more and more. By the early '50s the memorable silver run at Lake Wenatchee was a thing of the past.

Now, when you catch a "silver" at Lake Wenatchee, it's just one of the few sockeyes that unnaturally stayed behind.

Appendix 1. Wenatchee World, May 27, 1983.

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Determinants of abundance of sockeye salmon (Oncorhynchus nerka) in the Columbia River are examined with reference to the Grand Coulee Fish-Maintenance Project (1939-1960's), the revival of runs associated with the project (1945-1960's), and the decline in numbers of fish returning to the river that followed (1960's-80's).

This attempt at holistic interpretation of a vast array of information pertaining to Columbia River sockeye revealed several management implications: (1) natural production potential of remaining nursery lakes was perhaps only moderately less than the goal of 250,000 returning adults; (2) any shortfall might be made up by enhancement of the food supply in Lake Wenatchee; (3) the primary barrier to such enhancement is the societal conflict inherent in simultaneous management for resident and anadromous salmonids; and (4) providing sport fishing opportunity for returning adult sockeye salmon in North Central Washington constitutes strong incentive in alleviating such conflict.

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