Life history and ecology of bull trout

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Life History and Ecology of Bull Trout (Salvelinus confluentus) in a Large Lake-River System

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ABSTRACT

Life history, ecology and population trends of adfluvial bull trout (Salvelinus confluentus) were investigated in the Flathead Lake and River system of northwest Montana. Annual growth increments for bull trout in the lake were relatively constant (averaging 90 mm) from age 4-9. We estimated that about half of the adult bull trout in the lake embarked on a spawning migration each year. Bull trout matured at 5 or 6 years of age, and migrated in May through July from 88-250 km to reach tributaries of the North and Middle forks of the Flathead River. Bull trout spawned in the tributaries from late August through early October. Most spawners were 6 or 7 years old and they averaged 628 mm in length. Bull trout formed pairs near the tributary mouth, entered the tributaries when water temperatures dropped below 12 C, and began to spawn after water temperatures were below 9 C. They spawned in areas with low gradient, loosely compacted gravel, groundwater influence and holding cover. After spawning, females left the tributaries to return to the lake more quickly than males. Spawning was identified in 28 tributaries. Bull trout embryos incubated at 2 to 5 C from October through April. Fry emerged from the gravel at 25 mm, then doubled their length by the end of the first summer. Average length of juveniles in tributaries at annulus I, II, and III was 72, 108 and 140 mm. Juveniles were found in streams with summer maximum temperature less than 14 C, and they were closely associated with the stream bottom. Juveniles outmigrated from the tributaries from June through August, at age 1(18%), 2(49%), and 3(18%). Counts of completed redds in areas of tributaries selected for monitoring averaged 360 from 1979-1985, and peaked at 600 in 1982. We estimated that an average of 3,426 bull trout successfully spawned from 1980-82, based on drainage-wide redd counts and assuming 3.2 fish per completed redd. Changes in spawning and rearing habitat caused by timber and mineral development would impact the bull trout population in Flathead Lake. The population may be limited by a combination of juvenile rearing habitat, spawning habitat, and spawning escapement levels.

Key words: Bull trout, Salvelinus confluentus, Flathead Lake and River, life history, adfluvial, age and growth, water temperature, habitat selection, spawning escapement.

Topic phrases:

Life history and ecology of an inland char (bull trout) in the Flathead Lake and River system, Montana

Water temperature influences on migration, spawning and distribution of bull trout

Age structure and growth of adult and juvenile bull trout

INTRODUCTION

The bull trout (Salvelinus confluentus) is the largest fish native to the Flathead Drainage, attaining a length of nearly one meter and a weight of 10 kg. The bull trout inhabiting the inland waters of northwestern North America is considered a separate species from the smaller, coastal Dolly Varden (Salvelinus malma) (Cavender 1978). The bull trout population in the Flathead system is largely adfluvial, growing to maturity in lakes and migrating through the river system and into the tributaries to spawn. Juveniles rear in tributary streams from 1-3 years before migrating to the lakes.

Much information has been published concerning the life history of coastal Dolly Varden (eg. Heiser 1966, Blackett 1968, Armstrong and Morton 1969, Armstrong and Morrow 1980, Balon 1980). Published information on the bull trout is not as common. McPhail and Murray (1979), Leggett (1969), and Allan (1980) studied various aspects of the life history of bull trout in British Columbia and Alberta.

The Montana Department of Fish, Wildlife and Parks studied the bull trout population in the Flathead drainage beginning in 1953 (Block 1955, Hanzel 1976). More intensive work was undertaken from 1979-1984 during the EPA sponsored Flathead River Basin Studies (Graham et al. 1980, Fraley et al. 1981, Shepard et al. 1982, 1984a, Graham et al. 1982, Fraley and Graham 1982, Graham and Fredenberg 1982, Leathe and Graham 1982). We studied bull trout age and growth in the lake and river, harvest by anglers, the adult spawning migration, spawning site selection and use, and densities, habitat selection, and outmigration of juveniles rearing in tributaries. Methods included tagging, gill netting, stream trapping and electrofishing, creel survey, otolith and scale analysis, and redd counts.

The purpose of this paper is to summarize our knowledge of the life history, ecology and population status of adfluvial bull trout in the Flathead Lake and inlet river system.

STUDY AREA

The Flathead Lake-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 (Potter 1978). The upper 3 m of Flathead Lake is regulated by Kerr Dam, constructed on the outlet in 1938. The Flathead River enters the north end of the lake. This study was conducted in the upper Flathead Basin which includes Flathead Lake and the river system above Flathead Lake.

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. The upper North Fork drains southern British Columbia. The South Fork is regulated by Hungry Horse Dam, located 8 km above its mouth. The Swan River enters Flathead Lake near the mouth of the Flathead River.

Bull trout coexist with 23 other species of fish in the Flathead Lake-River system. Most bull trout which spawn in the North and Middle Fork drainages mature in Flathead Lake. Fish maturing in the large lakes of Glacier National Park may utilize some tributary streams for spawning. There are a few resident populations of bull trout in tributaries of the North Fork. Bull trout in Flathead Lake probably developed their migratory habits in Glacial Lake Missoula, which existed in the upper Columbia drainage to an elevation of 1341 m during the last glacial period. The lake drained approximately 12,000 years ago leaving Flathead Lake as its remnant.

Bull trout originally used the tributaries of all forks of the Flathead and the Swan River. The construction of Bigfork Dam in 1902 blocked bull trout migrations into the Swan River. A marginal fish ladder accommodates very limited movement of bull trout downstream from the Swan drainage, as evidenced by tag returns. Hungry Horse Dam, a 540 foot structure which was closed in 1951, blocked all movements of bull trout into the South Fork drainage and probably resulted in a substantial reduction of the population in Flathead Lake.

Tributaries used by spawning bull trout in the North and Middle Fork drainages are characterized by gravel-rubble substrate, low flows of 2-60 cfs, and maximum summer water temperatures less than 14 C.

LIFE HISTORY

Lake Residence

Bull trout populations residing in Flathead Lake include recently arrived migrating juveniles from the Flathead River system, subadult fish less than about 450 mm in length, and mature fish 5-6 years or more in age (Figure 2). Most bull trout in Flathead Lake matured at age 6. A similar age of maturity was reported for bull trout in Arrow Lakes, British Columbia (McPhail and Murray, 1979).

Bull trout in Flathead Lake were distributed throughout the water column, but exhibited seasonal responses to changes in temperature and prey species distribution. During the late summer, most bull trout were found below the thermocline in deeper waters.

The diet of bull trout in the lake consisted almost exclusively of fish (Leathe and Graham 1982). The lake whitefish (Coregonus clupeaformis), and pygmy whitefish (Prosopium williamsoni) were the most important year-round food item, followed by yellow perch (Perca flavescens), kokanee (Oncorhynchus nerka) and many non-game species. Kokanee were the major food item for bull trout in Pend Oreille Lake, Idaho (Jeppson and Platts 1959) while whitefish were the major food in Upper Priest Lake (Bjornn 1957). Bull trout in Priest Lake have recently been found to utilize oppossum shrimp (Mysis relicta).

The annual growth increment for bull trout in Flathead Lake, based on analysis of scales and otoliths ranged from 60-132 mm

(Figure 3). Back calculations of length at annulus formation were made from 1,814 scale samples. Aging was checked with otoliths from 451 of the fish. Agreement of aging between otoliths and scales ranged from 100% for fish 0-3 years of age, to 52% for older, mature fish. Growth was relatively constant after age IV, reflecting lake residence. Leathe and Graham (1982) reported that growth rates of bull trout in Flathead Lake were similar to that reported for some other waters in the Northwest.

Not all mature bull trout present in the lake embark on a spawning run each year. A smaller percentage of adult fish were found in the lake during the summer and fall, suggesting that between 38 and 69% (average 57%) left the lake on the annual spring migration each year (Leathe and Graham, 1982). The frequency of repeat spawning was thought to vary by age and sex. Alternate year spawning has been reported for inland Dolly Varden char (Armstrong and Morrow 1980).

Upstream Migration

Mature bull trout in Flathead Lake began their migration into the river system during April and moved slowly upstream, arriving in the North and Middle Forks during late June and July. Bull trout swam long distances during their spawning migration, traveling more than 250 km to reach North Fork tributaries in British Columbia. The shortest known migration of adult bull trout from Flathead Lake is 88 km to the mouth of Canyon Creek in the North Fork drainage. Observations and tag returns from 1974-1982 indicated that adult bull trout remained at the mouths of spawning tributaries for two weeks to a month. Feeding was thought to be limited after the adults reached the mouth of the tributary stream selected for spawning.

Adult bull trout entered tributary streams at night from July through September. Trapping indicated that the majority entered in August. Because the majority of bull trout moved through the traps in pairs, we believed that bull trout formed pairs near the mouth of the spawning tributary. Bull trout which entered the spawning tributaries were generally not in final spawning condition, but held in the tributaries for up to a month or more in deeper holes or near log or debris cover before spawning. Similar pre-spawning behavior and spawning timing was reported for bull trout in Mackenzie Creek (McPhail and Murray 1979) and John Creek (Leggett 1969) in British Columbia.

The majority of the bull trout spawners in the North and Middle Forks were six or seven years of age (Table 1). Most spawners in the Swan system were five or six years old (Leathe and Enk 1985).

Spawning

Most bull trout spawned during September and early October in the Flathead, similar to adfluvial bull trout populations in Idaho (Heimer 1965) and British Columbia (McPhail and Murray 1979). Initiation of spawning in the Flathead appeared to be related largely to water temperature, although photoperiod and streamflow probably also played a part. Bull trout began spawning when water temperatures dropped below a threshold level of 9-10 C. McPhail and Murray (1979) reported that 9 C was the threshold temperature for the initiation of spawning in Mackenzie Creek, British Columbia.

Bull trout selected aggrading areas in the stream channel for spawning, characterized by gravel substrates, low compaction and low gradient (less than 3%). Groundwater influence and proximity to holding cover were also important factors influencing spawning site selection. These relatively specific requirements for spawning sites resulted in a restricted distribution of spawning in the Flathead Drainage. Bull trout from Flathead Lake spawned only 28% of the 750 km of available tributary, according to basin-wide surveys from 1980-1982.

The female chose a spawning site through anal fin feeling, and constructed the redd. The male defended the area. Male bull trout in Trail Creek, a North Fork tributary, remained near the redd an average of two weeks after spawning. Completed bull trout redds in the Flathead drainage averaged 2.0 m x 1.0 m in size, and sometimes overlapped. A redd may be constructed by one male and one female, or by more than two fish. Block (1955) observed one male spawn with three females in succession, expanding the size of the redd each time. McPhail and Murray (1979), Leggett (1969), and Block (1955) provided detailed descriptions of spawning behavior and spawning site activities. After completion of the spawning act, the spent adults moved rapidly out of the tributary and downstream to the lake, possibly feeding on mountain whitefish during the journey. Adult spawners in the Flathead system averaged 630 mm, with little variation in average size over a wide range of collections (Table 2).

Fecundity varied with fish size. An average of 5,482 eggs per female was reported for a sample of 32 adults averaging 645 mm from the North Fork in 1977. One female bull trout collected in 1984 weighed 15 pounds and contained 12,000 eggs. Bull trout in Arrow Lakes, British Columbia were smaller and contained fewer than 2,000 eggs per female (McPhail and Murray 1979). The sex ratio of bull trout spawners averaged 1.4 females per male in Trail Creek in the North Fork drainage, and 1.37 females per male in the Swan Drainage.

Incubation and Emergence

After deposition in September and October, bull trout eggs incubated in the redd for several months before hatching in January (Weaver and White 1985). The alevins then remained in the gravel and absorbed the yolk sac, and emerged in April. Incubation time was dependent on temperature. Bull trout eggs required 113 days (340 temperature units) to 50% hatch in Coal Creek, a tributary of the North Fork of the Flathead River (Weaver and White 1985). The fry emerged from the gravel 223 days (635 temperature units) after egg deposition. Intergravel temperatures during the incubation period (October-March) in Coal Creek ranged from 1.2 - 5.4 C. McPhail and Murray (1979) reported the best survival of bull trout embryos at 2-4 C. Survival to emergence in Coal Creek averaged 53%.

In laboratory experiments, survival was shown to be inversely related to the percent fine material (<6.35 mm) in the gravels (Weaver and White 1985). Survival to emergence ranged from nearly 50% in mixtures which contained 10% fines, to 0% in mixtures which contained 50% fines.

Bull trout fry remained in the gravel for several weeks after yolk sac absorption (McPhail and Murray, 1979). The fry began feeding during this period, and after filling their air bladder, emerged from the gravel. Newly emerged fry averaged 23-28 mm in both the Flathead Drainage in Montana, and in Mackenzie Creek, British Columbia. Fry more than doubled their length during the first summer of growth. A group of 32 young of the year bull trout from Morrison Creek in the Middle Fork drainage collected on September 25, 1985 ranged from 55-71 mm in length.

Juvenile Rearing and Emigration

Juvenile bull trout were present in about half of the stream reaches surveyed during studies in the upper Flathead River Basin. Juveniles were present in many reaches which were not used by adult spawners. These juveniles apparently swam upstream to these sections to rear. Distribution was also influenced by water temperature as juvenile bull trout were rarely observed in streams with summer maximum temperatures exceeding 14 C. Oliver (1979), Allan (1980) and Pratt (1984) also reported that bull trout distribution was affected by temperature.

Young of the year bull trout were generally found in side channel areas and along the stream margins in Flathead tributaries. Blackett (1968) reported a similar habitat preference for juvenile Dolly Varden char in southeast Alaskan streams. McPhail and Murray (1979) found young of the year bull trout in areas of low velocity near the stream edges.

Densities of young bull trout in Flathead tributaries were generally similar in pools, runs, riffles and pocketwater habitat, and exhibited more flexibility in habitat use than bull trout in other drainages. Juvenile bull trout were found closely associated with stream substrate. Pratt (1984) studied microhabitat preferences in the Flathead Drainage and reported that small juveniles (less than 100 mm) were most often observed near the stream bottom, associated with instream cover such as the stream bed materials and submerged fine debris which provided pockets of slower current velocities. Juveniles 100 mm or longer were also associated with the stream bottom, and used dispersed instream cover, small pockets of slow water and larger instream debris. As the juvenile bull trout grew, they became less associated with the streambed.

During stream residence, juvenile bull trout were opportunistic feeders, ingesting mainly aquatic invertebrates (especially Diptera and Ephemeroptera) in similar percentages as they were available in the stream. Bull trout larger than 110 mm also ate small trout and sculpin. Diptera and Ephemeroptera were the major food items for juvenile Dolly Varden in southeast Alaskan streams (Armstrong and Morrow 1980).

Densities of juvenile bull trout in Flathead drainage tributaries estimated by snorkeling averaged 1.5 fish/100 m^2 of stream surface area (range:0.1-7.1). Juvenile bull trout are difficult to observe because of their close association with the stream bottom, so these numbers are probably underestimates. Electrofishing estimates ranged as high as 15.5 fish/100 m^2 in certain streams.

Most juvenile bull trout in the Flathead drainage remained in the tributaries for 1 to 3 years before emigrating to the river system. Ages were assigned, from scales and otoliths, to 246 juvenile bull trout captured in downstream traps placed in three tributaries to the North and Middle Forks (Figure 4). About half (49%) of the outmigrants were age II. Nearly a third (32%) left the tributaries at age III, while 18% were age I. Only 1% of the outmigrants were age IV. The age of emigrating juveniles were similar in Idaho and British Columbia (Bjorn 1957, Oliver 1979, McPhail and Murray 1979). The average length at annulus formation of Age I, II, and III juvenile bull trout in the Flathead System was 72, 108 and 140 mm respectively.

Emigration of juveniles from the tributaries into the Flathead River system took place largely from June through August (Figure 5), similar to the emigration period reported for the Wigwam drainage, British Columbia (Oliver 1979). After juvenile bull trout entered the river system they appeared to move rapidly down stream into the main stem Flathead River below the South Fork, arriving during August and September. Juvenile bull trout were found during electrofishing surveys in the main stem during all times of the year, but numbers peaked during the fall months (McMullin and Graham 1981). Based on snorkel observations, some juveniles rear along the stream margin of the Middle and North Forks. The degree of rearing or residence in the lower Flathead River before entry into Flathead Lake has not been well documented.

TRENDS IN SPAWNER ABUNDANCE

Drainage-wide counts of bull trout redds in 1980 (568), 1981 (714) and 1982 (1138) were used to index the number of adfluvial bull trout which successfully spawned in the river-tributary system. We converted the redd counts approximate fish numbers by making the following assumptions: 1) 75% of all redds were located, and 2) an average of 3.2 spawners entered the tributary for each completed redd. This ratio of spawners per redd was based on comparisons of trap counts of spawners and redds completed in North Fork streams. From partial trapping results on several tributaries in 1977-1981, we estimated a spawner:redd ratio of 3.2:1. In 1953, 55 bull trout entered Trail Creek and constructed 18 redds for a spawner:redd ratio of 3.2:1. During 1954, 160 bull trout constructed 48 redds in Trail Creek, yielding a ratio of 3.3:1. Based on these assumptions, we calculated that an average of 3,426 bull trout successfully spawned annually in the Flathead drainage from 1980-1982.

Bull trout spawned in 28 tributaries to the North and Middle forks (See Figure 1), but only a small percentage of the stream reaches available to bull trout were utilized for spawning. Major

North Fork spawning tributaries were Howell, Trail, Whale, Big and Coal creeks. Major spawning tributaries in the Middle Fork were Morrison-Lodgepole, Granite, Ole, Trail and Dolly Varden creeks. The portion of the drainage in Canada supported 23-31% (mean 29%) of the spawning in the North Fork drainage during the period. Howell Creek supported 13-19% (mean 16%) of all North Fork spawning.

Monitoring of bull trout spawning in the drainage at selected major sites indicates that the escapement was highest in 1982, but has been variable with no definite trend (Table 3). These monitoring areas are considered representative of the drainage, and comprised 32, 30 and 31% of the total drainage-wide counts in 1980, 1981 and 1982, respectively. Counts in the monitoring areas during the 1980-82 period accurately reflected drainage-wide trends.

Juvenile bull trout densities could also be viewed as reflective of population status. Juvenile bull trout populations in Coal and Morrison creeks have been monitored for only a limited period of record (Table 4). Numbers of juvenile bull trout were highest in 1985 for both streams. Continued population estimates in these streams will serve as valuable information for future monitoring.

Sampling for bull trout on Flathead Lake indicated that the population has been relatively stable. Average catches of bull trout in sinking nets were 1.2-2.1 fish per net in 1967-1970, 2.2-2.9 fish per net in 1980-81 (Leathe and Graham 1982). The average bull trout sampled in Flathead Lake was 24 mm larger in 1980-81 than in 1967-70. A larger percentage of the fish were greater than 500 mm in the 1980-81 sampling period. The percentage of trophy fish (greater than 634 mm) was similar in both sampling periods. Migrating spawners, captured in the river system, were similar in size from 1957 through 1981 (see table 2).

SENSITIVITY TO ENVIRONMENTAL DISTURBANCE

All bull trout life stages are sensitive to environmental disturbances. The population in the Flathead System is threatened by several major forms of resource development. The proposed Cabin Creek coal mine in the North Fork drainage in British Columbia has received Stage II approval by the Canadian government and has been referred by the U.S. and Canadian Governments to an International Joint Commission for review. This mine could impact bull trout spawning in the upper North Fork and in Howell Creek, the major spawning tributary in the Canadian portion of the drainage, through increased sedimentation and alteration of flow and water quality. Timber harvest and road construction in both the North and Middle fork drainages are potential threats to bull trout spawning and rearing habitat.

Increased fishing pressure is often associated with resource development. Because of the restricted distribution of bull trout spawning in the basin and the limited size of the known annual escapement (3,000-4,000 individuals), harvest of fish by anglers can have a dramatic impact on the population. Any increase in harvest by anglers in a particular area or subbasin could result in a loss of recruitment from that site, in turn reducing the overall population in Flathead Lake.

Large bull trout spawners are highly visible in the upper river-tributary system and are vulnerable to anglers. The upper river stocks are subject to a disproportionally high harvest because of greater visibility and longer migration routes. The Montana Department of Fish, Wildlife and Parks reduced the creel limit from two to one bull trout in 1982. This measure should result in decreased harvest on the spawning run, which could have been as high as 40% in 1981, assuming no other sources of pre-spawning mortality. The British Columbia Ministry of the Environment reduced the limit to one fish in 1983 and closed spawning tributaries to angling. Most major bull trout spawning tributaries in the U.S. portion of the drainage were closed to angling in the early 1960's. Other mortality factors affecting the adults during the time they are in the river and tributaries are unquantified, but could be significant, considering that these fish spend five to six months in the river system.

The long overwinter incubation and development phase for bull trout embryos and alevins (223 days in Coal Creek) leaves them particularly vulnerable to changes in streambed material, increases in fine sediments, and degradation of water quality. Weaver and White (1985) and Shepard et al. (1984b) reported that bull trout incubation success was affected by fine sediments. Juvenile bull trout would be greatly affected by streambed changes because of their close association with the substrate.

As our studies of bull trout in the system continue, we hope to better define the limiting factors which act on the population. It is not clear whether the tributaries are at carrying capacity for juvenile bull trout, or whether juvenile densities are limited by spawner escapement levels. The answer to these questions will require monitoring the escapement levels and resulting juvenile densities in the tributaries over a longer period of time. McPhail and Murray (1979) suggested that limitations to juvenile densities in tributary rearing streams may form an "ecological bottleneck", greatly affecting overall population levels of bull trout.

Bull trout in the Flathead are dependent on the habitat quality and management of the interconnected river, lake and tributaries. Cumulative losses of spawning and rearing habitat would reduce the bull trout population in Flathead Lake.

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Table 1. Age of bull trout spawners in the Flathead system.

Stream	Percent by Age				
	5	6	7	8	9
North Fork Flathead River 1954 (N-41)	24	39	34	3	0
Middle Fork Flathead River 1981 (N=31)	10	48	35	10	0
Swan River 1983 (N=57)	33	35	23	9	<1
Swan River 1984 (N=76)	43	37	17	3	0

Table 2. Total lengths of adult bull trout spawners in the Flathead drainage.

Stream	Year	Average Length (mm)	Number of Fish
North Fork	1979	638	36
	1977	645	32
	1953	617	165
Middle Fork	1980	618	35
	1957	622	87
Both Forks	1975	628	46

Table 3. Bull trout redd counts for selected areas of tributaries chosen for monitoring in the Flathead Drainage.

	1979	1980	1981	1982	1983	1984	1985
North Fork:							
Big	10	20	18	41	22	9	9
Coal	38	34	23	60	73	61	40
Whale	35	45	98	211	141	133	94
Trail	34[a/]	31[a/]	78	94	56	32	25
Total North Fork	117	130	217	406	292	235	168[b/]
Middle Fork:							
Morrison	25[a/]	75	32[a/]	86	67	38	99
Granite	14	34	14[a/]	34	31	47	24
Lodgepole	32	14	18	23	23	23	20
Ole		19	19	51	35	26	30
Total Middle Fork	71	142	83	194	156	134	173[b/]
Total Drainage	188	272	300	600	448	369	341

a/ Counts may be underestimated due to incomplete survey.

b/ High flows may have obliterated some of the redds.

Table 4. Juvenile bull trout densities in a North Fork tributary (Coal Creek) and a Middle Fork tributary (Morrison Creek) from 1980-1985.

	Date	Population Estimate (Number/150 m section)	95% Confidence Interval
Coal Creek (at Deadhorse Bridge)	08/05/82	130	±36
	08/23/83	99	±33
	08/31/84	89	±27
	08/26/85	167	±66
Morrison Creek	09/23/80	91	±48
	09/01/82	93	± 5
	08/18/83	62	±11
	09/25/85	93	±27

Figure legends

Figure 1. The upper Flathead River Basin. The 28 tributaries shown were identified as bull trout spawning areas.

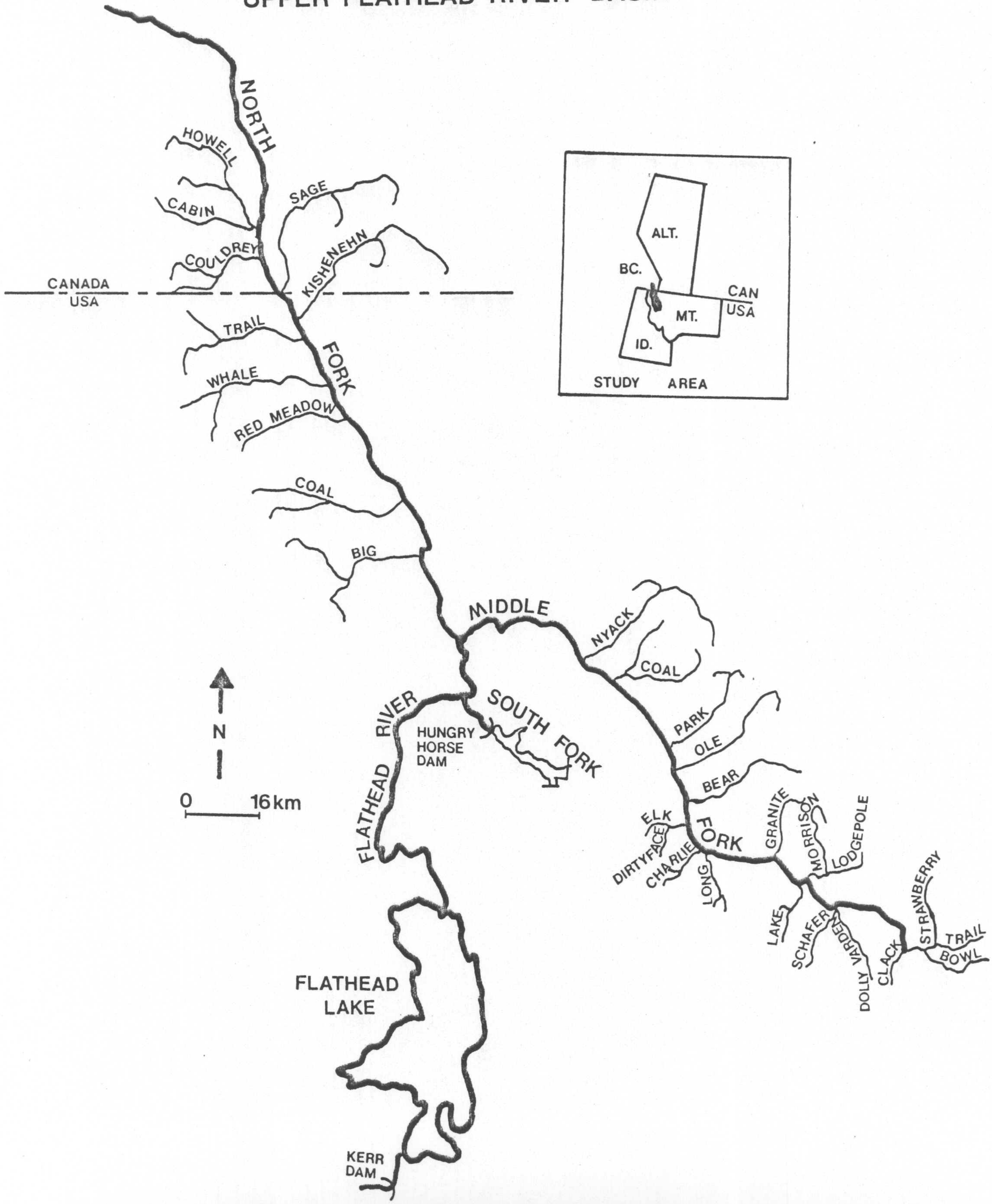
Figure 2. Bull trout life history stages and associated mortalities.

Figure 3. Average growth rate and annual growth increment from analysis of scale samples for bull trout in the Flathead system (N=1814).

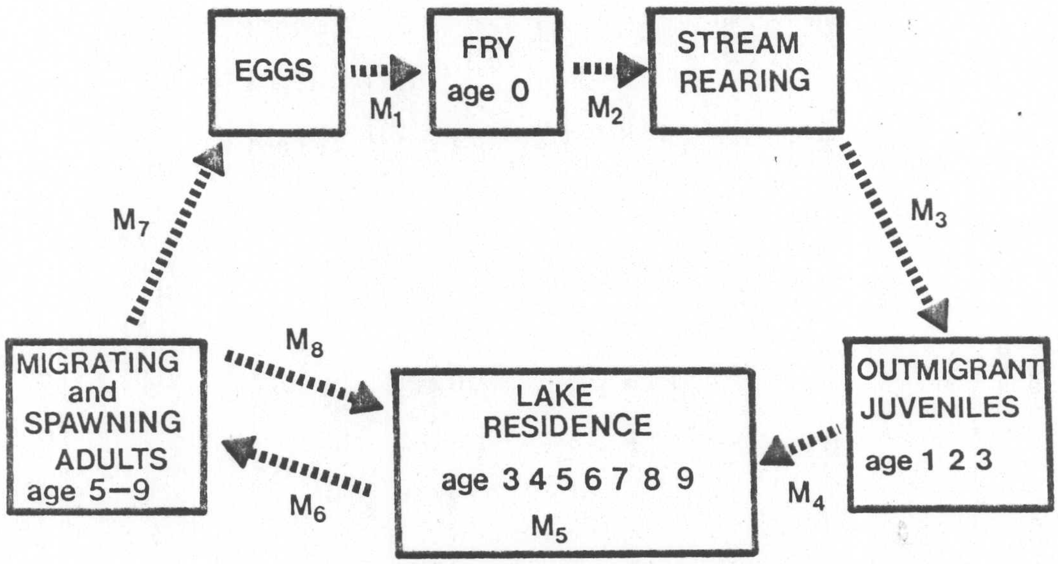
Figure 4. Percent outmigrating juvenile bull trout of each age class in Flathead river tributaries.

Figure 5. Number of juvenile bull trout passed through downstream traps, number of juvenile bull trout per trap day, by month for Flathead system tributaries (N=1328). Trap locations were near the tributary mouths, and all fish moving downstream were assumed to be outmigrants.

UPPER FLATHEAD RIVER BASIN

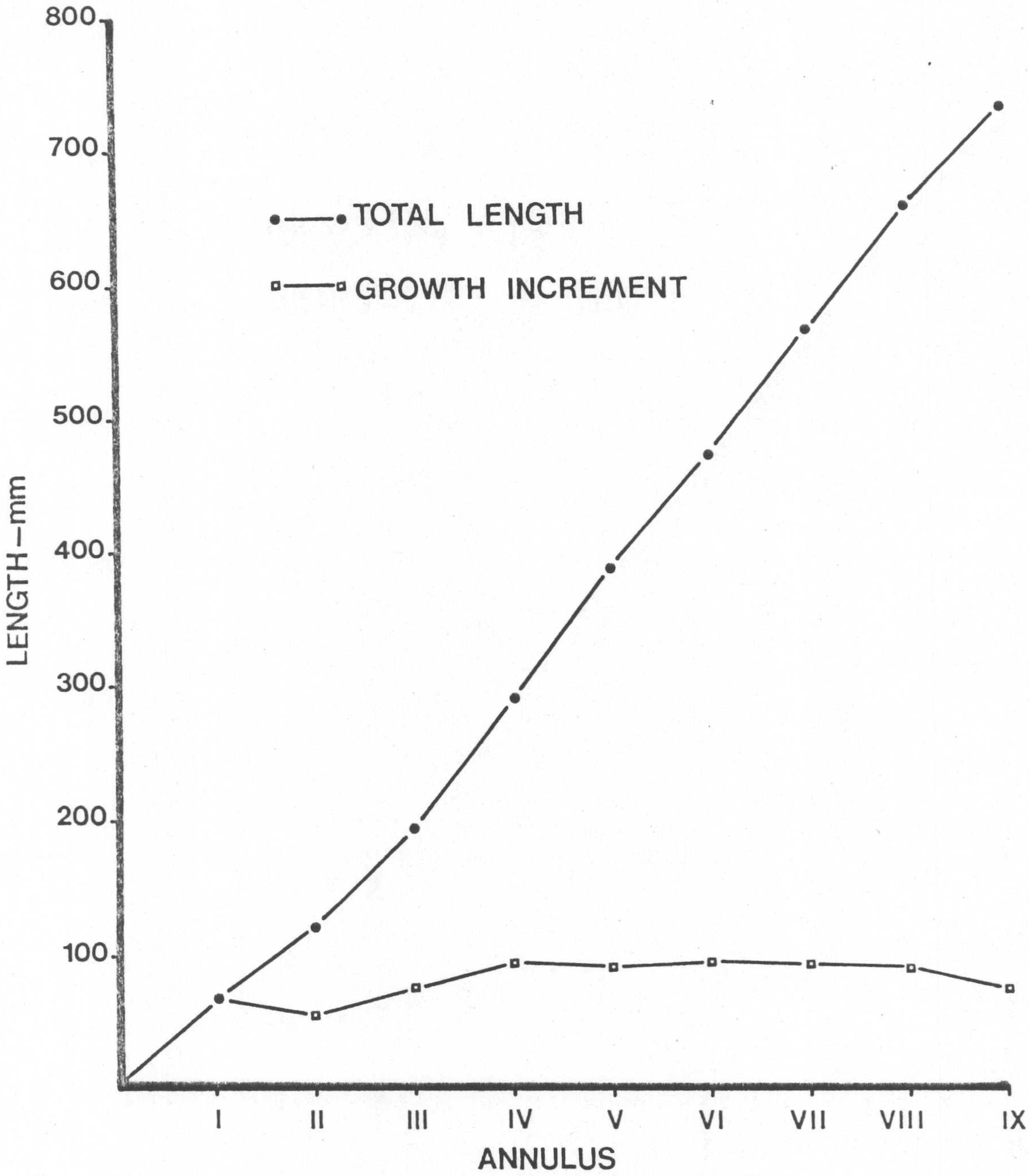


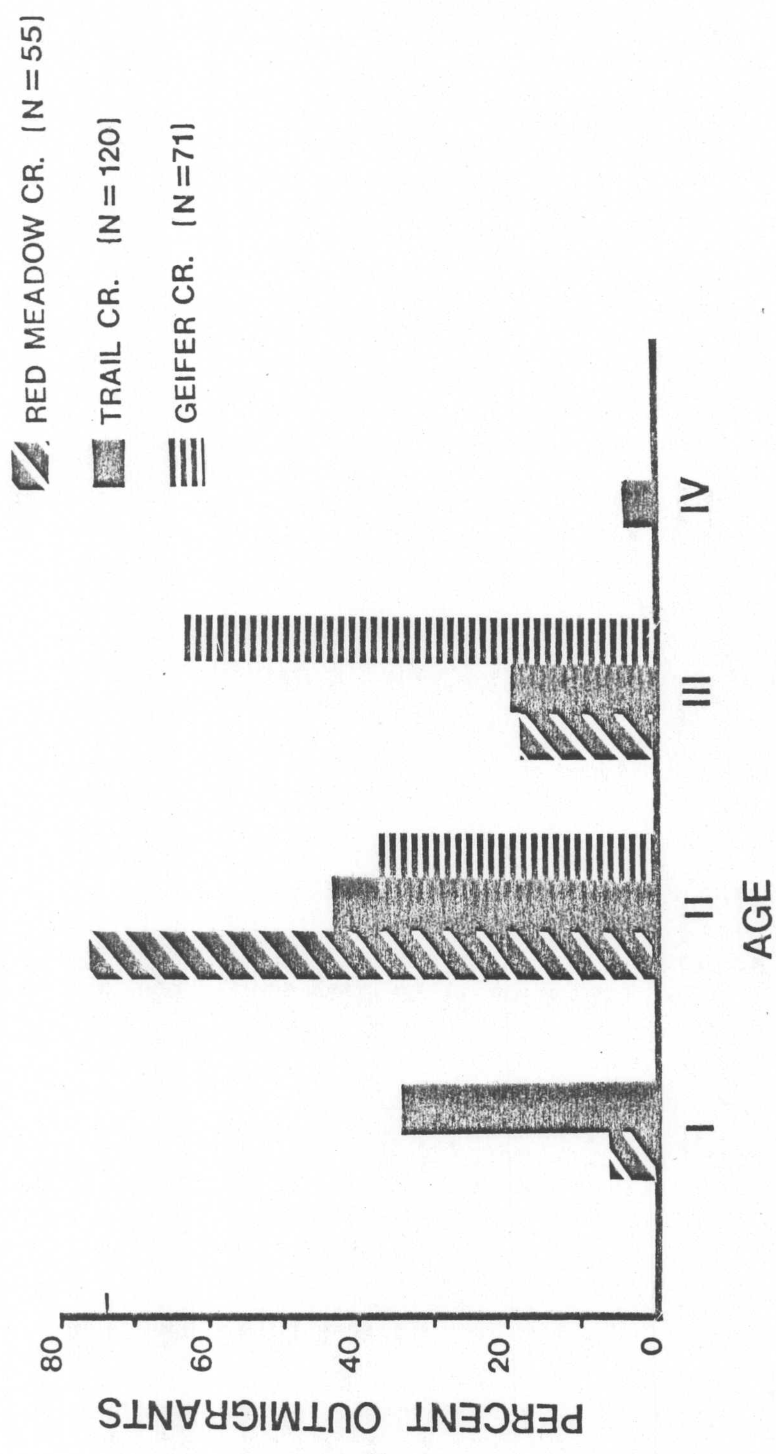
BULL TROUT LIFE HISTORY STAGES

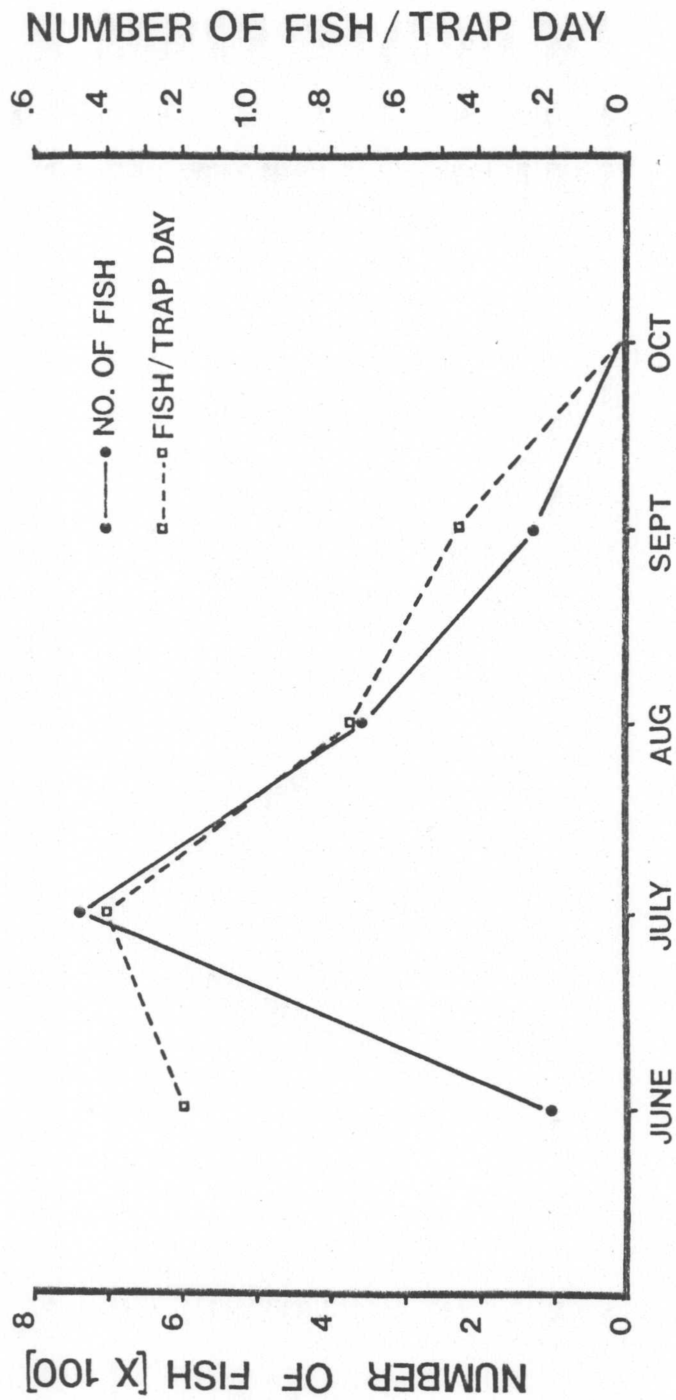


Mortalities (M_i): Associated with the following:

M_1 Egg development and hatching
M_2 Early development
M_3 Rearing (age 0-3)
M_4 Migration of juveniles through the river system to the lake
M_5 Maturation in the lake
M_6 Upstream spawning migration (natural stresses, fishing mortality)
M_7 Spawning act
M_8 Downstream migration of spawned-out adults to the lake


800
700
600
500
400
300
200
100
LENGTH—mm
TOTAL LENGTH
GROWTH INCREMENT
I
II
III
IV
V
VI
VII
VIII
IX
ANNULUS


RED MEADOW CR. (N=55)
TRAIL CR. (N=120)
GEIFER CR. (N=71)
PERCENT OUTMIGRANTS
80
60
40
20
0
I
II
III
IV
AGE


NUMBER OF FISH / TRAP DAY
.6
.4
.2
1.0
.8
.6
.4
.2
0
NO. OF FISH
FISH/TRAP DAY
JUNE
JULY
AUG
SEPT
OCT
NUMBER OF FISH [X 100]
8
6
4
2
0