North American Journal of Fisheries Management 6:560–568, 1986

Effects of Hydroelectric Operations on the Kokanee Population in the Flathead River System, Montana

JOHN J. FRALEY

Montana Department of Fish, Wildlife and Parks
Post Office Box 67, Kalispell, Montana 59901, USA

STEVE L. MCMULLIN

Montana Department of Fish, Wildlife and Parks
1125 Lake Elmo Drive, Billings, Montana 59105, USA

PATRICK J. GRAHAM

Montana Department of Fish, Wildlife and Parks
1420 East Sixth Avenue, Helena, Montana 59620, USA

Abstract.—Kokanee (*Oncorhynchus nerka*) were introduced into Flathead Lake in 1916 and developed both lakeshore and inlet river system spawning populations. River system spawning, including that in the main stem of the Flathead River and in McDonald Creek, was a major source of kokanee recruitment in the 1960s and 1970s. Changes in the operation of Hungry Horse Dam on the South Fork of the Flathead River in the early 1970s, coupled with angler harvest, resulted in a rapid 90% decline of main-stem kokanee spawning escapement in the late 1970s. Strong relationships existed between kokanee year-class strength and river flow conditions during 1966–1984 ($r = -0.93$). Hungry Horse Dam operations caused dewatering of kokanee spawning beds and high winter incubation mortality. This resulted in a rapid decline of the spawning run. Management of flow levels in the Flathead River is critical to the recovery of the kokanee run. The Montana Department of Fish, Wildlife and Parks recommended a stable flow release of 3,500–4,500 ft^3/s during the fall spawning period, and a minimum flow of 3,500 ft^3/s during the winter incubation period to eliminate dewatering of spawning areas. Managing flows and angler harvest in the system could result in recovery of the population to optimum levels by the late 1990s. Timing of the recovery could vary depending on natural fluctuations in kokanee survival rates from egg to fry and fry to adult, and changes in the carrying capacity of Flathead Lake.

Kokanee, the landlocked form of sockeye salmon (*Oncorhynchus nerka*), were introduced into Flathead Lake in northwestern Montana in 1916 and developed both lakeshore and river inlet system spawning populations (Alvord 1975). A thriving sport fishery developed by the early 1930s in Flathead Lake and the species became the most popular game fish in the drainage, supporting a summer trolling fishery in the lake and an intense fall snag fishery in the Flathead River system. Kokanee made up over 80% of the estimated annual game fish harvest of approximately 600,000 in the Flathead Lake and Flathead River system during both 1975 and 1981 (Hanzel 1977; Fredenberg and Graham 1982; Graham and Fredenberg 1982).

Two hydroelectric developments have affected kokanee in the Flathead Lake and river system. Kerr Dam, constructed at the outlet in 1938, regulates seasonal lake levels and has affected kokanee spawning along the shoreline. Hungry Horse Dam, completed on the South Fork of the Flathead River 8 km upstream from its mouth in 1953, altered natural flow and temperature regimes in the South Fork and in the main stem of the Flathead River downstream to Flathead Lake. Kokanee spawning runs increased in the Flathead River after the construction of Hungry Horse Dam and, from the late 1950s through the mid-1970s, large runs of kokanee migrated upstream from Flathead Lake to spawn in the river below the mouth of the South Fork.

A rapid decline in the main-stem spawning run became evident during the late 1970s. The decline was thought to be related to changes in the operation of Hungry Horse Dam. Most of the kokanee redds in the Flathead River were constructed in shallow areas such as side channels and along the margins of the river. In the early 1970s, operation of the dam for fall power peaking resulted in daily water level fluctuations of up to 2.0 m in the South Fork and 1.4 m in the main stem. Seasonal flood control operations as well as peaking affected incubation mortality. Flows were high during the fall spawning period and low during the winter incubation period.

Eggs deposited during periods of higher flows were subsequently dewatered and exposed to freezing. It is probable that incubation mortality was the major factor in the decline of the mainstem kokanee spawning run. Other workers have documented the importance of incubation mortality in controlling year-class strength of pink salmon (*Oncorhynchus gorbuscha*) and sockeye salmon (McNeil 1968).

Major objectives of this study were to (1) determine the effects of discharges from Hungry Horse Dam on the kokanee populations spawning in the Flathead River, and (2) recommend a flow regime that would result in recovery of the population. The overall management goal of the Montana Department of Fish, Wildlife and Parks is to provide a balance of size and numbers of kokanee for angling and spawning escapement while maintaining a diversity of spawning areas. The production goal for the Flathead River is approximately 330,000 spawners averaging 320–330 mm in length.

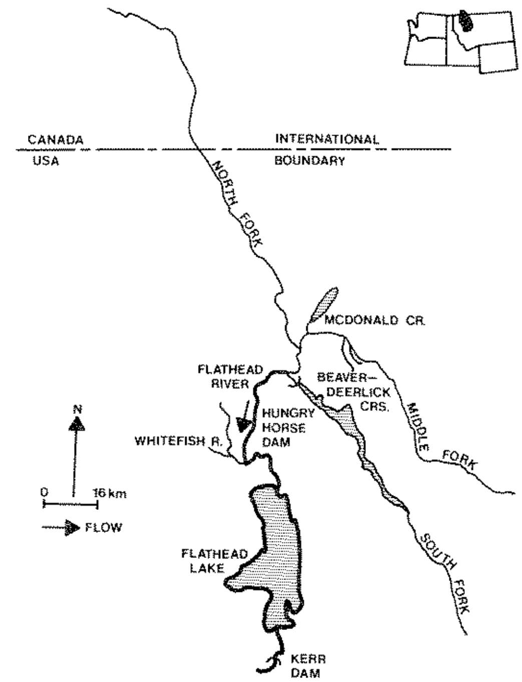

FIGURE 1.—Location of Flathead Lake, Montana, and of the upper Flathead River and its tributaries.

Study Area

The Flathead Lake and Flathead River drainage is the northeastern-most drainage in the Columbia River basin (Figure 1). Flathead Lake is a large oligomesotrophic lake with a surface area of 476 km^2 and a mean depth of 32.5 m (Potter 1978). The upper 3 m of Flathead Lake is regulated by Kerr Dam. The lower 35 km of the Flathead River inlet also is affected by Kerr Dam and is slough-like with a silt bottom. The remainder of the river (55 km) to its forks has a moderate gradient and gravel–rubble bottom. The South, Middle and North forks drain areas of approximately equal size in portions of the Great Bear and Bob Marshall wildernesses, Glacier National Park, and the Flathead National Forest.

Kokanee spawn in the lower portion of the South Fork of the Flathead River, the Flathead River for 32 km downstream from the South Fork, the Whitefish River, and along the shoreline of Flathead Lake. Spawning in the lower portion of the drainage generally takes place from mid-October to mid-December.

Kokanee also spawn in the Middle Fork of the Flathead River, as well as McDonald, Beaver, and Deerlick creeks, which are tributaries to the Middle Fork. Kokanee generally spawn in these upper drainage areas from mid-September through November, and there is some interchange among fish spawning early and later. McDonald Creek is 100 stream kilometers above Flathead Lake and is the largest tributary to the Middle Fork. The 4 km of stream below McDonald Lake has been a major spawning area for kokanee since the 1930s. A large concentration of migrating bald eagles (*Haliaeetus leucocephalus*) feeds on kokanee in this portion of McDonald Creek, located entirely within Glacier National Park (McClelland et al. 1982). The temperature and discharge of this stream are moderated by McDonald Lake and the bottom material consists of loosely compacted gravel and cobble.

Beaver and Deerlick creeks are spring-fed tributaries upstream from McDonald Creek with nearly constant flows and water temperatures and loosely compacted gravel substrates. Spawning kokanee have used these tributaries since the mid-1960s. Few kokanee spawn in the North Fork of the Flathead River.

Recent Status of the Population

Kokanee spawner escapement trends were estimated by counting redds in most areas of the river system and by determining spawner–redd ratios in confined areas of the river system. Escapement of spawners was estimated by multiply-

TABLE 1.—Estimated numbers of postharvest kokanee spawners (rounded to the nearest 100) in the Flathead River and lake system, 1979–1984. The percent contribution for each area is in parentheses.

Spawning area	Estimated number of spawners						
	1979	1980	1981	1982	1983	1984	Mean
McDonald Creek	65,000 (91)	49,500 (96)	103,500 (78)	31,000 (74)	34,300 (56.3)	86,500 (73.3)	61,600 (74.4)
Main stem Flathead River	6,800 (9)	1,100 (2.1)	19,000 (14.3)	3,700 (8.8)	16,300 (26.7)	17,700 (15.0)	10,800 (13)
Whitefish River		1,000 (1.9)	1,000 (0.8)	1,800 (4.3)	1,300 (2.1)	2,400 (2.0)	1,500 (1.8)
South Fork Flathead River			700 (0.5)	500 (1.2)	5,200 (8.5)	7,500 (6.3)	3,500 (4.2)
Beaver–Deerlick creeks	0		1,800 (1.3)	100 (0.2)	2 (<0.1)	0	400 (0.5)
Middle Fork Flathead River			5,500 (4.1)	1,800 (4.3)	1,300 (2.1)	400 (0.3)	2,300 (2.7)
Flathead lakeshore[a]			1,400 (1.0)	2,500 (6)	1,700 (3)	2,400 (2.0)	2,000 (2.4)
Swan River				500 (1.2)	800 (1.3)	1,300 (1.1)	900 (1.0)
Total	71,800	51,600	132,900	41,900	60,902	118,200	82,900

[a] From Decker-Hess and Clancey (1984).

ing redds counted by 2.4. Escapement could be underestimated for areas where redd superimposition takes place. Kokanee escapement in McDonald Creek was estimated by direct counts of fish (snorkeling).

During a 6-year period (1979–1984), only 13% of the total drainage spawning occurred in the main stem Flathead River (Table 1). McDonald Creek has been the major spawning area. The South and Middle forks of the Flathead River, the Whitefish River, the Beaver and Deerlick creeks, and the Flathead Lake shoreline each supported less than 5% of the spawning escapement.

The Flathead River spawning run declined dramatically during the late 1970s. The postharvest population of main-stem spawners fell from an estimated level of over 150,000 fish in 1975 (considered an average year prior to the decline) to an average of only 10,800 during 1979–1984. As a result, the McDonald Creek spawning run averaged 73% of the total spawning escapement during the same period.

From the late 1950s through the mid-1970s, the Flathead River kokanee spawning run probably was equal to or greater than the McDonald Creek run in terms of total escapement from Flathead Lake (Fraley and Graham 1982). Hanzel (1964) reported that the main-stem spawning run was larger than the McDonald Creek run during the early 1960s.

These population changes were reflected in the fall kokanee snag fishery in the river system. Angling pressure during the mid-1970s was concentrated on the run of fish that spawned in the main stem below the South Fork during October, November, and early December (Hanzel 1977). With the decline of the Flathead River run, angler effort and harvest shifted almost entirely to the earlier runs of fish bound for McDonald Creek and the Middle Fork during September. During the 1975 fishery, 88% of the total kokanee harvest from the river system was from the later main-stem run. During 1981, 1982, and 1983, only 12, 2, and 16% of the kokanee harvest in the river system was from the later main-stem run. Kokanee harvest in the latter 3 years was concentrated on the earlier spawning run bound for McDonald Creek and the Middle Fork.

Year-Class Strength and Flow Conditions

Historical relationships between year-class strength of kokanee spawners and flow conditions indicated kokanee spawning in the Flathead River was affected directly by the operation of Hungry Horse Dam. Most kokanee redds are located in the shallows and are subject to dewatering from only a small drop in water levels.

Historical flow conditions were determined by the differences in average river gauge height between the main kokanee spawning period (November) and the incubation period (December–March). Positive differences were deemed favorable for kokanee egg survival whereas negative differences indicated dewatering of spawning beds and conditions unfavorable for egg survival.

Total length of female kokanee spawners was used as the measure of year-class strength in the Flathead system. Females were collected at spawning areas throughout the river system and along the lakeshore. It was assumed that growth was inversely related to population size. Many workers have reported that growth of juvenile anadromous and landlocked sockeye salmon was density-dependent (Foerster 1944, 1968; Bjornn 1957; Johnson 1965; Rogers 1973; Goodlad et al. 1974). Total length has been used as the measure of year-class strength in Pend Oreille and Priest lakes in Idaho (Rieman and Bowler 1980).

Growth of kokanee also can be affected by interactions between and within year classes (Ward and Larkin 1964), accentuated by the close association of the species in schools. We assumed that age-0 fish interact both with others in their cohort and with age-I fish, but not with older fish. Age-0 and age-I fish appear to occupy different habitats than do older kokanee, based on purse seining in the lake. In subsequent years, interactions take place within cohorts and between a cohort and adjacent year classes. Most of the kokanee in Flathead Lake mature and spawn after four growing seasons (age III+), then die. In summary, an age-class interacts with the previous age-class for 3 years, 4 years within its cohort, and 3 years with the following year class (McMullin and Graham 1981).

To account for these interactions, a 3-year weighted moving average was used to calculate gauge height differences (GHD) between spawning and incubation periods. Female kokanee lengths for each spawning year from 1966 to 1984 were correlated against the weighted mean gauge height differences for the years in which they had hatched. For example, the length of 1983 spawners was correlated against (3 × 1978 GHD + 4 × 1979 GHD + 3 × 1980 GHD)/10. Our analysis of the data began with the 1962 water year because, prior to that time, kokanee populations were increasing rapidly and did not stabilize during the first several generations of fish produced after the completion of Hungry Horse Dam in 1953.

It was assumed that the Flathead River contributed a substantial portion of the total recruitment to Flathead Lake during the 1960s and 1970s. We assumed that strong year classes of kokanee in Flathead Lake (as indicated by smaller lengths of spawners) were produced when river flow conditions were favorable; weaker year classes resulted when river flows were unfavorable. Recruitment from McDonald Creek and the upper drainage also was substantial but almost constant due to spawning gravel limitations. Annual estimates of fry emigrating from McDonald Creek were similar between 1982 and 1984, despite a 3-fold difference in spawner numbers (Fraley 1984). Recruitment from the lower drainage areas, such as the Whitefish River and Flathead River spring areas, probably was relatively constant as well, but Flathead Lake spawning probably declined during the period (Decker-Hess and Clancey 1984).

For the purpose of this analysis, we assumed that kokanee harvest in Flathead Lake has been relatively constant during the 1966–1984 period. Creel surveys conducted during the summer fishery in 1962 and 1981 resulted in kokanee harvest estimates of 317,000 and 340,000, respectively.

Results of the Analysis

Kokanee spawner length was strongly correlated with the weighted gauge height difference between spawning and incubation periods for the years 1966 through 1984 ($r = -0.93$; $P = 0.99$: Figure 2). A large proportion (87%) of the variation in spawner length could be attributed to differences in gauge heights at spawning and incubation periods in the Flathead River, if our assumptions are valid. Flathead Lake levels also have affected kokanee year-class strength from 1966 to 1984 (Decker-Hess and Clancey 1984). The addition of a variable describing the number of days of lake elevation less than 2,885 ft above mean sea level during the incubation period each year was added to the analysis. This lake level was chosen because most kokanee redds built above minimum pool would be dewatered below 2,885 ft. The addition of the variable raised the R^2 of the gauge height model from 0.87 to 0.93.

The close fit of the relationships indicate that optimum yield of kokanee numbers and size in the Flathead system could be produced through management of reservoir operations and the harvest. Angler harvest also probably contributed to the decline in the main-stem kokanee numbers and will have to be controlled to allow population recovery.

Unexplained variation in kokanee year-class strength may be related to other factors affecting incubation success (Wickett 1962), growth of kokanee in the lake (Goodlad et al. 1974), or differential recruitment to the lake population from other spawning areas (Killick and Clemens 1963).

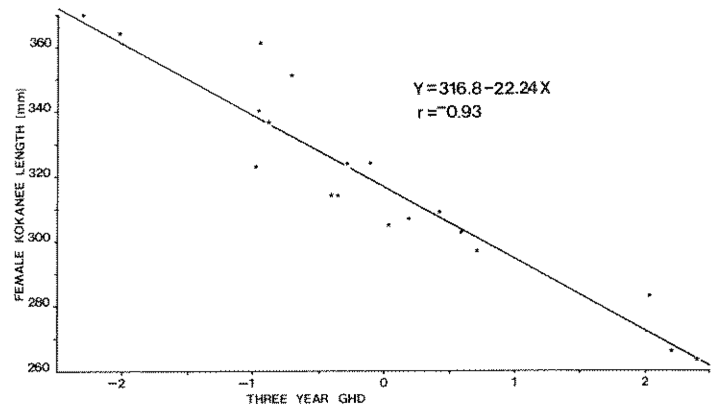

FIGURE 2.—Relationship between total length of female kokanee spawners and 3-year averages in gauge height difference (GHD in feet) for the years that produced the respective spawner cohorts, 1966–1984.

Age composition of the river system kokanee run does not appear to have affected spawner lengths from 1970 to 1983. During the 1981–1983 period, kokanee spawner lengths were the largest recorded, yet only 6–14% of the run was composed of older (age IV+) fish. The age composition of kokanee spawners in the river system spawning population averaged approximately 80% age III+ fish and 20% age-IV+ fish from 1970 to 1984 (Hanzel 1984). A small number of age-II+ fish spawn each year.

Flow Recommendations for Population Recovery

The goal for management of the Flathead drainage kokanee fishery is a balance between the number and size of fish (adult spawner length of approximately 320 mm). This goal would provide a main-stem spawning run similar to that of 1975 when an estimated 165,000 fish spawned in the Flathead River and about the same number were harvested before spawning. Recovery of the river spawning run will enhance recruitment to the Flathead Lake fishery and also provide a dependable fishery for adult kokanee in the river. Also included in the management goal is the maintenance of present levels of spawning escapement in other segments of the river system (McDonald, Beaver, and Deerlick creeks and the Whitefish River) to ensure a diversity of spawning areas and stability of the spawning population.

Management of seasonal and daily flow levels in the Flathead River below the South Fork is critical to the recovery of the kokanee population. A flow regime in the main stem that would enhance kokanee reproduction was recommended to the Northwest Power Planning Council and U.S. Bureau of Reclamation in 1981, and adopted by the council in 1982 as part of the Columbia River Basin Fish and Wildlife Program (Northwest Power Planning Council 1984). The flow recommendations included a stable discharge of 3,500–4,500 ft^3/s for kokanee spawning from 15 October through 15 December, and a minimum flow of 3,500 ft^3/s for egg incubation, alevin development, and fry emergence from 15 December through 30 June. The recommended flows during the spawning period allow some flexibility in operations (be-

TABLE 2.—Percent egg-to-fry survival of kokanee and sockeye salmon in various waters.

Area	Species	Survival (%)	Source
Flathead River system			
1982	Kokanee	21	This study
1983	Kokanee	35	This study
Sullivan Springs, Idaho	Kokanee	7	Jeppson (1960)
Odell Lake, Oregon	Kokanee	20	Lewis (1974)
Cedar River, Washington	Sockeye	1–8	Stober and Hamalainen (1980)
Sashin Creek, Alaska	Sockeye	11–19	Mead and Woodall (1968)
Average, several areas	Sockeye	11	Foerster (1986)

tween 3,500 and 4,500 ft³/s), yet prevent kokanee from building redds in shallow areas that would be subject to subsequent dewatering. Kokanee construct redds and deposit eggs during the daylight hours and the flows should be maintained 24 h/d. The recommended flows will eliminate most incubation mortality due to dewatering and should result in the recovery of the main-stem run to levels observed prior to the late 1970s. Specific management goals for the Flathead Lake shoreline spawning population and operation recommendations for Kerr Dam are yet to be determined.

Population Recovery Model

Model Development

Recovery of the Flathead River kokanee population was projected based on an average egg-to-fry survival rate of 20%. This survival was determined to be 21% during 1983 and 35% during 1984 for the Flathead River drainage spawning areas, by use of drift-netting techniques to capture kokanee fry. Values reported for kokanee and sockeye salmon in other areas of North America range from 7 to 20% (Table 2). Egg-to-fry survival rates are expected to fluctuate during the recovery period, but 20% appeared to be a reasonable average. A 2% survival from fry to returning adult was determined by observations in McDonald Creek, where the data indicated an adult return in 1981 of 1.7% of the estimated fry numbers produced by the 1977 year class.

At the assumed survival rates, a doubling of the kokanee population would take place in each successive 4-year period. The number of kokanee spawners returning each year from 1984 to 2033 was projected by a computer simulation that started from the kokanee escapement of 1979–1983 and assumed 1,000 eggs/female, a 1:1 sex ratio, a 20% egg-to-fry survival, a 2.0% survival of fry to returning adult, and a 4:1 ratio of age-III+ and age-IV+ spawners. Recovery also was projected for various other rates of egg-to-fry and fry-to-adult for comparison purposes. Several hypothetical harvest rates, ranging from 0 to 50%, were used in the analysis. Larkin (1971) used a similar simulation model to project sockeye salmon populations in the Adams River, British Columbia.

Timing of the Population Recovery

The timing of the recovery of the main-stem kokanee population could vary substantially, depending on the level of natural reproductive success and the survival of each year class of fish in

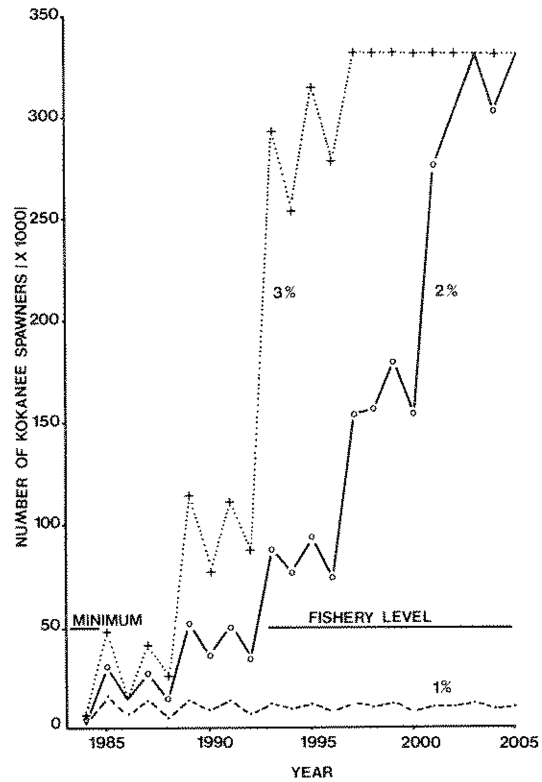

FIGURE 3.—Projected growth of the main-stem Flathead River kokanee spawning population for a constant 20% egg-to-fry survival and a 1, 2, or 3% fry-to-adult survival (no angler harvest). An escapement of 50,000 spawners is the smallest that could sustain a fishery.

Flathead Lake (Figure 3). Changes in the carrying capacity of Flathead Lake also would affect kokanee population recovery. Recovery of the population from its present depressed level could not occur at a fry-to-adult return rate of 1.0% and an assumed 20% egg-to-fry survival. At a 2.0% fry-to-adult return rate and no river harvest, a fishable main-stem population would be reached by 1993 and more than 150,000 spawners would return annually by 1997. The maximum assigned level of 330,000 spawners would be reached by the year 2003. A survival rate of 3.0% could result in a fishable population by 1989 and maximum returns by 1997.

Due to the present low density of spawners, reproductive success in the early years of the recovery could be substantially greater than expected. The 1984 main-stem kokanee run of 17,700 spawners was eight times greater than would be expected from a doubling of the 1980 parental run. However, straying from the McDonald Creek run,

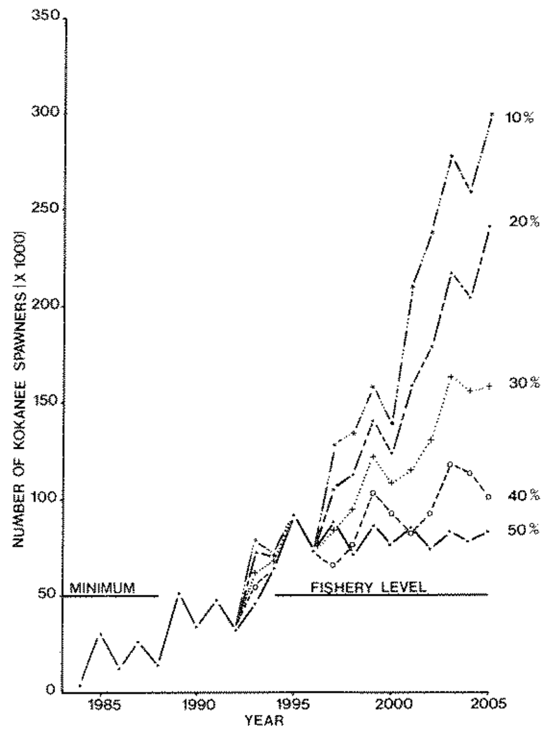

FIGURE 4.—Projected growth of the main-stem Flathead River kokanee spawning run for a constant 20% egg-to-fry survival, a constant 2% fry-to-adult survival rate, and 10, 20, 30, 40, or 50% harvest rates after 1992. A minimum escapement of 50,000 spawners could sustain a fishery.

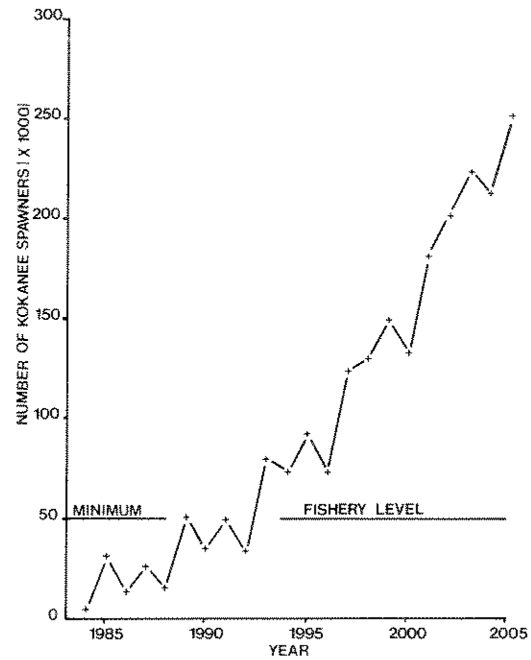

FIGURE 5.—Projected growth of the main-stem Flathead River kokanee spawning run for constant 20% egg-to-fry and 2% fry-to-adult survival rates, and a harvest rate that shifts between 10 and 50% as the number of spawners ranges from 50,000 to 330,000.

increased incubation success due to low spawner density, and recent lower harvest rates in Flathead Lake probably contributed to the larger than expected numbers. Spawning by younger fish (age-II+ spawners) from the 1985 year class also increased spawner escapement.

Quadrennial or cyclic dominance in kokanee and sockeye populations may also be a factor in year-class strength variation (Killick and Clemens 1963). A larger data base is needed before any conclusions can be made about cyclic dominance in the Flathead system. Ward and Larkin (1964) and Larkin (1971) presented conclusive evidence of variations in year-class strength resulting from quadrennial dominance in sockeye populations of the Adams River.

TABLE 3.—Hypothetical harvest management plan for the main stem Flathead River kokanee run.

Projected preharvest population level (number of fish)	Estimated time period	Mean harvest rate (%)	Mean number of kokanee harvested
0–50,000	1984–1992	0[a]	0
50,000–100,000	1993–1996	14	11,473
100,000–200,000	1997–2001	24	34,093
200,000–300,000	2002–2008	39	95,749
>300,000	2009–2033	50	162,235

[a] A restricted lure fishery resulted in a harvest of less than 10%.

Management of Harvest Rates

A spawning run of 50,000 kokanee in the main stem was estimated as the minimum population that could support a harvest without impairment of the population's recovery rate. The main-stem Flathead River spawning run should be safely above the 50,000 fish level by 1993. The rate at which the main-stem population is harvested from that point would greatly affect the future rate of population growth and recovery (Figure 4). A desirable harvest rate for management of the main-stem kokanee population would be one that could be adjusted based on the number of spawners that return each year. This shifting harvest rate could begin at 10% of the spawning run when the minimum escapement of 50,000 fish is reached and be increased to 50% at the presumed maximum population level of 330,000 spawners (Figure 5; Table 3). With this shifting harvest rate, the main-stem population would increase to over 200,000 spawners after four or five generations and to over 300,000 spawners by the year 2007. This harvest strategy would allow for a reasonable balance between population recovery and angler harvest. However, this analysis assumes a fixed harvest rate for the fishery in Flathead Lake.

The river snag fishery with a 35-fish limit was converted to a lure fishery with a limit of 10 fish during 1983 and 1984. The purpose of those regulation changes was to reduce the harvest rate below 10% as outlined in the hypothetical harvest management strategy. An estimated 1,022 kokanee were harvested in 1983 from an estimated main-stem preharvest population of 17,301, for a harvest rate of 6% in 1983. The lure fishery regulations were effective in reducing harvest rates in the Flathead River run from the traditional 40–50% experienced during the snag fishery.

The lure fishery was closed after a harvest of 12,000 spawners was reached in 1984. It was assumed that most of this harvest came from the early upper river runs because the season was closed in mid-September before many main-stem spawners had entered the fishing area. The lure fishery will remain in effect until the population recovers to the level where it can again support the 40–50% harvest rates of the past.

Acknowledgments

The authors gratefully acknowledge the efforts of the dedicated people involved in the fieldwork portion of the project, including Mark Gaub, Jon Cavigli, Paul Leonard, Rick Adams, Ken Frazer, Paul Suek, and Tim Bodurtha. Mark Gaub prepared the graphics and assisted in manuscript preparation. Personnel of the U.S. Bureau of Reclamation and Bonneville Power Administration were very helpful in providing data and assistance, especially Richard Prange, Roger Larson, Tom Vogel, Dick Taylor, and Rich Clark. Personnel at Glacier National Park were helpful throughout the study. The staff of Region 1 of the Montana Department of Fish, Wildlife and Parks, including Bob Schumacher, Jim Vashro, Joe Huston, Laney Hanzel, Scott Rumsey, Bob Domrose, and Gary Anderson, provided equipment and guidance. This study was funded by the Bonneville Power Administration and the U.S. Bureau of Reclamation.

References

Alvord, W. 1975. History of the Montana fish and game. Montana Department of Fish, Wildlife and Parks, Helena.

Bjornn, T. C. 1957. A survey of the fishery resources of Priest and Upper Priest lakes and their tributaries, Idaho. Idaho Department of Fish Game, Federal Aid in Fish Restoration, F-24-R, Completion Report, Boise.

Decker-Hess, J., and P. Clancey. 1984. Impacts of water level fluctuations on kokanee reproduction in Flathead Lake. Montana Department of Fish, Wildlife and Parks, Kalispell.

Foerster, R. E. 1944. The relation of lake population density to size of young sockeye salmon (*Oncorhynchus nerka*). Journal of the Fisheries Research Board of Canada 6:267–280.

Foerster, R. E. 1968. The sockeye salmon (*Oncorhynchus nerka*). Fisheries Research Board of Canada Bulletin 162.

Fraley, J. J. 1984. Effects of the operation of Hungry Horse Dam on the kokanee fishery in the Flathead River system. Annual report to the Bonneville Power Administration, Contract DE AI79-83BP39641, Project 81S-5, Portland, Oregon.

Fraley, J. J., and P. J. Graham. 1982. The impact of Hungry Horse Dam on the fishery of the Flathead River. Completion report to U.S. Bureau of Reclamation, Boise, Idaho.

Fredenberg, W., and P. J. Graham. 1982. Flathead River fisherman census. Montana Department of Fish, Wildlife and Parks, Kalispell.

Goodlad, J. C., T. W. Gjernes, and E. L. Brannon. 1974. Factors affecting sockeye salmon (*Oncorhynchus nerka*) growth in four lakes of the Fraser River system. Journal of the Fisheries Research Board of Canada 31:871–892.

Graham, P. J., and W. Fredenberg. 1982. Flathead Lake fisherman census. Montana Department of Fish, Wildlife and Parks, Kalispell.

Hanzel, D. A. 1964. Evaluation of kokanee spawning and population density in Flathead Lake and tributaries. Montana Department of Fish, Wildlife and Parks, Federal Aid in Fish Restoration, F-7-R-12, Job II, Completion Report, Kalispell.

Hanzel, D. A. 1977. Angler pressure and gamefish harvest estimates for 1975 in the Flathead River system above Flathead Lake. Montana Department of Fish, Wildlife and Parks, Kalispell.

Hanzel, D. A. 1984. Measurement of annual trends in recruitment and migration of kokanee populations and identification of major factors affecting trends. Montana Department of Fish, Wildlife and Parks, Federal Aid in Fish Restoration, F-33-R-18, Job I-b, Boise.

Jeppson, P. 1960. Evaluation of kokanee and trout spawning areas in Pend Oreille Lake and tributary streams. Idaho Department of Fish and Game, Federal Aid in Fish Restoration, F-3-R-10, Job Progress Report, Boise.

Johnson, W. E. 1965. On mechanisms of self-regulation of population abundance in *Oncorhynchus nerka.* Mitteilungen Internationale Vereinigung fuer Theoretische und Angewandte Limnologie 13:66–76.

Killick, S. R., and W. A. Clemens. 1963. The age, sex ratio and size of Fraser River sockeye salmon 1915 to 1960. International Pacific Salmon Fisheries Commission Bulletin 14.

Larkin, P. A. 1971. Simulation studies of the Adams River sockeye salmon (*Oncorhynchus nerka*). Journal of the Fisheries Research Board of Canada 28: 1493–1502.

Lewis, S. L. 1974. Population dynamics of kokanee salmon in O'dell Lake. Oregon Wildlife Commission, Federal Aid in Fish Restoration, F-71-R-11, Research Project Segment, Portland.

McClelland, B., L. Young, D. Shea, P. McClelland, H. Allen, and E. Spettigue. 1982. The bald eagle concentration in Glacier National Park, Montana: origin growth and variation in numbers. Living Bird 19:133–155.

McMullin, S. L., and P. J. Graham. 1981. The impact of Hungry Horse Dam on the kokanee fishery on the Flathead River. Report to the U.S. Bureau of Reclamation, Boise, Idaho.

McNeil, W. J. 1968. Migration and distribution of pink salmon spawners in Sashin Creek in 1965, and survival of their progeny. U.S. Fish and Wildlife Service Fishery Bulletin 66:575–586.

Mead, R. W., and W. L. Woodall. 1968. Comparison of sockeye salmon fry produced by hatcheries, artificial channels and natural spawning areas. International Pacific Salmon Fisheries Commission Bulletin 20.

Northwest Power Planning Council. 1984. Columbia River basin fish and wildlife program. Northwest Power Planning Council, Portland, Oregon.

Potter, D. S. 1978. The zooplankton of Flathead Lake: an historical review with suggestions for continuing lake resource management. Doctoral dissertation. University of Montana, Missoula.

Rieman, B. E., and B. Bowler. 1980. Kokanee trophic ecology and limnology in Pend Oreille Lake. Idaho Department of Fish and Game, Fisheries Bulletin 1, Coeur d'Alene.

Rogers, D. E. 1973. Abundance and size of juvenile sockeye salmon, *Oncorhynchus nerka,* and associated species in Lake Aleknagik, Alaska, in relation to their environment. U.S. National Marine Fisheries Service Fishery Bulletin 71:1061–1075.

Stober, Q. J., and A. H. Hamalainen. 1980. Cedar River sockeye salmon production. Washington State Department of Fisheries, Olympia.

Ward, F., and P. Larkin. 1964. Cyclic dominance in Adams River sockeye salmon. International Pacific Salmon Commission Progress Report 11.

Wickett, W. P. 1962. Environmental variability and reproduction potential of pink salmon in British Columbia. Pages 73–86 *in* N. J. Wilimovsky, editor. Symposium on pink salmon. H. R. MacMillan Lectures in Fisheries, University of British Columbia, Vancouver.