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EFFECTS OF STREAM AND LAKE REGULATION ON REPRODUCTIVE SUCCESS OF KOKANEE IN THE FLATHEAD RIVER SYSTEM, MONTANA, U.S.A.

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ABSTRACT

Kokanee (*Oncorhynchus nerka*) provided an important recreational fishery in the Flathead River–Lake system (Columbia River Basin, U.S.A.–Canada) until the late 1970s when populations declined dramatically. The declines coincided with peaking river discharge from Hungry Horse Dam during the autumn spawning period and an increase in the duration of lake drawdown caused by the operation of Kerr Dam on the outlet of Flathead Lake. Redds of both river and lakeshore spawners were, therefore, dewatered in winter, causing high freezing and desiccation mortality of eggs during the incubation period. It appeared that growth rates of kokanee were density dependent. Female kokanee from strong year classes (i.e., those produced during years of favourable water levels and flow conditions during the incubation period) were smaller than those from weak year classes when unfavourable conditions for incubation prevailed. A highly significant relationship ($r^2 = 0{\cdot}929$, $p < 0{\cdot}001$) was demonstrated between female kokanee spawner length, river gauge heights, and lake levels during years which produced each year class. The close fit of the relationship was further validated by the strong correlation ($r = 0{\cdot}964$) between actual kokanee lengths and predicted lengths. Other factors which could have influenced kokanee year class strength include hatchery plants of kokanee fry, harvest of kokanee by anglers, variations in the carrying capacity of Flathead Lake, and natural fluctuations in egg and fry mortality.

KEY WORDS Kokanee Flathead River and Lake Montana, USA Stream and lake regulation Incubation mortality Year class strength.

INTRODUCTION

Kokanee (*Oncorhynchus nerka*) is the landlocked form of sockeye salmon. The original range of kokanee in North America was the Pacific Coastal drainages from Oregon to Alaska (Scott and Crossman, 1973). Kokanee have been widely introduced in coldwater lakes throughout western North America.

Kokanee were introduced into Flathead Lake in northwestern Montana in 1916, and developed both lakeshore and inlet river system spawning populations. An important sport fishery developed by the early 1930s in Flathead Lake. By 1975, kokanee constituted over 80 per cent of the estimated 500,000 game fish harvested annually in the Flathead system (Hanzel, 1977; Graham and Fredenberg, 1982). Kokanee also provide forage for bull trout (*Salvelinus confluentus*) and lake trout (*S. namaycush*).

The overall objective of this study was to determine the effects of stream and lake regulation on kokanee spawning success in the Flathead system. The investigation was prompted by severe population declines first noted in the late 1970s. A management plan to induce recovery of the river fishery is presented elsewhere (Fraley *et al.*, 1987).

STUDY AREA

The Flathead River system 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

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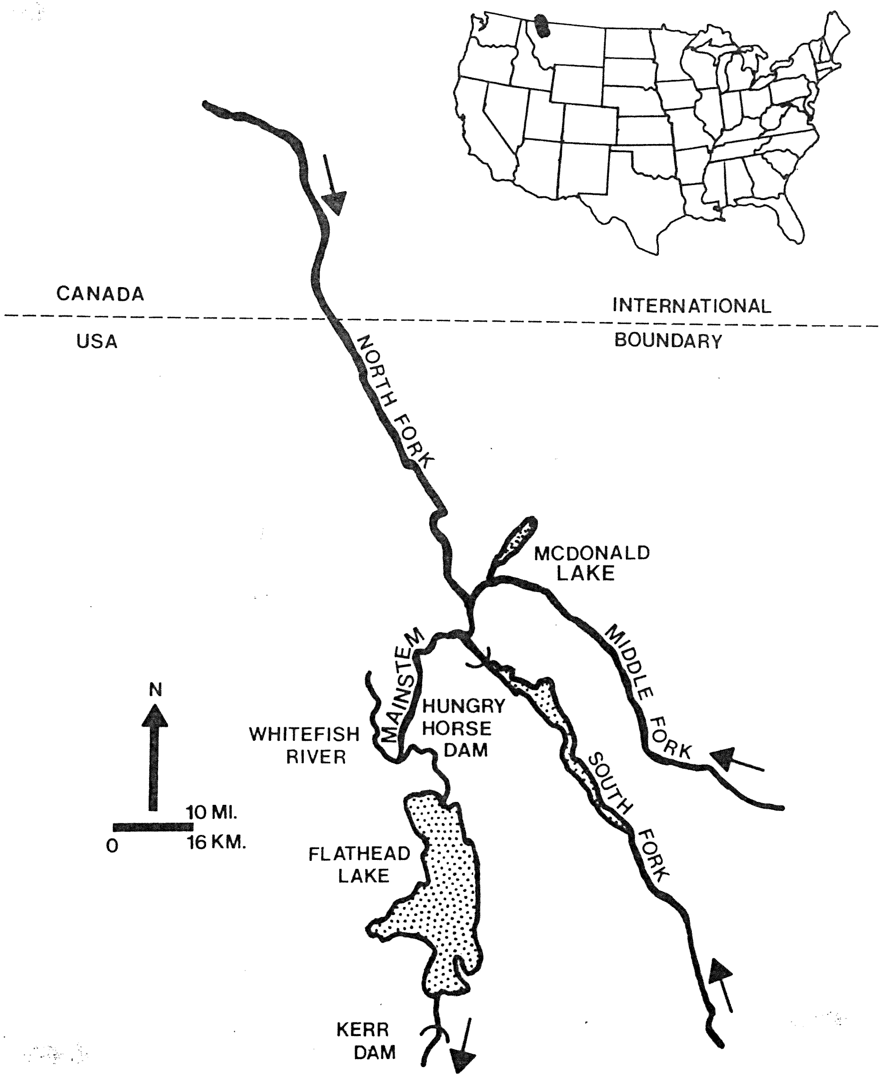

Figure 1. The upper Flathead Basin. Arrows indicate the direction of flow

(Potter, 1978). Approximately 50 per cent of the 200 km shoreline is composed of gravel and cobble which could provide suitable spawning substrate for kokanee.

The Flathead Lake–River system has been affected by two major hydroelectric developments. Kerr Dam (168 megawatt capacity), located 7 km downstream of the natural lake outlet, was closed in 1938. Prior to impoundment, the water level of Flathead Lake remained relatively constant near 879 m *a.s.l.* from September to mid-April. Spring runoff typically increased the lake elevation to the annual maximum (881·8 m) in May and June. Since impoundment, maximum lake elevation has been maintained from May into September. Drawdown usually begins in mid-September. Flood control and recreational constraints on the project require that an elevation of 878·7 m be attained by 15 April, and elevation of 880·9 m by 30 May, and maximum pool level be maintained through 1 September.

Hungry Horse Dam, with a 328 megawatt capacity and a hypolimnetic drain, was constructed from 1948–1953 eight km upstream from the mouth of the South Fork (Figure 1). Operations of Hungry Horse and Kerr Dams are regulated in concert with the complex network of electrical energy producing systems, water consumption needs, and flood control requirements throughout the Pacific Northwest. Neither Kerr nor Hungry Horse Dams are equipped with fish passage facilities.

Kokanee mature in Flathead Lake then return to various natal grounds to spawn. Spawning in the Flathead system usually occurs at the end of the fourth growing season. Kokanee spawn in a diversity of habitats, including springs, lake outlet streams, larger rivers, and lakeshore areas. Kokanee spawning areas in the upper portion of the drainage include the Middle Fork of the Flathead River, and McDonald, Beaver, and Deerlick creeks, tributaries to the Middle Fork (Figure 1). Spawning areas located in the lower portion of the drainage include Flathead Lake shoreline, the Swan River, the Whitefish River, and the main stem Flathead River between Flathead Lake and the confluence with the South Fork Flathead River.

METHODS

Kokanee spawning success was monitored through redd counts, trapping, and snorkeling, from 1979 through 1984. Relationships between year class strength of kokanee spawners and hydropower operations were examined to assess effects of Kerr and Hungry Horse Dams on spawning success in the main stem Flathead River and Flathead Lake shoreline. Historic flow conditions in the Flathead River were measured by the difference in average river gauge height between the kokanee spawning (November) and incubation (December–March) periods. Positive gauge height differences (i.e., an increase in water levels from spawning through the incubation period) was presumed to be favourable for kokanee egg survival, whereas negative gauge height differences were indicative of dewatering of spawning beds.

The number of days the lake was held below various water level increments during the incubation period was also investigated based on evidence that prolonged exposure of salmonid embryos by lake drawdown could cause significant mortality. Initially, the length of time the lake was held between 879·3 and 880·6 m was analysed because less than two per cent of the redds built above minimum pool were constructed above or below these levels in 1981, 1982, and 1983. The change in the number of days the lake was below 879·3 m was further investigated because 80–90 per cent of the redds constructed in spawning areas above minimum pool in 1981, 1982, and 1983 were built above this level.

Total length of female kokanee spawners was used as the measure of year class strength in the Flathead system. 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 and 1968; Johnson, 1965; Rogers, 1973; Goodlad *et al.*, 1974). Adult kokanee length has been used as a measure of year class strength in Pend Orielle and Priest Lakes, Idaho (Rieman and Bowler, 1980).

Growth of kokanee can also 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 fry or age 0+ fish interact with their cohorts and age I fish, but not with older fish. In subsequent years, interactions take place within cohorts and between a cohort and adjacent year classes. The majority of kokanee in Flathead Lake mature and spawn after four seasons (age III+), leaving the fishery. In summary, an age class interacts three years with the previous age class, four years within the cohort, and three years with the following year class (McMullin and Graham, 1981).

To account for these age class interactions, a three year weighted moving average was used in calculating spawning–incubation period gauge height differences. Total length of female kokanee collected from river and lakeshore spawning sites was used as the dependent variable. Females were used because they exhibited less morphological change than males during spawning. Female kokanee lengths for each spawning year from 1966–1984 were correlated to the weighted mean gauge height differences and lake level days which produced them. For example, length of 1983 female spawners was correlated with: [((3;1978 GHD) + ((4)1979 GHD) + ((3)1980 GHD)]/10. This equation yields the river gauge height independent variable, with the same equation used for lake levels for the second independent variable. We began the analysis with the 1962 water year (1966 spawn year) because prior to that, kokanee populations were increasing rapidly and probably did not stabilize for several generations after the completion of Hungry Horse Dam in 1953.

We assumed that the main stem Flathead River and the Flathead lakeshore contributed a substantial portion of the total recruitment to Flathead Lake during the 1960s through mid 1970s (Fraley and Graham, 1982). Strong year classes of kokanee in Flathead Lake were produced when flow and lake level conditions were favourable. Recruitment from McDonald Creek and the upper drainage was also substantial but was probably relatively constant, due to spawning gravel limitations. Recruitment from the other lower drainage areas such as the Whitefish River and Flathead River spring areas was assumed to be relatively constant.

RESULTS AND DISCUSSION

Population Decline and Present Status

From 1979 through 1984, McDonald Creek supported an average of 74·4 per cent of the total spawning run (Table I). The main stem Flathead below the dam supported an average of 13 per cent, the South Fork 4·2 per cent, the Middle Fork 2·7 per cent, and the Flathead Lake shoreline 2·4 per cent. The Swan River, Whitefish River and Beaver–Deerlick Creeks each supported less than 2 per cent of the run.

Formerly, the Flathead River and Flathead lakeshore supported a major portion of the kokanee spawning run (Fraley and Graham, 1982; Decker-Hess and Clancey, 1984). Spawning in the Flathead River increased markedly after the completion of Hungry Horse Dam in 1953, aided by hypolimnial discharges which resulted in warmer winter water temperatures. During the late 1970s, the main stem spawning run declined rapidly. We believe that the decline was related to changes in the operation of Hungry Horse Dam. The majority of kokanee redds in the main stem Flathead are 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 vertical water level fluctuations of up to 2·0 m in the South Fork and 1·4 m in the main stem. Seasonally, operations shifted to higher flows during the fall spawning period and lower flows during the winter incubation period (Figure 2). This operational pattern led to subsequent dewatering and freezing of incubating kokanee eggs deposited during periods of higher flows (Fraley and Graham, 1982). High incubation mortality was probably the major factor in the decline of the main stem kokanee spawning run, which fell from an estimated several hundred thousand fish in the mid-seventies, to an average of 10,800 from 1979–1984.

Shoreline spawning areas in Flathead Lake were used extensively and successfully into the early 1970s. Stefanich (1954) documented kokanee spawning use in 30 shoreline areas, evenly divided on the east and

Table I. Estimated per cent of total post-harvest kokanee spawners in the Flathead River and Lake system, 1979–1984. Dashed lines indicate no available count

	Per cent by spawning area 1979	1980	1981	1982	1983	1984	Mean
McDonald Creek	91	96	78	74	56·3	73·3	74·4
Main stem Flathead River	9	2·1	14·3	8·8	26·7	15·0	13
Whitefish River	—	1·9	·8	4·3	2·1	2·0	1·8
South Fork Flathead River	—	—	·5	1·2	8·5	6·3	4·2
Beaver–Deerlick Creeks	0	—	1·3	·2	<·	0	·5
Middle Fork Flathead River	—	—	4·1	4·3	2·1	0·3	2·7
Flathead lakeshore	—	—	1·0	6	3	2·0	2·4
Swan River	—	—	—	1·2	1·3	1·1	1·0
TOTAL NUMBERS	71,800	51,600	132,900	41,900	60,902	118,200	82,900

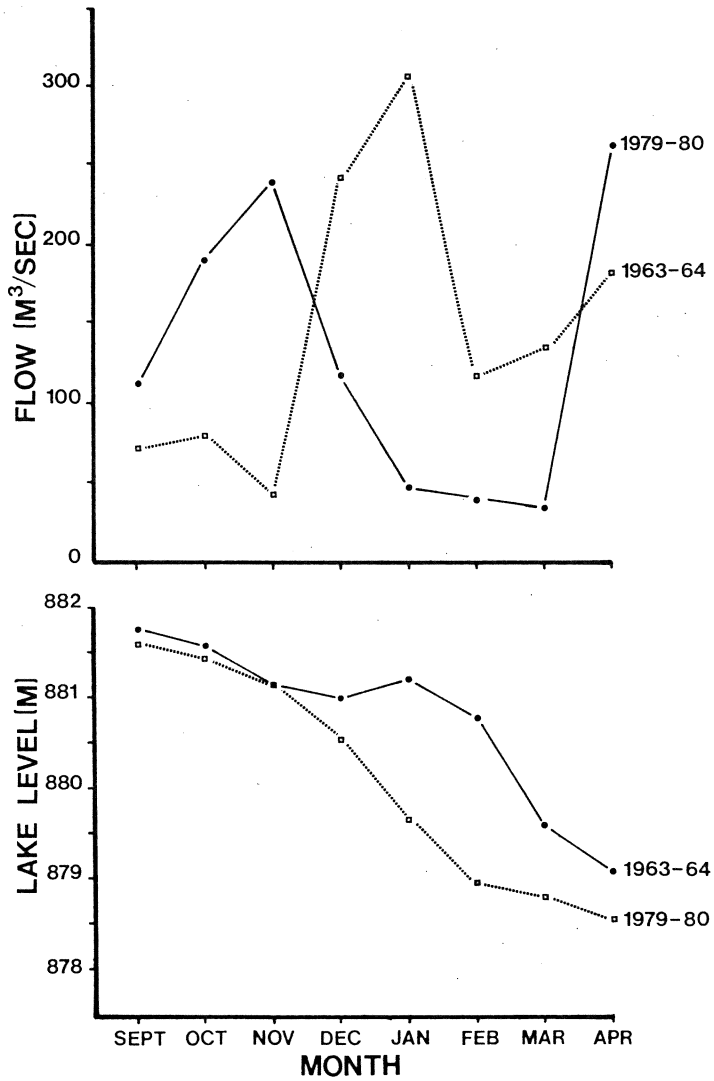

Figure 2. Comparison of Flathead River flows and Flathead Lake levels during a typical favourable year (1963–1964) and a typical unfavourable year (1979–1980) for kokanee reproduction. The autumn spawning period is from late October through November, and the winter incubation period is from December through March

west shores in the 1950s. Egg taking in shoreline areas by hatchery personnel provided millions of eggs to the Station Creek Hatchery into the late 1950s and to the Somers Hatchery into the late 1960s. A general decline in the early 1970s of the numbers of adult kokanee using shoreline areas was noticed by fishery personnel as well as the angling public (Decker-Hess and Clancey, 1984). Kokanee now spawn in only 12–16 areas along the east lakeshore. Only two westshore spawning areas recently have been used by kokanee.

The length of drawdown of Flathead Lake increased dramatically in the mid 1970s (Figure 2). Through natural redd sampling and artificial egg plants, we documented the negative effects of the lengthened drawdown period on incubating embryos in shoreline areas (Decker-Hess and Clancey, 1984). Embryos, prior to hatching, were unable to tolerate extended periods of dewatering when winter air temperatures were below −10°C. Complete mortality was observed after 48 hours following hatching if groundwater flow was insufficient.

Kokanee Year Class Strength and Hydropower Operations

There was a strong relationship between total length of female kokanee spawners and flow levels during the years which produced them from 1966–1984 (Table II). Female kokanee in the 1966–1976 year classes averaged 299·5 (SD 19·8) mm. Water level and flow conditions during the incubation period were favourable. Lake levels were below 879·3 m an average of only 26·2 days (SD 5·3), and river incubation flow levels averaged higher than spawning flow levels in eight of the 11 years. Female kokanee in the 1977–1984 year classes were larger, averaging 345 mm (SD 18·7), and were produced by far less favourable water level and flow conditions. Lake levels were below 879·3 m an average of 58·4 days (SD 19·3), and the river incubation flow levels averaged lower than spawning levels in all eight years. These unfavourable water level conditions apparently increased incubation mortality, resulting in reduced year class strengths and larger size of female kokanee.

The relationship between female kokanee spawner length, river gauge heights, and lake levels during the years which produced each year class was highly significant ($R^2 = 0{\cdot}929, p < 0{\cdot}001$). The form of the equation used to estimate Y was:

$$Y = -17{\cdot}17\ (\text{GHD}) + 0{\cdot}4767\ (LL) + 298{\cdot}7$$

where: Y = predicted female kokanee spawner length (mm); GHD = river spawning–incubation gauge height difference (3-year average); LL = number of days lake levels were below 879·3 m during the incubation period (3-year average); Y intercept = 298·7.

The R^2 value from the relationship indicates that a significant proportion of the variation in kokanee year class strength, as indicated by female spawner length, could be attributed to variations in river and lake levels. These levels were directly influenced by the operations of Kerr and Hungry Horse Dams. The higher partial correlation coefficient attributed to the river gauge height variable, 0.893, as compared to

Table II. Water level variables and female kokanee lengths from 1966–1984 in the Flathead system. Historical river gauge height data are in feet, so all analyses of river flow were run with English units of measurement. However, the data reported herein have been converted to metric units for uniformity of presentation

Year class	Female kokanee length (mm)	Water level conditions which produced the year class: Water years (in 3-year means)	Incubation spawning river gauge height difference (m)	Number of days lake levels were below 879·3 m
1966	283	1962–64	0·63	35
1967	263	1963–65	0·74	22
1968	266	1964–66	0·67	27
1969	303	1965–67	0·20	30
1970	314	1966–68	−0·11	34
1971	324	1967–69	−0·09	20
1972	324	1968–70	−0·04	23
1973	297	1969–71	0·07	30
1974	307	1970–72	0·07	26
1975	309	1971–73	0·12	23
1976	305	1972–74	0·02	18
1977	314	1973–75	−0·13	32
1978	323	1974–76	−0·30	30
1979	337	1975–77	−0·27	47
1980	351	1976–78	−0·15	56
1981	361	1977–79	−0·29	76
1982	370	1978–80	−0·70	84
1983	364	1979–81	−0·63	76
1984	346	1980–82	−0·28	66

0.675 for the lake level variable indicated that river flows, as influenced by the operation of Hungry Horse Dam, had the larger influence on year class strength. Operations of the two projects are related, but tests for collinearity indicated that the lake level variable was more significantly related to female kokanee length than to the river flow variable.

Mean minimum air temperatures during the incubation period were not significantly related to female kokanee spawner length. Minimum air temperatures are probably always cold enough to cause significant mortality in kokanee redds not influenced by groundwater or springs. There was no significant relationship between female kokanee spawner length and the age structure of the spawning run (Hanzel, 1984).

The close fit of the relationship was further validated by a comparison of actual kokanee lengths and those predicted from the river–lake level equation (Figure 3). Predicted lengths agreed closely ($r = 0{\cdot}964$) with measured lengths throughout the observed size range from 1966 through 1984.

Unexplained variation in kokanee year class strength may be related to: (1) other factors affecting incubation success (Wickett, 1962); (2) other factors affecting growth of the various age classes of kokanee in the lake (Goodlad *et al.*, 1974); (3) differential recruitment from other spawning areas to the lake population; (4) quadrennial or cyclic dominance (Killick and Clemens, 1963; Larkin, 1971); and (5) changes in the carrying capacity of Flathead Lake. Harvest of kokanee by anglers probably contributed to variations in year class strength following the initial decline of the population in the mid 1970s.

Kokanee fry were planted sporadically in Flathead Lake throughout the analysis period, possibly influencing year class strength in some years. However, there was no consistent relationship between numbers of fry planted in the spring and year class strength three years hence. The number of fry planted usually was not significant in comparison with the number of fry assumed to be produced by natural reproduction.

Mysis relicta is a competitor with kokanee for the *Daphnia* food supply in Flathead Lake, but did not begin increasing in numbers until 1982. Competition with *Mysis* should not have influenced numbers of adult kokanee during the 1966–1984 period.

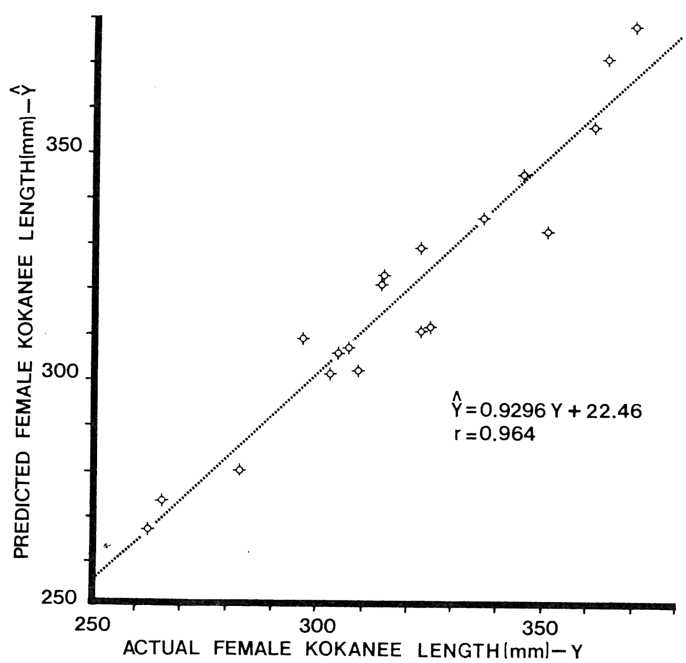

Figure 3. Comparison of Flathead drainage female kokanee spawner length and length predicted by the river–lake equation from 1966 through 1984

CONCLUSIONS

Water level fluctuations beginning in the early 1970s along the Flathead River and Flathead lakeshore greatly increased incubation mortality and reduced kokanee spawning success in spawning sites not influenced by springs. Mortality resulted from water level or flow reductions during the egg incubation and hatching period, exposing embryos to desiccation and freezing. This increased incubation mortality appeared to be the major factor in the observed decline of kokanee spawner numbers, as evidenced by an increase in female kokanee spawner length, during the mid to late 1970s. The water level fluctuations were caused by daily and seasonal changes in the water releases from Hungry Horse and Kerr Dams, linking the operation of the two hydropower projects to kokanee year class strength in the Flathead system.

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