AGE, MORPHOLOGY, DEVELOPMENTAL BIOLOGY, AND BIOCHEMICAL GENETIC VARIATION OF YUKON RIVER FALL CHUM SALMON, *ONCORHYNCHUS KETA*, AND COMPARISONS WITH BRITISH COLUMBIA POPULATIONS

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ABSTRACT

Fall chum salmon, *Oncorhynchus keta*, populations spawning in the Yukon River drainage were surveyed for variation in age, size and shape at maturity, developmental biology, and biochemical genetics. Yukon River fall chum salmon matured at older ages and smaller sizes than chum salmon in British Columbia. They also had proportionately smaller heads, thinner caudal peduncles, and smaller fins than British Columbia chum salmon, perhaps illustrating morphometric adaptation to long distance freshwater migration. Yukon River chum salmon were less fecund and had smaller eggs than those in British Columbia, and they also tended to have faster development to alevin hatching and fry emergence than most British Columbia populations. Maximum alevin and fry size of Yukon River salmon occur at lower water temperatures during development than for most British Columbia populations, possibly indicating a developmental adaptation to low winter water temperatures. Genetic differentiation among chum salmon populations in the Yukon River drainage was observed.

The Yukon River is a major North American river, originating in British Columbia and flowing over 3,200 km through the Yukon Territory and Alaska to the Bering Sea, and draining an area of approximately 860,000 km². Five species of Pacific salmon (*Oncorhynchus*) occur in the Yukon River (Gilbert 1922), but chinook, *O. tshawytscha*, and chum salmon, *O. keta*, are the most abundant and are exploited in commercial and subsistence fisheries (McBride et al. 1983). Chum salmon in the Yukon River are characterized by distinct seasonal races (Gilbert 1922). The early-maturing or "summer" chum salmon return to the Yukon River between early June and mid-July and spawn in the lower 800 km of the drainage (Buklis 1981). Later-maturing or "fall" chum salmon enter the Yukon River from mid-July through late August and spawn in the up-river portions of the drainage, migrating as far as 2,800 km upstream (Milligan et al. 1986). Fall chum salmon are also larger than summer chum salmon (Buklis 1981; Buklis and Barton 1984), and generally have higher fecundity and younger age compositions than summer chum salmon (Sano 1966).

Chum salmon generally spawn in rivers only a short distance from salt water (≤200 km), a trait very different from the long distance freshwater migrations of Yukon River fall chum salmon. Yukon River fall chum salmon are noted for their high oil content upon entering the river (Gilbert 1922), an adaptation necessary to provide sufficient energy reserves for the freshwater migration, as in Amur River chum salmon in the Soviet Union (Nikol'skii 1961). Adaptations in other biological characters may reflect the environmental conditions experienced by Yukon River fall chum salmon. Thus we examined the variation in life history traits of Yukon River fall chum salmon, and compared this variation to that found in chum salmon in British Columbia.

In 1984, we began a survey of variation in biological characters of fall chum salmon in the Yukon River. Regional biochemical genetic variation had previously been reported for chum salmon in British Columbia (Beacham et al. 1987), and we investigated the biochemical genetic differentiation of Yukon River fall chum salmon. We had previously examined the adaptive nature of the variation in some morphometric and life history traits of chum salmon in British Columbia (Beacham and Murray 1987) and used this for comparison for Yukon River fall chum salmon.

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METHODS AND MATERIALS

Age and Morphology

Chum salmon were collected with gill nets. After capture in 1984, postorbital-hypural length (Vladykov 1962), caudal peduncle depth, and length of the base and height of the anal and dorsal fins were all recorded on the left side in the field to the nearest millimeter. The number of gill rakers on the left anterior arch was recorded, as well as the number of branchiostegal rays on the left side. Five scales and two otoliths were collected from each individual for age determination, and the sex of an individual was confirmed by internal inspection. When the age of an individual estimated from scales and from otoliths disagreed, the age determined from scales was assigned. In 1985, only postorbital-hypural length and sex were recorded for individuals, and only scales were collected for age determination.

Population differences and sexual dimorphism in the meristic characters were examined by two-way analysis of variance, with population and sex as the indices. Population is used in the manner as described by Ricker (1972), as a group of fish spawning in a particular river at a particular season, and there is no substantial interbreeding with another group spawning in a different river. Morphometric measurements of both males and females were standardized to a postorbital-hypural length of 520 mm by the method outlined by Beacham and Murray (1983):

$$M_t = M_o \left(\frac{\bar{L}}{L_o}\right)^b$$

where M_t = size of standardized morphometric character,
M_o = observed character size,
$\bar{L}$ = length that characters are standardized to (520 mm),
L_o = observed postorbital-hypural length, and b is the regression coefficient of $\log_e M_o$ on $\log_e L_o$ (stocks and sexes separate).

Two-way analysis of variance was again used to examine population differences and sexual dimorphism in the morphometric characters.

Developmental Biology

We estimated fecundity of Yukon River chum salmon by collecting and freezing both ovaries from 14 females in the Dawson City commercial fishery in 1985 (we also collected length and scales); we subsequently thawed both ovaries and made total egg counts for each female. The methodology of the survey of developmental biology was similar to that outlined by Beacham and Murray (1987). Gametes were collected from five male and five female Kluane River chum salmon on 17 October 1985. The gametes were then shipped to the laboratory on ice, the eggs fertilized at 8°C, and then subsequently reared in controlled water temperatures of 4°, 8°, and 12°C in vertical stack incubators. Five full-sib families were obtained from the crosses, with each family replicated in each incubator. Water temperatures were recorded daily, and mean temperatures in the incubators during the study were 4.1° (SD = 0.29), 8.0° (SD = 0.44), and 12°C (SD = 0.40), respectively.

Egg diameter (millimeters) and weight (milligrams) for each female were determined from 30 water-hardened eggs preserved for at least 3 months in 10% formalin. During incubation, dead eggs were removed from each family, stored in Stockard's solution, and later inspected to remove unfertilized eggs. Egg survival rates were then calculated based upon the number of eggs initially fertilized. Once hatching began in each family, we recorded the number of newly hatched alevins daily, and within 1 day of 50% hatching we anesthetized and preserved 30 per family in 10% formalin for subsequent determination of alevin length and weight. Fork length was recorded to the nearest 0.1 mm, total weight recorded to the nearest milligram, the yolk separated from the rest of the body and weighed (milligrams), and then tissue weight (milligrams) determined by subtraction. Dead alevins were also removed and counted in order to determine alevin survival rates. The timing of fry emergence (swim-up) for each family was determined by placing the alevins in an emergence trap modified from Mason (1976), where the alevins were classified as newly emergent fry only when they became neutrally buoyant and positively phototactic. When 50% of the fry from a particular family had emerged, all of the family remaining in the incubator was anesthetized and then preserved in 10% formalin, and 30 fry were randomly drawn from the preserved samples and fry length and weight determined as for alevins.

Variation in egg size was analyzed with a one-way (female was the index) analysis of variance. Variation in survival rates was analyzed by first determining survival rates for each group as proportions and then transforming them to radians with the arcsine

square root transformation to normalize the data. We then used an analysis of variance model:

$$Y_{ijkl} = \mu + T_i + F_j + TF_{ij} + R_{ijk} + e_{ijkl}$$

where Y_{ijkl} = transformed survival rate,
  μ = overall mean,
  T_i = fixed effect of temperature (i = 1–3),
  F_j = random effect of family (j = 1–5),
  TF_{ij} = random interaction between temperature and family,
  R_{ijk} = random effect of replicate (k = 1–2), and
  e_{ijkl} = error term for lth observation in subgroup ijk.

Variation in alevin and fry size characters was ana-lyzed with the same model. Satterthwaite's (1946) approximation was necessary to calculate an appropriate mean square to test the effect of family.

Biochemical Genetics

Biochemical genetic sampling began on Canadian populations in 1984 and was expanded in 1985 to include United States populations (Fig. 1). Methodology of sample collection has been outlined by Beacham et al. (1985). Summarized briefly, heart, liver, and muscle samples were collected from adult chum salmon, frozen, and stored at $-20°C$ for later electrophoretic analysis by a consultant. We verified the scoring of all gels from a complete photographic record. Horizontal starch gel electrophoresis, described by Utter et al. (1974), was used to detect protein variation. The loci and buffer systems used
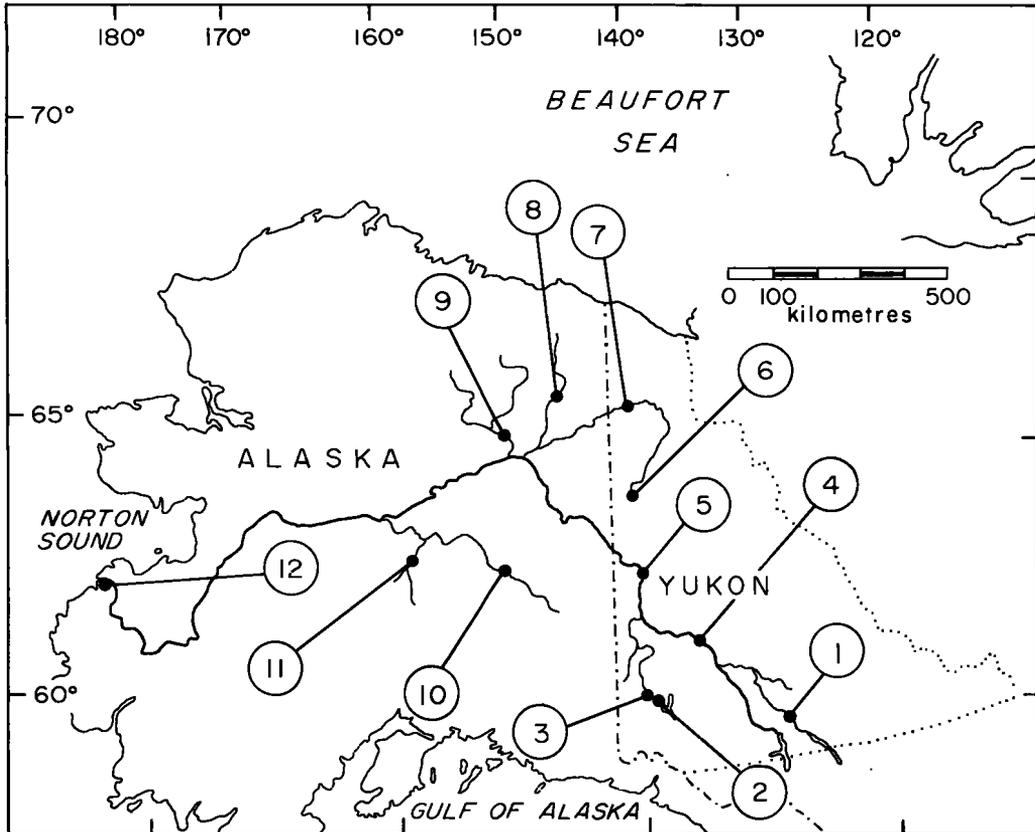

FIGURE 1.—Locations in Yukon River drainage where chum salmon were sampled during 1984–1986. Listed in ascending order are (1) Teslin River, (2) Kluane River, (3) Koidern River, (4) Yukon River at Minto, (5) Dawson City, (6) Fishing Branch River, (7) Porcupine River at Old Crow, (8) Sheenjek River, (9) Chandalar River, (10) Delta River, (11) Toklat River, (12) Yukon River at Emmonak.

are outlined in Beacham et al. (1985). *Lgg* was re-named as *Tapep* and was scored as a four-allele locus (L. Seeb[2]) (although only three were present in the stocks we surveyed) on both a Tris-boric acid-EDTA buffer described by Markert and Faulhaber (1965) and an amine citrate buffer described by Clayton and Tretiak (1972). *Me* was renamed as *MdhP*, *6-Pg* as *Pgdh*, *Pmi* as *Mpi*, and *Agp* as *G3pdh*.

We determined allelic frequencies for each locus by summing the numbers of each allele and dividing by the total number of alleles counted. Genotypic frequencies at each polymorphic locus in each population were tested for departures from Hardy-Weinberg equilibrium by chi-square. We used the log-likelihood ratio statistic (*G*-test) (Sokal and Rohlf 1969) to test equality of allelic frequencies between countries, among populations within countries, and between years for samples taken from the same population. An approximate *F*-ratio (*G*-statistic summed over all loci/degrees of freedom) was used to test the relative magnitude of the sources of variation. We calculated genetic distance among populations using Nei's (1978) statistic and the 7 loci indicated in Table 7 and constructed a denogram from the matrix of the distances using the unweighted pair group mean method of Sneath and Sokal (1973).

RESULTS

Age and Morphology

Age of Maturity

The dominant age of maturity for fall chum salmon returning to Canadian rivers during 1984 and 1985 was four years, with age 3 and age 5 chum salmon each comprising less than 15% of the total return (Table 1). The proportion of chum salmon returning at three or five years of age varied annually within a population, possibly reflecting different production from the respective brood years. Yukon River chum salmon matured at a significantly older age than chum salmon in British Columbia ($X_2^2 = 193.9$, $P < 0.01$), but four years was the dominant age of maturity in both areas. Of 227 chum salmon sampled in 1984 from which age could be determined from both otoliths and scales, the same age was recorded in 184 (83%) of the cases. For the 43 other fish, the age estimated from scales was one year older than that estimated from otoliths in 22 cases, whereas in the remaining 21 fish, the age

estimated from otoliths was either one year (19 cases) or two years (2 cases) older than that estimated from scales. In 1984, age could not be determined from 16% (48 fish) of the scales collected and 9% (26 fish) of the otoliths collected. In 1985, age could not be determined from 18% (124 fish) of the scales examined due to scale resorption. Age of maturity was more likely to be determined from otoliths than from scales.

TABLE 1.—Percentage of chum salmon returning at ages 3–5 years and mean age of return for Yukon River populations sampled on the spawning grounds during 1984–85. The mean for British Columbia chum salmon was derived from Beacham and Murray (1987).

| Population | Year | N | Age (yr) | | | Mean age (yr) |
			3	4	5	
Yukon River						
Kluane	1984	100	16.0	78.0	6.0	3.90
	1985	96	29.2	70.8	0.0	3.71
Total		196	22.4	74.5	3.1	3.81
Minto	1984	100	13.0	69.0	18.0	4.05
	1985	99	25.3	72.7	2.0	3.77
Total		199	19.1	70.9	10.0	3.91
Fishing Branch	1984	100	14.0	82.0	4.0	3.90
	1985	77	1.3	72.7	26.0	4.25
Total		177	8.5	78.0	13.5	4.05
Porcupine	1985	67	1.5	85.1	13.4	4.12
Teslin	1985	64	0.0	56.3	43.7	4.44
Koidern	1985	81	0.0	74.1	25.9	4.26
Total						
Mean		784	12.5	73.7	13.8	4.01
British Columbia						
Total						
Mean		11,749	32.4	62.1	5.5	3.73

Meristics

No sexual dimorphism was observed in the number of gill rakers or branchiostegal rays ($P > 0.05$). No population differences in gill raker number were observed ($P > 0.05$), but significant differences among populations were observed in branchiostegal ray number ($F_{2,297} = 4.36$, $P < 0.05$). The population with the greatest number of gill rakers (Fishing Branch) also had the greatest number of branchiostegal rays (Table 2). Yukon River chum salmon had more gill rakers and branchiostegal rays than the average British Columbia chum salmon.

Morphometry

Yukon River male chum salmon were longer than

females at all ages examined ($P < 0.05$) (Table 3). Although there could be significant variation in mean length-at-age among populations ($P < 0.05$), Yukon River chum salmon were substantially smaller than chum salmon of the same age spawning in British Columbia ($P < 0.05$). Size differences between Yukon River and British Columbia chum salmon increase with age, with age 3 Yukon River males 94% of the length of age 3 British Columbia males, but age 5 Yukon River males are 86% of the length of their British Columbia counterparts. Similar results were also observed for females.

We examined whether there was any differentiation of selected morphometric characters with respect to sexual dimorphism or distance of freshwater migration. With the morphometric measurements of both males and females standardized to a postorbital-hypural length of 520 mm, males had longer postorbital head lengths, thicker caudal peduncles, longer base length of the dorsal fin, and longer dorsal and anal fins (all $P < 0.05$) (Table 4). No sexual dimorphism in base length of the anal fin

was observed. Significant population differences in the relative sizes of the morphometric characters were also observed, with the Kluane River population having the relatively smallest characters, and the Fishing Branch River population having the proportionally largest characters.

Substantial differences exist in length of freshwater migration between Yukon River fall chum salmon and chum salmon in British Columbia. The relative sizes of the morphometric characters examined are all smaller for Yukon River chum salmon than for chum salmon in British Columbia (Table 4), perhaps illustrating morphometric adaptation of Yukon River chum salmon to the long freshwater migration.

Developmental Biology

Fecundity and Egg Size

The fecundity-length relationship for 14 female chum salmon is described by

$$F = 0.100\ L^{1.60}$$

where F = number of eggs and L is postorbital-hypural length (mm). Mean fecundity of age 4 females was 2,271 eggs (SD = 208, n = 7), and that of age 5 females was 2,451 eggs (SD = 106, n = 3).

Mean egg weight of the five Kluane River females used in the study of developmental biology ranged from 145 mg (SD = 6 mg) to 210 mg (SD = 5 mg). Mean diameters ranged from 6.66 mm (SD = 0.21 mm) to 7.25 mm (SD = 0.18 mm). Mean egg size of Yukon River chum salmon is substantially smaller than the mean weight of 290 mg and mean diameter of 8.39 mm for egg size of chum salmon in

TABLE 2.—Mean number of gill rakers on left anterior gill arch and mean number of branchiostegal rays on left side for Yukon River fall chum salmon sampled during 1984. Standard error of mean is in parentheses. One hundred fish were sampled per population. Data for 9,206 British Columbia chum salmon are from Beacham and Murray (1987).

Population	Gill rakers	Branchiostegal rays
Yukon River		
Kluane	22.88 (0.10)	13.72 (0.07)
Minto	22.90 (0.09)	13.58 (0.08)
Fishing Branch	23.13 (0.09)	13.89 (0.07)
Mean	22.97 (0.05)	13.73 (0.04)
British Columbia		
Mean	22.62 (0.01)	13.42 (0.01)

TABLE 3.—Mean postorbital-hypural length-at-age (mm) for chum salmon sampled on the spawning grounds during 1984–85. Sample sizes are given in parentheses. The mean length-at-age for British Columbia chum salmon was derived from Beacham and Murray (1987).

Population	Male age						Female age					
	3		4		5		3		4		5	
Yukon River												
Kluane	509	(19)	516	(59)	556	(4)	490	(25)	501	(87)	526	(2)
Minto	525	(13)	528	(46)	541	(8)	509	(25)	516	(95)	525	(12)
Fishing Branch	477	(5)	524	(64)	548	(5)	487	(10)	504	(74)	519	(19)
Porcupine			541	(41)	546	(4)	462	(1)	514	(16)	531	(5)
Teslin			521	(17)	521	(14)			492	(19)	506	(14)
Koidern			510	(29)	514	(10)			468	(31)	503	(11)
Mean	510	(37)	524	(256)	531	(45)	497	(61)	505	(322)	515	(63)
British Columbia												
Mean	543	(1974)	595	(3186)	621	(344)	532	(1357)	579	(2879)	605	(255)

TABLE 4.—Mean measurements (mm) for six morphometric characters for chum salmon sampled during 1984. Measurements for each individual were standardized to a postorbital-hypural length of 520 mm. Standard deviations are indicated in parentheses. The size (%) of each standardized character relative to body length is indicated for both Yukon and British Columbia chum salmon. Data for 4,862 male and 4,044 female British Columbia chum salmon were standardized to 600 mm postorbital-hypural length and were derived from Beacham and Murray (1987).

| | Kluane | Minto | Fishing Branch | % of length | |
				Yukon	B.C.
Males					
Head length	79.4 (4.3)	80.7 (3.3)	81.3 (2.9)	15.48	16.02
Caudal peduncle	39.9 (2.8)	41.5 (2.3)	41.2 (2.5)	7.85	8.37
Anal fin base	67.4 (4.4)	70.0 (3.5)	69.3 (4.4)	13.25	13.68
Anal fin height	57.8 (3.9)	59.5 (3.1)	58.7 (4.5)	11.28	11.65
Dorsal fin base	62.9 (5.6)	66.1 (4.0)	63.9 (4.6)	12.34	13.01
Dorsal fin height	88.1 (6.2)	90.2 (5.4)	92.0 (5.6)	17.33	17.64
Sample size	37	32	39		
Females					
Head length	73.5 (4.3)	74.7 (4.0)	76.3 (3.5)	14.38	14.64
Caudal peduncle	37.7 (3.1)	38.9 (3.3)	39.5 (2.2)	7.44	8.06
Anal fin base	67.8 (5.2)	68.0 (4.8)	68.8 (4.8)	13.12	13.79
Anal fin height	56.0 (4.0)	57.6 (4.8)	58.0 (4.5)	11.00	11.65
Dorsal fin base	58.2 (4.1)	58.4 (4.4)	59.1 (4.4)	11.26	11.79
Dorsal fin height	79.8 (6.5)	82.7 (5.3)	84.4 (5.4)	15.83	16.24
Sample size	63	68	61		

British Columbia (Beacham and Murray 1987).

Survival Rates

Embryo survival rates were lowest at a 4°C incubation temperature and highest at 12°C, with significant differences observed among incubation temperatures ($P < 0.05$) (Table 5). Significant differences were also observed in embryo survival rates among families ($P < 0.0$), but not between replicates within families ($P > 0.10$). An interaction between family and incubation temperature occurred ($P < 0.01$), illustrating that trends in embryo survival with respect to incubation temperature were not the same for all families.

Alevin survival rates were uniformly high (Table 5), with no significant difference observed among temperatures, among families, or between replicates within families. The interaction between family and incubation temperature also occurred for alevin survival rates ($P < 0.05$).

Hatching and Emergence Time

Warmer water temperatures during incubation enhanced the development rate of Kluane River chum salmon (Table 5). Timings of both alevin hatching and fry emergence at a specific incubation temperature were comparable with that of a British Columbia chum salmon population spawning in late

TABLE 5.—Survival rates of embryos and alevins for Kluane River chum salmon maintained at constant water temperatures of 4°, 8°, and 12°C. Time of 50% hatching (days) of the alevins and 50% emergence (days) of the fry is also indicated. N is number of fertilized eggs (for embryo survival rates) or alevins hatched (for alevin survival rates). Standard deviations of 50% hatching and emergence times are in parentheses.

Temperature (°C)	N	Survival rate	Time to 50% hatching or emergence
Embryos			
4.1 (0.28)	2,172	0.767	113.9 (2.3)
8.0 (0.21)	2,387	0.906	65.7 (0.6)
12.0 (0.35)	2,432	0.955	43.7 (0.9)
Alevins			
4.1 (0.29)	1,666	0.975	182.2 (1.9)
8.0 (0.20)	2,162	0.998	111.6 (1.2)
12.0 (0.35)	2,323	0.991	79.6 (1.1)

December or early January (Beacham and Murray 1986, 1987), nearly three months later than the spawning time of the Kluane River population.

Alevin and Fry Size

Alevin and fry length and weight were influenced by the water temperature during development. The longest and heaviest alevins and fry were observed at 4°C (Table 6). Significant differences in alevin length and weight were observed among incubation temperatures, among families, and between repli-

cates within families (all $P < 0.05$). Significant interactions between temperature and family were also observed for all alevin size characters (all $P < 0.05$), again illustrating that alevin size characters did not respond consistently among families to changes in incubation temperature.

The effect of different incubation temperatures on fry size characters was similar to that for the alevin size characters. Significant differences in fry length, total weight, and tissue weight were observed among temperatures, among families, and between replicates. The amount of yolk remaining at the time of fry emergence was similar at all incubation temperatures ($P > 0.05$) (Table 6). Interactions between family and incubation temperature were present for all fry size characters (all $P < 0.05$).

Biochemical Genetics

Regional differentiation of allelic frequencies for chum salmon stocks in Alaska and the Yukon Territory was observed. Chum salmon from Alaska generally had a lower frequency of Idh-1[100] and a higher frequency of Tapep (Lgg)[75] than those from the Yukon Territory (Table 7). Regional differentiation in allelic frequencies was also observed for the other loci examined. The Delta and Toklat River populations, both tributaries of the Tanana River, had higher frequencies of Idh-3[100] than all other populations except the Teslin River population. Only one genotypic frequency was not in Hardy-Weinberg equilibrium, that being Pgdh in the Toklat River population. The disequilibrium was due to a heterozygote deficiency.

Variation in allelic frequencies among populations

TABLE 6.—Fork length, total weight, yolk weight, and tissue weight for Kluane River chum salmon alevins and fry maintained at constant 4°, 8°, and 12°C water temperatures. N is the number of alevins and fry measured and weighed for all families combined. Standard deviations are in parentheses.

Temperature (°C)	N	Fork length (mm)	Total weight (mg)	Yolk weight (mg)	Tissue weight (mg)
Alevin					
4	150	21.1 (1.4)	222.2 (38.2)	136.9 (19.1)	85.3 (22.4)
8	150	20.8 (0.7)	108.9 (18.9)	106.7 (12.7)	74.2 (8.0)
12	149	20.4 (0.9)	176.6 (20.1)	109.8 (12.9)	66.8 (9.4)
Fry					
4	150	32.3 (1.8)	308.4 (52.9)	30.0 (8.7)	278.4 (51.3)
8	150	31.0 (0.9)	277.5 (27.4)	28.0 (7.2)	249.5 (23.5)
12	150	30.5 (1.1)	277.6 (28.1)	30.7 (6.4)	247.5 (27.2)

within a region was greater than annual variation in allelic frequencies within a population ($F_{67,48} = 4.00$, $P < 0.01$) (Table 8). Annual stability of allelic frequencies was examined for the loci for which two years of data was available in each population. Of 39 comparisons made, 3 (8%) were significant (Table 8).

Heterozygosity of populations from Alaska was generally higher than that from the Yukon Territory. Mean heterozygosities were 0.156 (SD = 0.009) and 0.138 (SD = 0.019), respectively, for the loci outlined in Table 7. Heterozygosity values are dependent upon the number of polymorphic and monomorphic loci included in the calculations, and thus will vary among studies.

The analysis of genetic distance for all pairwise combinations of the 10 populations sampled ranged from 0.0000 to 0.0072. A dendogram based upon the unweighted pair group mean analysis (UPGMA) illustrated two main clusters of populations (Fig. 2).

FIGURE 2.—Dendogram produced from cluster analysis using Nei's (1978) genetic distance value. Codes are C = Canadian and US = United States.
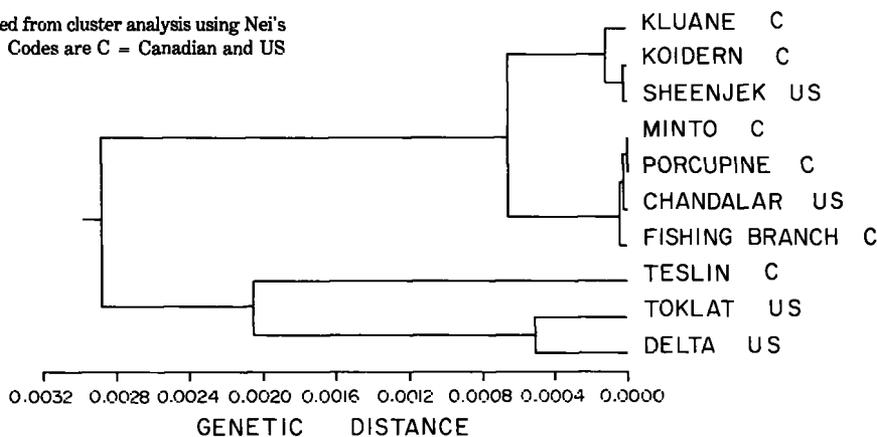

KLUANE C
KOIDERN C
SHEENJEK US
MINTO C
PORCUPINE C
CHANDALAR US
FISHING BRANCH C
TESLIN C
TOKLAT US
DELTA US

0.0032 0.0028 0.0024 0.0020 0.0016 0.0012 0.0008 0.0004 0.0000

GENETIC DISTANCE

TABLE 7.—Observed allelic frequencies at polymorphic loci for 10 Yukon River drainage
and other alleles were assigned numbers

Stock	Year	Idh-1		Idh-3				MdhP	
		N	100	N	100	40	85	N	100
Kluane	1984	107	1.000	106	0.358	0.585	0.057	107	0.977
	1985	106	1.000	106	0.396	0.552	0.052	106	0.991
	Pooled	213	1.000	212	0.377	0.568	0.054	213	0.984
Minto	1984	130	1.000	130	0.481	0.508	0.012	130	0.904
	1985	114	1.000	114	0.482	0.461	0.057	114	0.899
	Pooled	244	1.000	244	0.482	0.486	0.033	244	0.902
Fishing Branch	1984	126	1.000	126	0.460	0.512	0.028	126	0.944
	1985	99	1.000	98	0.444	0.510	0.046	99	0.914
	Pooled	225	1.000	224	0.453	0.511	0.036	225	0.931
Teslin	1985	90	1.000	90	0.611	0.361	0.028	90	0.889
Koidern	1985	100	1.000	100	0.405	0.570	0.025	100	0.980
Porcupine	1985	81	1.000	81	0.463	0.506	0.031	81	0.938
Toklat	1985	120	0.946	120	0.579	0.350	0.071	120	0.887
	1986	124	0.952	124	0.512	0.399	0.089	124	0.911
	Pooled	244	0.949	244	0.545	0.375	0.080	244	0.900
Delta	1985	146	0.990	145	0.538	0.417	0.045	146	0.877
	1986	147	0.990	146	0.490	0.449	0.062	147	0.884
	Pooled	293	0.990	291	0.514	0.433	0.053	293	0.881
Sheenjek	1985	143	0.993	147	0.398	0.585	0.017	144	0.962
	1986	150	0.987	124	0.415	0.528	0.056	150	0.907
	Pooled	293	0.990	271	0.406	0.559	0.035	294	0.934
Chandalar	1986	147	1.000	143	0.448	0.497	0.056	147	0.939

TABLE 8.—Analysis of heterogeneity of allelic frequencies between countries, among
sampled during

Source of variation	Idh-1		Idh-3		MdhP		Mpi	
	df	G	df	G	df	G	df	G
Between countries	1	45.4**	2	12.6**	1	9.6**	1	4.5*
Among populations within countries	8	35.7**	16	77.4**	8	59.2**	8	13.9
Canada	5	0.0	10	34.7**	5	45.2**	5	10.0
United States	3	35.7**	6	42.7**	3	14.0	3	3.9
Between years within populations	6	0.3	12	21.5	6	8.7	6	4.5
Kluane	1	0.0	2	0.6	1	0.6	1	1.3
Minto	1	0.0	2	8.7**	1	0.0	1	0.1
Fishing Branch	1	0.0	2	1.1	1	1.1	1	1.7
Toklat	1	0.0	2	2.3	1	0.5	1	1.2
Delta	1	0.2	2	1.8	1	0.0	1	0.2
Sheenjek	1	0.1	2	7.0	1	6.5**	1	0.0

The Toklat and Delta River populations were distinctive from other populations surveyed. The population from Chandalar River, a tributary of the Porcupine River, was similar to the Porcupine River population (sampled at the Old Crow fishery) and to the Fishing Branch River population, also a tributary of the Porcupine River. The populations from Kluane and Koidern Rivers, tributaries of the White River, were also similar to each other, as well as to the Sheenjek River population in Alaska.

DISCUSSION

Yukon River fall chum salmon undertake the longest freshwater spawning migration of chum salmon in North America and spawn in locations where winter environmental conditions are very severe. They are also relatively abundant, with an average of almost 450,000 chum salmon harvested annually during 1974–83 (Buklis and Barton 1984). Their abundance indicates that they have adapted success-

fall chum salmon populations during 1984–86. The most common allele at a locus was designated 100, according to the mobility relative to that of the 100 allele.

Stock	Year	Mpi		Pgdh		G3pdh-2		Tapep			
		N	100	N	100	N	100	N	100	50	75
Kluane	1984	105	0.910	107	0.991	106	0.887				
	1985	106	0.943	105	0.990	104	0.856	106	0.901	0.099	0.000
	Pooled	211	0.927	212	0.991	210	0.871	106	0.901	0.099	0.000
Minto	1984	130	0.923	130	0.962	130	0.888				
	1985	114	0.934	114	0.956	114	0.842	114	0.842	0.158	0.000
	Pooled	244	0.928	244	0.959	244	0.867	114	0.842	0.158	0.000
Fishing Branch	1984	126	0.893	126	0.960	113	0.854				
	1985	97	0.933	99	0.995	96	0.880	99	0.803	0.197	0.000
	Pooled	223	0.910	225	0.976	209	0.866	99	0.803	0.197	0.000
Teslin	1985	90	0.972	90	0.994	89	0.983	90	0.861	0.139	0.000
Koidern	1985	100	0.945	100	1.000	99	0.879	97	0.845	0.155	0.000
Porcupine	1985	79	0.943	81	0.981	75	0.847	80	0.806	0.194	0.000
Toklat	1985	120	0.917	120	0.971	112	0.848	120	0.808	0.158	0.033
	1986	124	0.883	123	0.976	111	0.833	122	0.852	0.119	0.029
	Pooled	244	0.900	243	0.973	223	0.841	242	0.831	0.138	0.031
Delta	1985	141	0.922	146	0.949	134	0.888	146	0.818	0.147	0.034
	1986	147	0.935	147	0.939	104	0.880	142	0.852	0.106	0.042
	Pooled	288	0.929	293	0.944	238	0.884	288	0.835	0.127	0.038
Sheenjek	1985	150	0.913	144	0.972	129	0.876	150	0.847	0.147	0.007
	1986	150	0.913	148	0.973	120	0.879	149	0.822	0.158	0.020
	Pooled	300	0.913	292	0.973	249	0.878	299	0.834	0.152	0.013
Chandalar	1986	145	0.897	147	0.973	85	0.871	145	0.834	0.148	0.017

populations within countries, and between years within populations for Yukon River fall chum salmon 1984–86. $P < 0.01$; $P < 0.05$.

Source of variation	Pgdh		G3pdh-2		Tapep		Total		Standardized F-statistic
	df	G	df	G	df	G	df	G	
Between countries	1	7.9*	1	0.7	2	48.3**	9	129.0**	14.33
Among populations within countries	8	32.0**	8	34.6**	11	20.6*	67	273.4**	4.08
Canada	5	22.6*	5	30.3*	5	10.3	40	153.1**	3.83
United States	3	9.4	3	4.3	6	10.3	27	120.3**	4.46
Between years within populations	6	5.1	6	3.0	6	5.8	48	48.9	1.02
Kluane	1	0.2	1	0.6					
Minto	1	0.0	1	1.9					
Fishing Branch	1	4.8**	1	0.4					
Toklat	1	0.0	1	0.1	2	1.7			
Delta	1	0.1	1	0.0	2	1.8			
Sheenjek	1	0.0	1	0.0	2	2.3			

fully to a long distance freshwater migration and extreme winter conditions.

Several biological characters differ between chum salmon in the Yukon River and in British Columbia. For Yukon River fall chum salmon, approximately equal numbers of salmon mature, on average, at three and five years of age, although there is annual variation (Buklis and Barton 1984). In the Amur River, fall chum salmon mainly mature at four and five years of age (Smirnov 1975). Similar results

were recorded in our study. Yukon River chum salmon matured at older ages and at smaller mean lengths-at-age than did chum salmon in British Columbia. A general trend of younger ages at maturity and increased mean lengths-at-age in southern as compared with northern chum salmon populations has been reported by Salo (in press). This trend may be a result of the earlier timing of fry emergence and later timing of adult spawning of more southern populations, allowing more time for

ocean growth, particularly in the year of maturity.

Body shape of Yukon River and British Columbia chum salmon was different, with Yukon River chum salmon having a shorter head, thinner caudal peduncle, and smaller fins than British Columbia chum salmon. This more fusiform body shape is presumably an adaptation to the long migration in fresh water, as selection should result in a body shape that would minimize energy consumption during migration. Morphological differentiation with respect to distance of upstream migration has been reported to occur in other *Oncorhynchus* species (Eniutina 1954; Taylor and McPhail 1985), as well as with respect to river size (Hjort and Schreck 1982; Beacham and Murray 1987).

The mean fecundity of 2,325 eggs per female for Yukon River fall chum salmon reported in our study is similar to other results. Elson (1975) reported mean fecundities of 2,360 eggs and 2,513 eggs per female for Porcupine River chum salmon sampled in 1971 and 1973, respectively. Raymond (1981) reported mean fecundities of Tanana River chum salmon of 2,355 eggs in 1977 and 2,762 eggs in 1978. Fecundities of Yukon River fall chum salmon are less than those reported for many chum salmon stocks in British Columbia (Beacham 1982), and also less than fall chum salmon in the Amur River (3,200 to 4,300 eggs) (Smirnov 1975). Mean egg size of Yukon River fall chum salmon is also less than that of Amur River chum salmon (180 to 300 mg, 6.7 to 9.0 mm diameter) (Smirnov 1975).

The different fecundities and ages at maturity of Yukon River and British Columbia chum salmon present an interesting contrast in life history characters. Yukon River fall chum salmon mature at an average age of 0.28 years older than British Columbia salmon, which means that they incur an additional 5% mortality if the instantaneous mortality rate during the last year of life for chum salmon is 0.013 per month (Ricker 1976). The lower fecundity and older age at maturity of Yukon River salmon indicate that they are not as productive as chum salmon in British Columbia or that mean survival rates of the two groups are not equivalent. Egg-to-fry survival rates for Yukon River chum salmon have been reported as a mean of about 2.5% (Buklis and Barton 1984), whereas those for British Columbia chum salmon average about 10% (Bakkala 1970; Beacham and Starr 1982). If Yukon River chum salmon are as productive as those in British Columbia, then ocean survival rates of Yukon River chum salmon must be higher than those of British Columbia chum salmon.

When incubated under the same water temperatures, Yukon River chum salmon alevins hatch and the fry emerge sooner than most chum salmon populations in British Columbia (Beacham and Murray 1987). The faster development rates presumably occur as a response to lower water temperatures during the winter in the Yukon River tributaries than in rivers in British Columbia. Yukon River chum salmon alevins and fry are shorter and lighter than those from British Columbia (Beacham and Murray 1987), presumably reflective of smaller initial egg size of Yukon River chum salmon. At incubation temperatures of 4°, 8°, and 12°C, maximum alevin and fry size for Yukon River chum salmon was observed at 4°C, but for British Columbia stocks, maximum alevin and fry size was generally observed at 8°C. These results suggest that Yukon River chum salmon are better adapted for development under low water temperatures than are British Columbia chum salmon.

Yukon River chum salmon are generally distinctive in electrophoretic characteristics from chum salmon in Cook Inlet in Alaska (Okazaki 1981) and British Columbia (Okazaki 1981; Beacham et al. 1985, 1987). For example, the allelic frequency of $Idh-3^{25}$ is 0.28 in Queen Charlotte Islands populations and 0.17 in populations in northern British Columbia (Beacham et al. 1987), but this allele was not detected in our study of Yukon River chum salmon. Heterozygosity of Yukon River chum salmon was lower than that observed for British Columbia salmon (the same loci were included in the analysis) (Beacham et al. 1987). Kijima and Fujio (1984) reported that average heterozygosity is related to effective population size in Japanese chum salmon populations, with more abundant populations having increased genetic variance. Abundance of the Yukon River populations examined in our study is unknown, but the catch data suggest that the individual Yukon River populations may not be as abundant as major chum salmon populations in British Columbia.

Allelic frequencies for most salmon populations are reported to show little annual variation (Grant et al. 1980; Utter et al. 1980; Beacham et al. 1985, 1987), allowing for pooling of samples from a particular population over several years. It should thus not be necessary to conduct annual sampling in order to characterize the populations contributing to fisheries. Stock identification based on stable traits, such as allelic frequencies, reduces annual sampling costs for the baseline stocks. This differs from scale analysis, in which variation in the char-

acters used for stock identification makes annual sampling of the baseline stocks necessary (e.g., Wilcock and McBride 1983; Wilcock 1984), and restricts the incorporation of results into management decisions during the fishing season.

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