

POPULATION BIOLOGY OF CHUM SALMON, *ONCORHYNCHUS KETA*, FROM THE FRASER RIVER, BRITISH COLUMBIA

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ABSTRACT

Population biology of Fraser River chum salmon, *Oncorhynchus keta*, was investigated. Mean age of chum salmon during the run declined from 3.98 years in October to 3.78 years in December in the 1970s. Females were more abundant than males in 4-year-old chum salmon, but males were more abundant than females in 3- and 5-year-old chum salmon. Fecundity of females was 3,250 eggs/female at a standard length of 58.0 cm and did not vary among years sampled. Fry tended to migrate downstream earlier when the previous winter had been warm than when it was cold. Egg-to-fry survival was correlated with rainfall, air temperature, and number of eggs deposited. Mean age of return of a brood year was positively correlated with its abundance. The return to escapement ratio for even-numbered brood years was inversely correlated with the abundance (catch plus escapement) of the previous brood year, which suggests that marine survival of chum salmon may be density-dependent. The return to escapement ratio for odd-numbered brood years was positively correlated with early downstream migration of chum salmon fry relative to pink salmon, *O. gorbuscha*, fry and with increased chum salmon spawning escapements relative to those of pink salmon.

Stocks of chum salmon, *Oncorhynchus keta*, in British Columbia and Alaska have fluctuated considerably in abundance (Hoar 1951; Wickett 1958; Hunter 1959; Helle 1979). These fluctuations have been attributable to variability in freshwater and marine survival, and have been related to climatic factors such as rainfall (Wickett 1958) and to population density or predation on fry (Hunter 1959). Chum salmon in British Columbia return to spawn in their natal streams mainly as 3- and 4-yr-olds, and to a lesser extent as 5-yr-olds. The mean age of returning adults tends to be greater for stocks from northern British Columbia than from southern British Columbia (Pritchard 1943; Ricker 1980). Chum salmon tend to spawn later in the fall than other species of *Oncorhynchus*, and the fry migrate downstream in the spring, within a few days after emerging from spawning beds.

The chum salmon stocks of the Fraser River have supported commercial fisheries in Johnstone Strait, the Strait of Georgia, and the Fraser River for many years (Palmer 1972) (Fig. 1). Annual catches of chum salmon were extensive

in Johnstone Strait during 1951-54, ranging from 0.7 to 2.0 million fish, and in the Fraser River, ranging from 274,000 to 479,000 fish. However, the annual contribution of Fraser River chum salmon to the Johnstone Strait catch is unknown before 1964. Catches of chum salmon declined substantially during 1965-69, ranging from 23,000 to 649,000 fish in Johnstone Strait (an estimated 0 to 228,000 Fraser River chums), and 10,000 to 196,000 fish in the Fraser River. Catches have continued to vary widely in the 1970s. Fraser River chum salmon have thus shown marked fluctuations in abundance, and these fluctuations have not been satisfactorily accounted for. It is not currently possible to identify stocks of Fraser River chum salmon, so for purposes of the analysis, Fraser chum salmon were treated as a unit stock. This paper describes the population biology of Fraser River chum salmon and results of studies on the causes of variability in the number of returning adults.

MATERIALS AND METHODS

Estimates of abundance of returning adult and downstream migrating fry were derived by different sampling methods. Fry were enumerated during 1965-81 on the lower Fraser River near Mission City (Fig. 1) using techniques previously described by Todd (1966) and Bailey

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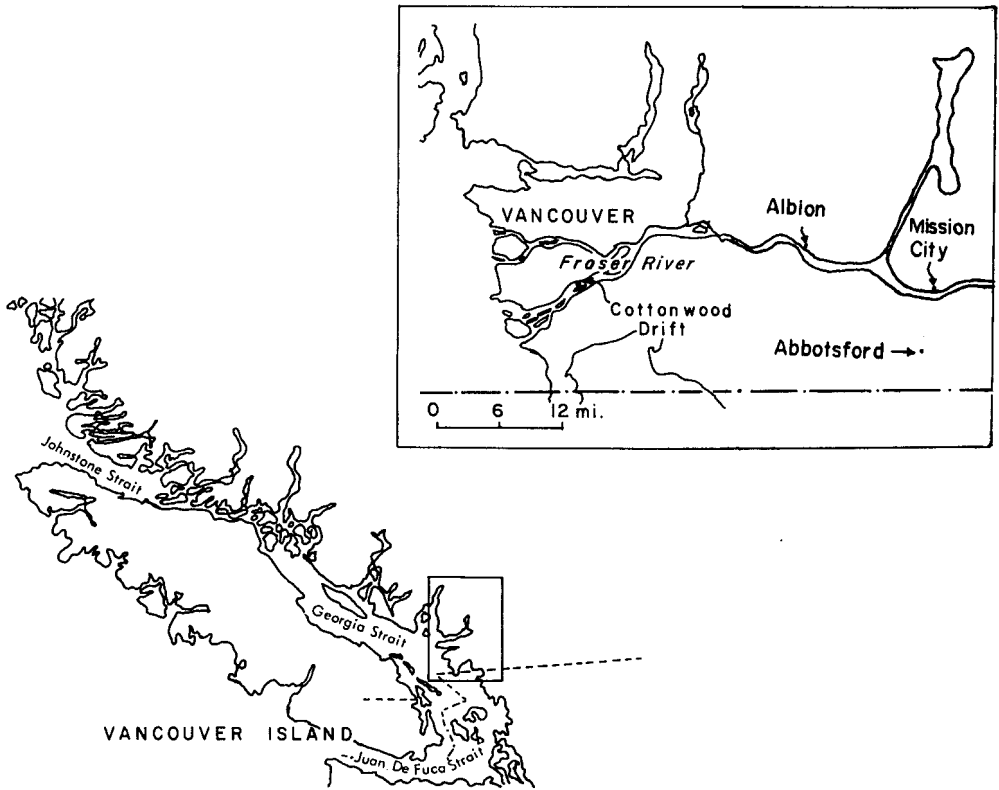


FIGURE 1.—Areas in British Columbia where Fraser River chum salmon are caught in the commercial fishery. Inset shows areas in the lower Fraser River where fry and returning adults were sampled.

(1979³). Briefly, the sampling procedure consisted of suspending traps at various depths from the surface to 3.7 m (12 ft) from either side of a boat travelling at a constant velocity relative to the water for 15-min periods. Samples were taken in this manner between 0500 and 1300 h. Preliminary sampling had established that chum fry migrating past Mission City were most active during this period. Sampling occurred during this period, 5 d a week from beginning of March to end of May. Daily sampling was continued for 24 h 2 or 3 d/wk so that estimates of the daily proportion of fry migrating during the standard shift (0500 to 1300 h) could be made, and daily totals of chum fry migrating past Mission City calculated. Sampling was also performed at different sites across the 527 m (1,725 ft) width of the Fraser River at Mission City. The depth and

cross-sectional area of the river were known at each sampling site, as well as the area sampled by the fry traps, so that, by extrapolation, the number of fry migrating downstream daily could be estimated. Abundance of chum salmon fry used in the present analysis was taken from Bailey (footnote 3), as were the dates when 50% of the chum and pink, *O. gorbuscha*, salmon fry were estimated to have migrated past the sampling site. Weekly mean lengths (mm) of fry were determined in 1978.

Sex ratios, age composition, length-at-age, and fecundity of adult chum salmon arriving at the river mouth were derived from test fishing conducted at Cottonwood Drift from 1962 to 1979 and Albion from 1978 to 1979 (Fig. 1). A 274 m (150-fathom) long, 60-mesh deep gill net having 16.9 cm (6 $\frac{3}{4}$ in) mesh was set for a standard 30-min drift twice a day during the slack period of the lowest tide of the day. Smaller fish may have avoided capture on account of gill net selectivity (McCombie and Berst 1969; Todd and Larkin

³Bailey, M. D. 1979. Enumeration of salmon in the Fraser River. Unpubl. manusc., 122 p. Department of Fisheries and Oceans.

1971), which could possibly bias adult age composition, sex ratios, and fecundity estimates. However, we believe that any bias present was not of sufficient magnitude to mask trends in abundance of individual brood years. Daily test fishing 5 d/wk was usually conducted from late September until mid-December, although sampling within this period was not conducted when the commercial fishery was operating in the river. Ages of chum salmon were determined from scales. Bilton and Ricker (1965) and LaLanne and Safsten (1969) have outlined the methodology of using scales for aging chum salmon. Lengths were recorded as either fork length or postorbital-hypural length to the nearest millimeter. Fecundity was determined by direct counts of the number of eggs in both ovaries. Age composition in the escapement was assumed to be the same as that in the test fishery. Escapement was estimated during the 1960s by visual counts on spawning beds, by test fishing, and by a tagging program (Palmer 1972), whereas in the 1970s, escapement was estimated from visual counts and test fishing only. Total returns for a brood year included the catch plus escapement.

Fraser River chum salmon are taken by the fishery which operates near the river mouth, and by fisheries in Johnstone Strait, the Strait of Georgia, and at Point Roberts in the United States. The proportion of Fraser River chum salmon in the Johnstone Strait fishery was estimated seasonally based on the tagging studies reported by Palmer (1972). Since the fishery in the Strait of Georgia exploits mixed stocks of chum salmon, it was not possible to estimate the contribution of Fraser River chum salmon in this fishery, although it is small compared with the catch in Johnstone Strait. Catches in the Fraser River, as well as 100% of the catches off Point Roberts, and the Fraser River contribution to Johnstone Strait were summed to estimate the total annual catch of Fraser River chum salmon. Although not all chum salmon caught off Point Roberts, 20 km south of the Fraser River mouth, may be bound for the Fraser River, any overestimation of the Fraser River contribution to the Point Roberts catch is compensated for by underestimation of the Fraser River contribution to the Strait of Georgia catch. Escapements of pink salmon used in the present study were those listed in the annual report of the International Pacific Salmon Fisheries Commission for 1979 (Anonymous 1980).

RESULTS

Marine Growth

High-seas scale and tagging studies have indicated that chum salmon from British Columbia and Alaska range from lat. 45°N to 60°N and from long. 130°W to 180° in the North Pacific Ocean (Shepard et al. 1968). Specific distributions of Fraser River chum salmon were not available. However, the effect of variability in ocean water temperatures on growth rate was investigated by comparing the mean monthly temperature from March through August (major part of growing season) at Station P (lat. 50°N, long. 145°W) and mean length-at-age of returning adults. Fork lengths of returning adults during 1960-69 were taken from Palmer (1972) and were converted to postorbital-hypural lengths by the regressions:

$$\begin{aligned} \text{Males: } H &= 1.08 FL - 219 \quad (N = 100, r = 0.72) \\ \text{Females: } H &= 1.00 FL - 130 \quad (N = 100, r = 0.89) \end{aligned}$$

where FL = fork length in millimeters and H = postorbital-hypural length in millimeters. These regressions were derived from chum salmon taken by the Fraser River commercial fishery in 1962 and 1963. Postorbital-hypural lengths of returning adults during 1970-78 were derived from the test fishery at Cottonwood Drift. For the period of 1960-78, mean lengths-at-age of 4-yr-old chum salmon were correlated with water temperature at Station P during the penultimate growing season for males ($r = 0.49$, $n = 19$, $P < 0.05$) and females ($r = 0.44$, $n = 19$, $P < 0.06$). However, there was no correlation for mean length-at-age and water temperature at Station P during the penultimate growing season for age-3 fish (males: $r = 0.17$, $n = 19$, $P > 0.10$; females: $r = -0.08$, $n = 19$, $P > 0.10$) or in the year of return and mean length-at-age for age-3 fish (males: $r = 0.17$, $P > 0.10$; females: $r = 0.10$, $P > 0.10$). The relatively stable mean length-at-age for returning age-3 chum salmon is undoubtedly due to selectivity of the sampling gear, with possibly only the larger age-3 fish susceptible to capture in a 16.9 cm mesh gill net.

Age Composition and Sex Ratios of Returning Adults

The mean monthly age composition of chum salmon migrating upstream during the years

1970-79 indicated that the proportion of age-5 fish in the run decreased from October through December, whereas the proportion of age-3 fish increased (Table 1). Age-4 chum salmon comprised about 74% of the run in each month, while age-3 comprised 24% of the run in December but only 14% in October.

Sex ratios were variable among ages, with more male chum salmon returning at age 3 ($X^2 = 23.7$, $df = 1$, $P < 0.01$) and age 5 ($X^2 = 10.7$, $P < 0.01$) than did females (Table 2). More female chum salmon returned at age 4 than did males ($X^2 = 70.6$, $P < 0.01$). Since the mean age of chum salmon in the run decreased through time, and sex ratios vary with age, the sex ratio of the run may also vary through time. However, an application of the sex ratios by age in Table 2 to the age compositions in Table 1 shows that sex ratios of the total run were nearly the same each month (52.9% females in October, 53.1% in November, and 52.9% in December).

TABLE 1.—Percentage age composition by month (October-December) of chum salmon sampled in the Fraser River test fishery, 1970-79. Sample sizes are in parentheses.

Age	October	November	December
3	13.7 (326)	21.7 (715)	23.8 (307)
4	74.3 (1,826)	74.3 (2,443)	73.4 (947)
5	12.0 (304)	4.0 (132)	2.6 (36)
Total	100.0 (2,456)	100.0 (3,290)	100.0 (1,290)
Mean age (yr)	3.98	3.82	3.78

TABLE 2.—Sex ratios (males:females) of age-3, -4, and -5 chum salmon sampled in the Fraser River test fishery, 1960-79.

Age:	3	4	5
Ratio	1.19	0.79	1.30
Sample size	3,172	5,378	626

Fecundity

Fecundity was determined from samples of chum salmon taken in 1966, 1968, and 1978 with females ranging in postorbital-hypural length from 50 to 66 cm. Females sampled in 1978 were generally larger than those in 1966 and 1968 (Table 3). A two-way analysis of covariance with sampling year and age as factors and length as a co-variate (co-variate was accounted for before factors were tested) indicated that there was no significant difference in fecundity (F) among years ($F = 0.92$, $df = 2$ and 228 , $P > 0.05$) or among

ages ($F = 2.66$, $P > 0.05$). The mean fecundity for all samples was 3,250 eggs/female (Table 3).

The relationship between fecundity and length of 234 females sampled was described by:

$$\log_e F = 2.8659 + 0.8193 \log_e L \quad (r = 0.29) \quad (1)$$

where F = fecundity and L = postorbital-hypural length in millimeters. The regression was significant ($F = 20.1$, $P < 0.01$), but accounted for about only 9% of the variability in fecundity (Fig. 2). Most of the females sampled were between 54 and 63 cm in length, and with high variability in fecundity within this short length range, little of the variability in fecundity could be accounted for by the regression.

TABLE 3.—Number of females sampled, mean length (cm), mean age (yr), and mean fecundity of chum salmon from the Fraser River. SE = standard error of mean.

Year:	1966	1968	1978	Total
<i>n</i>	109	76	49	234
Length	57.4	57.9	59.5	58.0
SE of length	0.2	0.3	0.4	0.2
Age	3.90	3.89	3.90	3.90
Fecundity	3,227	3,276	3,261	3,250
SE of fecundity	39.5	46.6	60.1	27.7
Age:	3	4	5	
<i>n</i>	26	194	2	
Length	55.8	58.1	58.3	
SE of length	0.6	0.2	1.3	
Fecundity	3,292	3,246	3,091	
SE of fecundity	83.6	28.4	287.9	

Fry Migrations and Survival

The major portion of the downstream migration of chum salmon fry passed the Mission City sampling site from mid-March to the end of April. Usually 50% of the fry had passed the sampling site between April 13th and the 23d (Fig. 3), although 50% of the fry have passed the sampling site as early as April 3 (1976 brood year) and as late as May 3 (1971 brood year). About 80% of the chum salmon fry migrate downstream at a length of <40 mm. However, the proportion of fry >40 mm long during the downstream migration tends to increase with time. By the second week of May 1978, 20% of the fry were >43 mm long and weighed 1.0 g, which suggests a period of freshwater rearing for these fry.

Linear regression was used to determine the relationship of air temperature (T), determined as the mean of monthly air temperatures at the Abbotsford airport from December through February, to timing of the fry migration (F),

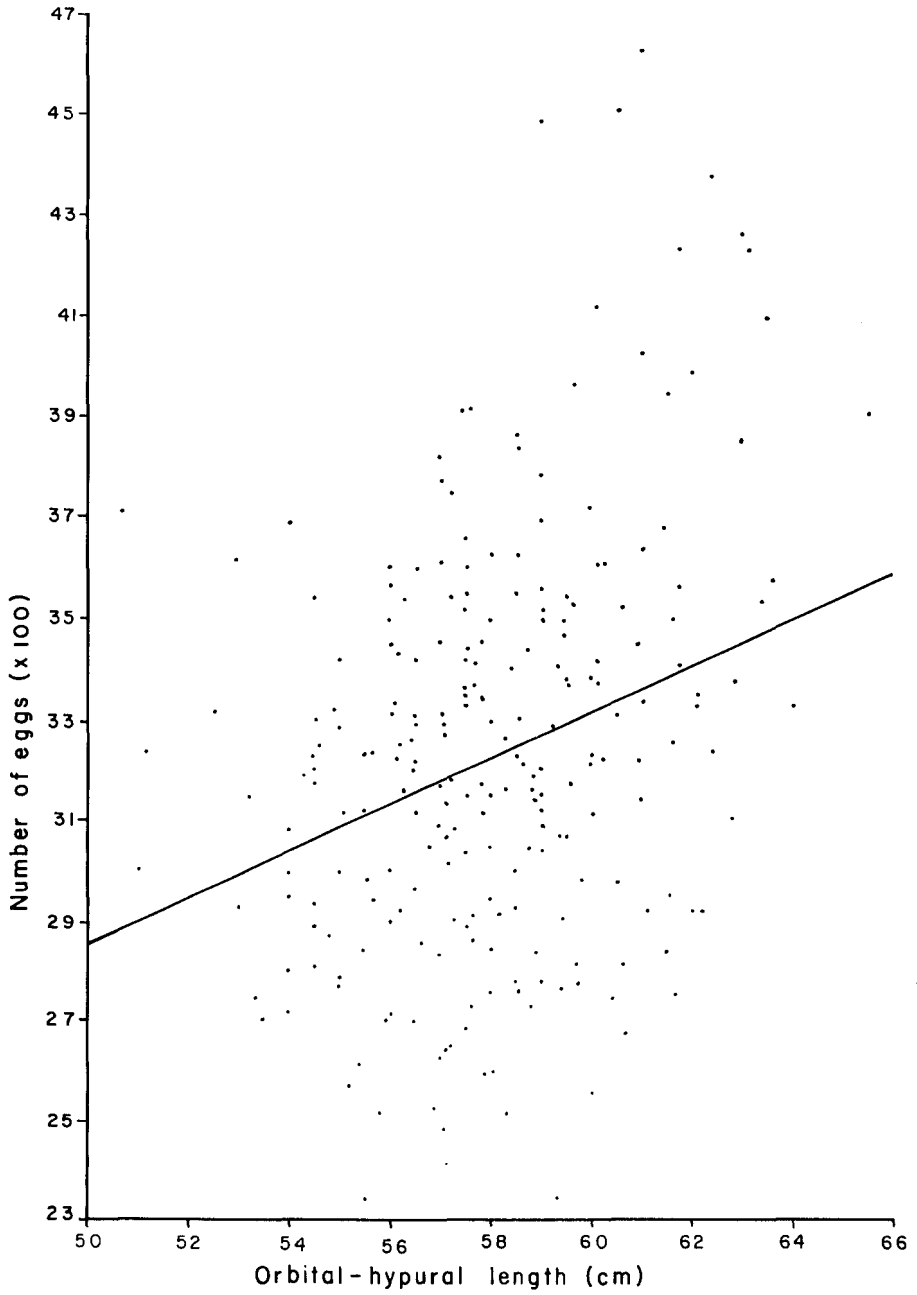


FIGURE 2.—The relationship between fecundity and length in female chum salmon sampled from the test fishery in 1966, 1968, and 1978.

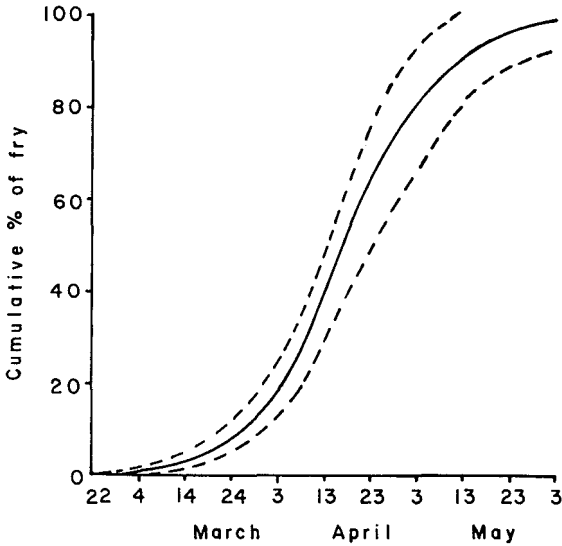


FIGURE 3.—Mean time of chum fry downstream migrations on the Fraser River, 1965-80. Dotted lines indicate 95% confidence limits.

measured as the days from April 1 to the date of 50% migration. Abbotsford airport is located near many major chum salmon spawning areas (Fig. 1). The model fitted was:

$$F = \frac{25.53}{T^{0.444}} \quad (n = 15) \quad (2)$$

and the regression was significant ($r = 0.61$, $P < 0.05$) (Fig. 4). Fry tend to migrate downstream earlier following a warmer winter than following a colder winter, presumably because warmer temperatures accelerate egg development.

Based on estimates of the number of migrating fry and egg deposition (Table 4), egg-to-fry survival varied from 6% to about 35% in the 1961-78 brood years. Multiple regression was used to determine the relationship of rainfall, egg numbers, air temperature, and their interactions on variability in egg survival. The model fitted through stepwise regression was:

$$S = a T + b T \times \frac{1}{R} + c T \times \frac{1}{E} + d T \times \frac{1}{R} \times \frac{1}{E} + e \quad (3)$$

where $S = \% \text{ egg to fry survival}$

$T =$ mean monthly air temperature at Abbotsford airport from December through February

$R =$ total rainfall in cm at Abbotsford airport from November through January

$E =$ number of eggs deposited $\times 10^6$.

The analysis yielded:

Variable	Coefficient	SE	t
T	-7.62	2.51	-3.03
T/R	615.90	130.42	4.72
T/E	4,369.52	1,375.07	3.18
T/RE	-266,517.54	77,530.32	-3.44
Constant	5.99		

The regression was significant ($R^2 = 0.77$, $F = 10.75$, $df = 4$ and 13 ; $P < 0.01$), and the correlation matrix for the model is shown in Table 5. The individual factors of rainfall ($r = -0.28$) and egg numbers ($r = -0.005$) were not significantly correlated with egg survival, but their interactions with temperature were. Egg survival tended to increase during drier winters, but if these drier winters were also relatively cold, then egg survival was lowered. If the winter was both relatively dry and warm, then egg survival was good, as was the case for the 1976 brood year (Table 4).

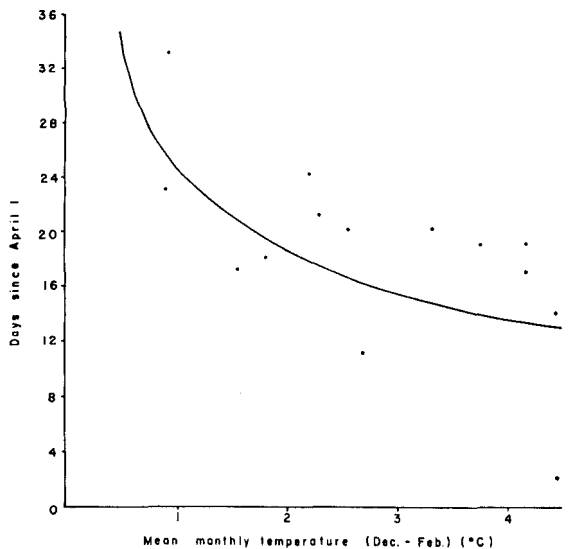


FIGURE 4.—Median date of downstream chum fry migration versus mean monthly temperature from December through February as measured at the Abbotsford airport.

TABLE 4.—Escapements, survivals, returns-at-age, mean age of return, and return to escapement ratios of Fraser River chum salmon, 1961-74 brood year. Percentage age composition for each brood year is in parentheses.

Brood year	Spawning escapement	No. of females	Egg deposition (x10 ⁶) at 3,250/female	No. of fry (x10 ⁶)	% egg to fry survival	Adult returns (x10 ³)	% fry to adult survival	Return at age (x10 ³)			Mean age of return (yr)	Total return (x10 ³)	Return to escapement
								3 yr	4 yr	5 yr			
1961	164,000	83,800	272.4	25.8	9.5	236.3	0.91	98.6 (41.7)	132.0 (55.9)	5.7 (2.4)	3.61	236.3	1.44
1962	180,000	90,000	292.5	42.5	14.5	468.1	1.10	63.4 (13.5)	396.5 (84.7)	8.2 (1.8)	3.88	468.1	2.60
1963	214,000	107,000	347.8	54.8	15.8	178.2	0.33	50.7 (28.5)	123.6 (69.4)	3.9 (2.1)	3.74	178.2	0.83
1964	325,000	135,850	441.5	53.6	12.1	1,293.9	2.41	171.2 (13.2)	1,108.7 (85.7)	14.0 (1.1)	3.88	1,293.9	3.98
1965	185,000	109,930	357.3	32.4	9.1	579.8	1.79	211.9 (36.6)	363.9 (62.7)	4.0 (0.7)	3.64	579.8	3.13
1966	430,000	236,500	768.6	75.2	9.8	925.8	1.23	257.3 (27.8)	627.0 (67.7)	41.5 (4.5)	3.77	925.8	2.15
1967	212,000	102,600	333.5	69.0	20.7	325.4	0.47	53.5 (16.4)	224.5 (69.0)	47.4 (14.6)	3.98	325.4	1.53
1968	822,000	392,910	1,277.0	72.5	5.7	1,933.9	2.67	146.0 (7.6)	1,549.9 (80.1)	238.0 (12.3)	4.05	1,933.9	2.35
1969	390,100	206,360	670.7	107.4	16.0	1,434.6	1.34	58.5 (4.1)	1,174.4 (81.9)	201.7 (14.0)	4.10	1,434.6	3.68
1970	303,100	175,890	570.4	48.7	8.5	534.2	1.10	47.9 (9.0)	477.7 (89.4)	8.6 (1.6)	3.93	534.2	1.76
1971	356,700	142,980	464.7	58.2	12.5	367.7	0.63	161.0 (43.8)	200.7 (54.6)	6.0 (1.6)	3.58	367.7	1.01
1972	579,700	333,330	1,083.3	109.5	10.1	1,239.1	1.13	242.8 (19.6)	984.4 (79.4)	11.9 (1.0)	3.82	1,239.1	2.14
1973	453,000	250,510	814.2	130.8	16.1	653.0	0.50	205.7 (31.5)	427.5 (65.5)	19.8 (3.0)	3.72	653.0	1.42
1974	565,300	291,130	946.2	114.4	12.1	1,210.5	1.06	136.7 (11.3)	1,022.6 (84.5)	51.2 (4.2)	3.93	1,210.5	2.16
1975	235,300	125,890	409.1	73.0	17.8	158.9		158.9	227.4				
1976	588,700	310,830	1,010.2	358.2	35.4								
1977	538,800	271,020	880.8	124.3	14.1								
1978	466,600	268,603	873.0	86.1	10.1								
1979	327,700	173,700	564.5	109.4	19.4								

TABLE 5.—Correlation matrix for the egg-to-fry survival model. Variables are listed in the text.

	Variable				
	S	T	T/R	T/E	T/E x R
S	1.00	0.52	0.73	0.22	0.29
T		1.00	0.80	0.66	0.60
T/R			1.00	0.49	0.64
T/E				1.00	0.93
T/E x R					1.00

There was a slight tendency for egg survival to decline with increasing numbers of eggs deposited and this effect was enhanced by a cold winter. Thus spawning escapement (egg deposition), rainfall, and temperature interact to produce variable freshwater survival. Fry-to-adult survival was inversely correlated with egg-to-fry survival ($r = -0.62, n = 14, P < 0.05$), which suggests a density-dependent response of chum salmon fry survival.

Age of Return

Total returns from the 1961 through the 1974 chum salmon brood years have ranged from 180,000 to 1,930,000 fish (Table 4). The proportion of the brood year returning at age 3 has ranged from 4% to about 42%. To determine if the mean age at maturity from a brood year was dependent upon the total number of adults produced from that brood year, we regressed mean age at maturity (in years) on total return (Fig. 5). This regression produced:

$$\text{Mean age} = 3.67 + 1.923 \times 10^{-7} \text{ Returns} \quad (n = 14) \quad (4)$$

where $r = 0.63 (P < 0.05)$. The mean age at maturity of a brood year increased as did the total num-

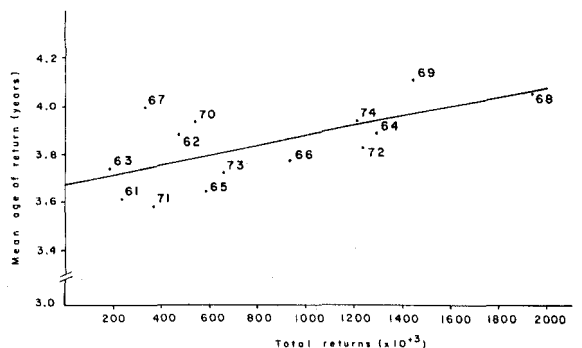


FIGURE 5.—Mean age of return of a brood year of chum salmon versus its abundance.

ber of returning adults, which suggests that if the timing of returns is size dependent, then density-dependent growth may occur during the ocean residence of chum salmon. Pink salmon return to the Fraser River in abundance in odd years, but return in negligible amounts in even years. The mean age at maturity and number of returning chum salmon adults tended to be higher in even brood years than in odd ones (Fig. 5), so that pink salmon may indirectly influence mean age at maturity of chum salmon through an effect on survival of chum salmon.

The proportion of a brood year returning at age 3, 4, and 5 is frequently of importance in predicting annual returns. For Fraser River chum salmon, the percentage age composition of the returns from a brood year is related to the mean age of return of the brood year as follows:

$$\% \text{ age 3} = 321.56 - 78.26 \text{ mean age} \quad (r^2 = 0.93) \quad (5)$$

$$\% \text{ age 4} = -141.68 + 56.20 \text{ mean age} \quad (r^2 = 0.63) \quad (6)$$

$$\% \text{ age 5} = -79.88 + 22.06 \text{ mean age} \quad (r^2 = 0.50). \quad (7)$$

If the returns from a brood year can be predicted, then the mean age of return of a brood year can be obtained from Equation (4) and applied to Equations (5)-(7) in order to obtain numbers returning at each age.

Return to Escapement

The ratio of total returns for a brood year to escapement (R/S) has varied from 0.8 to 4.0 for the 1961 through 1974 brood years. The available evidence suggests that for escapements below 850,000 adults, egg-to-fry and fry-to-adult survivals will generally be large enough to allow the number of returning chum salmon to remain above replacement levels (Fig. 6). However, only the 1968 escapement was above 600,000 adults, so further information on the R/S ratio for escapements $>500,000$ adults is required in order to evaluate the effect of varying escapements on chum salmon survival. There was no evidence to indicate a decline in recruits per spawner at escapements $>500,000$ fish, and thus the optimal escapement is uncertain. Optimal escapements will not be established with confidence until declines in recruits per spawner (or density-dependent mortality) is observed at high spawning stock sizes.

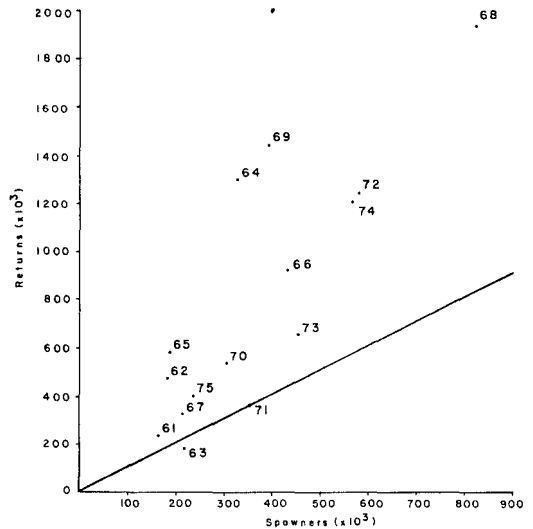


FIGURE 6.—Total return versus numbers of spawners for the 1961-75 brood years of Fraser River chum salmon.

Fry-to-adult survival has been variable, ranging from 0.3% to 2.4% (Table 4). The average survival for the even brood years was 1.53%, whereas survival for the odd brood years was 0.85%. The effect of fry abundance on variability in fry-to-adult survival was investigated for odd brood years by summing the estimated numbers of chum salmon and pink salmon fry, and for even brood years by assuming that the number of pink salmon fry produced was negligible. The data suggested that chum salmon fry survival tended to increase when the abundance of chum and pink salmon fry decreased (Fig. 7). This relationship can be expressed by:

$$\% \text{ survival} = 0.73 + \frac{46.53}{\text{Fry abundance (millions)}} \quad (r = 0.52) \quad (8)$$

for the 1961-75 brood years. All of the fry-to-adult survivals for the odd brood years, except for the 1965 and 1969 brood years, were below 1.0%, whereas all of the fry-to-adult survivals for the even brood years were above 1.0%, with the 1964 and 1968 brood year fry survival being higher than the rest.

Some of the variability in fry-to-adult survival was due to the timing of the downstream fry migration. The higher survival of the 1965 and 1969 brood year fry when compared with other odd

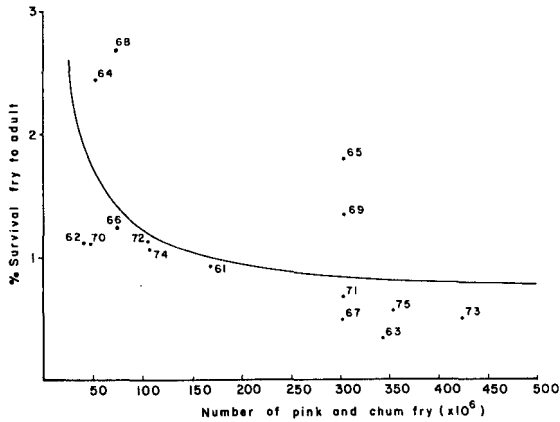


FIGURE 7.—Fry-to-adult survival for chum salmon versus total abundance of pink and chum salmon fry. The abundance of pink fry from even-numbered brood years was assumed to be negligible.

brood years may be accounted for by the early downstream migration, and the same condition may apply to even brood years (Fig. 8).

With fry-to-adult survivals of Fraser River chum salmon generally lower in odd brood years than in even ones, odd- and even-numbered brood years were separated in a further analysis of variability in the returns to spawners relationship. The R/S ratio for even brood years was inversely related with the total number of returning adults of the previous odd brood year (Fig. 9). This relationship was determined through regression and is described by:

$$\frac{R_t}{S_t} = 1.367 + \frac{0.3867}{R_{t-1}} \quad (n = 7) \quad (9)$$

where R_t = total returns for even-numbered brood year

S_t = spawning escapement producing that brood year

R_{t-1} = total returns of previous brood year in millions

and the correlation between R_t/S_t and $1/R_{t-1}$ was significant ($r = 0.91, P < 0.01$). This equation can be rearranged to give a prediction of total number of returning adults in year t , given escapement and total return of the previous brood year. The above suggests that survival of chum salmon in the marine environment is dependent upon the abundance of conspecifics in the previous brood year. Marine survival may thus be density-de-

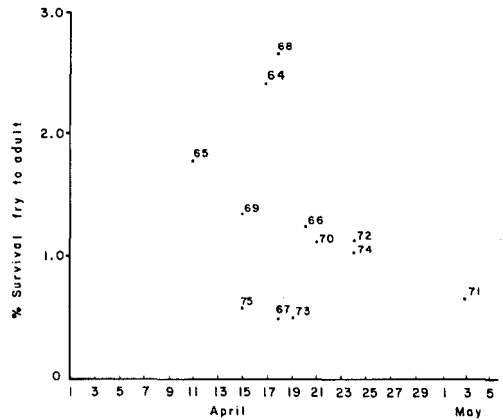


FIGURE 8.—Fry-to-adult survival of chum salmon versus median date of downstream migration.

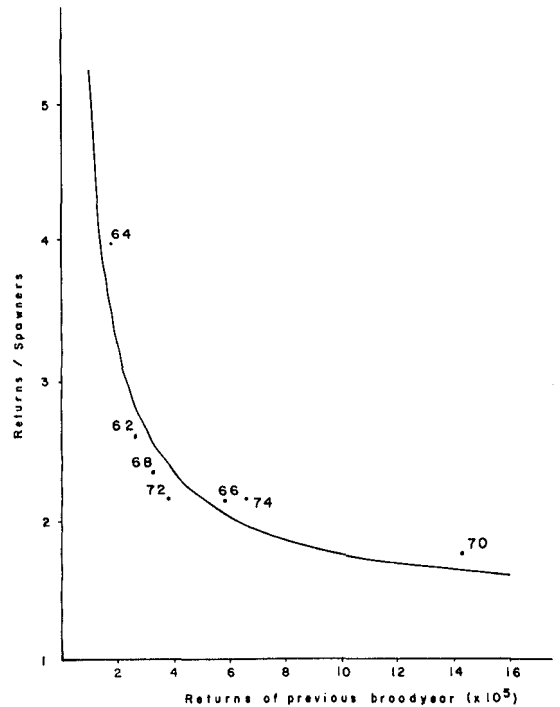


FIGURE 9.—Ratio of returns/spawners for even-numbered brood years of Fraser River chum versus chum abundance in previous brood year.

pendent, and interbrood year interactions, possibly through competition for food, may affect marine survival of chum.

Pink salmon have been implicated in the present study as impacting population dynamics of Fraser River chum salmon during odd brood

years. Multiple regression was used to describe the effect of pink salmon on chum salmon fry survivals by:

$$\frac{R}{S} = a \frac{S}{P} + b(D) + c \quad (10)$$

where R = total returns from a given brood year

S = spawning escapement of chum salmon that produced a given brood year

P = spawning escapement of pink salmon in same brood year

D = median time of downstream pink salmon fry migration minus median for chum salmon fry in days

c = regression constant.

The analysis yielded:

Variable	Coefficient	SE	<i>t</i>
S/P	13.268	4.928	2.69
D	0.136	0.034	3.93
Constant	-1.469		

The regression was significant ($F = 9.60$, $df = 2$, and 3 , $P < 0.05$) and accounted for 85% of the variation in R/S in odd brood years ($R = 0.92$). The chum salmon R/S ratio increases the earlier that chum salmon fry migrate downstream relative to pink salmon fry (Table 6). If chum salmon escapement is 10% of that of pink salmon, then the time of the median downstream migration of chum salmon fry must be at least 9 d earlier than that of pink salmon fry if the chum salmon spawners are just to replace themselves ($R/S = 1.0$) (Fig. 10). However, if chum salmon escape-

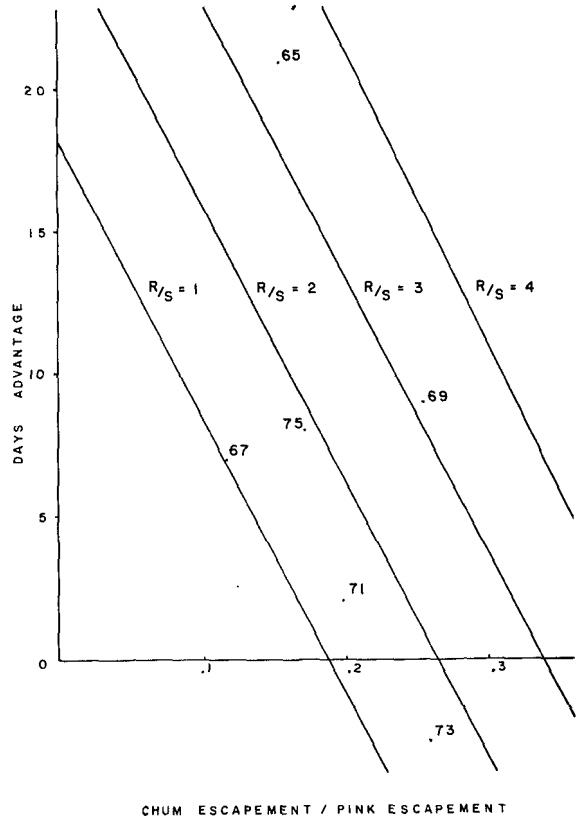


FIGURE 10.—Contour plot for returns/spawners for odd-numbered brood years of Fraser River chum in relation to timing of pink and chum fry migrations and relative spawning escapements of pink and chum. Contour lines of $R/S = 1.0, 2.0, 3.0,$ and 4.0 are plotted.

ment is 30% of the pink salmon escapement and chum salmon fry still have a 9-d advantage over pink salmon fry, then the R/S ratio for chum salmon will be between 3.0 and 4.0, as happened for the 1969 brood year (Fig. 10). The chum salmon R/S ratio will still be between 3.0 and 4.0 if the chum salmon escapement is 15% of the pink salmon escapement, provided the chum salmon fry have at least a 19-d advantage over the pink salmon fry, similar to the 1965 brood year (Fig. 10).

TABLE 6.—Dates when 50% of the fry were estimated to have migrated downstream and estimated spawning escapements for odd-numbered brood years, 1965-77.

Brood year	Date of 50% fry migration		Spawning escapements ($\times 10^3$)	
	Chum	Pink	Chum	Pink
1965	11 April	2 May	185.0	1,191.1
1967	17 April	24 April	212.0	1,831.4
1969	15 April	24 April	390.0	1,529.5
1971	3 May	5 May	356.7	1,803.8
1973	19 April	16 April	453.0	1,754.1
1975	15 April	23 April	235.3	1,367.3
1977	20 April	25 April	538.8	2,387.8

DISCUSSION

Mean lengths at maturation for 4-yr-old chum salmon in the present study were found to be significantly correlated with oceanic water temperatures in the penultimate growing season but not in the final one. Helle (1979) found that oceanic

environmental factors during the final ocean year strongly influenced length at maturity of chum salmon from Olsen Creek, Alaska. The causes of the different results of the two studies are uncertain, but may in some way be related to the timing of the attainment of a threshold length for spawning.

The fecundity of Fraser River chum salmon (3,250 eggs/female) reported in the present study was greater than that reported by Foerster and Pritchard (1936) for Fraser River chum salmon (2,943 eggs/female), for Nile Creek chum salmon (2,726 eggs/female) (Neave 1953), and for Hooknose Creek chum salmon (2,083-3,097 eggs/female) (Hunter 1959). Only a few of the mean fecundities listed by Bakkala (1970) for North American and Asian chum salmon were greater than that of Fraser River chum salmon. However, size and age compositions of chum salmon sampled for fecundity in the former studies were unavailable, and it may be that larger sized chum salmon were sampled in the Fraser than in other areas because smaller females may have avoided the test fishery.

In chum salmon, males have been reported to predominate in the early part of the run and females in the later part (Gilbert 1922; Henry 1954). In the present study, sex ratios as measured by the test fishery remained relatively constant during the fall upriver migration. This result was probably due to differences in run timing of stocks in the Fraser River, so that stocks in different stages of completeness of the run were sampled at the same time, and thus temporal shifts in sex ratios may have been obscured.

Freshwater and marine survival of Fraser River chum salmon have varied about sixfold and fivefold, respectively. Rainfall and gravel permeability have been implicated in variable freshwater survival elsewhere, with higher rainfall in the fall (except in flood years) and looser, more permeable gravel resulting in higher survival (Wickett 1958). Freshwater survival of chum salmon in Hooknose Creek was inversely related to the total number of pink and chum salmon eggs deposited (Hunter 1959). The present study indicated that freshwater survival of Fraser River chum salmon was inversely related to the amount of winter rainfall, and that much of the variability in freshwater survival was attributable to interactions among temperature, rainfall, and egg abundance.

Mortality among young fry has been suggested

to be a major influence in determining the abundance of returning adults from a brood year of pink or chum salmon (Neave 1953; Hunter 1959; Parker 1965). Egg-to-fry survival in Fraser River chum salmon was largely dependent upon physical environmental fluctuations, whereas fry-to-adult survival may be dependent upon chum and pink salmon abundance. The effects of favorable or unfavorable environmental conditions during incubation appear to be compensated for by density-dependent responses of survival during the marine life history stage of chum salmon. Density-dependent survival during the marine residence period has been suggested for several *Oncorhynchus* species, with possible interactions within and among brood years (Peterman 1978). The present study indicated that for even brood years of Fraser River chum salmon, marine survival may be inversely associated with the abundance of the previous brood year, which suggests that the number of returns from a brood year is not determined until the mixing of underyearlings and older chum salmon in the ocean. Although early fry mortality is undoubtedly heavy in chum salmon, as it is in other marine fish, and although it has been suggested that the determination of year-class abundance occurs soon after hatching in marine fishes (Cushing and Harris 1973), some evidence does suggest that year-class abundance is not determined in the first year of life of marine fishes (Ponomarenko 1973; Lett et al. 1975).

The present study indicated that the mean age of returns of a brood year increased with brood year abundance. Similar observations have been reported by Birman (1951) for chum salmon in the Amur River in the Soviet Union and Helle (1979) for chum salmon in Olsen Creek in Alaska. This result implies that growth during ocean residence is density-dependent, as has been reported in other marine fishes (Sonina 1965; Paloheimo and Kohler 1968; Templeman et al. 1978). Competition for food may be one of the mechanisms of this density-dependence. The present study also indicated that higher marine water temperatures were accompanied by increased growth rates, as indicated by annual variability in size of returning 4-yr-old chum salmon.

The present study suggests that there may be competition between chum and pink salmon fry in the Fraser River estuary or Strait of Georgia. Phillips and Barraclough (1978) found that chum salmon fry in the Strait of Georgia near the Fraser estuary were larger in 1967 and 1969 when

pink salmon fry abundance would be low than those in 1966 and 1968 when pink salmon fry would be abundant. When chum and pink salmon fry migrated at similar times, chum salmon fry-to-adult survival was lower than when chum salmon fry migrated earlier than pink salmon fry. Pink salmon grow faster than do chum salmon (Ricker 1964), and this faster growth rate may allow them to outcompete chum salmon fry for food. The influence of pink salmon on egg-to-fry survival of chum salmon was not examined, but we expect it would be minimal relative to environmental influences as pink salmon spawn earlier in the Fraser River than do chum salmon.

The present study suggests some areas that need to be explored further. Interspecific interactions between pink and chum salmon fry may be investigated by marking and varying the size and time of release of chum salmon fry in years when pink salmon fry are present and measuring rates of adult returns for these sets of fry, similar to the studies of Fraser et al. (1978) for chum on the Big Qualicum River and Bilton (1978) for coho salmon, *Oncorhynchus kisutch*.

ACKNOWLEDGMENTS

We are indebted to those who sampled and aged the salmon caught in the test fishery and sampled the fry during their downstream migrations. Tom Bilton provided the data used to convert chum fork lengths to postorbital-hypural length. M. C. Healey and B. E. Riddell made many helpful suggestions which improved the manuscript. The manuscript was prepared with the assistance of the staff at the Pacific Biological Station.

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