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ENERGY SOURCES AND EXPENDITURES IN FRASER RIVER SOCKEYE SALMON DURING THEIR SPAWNING MIGRATION

by
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ABSTRACT

Constituent proportions in body components of several races of Fraser River sockeye were measured at various stations along the estuary and river migration paths, demonstrating decreasing fat and protein, and increasing water. Accompanying physical measurements indicated weight loss during migration and spawning with possible length decrease. Total weight, specific gravity and percent fat decreased in later segments of a racial migration passing a sampling station, suggesting increasing maturity. Within samples, constituent composition was correlated with condition. Racial differences were found in gonad development and in composition of testes. Percentage fillets (body muscle) decreased in relative weight during river migration while percentage trimmings (head, skin, fins, bones) increased in relative weight. Females entered the estuary with larger relative energy stores, allotted more reserves to gonad development, transferred less protein to secondary sexual characters, and used generally more energy per mile or day on migration than males. Spawning occurred in a narrow range of constituent percentage values. Between 5% and 26% of the fat and 40% to 70% of the protein remained in dead sockeye, with males retaining more than females. Viscera excluding gonads provided less than 5% of energy expenditure. Energy expenditure per kg per mile varied with the 0.43 power of average river slope. Post-spawning energy stores and other information indicate that spawning cannot be delayed appreciably beyond the normal time.

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INTRODUCTION

Maturing Fraser River sockeye (*Oncorhynchus nerka*) largely cease feeding upon entering the Strait of Juan de Fuca (Gilbert 1913) some 200 miles from the Fraser River and an additional 60 miles to 650 miles from the spawning grounds of the various populations or races. Fraser sockeye must thereafter derive their energy from stores of fat and protein, which enable them to complete their migration to the stream of origin and spawn successfully.

Early investigations of energy stores of anadromous salmonids disclosed the reduction in concentration of fat and protein in the body and the growth of the gonads during migration and spawning (Miescher-Rüsch 1880; Paton *et al.* 1898; Greene 1926; Pentegov *et al.* 1928; Davidson and Shostrom 1936; and Kizevetter 1948). Previous investigation of Fraser River sockeye (Idler and Clemens 1959) presented data for the Chilko and Early Stuart runs in 1956. Further investigations were made of these and other runs in 1957, 1958, and 1959 to examine differences between races, as well as differences within a race for different parts of a migration and between years.

The sampling, and chemical and physical measurements necessary to the studies were carried out as a joint project of the International Pacific Salmon Fisheries Commission and the Vancouver Technological Station of the Fisheries Research Board of Canada.

SOCKEYE RUNS STUDIED

Fraser River sockeye are divided into several "stocks" or "races" for management purposes. The term "race" implies genetic divergence, for which evidence is gradually accumulating (Thompson 1945; Gilhousen 1960; Brannon 1972). Sampling was therefore designed to discover if differences occurred between races, which make migrations of different distances at different times, as well as show the general situation for Fraser sockeye.

Sockeye from the Fraser make extensive feeding migrations in the northeastern Pacific Ocean. Recoveries of sockeye tagged at sea (Margolis *et al.* 1966) have shown that Fraser sockeye occur up to 1,200 nautical miles west of Juan de Fuca Strait (FIGURE 1), with a north-south range from about 47°N to approximately 57° North Latitude. Nothing is known concerning the fat and protein content of Fraser sockeye on the high seas, other than that practically all their energy stores are acquired there. Maturing sockeye caught at the outer end of Juan de Fuca Strait usually have food in their stomachs but as they move toward the Fraser mouth the sockeye appear to cease feeding, and food is rarely found in stomachs at any other point on the spawning migration (Gilbert 1913).

Six races of Fraser sockeye were studied. Three of the Fraser races (Early Stuart, Chilko and Adams) were studied in detail because they had long river migrations and were easily separated from other races. The remaining Fraser sockeye races were sampled after they had entered a branch stream and had separated from other races.

These races cover a wide range of times of migration and spawning, and of distance of migration in fresh water (TABLE 1). The "coastal" variety of sockeye is represented by the races with short migration routes. Typically, these races have relatively early migration and late spawning, utilizing their stored energy to subsist during a long waiting period near the spawning grounds. At the other extreme are the "interior" runs of sockeye, which both migrate and spawn early, and utilize their stored energy during migration rather than during a long waiting period at the spawning grounds. This division between the two types of Fraser sockeye races is not sharp, however, as a great variety of migration distances and times are found.

One race of interior sockeye included in this study, the Adams River run, migrates late and spawns late in the season, with a lengthy delay off the mouth of the Fraser River. In 1958, the only year this race was sampled, the Adams River run was much later than average in migration (as were all the other runs of that year) and had a longer duration than normal (Gilhousen 1960). However, the Early Stuart run was sampled in 1956, 1957 and 1958, and provides a basis of comparison between years.

Because energy reserves might vary from year to year, sampling was generally confined to the 4_2 age group, the most abundant age class found in Fraser sockeye stocks.

TABLE 1—Timing of peak of runs, river migration distances, elevation of spawning grounds and slope of migration path for races of sockeye studied. Times not exact because variations of a week or more may occur.

Race	Time of River Entry	Distance (miles)	Elevation (feet)	Slope (ft/mi)	Time of Spawning
Early Stuart	Early July	675	2,300	3.4	Early August
Chilko	Late July to Early August	390	3,800	9.7	Late September
Adams	Mid-September	300	1,200	4.0	Mid-October
Pitt	Late July	60	Near sea level	—	Mid-September
Horsefly	Late July	500	2,500	5.0	Early September
Late Stuart	Late July	650	2,250	3.4	Mid-September

METHODS

In a quantitive study of the constituents of sockeye, assessment of changes in weight during migration and spawning is necessary. Lengths and weights were measured on the individual sockeye so that sample mean weight could be corrected to true population mean weight at any station through a length-weight relationship, using deviations of sample mean length from the population mean length determined from supplemental length measurements. The "standard fish" of Idler and Clemens (1959) is an estimate of the true population mean weight at a given station or stage, derived in this manner.
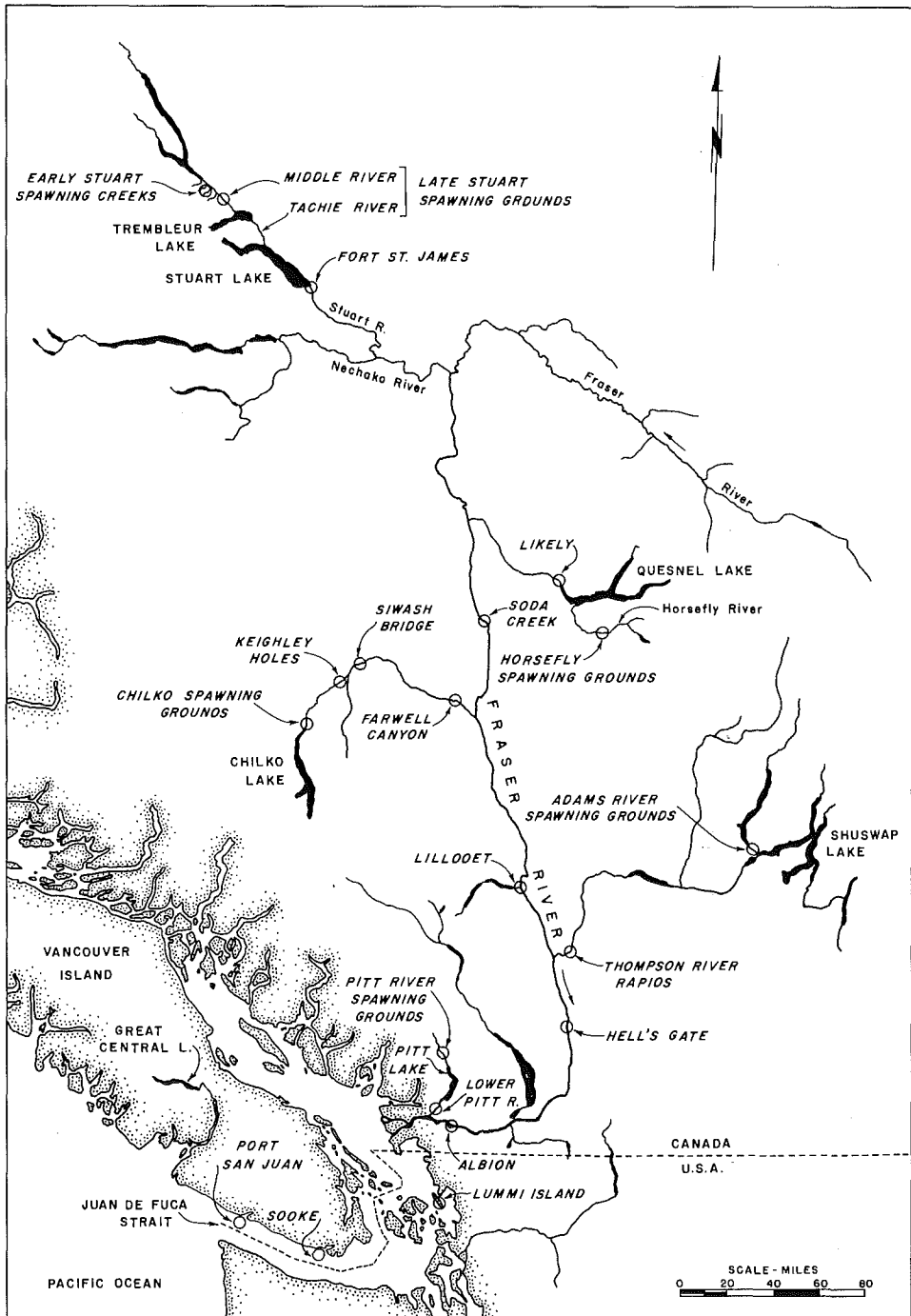
FIGURE 1—Fraser River, tributaries, and adjacent waters utilized by the sockeye races in the study of energy stores. Sampling locations shown by circles.

Specific gravity of eviscerated sockeye was investigated in 1957, 1958 and 1959 to ascertain whether this parameter would allow a better correction to standard fish weight than would adjustment to constant length (Idler and Clemens, *ibid.*).

Weights of various components of the sockeye such as viscera and gonads were measured to determine changes during migration. Since each race studied has a different migration schedule, data for each race were compared against the percentage water in the eviscerated fish, a basic parameter which is closely related to maturation.

Sampling Locations

Sockeye sampled for energy studies were taken at locations extending from Port San Juan to the spawning grounds. Location of sampling, dates, condition, and numbers of sockeye taken are given in TABLES 2, 3, 4 and 5. Locations and distances of the sampling stations are shown in FIGURE 1 and in TABLE 6.

TABLE 2—Numbers of male and female sockeye of the Early Stuart race sampled from various locations for determination of body constituents in 1956, 1957 and 1958.

Year	Sampling Station	Sampling Date	Segment of Run	Condition of Fish	No. of Sockeye		
					♂	♀	Total
1956	Port San Juan	July 4	Peak	Migrating	8	10	18
	Lummi Island	July 5	Peak	Migrating	7	13	20
	Albion	July 7-8	Peak	Migrating	9	9	18
	Hell's Gate	July 13	Peak	Migrating	9	4	13
	Lillooet	July 16	Peak	Migrating	7	13	20
	Soda Creek	July 20-21	Peak	Migrating	4	10	14
	Ft. St. James	July 26	Peak	Migrating	9	13	22
	Forfar Creek	July 31	Peak	Ripe	7	7	14
	Forfar Creek	August 7	Peak	Live-Spawned	12	12	24
	Forfar Creek	August 7	Peak	Dead-Fresh	10	12	22
				Totals	82	103	185
1957	Lummi Island	July 3	Peak	Migrating	23	33	56
	Albion	July 7	Peak	Migrating	22	17	39
	Albion	July 14	Late	Migrating	20	14	34
	Lillooet	July 13	Peak	Migrating	40	40	80
	Ft. St. James	July 22-23	Early	Migrating	19	19	38
	Ft. St. James	July 29-30	Peak	Migrating	24	16	40
	Ft. St. James	August 5-6	Late	Migrating	20	19	39
	Forfar Creek	July 31	Peak	Ripe	25	55	80
	Forfar Creek	July 31	Early	Live-Spawned	16	19	35
	Forfar Creek	August 9	Peak	Live-Spawned	4	14	18
	Forfar Creek	August 17	Late	Live-Spawned	19	20	39
				Totals	232	266	498
1958	Sooke	July 7	Early	Migrating	12	20	32
	Albion	July 9	Early	Migrating	16	23	39
	Lillooet	July 18	Early	Migrating	21	19	40
	Ft. St. James	August 4-5	Peak	Migrating	21	19	40
	Forfar Creek	August 10	Peak	Live-Spawned	19	18	37
	Forfar Creek	August 17	Peak	Dead-Fresh	20	20	40
				Totals	109	119	228

TABLE 3—Numbers of male and female sockeye of the Chilko race sampled from various locations for determination of body constituents in 1956 and 1959.

Year	Sampling Station	Sampling Date	Segment of Run	Condition of Fish	No. of Sockeye		
					♂	♀	Total
1956	Albion	July 30	Peak	Migrating	13	11	24
	Farwell Canyon	August 10	Peak	Migrating	9	19	28
	Keighley Holes	August 20	Peak	Migrating	13	16	29
	Chilko River	September 18	Peak	Live-Spawned	15	11	26
	Chilko River	September 23	Peak	Dead-Fresh	14	15	29
				Totals	64	72	136
1959	Lummi Island	August 4	Peak	Migrating	22	29	51
	Albion	August 6	Peak	Migrating	49	35	84
	Farwell Canyon	August 19	Peak	Migrating	29	48	77
	Siwash Bridge	August 28-29	Peak	Migrating	41	39	80
	Chilko River	September 15	Early	Ripe	39	38	77
	Chilko River	September 22	Early	Live-Spawned	39	38	77
	Chilko River	September 30	Early	Dead-Fresh	36	39	75
				Totals	255	266	521

TABLE 4—Numbers of male and female sockeye of the Adams River race sampled from various locations for determination of body constituents in 1958.

Year	Sampling Station	Sampling Date	Segment of Run	Condition of Fish	No. of Sockeye		
					♂	♀	Total
1958	Lummi Island	September 8	Peak	Migrating	38	40	78
	Albion	September 28	Early	Migrating	40	40	80
	Albion	October 5	Peak	Migrating	41	36	77
	Albion	October 16-18	Late	Migrating	38	44	82
	Albion	October 28	Very Late	Migrating	26	30	56
	Hell's Gate	October 12	Peak	Migrating	41	39	80
	Thompson Canyon	November 2	Very Late	Migrating-Weak	38	41	79
	Adams R. Mouth	October 15	Early	Ripe	18	22	40
	Adams R. Mouth	October 23	Peak	Ripe	40	44	84
	Adams R. Mouth	November 6	Late	Ripe	21	18	39
	Adams River	October 30	Peak	Live-Spawned	40	28	68
	Adams River	November 12	Peak	Dead-Fresh	39	41	80
	Adams R. Mouth	November 24	Very Late	Dead-Fresh -Unspawned	36	39	75
				Totals	456	462	918

Sampling Gear

Gear used for taking sockeye varied with the location of sampling. In the saltwater areas and in the lower Fraser River, commercial gear was used or fish were purchased from commercial fishermen. Purse seines, traps, and reef nets were used to obtain sockeye at Port San Juan, Sooke, and Lummi Island respectively. Gillnets were used as drift nets at Albion on the lower Fraser, and as anchored set nets at Fort St. James. The

most common sampling gear in the freshwater migration area was the native Indian dip net. Smaller dip nets were used on the spawning grounds. Samples from the Chilko River at Keighley Holes and Siwash Bridge were taken with a gaff pole. Beach seine gear was employed for catching live samples at certain spawning grounds. Samples of sockeye which had just died (fresh dead) were picked by hand along the bank of the spawning streams.

TABLE 5—Number of male and female sockeye of the Pitt, Horsefly and Late Stuart races sampled from various locations for determination of body constituents in 1957. All samples from peak of run.

Race	Sampling Location	Sampling Date	Condition of Fish	No. of Sockeye		
				♂	♀	Total
Pitt	L. Pitt River	July 29 & August 4	Migrating	14	9	23
	Boise Creek	September 23	Dead-Fresh	7	9	16
			Totals	21	18	39
Horsefly	Likely	August 22-26	Migrating	22	20	42
	Horsefly River	September 9-10	Dead-Fresh	21	21	42
			Totals	43	41	84
Late Stuart	Fort St. James	August 26-27	Migrating	23	11	34
	Middle River	September 16	Live-Spawned	20	20	40
			Totals	43	31	84

TABLE 6—Approximate distances of sampling stations by water from Port San Juan for the three Fraser sockeye races studied in detail.

Sampling Station	Distance in Miles		
	Early Stuart	Chilko	Adams
Port San Juan	0	0	0
Sooke Traps	50	—	—
Lummi Island	135	135	135
Albion*	215	215	215
Hell's Gate	305	—	305
Thompson Canyon	—	—	345
Lillooet	385	—	—
Farwell Canyon	—	485	—
Soda Creek	515	—	—
Siwash Bridge	—	540	—
Keighley Holes	—	555	—
Fort St. James	775	—	—
Spawning Grounds	850	585	475

* 40 miles above Fraser River mouth.

Sample Sizes and Sampling Times

Sample sizes varied from as few as 4 in each sex to as many as 55 (TABLES 2 through 5). Listed sample sizes are those which were analysed after loss or discard of

some fish from the original catches. In catches containing more than one race, sockeye of the desired race were determined by scale examination (using the methods of Henry 1961) and the remainder discarded. Since the racial identity of each fish was not always determinable, only those fish were retained which were clearly of the desired race. Only sockeye of age four (4_2) were retained except at Pitt river where five year old (5_2) sockeye predominated.

Most samples were taken from as near the peak of the run as practicable in order to be most representative of the total run but some samples from the 1958 Early Stuart and 1959 Chilko runs were taken from the early segment. Additional samples were taken from early, late, or very late segments of the 1957 Early Stuart and the 1958 Adams River runs at several sampling stations (TABLES 2 and 4). These non-peak samples were scheduled to be a week or more from the peak of the run.

Storage, Transportation and Dissection of Sockeye

On being caught, sockeye were sealed in heavy, individual plastic bags. Measurements and scales for age and racial determination were taken either before bagging or just before processing for constituent analysis. Sockeye were sometimes transported to the laboratory for immediate processing, but more often were taken to a cold storage facility, being cooled by ice or dry ice where a long journey was necessary.

Samples were taken to the laboratory of the Vancouver Technological Station, thawed, measured, dissected, and the components cut into small pieces by a cutting machine. The chopped material from each component of the fish was stirred, and a one pound can of each resulting mix was preserved by the usual methods of the food processing industry. Constituent analyses were made on individual sockeye in the 1956 samples. However, larger sample sizes without increased constituent analyses were desired, therefore, in 1957, 1958 and 1959, chopped material from several fish was combined before canning into four subsamples per sample. As a result, as many as 14 fish were included in a subsample.

In all cases, the eviscerated body and total viscera were treated as separate units. Viscera were divided into gonads and remainder in all but the 1956 samples. In some samples, the eviscerated body was separated into "fillets" and "trimmings", fillets being the body muscles which extend from the back of the head to the tail, and trimmings being the head (including gills), fins, skin and backbone. After dissection and canning, the labeled cans were stored at room temperature until analysed.

Physical Measurements

Total (fork) length, standard length (tip of nose to hypural plate terminus), and snout length (tip of nose to anterior edge of eye socket) of the fish were measured. Since the length of the vertebral column is not known to change on the spawning migration, the body length (standard length minus snout length) was usually used as an index of size.

Weights were obtained for all individual whole fish, all dissected parts, and the eviscerated fish. After the weight of the eviscerated fish was obtained in air, it was weighed again in water while suspended on a string or wire. Volume was then calculated as the weight in air less the weight in water, assuming that a gram of water had a volume of one milliliter. In cases where the sockeye floated, the weight in water, and thus volume,

was not determined. Specific gravity was calculated as the weight of the fish in air divided by the volume of the fish.

In comparisons between samples from different segments of the run, mean total weight of early and late samples within each sex at each sampling station were adjusted to the mean body length of the peak sample at that station. This procedure assumed that samples with longer or shorter body lengths were proportionately heavier or lighter than the population they were taken from. Although this assumption was not always correct, the adjusted total weights provided a better comparison than unadjusted weights. Adjustment of weight was made with the relationship $W = W_o (L/L_o)^b$, with b taken as 3.5, based on length-weight relationships in the data collected. Condition factor was calculated as C.F. $= kW/L^{3.5}$.

Constituent Analyses

The major constituents of a salmon are fat, protein, and water, of which fat and protein are sources of stored energy. Proportions of these constituents were determined by standard physical and chemical methods.

Procedure in determining constituent proportions began with subsampling of the canned samples of sockeye flesh and organs. Each can of material was whipped into a finely divided, homogeneous mass in a high speed blender. Three 10 gm subsamples were measured from each can, or six subsamples where duplicate analyses were made. Water content was determined by evaporation of moisture under infrared lamps until weight became constant. Fat (oil) content was determined by extraction with acetone and methylene chloride as described by Idler and Clemens (1959).

Protein was determined as nitrogen by the standard Macro-Kjeldahl method. A factor of 6.25 was used to convert nitrogen to protein. Because the nitrogen containing material in sockeye included 13 to 16 percent of non-protein compounds (Duncan and Tarr 1958; Wood 1958), the protein percentage determined is actually an index of the true value. Non-protein nitrogen appears to a relatively constant proportion of the total nitrogen throughout migration (Wood *ibid.*), therefore it may be included in the "protein" percentage with little practical effect on energy calculations. The sum of fat, protein and water will usually be found to total approximately 98% or 99%, the remainder being ash.

Although mean constituent percentages were available for eviscerated sockeye in all samples, not all the percentages were obtained in the same way. In those samples in which eviscerated sockeye were dissected into fillets and trimmings, constituent percentages for the eviscerated fish had to be calculated from data for the two components. Actual amounts of fat, protein, or water were calculated within subsamples for fillets and for trimmings, and the percentage which the sum for each constituent formed of the total eviscerated weight was obtained. Sample mean constituent percentage was derived by averaging the four subsample mean constituent percentages.

Energy Expenditure

Energy use was calculated between Lummi Island and Albion, and between Albion and arrival at the spawning ground, and also between Albion and dead in some cases and between arrival and dead in other cases, as the data permitted. Racial migrations in

different years were kept separate for comparison between years as well as between races.

Because various components of the sockeye had been dissected and analysed separately, sample mean weights of the components at the selected stations were assembled into tables, sexes separately. Complementary tables of mean percentages of protein and fat in the components were also constructed. Application of the mean percentage composition figures to the corresponding mean weights produced tables of mean content of fat and protein in the sockeye at the chosen stations. Changes in constituents from one station to the next were obtained and summed into two parts, that involved in migration or spawning ground activity, and that used in gonad growth or expulsion of sex products. An exception was the constituents used by the 1956 Chilko and 1958 Early Stuart runs for migration and for spawning ground activity. These items were not separated until energy use per kilogram was calculated. Lack of spawning ground arrival samples for the 1956 Chilko and 1958 Early Stuart runs necessitated the estimation of data for this stage in order to use the other information available for these runs. Estimates of gonad size at arrival was obtained by proportion from other years of the same race. Total fish weight for calculating energy use per kg of fish was likewise obtained. Mean constituent percentages for gonads were taken directly from the same race and station in another year, or the mean of two years was used. Constituent analyses were not made for gonads and other viscera in the 1956 sampling, therefore constituent percentages for these components were also taken from other years samples, as was the division of total viscera weight into gonads and remaining viscera.

Grams of fat or protein used were converted to kilocalories (kcal) by the factors 9.3 kcal/g of fat, and 4.1 kcal/g of protein (Idler and Clemens 1959). The sum of constituent use for each run, sex, and stage of migration or spawning was divided by the mean total fish weight between stations to obtain kcal/kg energy use. For runs not sampled at spawning ground arrival, the kcal/kg from arrival to death was taken as equal to that in another year of the same race, and kcal/kg for Albion to spawning ground arrival was obtained by subtracting the former energy value from the total energy per kg from Albion to death. Energy use per kg between stations per mile and per day was derived by dividing kcal/kg values by miles between stations or days between samples.

PHYSICAL FEATURES

Length

Mean body length in samples from the peak of three races studied in detail varied by less than three centimeters in the same sex in any year (TABLE 7). Difference between male and female mean body length at the same station averaged about a centimeter. In general, male and female mean body lengths show parallel deviations indicating factors which caused both to deviate in the same direction.

Mean body lengths were exceptionally short in the 1959 Chilko samples from the spawning grounds and from Siwash Bridge (TABLE 7). Large samples of dead fish from the spawning ground measured for other purposes also had similar short mean body lengths. No satisfactory explanation can be given for this difference.

There is a trend in some of the data of decreasing body lengths as the fish approach the spawning grounds (TABLE 7). However, dead fish were longer than spent fish in

TABLE 7—Mean body lengths (cm) of male and female sockeye in peak samples of the three major races studied.

	Early Stuart					
	Year					
	1956		1957		1958	
Station	Males	Females	Males	Females	Males	Females
Port San Juan	52.1	50.4				
Sooke					49.3*	48.8*
Lummi Island	51.0	50.5	50.0	49.3		
Albion	50.7	50.2	50.3	50.0	50.2*	49.2*
Hell's Gate	50.9	50.4				
Lillooet	51.7	51.3	50.2	49.3	50.4*	49.7*
Soda Creek	51.6	50.5				
Fort St. James	49.6	50.6	49.9	49.5	49.4	49.1
Forfar Cr. - Ripe	52.5	50.0	50.3	49.3		
Forfar Cr. - Spent	51.3	50.4	49.2	48.3	49.2	48.5
Forfar Cr. - Dead	50.7	50.1			48.3	47.7

	Chilko			
	Year			
	1956		1959	
Station	Males	Females	Males	Females
Lummi Island			50.1	49.1
Albion	50.5	50.3	49.9	49.4
Farwell Canyon	51.5	50.2	49.9	49.1
Keighley Holes	51.9	50.9		
Siwash Bridge			48.2	48.1
Chilko R. - Ripe			47.2*	46.5*
Chilko R. - Spent	50.7	49.7	48.4*	48.2*
Chilko R. - Dead	52.0	50.2	48.0*	47.3*

	Adams	
	1958	
Station	Males	Females
Lummi Island	51.5	49.9
Albion	49.8	49.5
Hell's Gate	50.9	49.2
Adams R. - Ripe	50.9	49.4
Adams R. - Spent	49.9	48.7
Adams R. - Dead	49.1	48.2

* Samples from early segment.

samples from the 1956 Chilko run. Some of the length decrease on the spawning grounds could be due to deterioration as the sockeye approach the end of life. The decrease between spent and dead fish could also result from measurement of spent sockeye prior to *rigor mortis*, whereas dead sockeye would almost always be measured during or after *rigor mortis*. The data do not indicate a statistically significant length decrease during migration except in the 1959 Chilko run. Mean body length variation between peak and non-peak samples at the same location (TABLE 8) show no consistent pattern.

TABLE 8—Mean body lengths (cm) for 1957 Early Stuart and 1958 Adams River sockeye in samples other than peak. Mean body lengths from peak shown for comparison.

Race	Year	Location	Males				Females			
			Early	Peak	Late	Very Late	Early	Peak	Late	Very Late
Early Stuart	1957	Albion	—	50.3	50.0	—	—	50.0	50.2	—
		Ft. St. James	48.8	49.9	50.9	—	48.7	49.5	49.7	—
		Forfar Creek Spawned	48.9	49.2	48.6	—	49.4	48.3	47.4	—
Adams River	1958	Albion	50.7	49.8	50.5	50.1	49.9	49.5	49.0	49.6
		Thompson Canyon	—	—	—	50.6	—	—	—	49.2
		Adams River Arrival	50.1	50.9	50.1	—	48.8	49.4	49.3	—
		Adams River Fresh Dead	—	49.1	—	49.1*	—	48.2	—	47.9*

* Died unspawned.

Total Weight

Mean total weight of peak samples (TABLE 9) decreased as much as 700 grams between salt water sampling and death. As with body length data, male and female weight generally followed parallel trends suggesting factors which affected both sexes similarly.

Males averaged 200 to 300 grams more than females in most samples but the difference between sample means at a location varied from less than 100 to over 500 grams (TABLE 9). At Albion and Fort St. James, where gillnets were used to capture sockeye, the difference in weight was often small (1957 Early Stuart, 1956 Chilko, and 1958 Adams at Albion; 1956 Early Stuart at Fort St. James).

Decrease in total weight of sockeye during migration and spawning would be expected where body material is being consumed without replacement by food intake. Static weight or gain in weight during migration suggests net water intake or non-representative samples. Data for Early Stuart, Chilko and Adams River sockeye indicate weight loss from saltwater to death at the spawning grounds although there are anomalies (TABLE 9).

Mean total weights in peak samples and adjusted mean total weights from early and late segment samples of a run passing a given sampling station show a fairly consistent trend toward lower total weight in later segments (TABLE 10). In 22 comparisons between adjacent segments at the same sampling station there were 19 weight decreases from an earlier to the next later sample, and 3 weight increases. These data suggest that the trend of weight decrease during passage of a run is highly significant. Decrease in mean total weight during passage of a sockeye run was also noted in large samples of females from the 1969 Horsefly run taken a few miles below the main spawning ground (Williams 1973).

TABLE 9—Mean total weight (gm) of male and female sockeye in peak samples of the three major races studied. Mean ovary weight for ripe female added to weight of spent and dead females.

Early Stuart

| | Year | | | | | |
| | 1956 | | 1957 | | 1958 | |
Station	Males	Females	Males	Females	Males	Females
Port San Juan	2,904	2,759				
Sooke					2,424*	2,327*
Lummi Island	2,714	2,456	2,503	2,376		
Albion	2,741	2,517	2,448	2,406	2,470*	2,394*
Hell's Gate	2,603	2,361				
Lillooet	2,572	2,378	2,371	2,156	2,536*	2,395*
Soda Creek	2,418	2,232				
Fort St. James	2,517	2,390	2,392	2,210	2,574	2,193
Forfar Cr. - Ripe	2,869	2,033	2,583	2,168		
Forfar Cr. - Spent	2,346	2,023[a]	2,133	1,865[b]	2,195	1,990[c]
Forfar Cr. - Dead	2,200	1,885[a]			2,030	1,787[c]

a - includes ovary wt. of 319 gm.
b - includes ovary wt. of 298 gm.
c - includes ovary wt. of 312 gm. estimated by proportion in other years.

Chilko

| | Year | | | |
| | 1956 | | 1959 | |
Station	Males	Females	Males	Females
Lummi Island			2,323	2,099
Albion	2,655	2,545	2,290	2,160
Farwell Canyon	2,439	2,086	2,086	1,963
Keighley Holes	2,781	2,481		
Siwash Bridge			1,901	1,809
Chilko R. - Ripe			2,218*	1,928*
Chilko R. - Spent	2,779	2,280[d]	2,076*	1,767[e]*
Chilko R. - Dead	2,642	1,950[d]	1,840*	1,646[e]*

d - includes ovary wt. of 299 gm. estimated from unpublished fecundity data.
e - includes ovary wt. of 268 gm.

Adams

| | 1958 | |
Station	Males	Females
Lummi Island	2,920	2,453
Albion	2,750	2,547
Hell's Gate	2,824	2,445
Adams R. - Ripe	3,042	2,477
Adams R. - Spent	2,638	2,420[f]
Adams R. - Dead	2,480	2,302[f]

f - includes ovary wt. of 414 gm.
* - samples from early segment.

TABLE 10—Comparison of peak sample mean total weight (gm) with adjusted mean total weight of early and late samples. Adjustment of weight to peak sample body length is described on page 8.

Race	Year	Location	Males				Females			
			Early	Peak	Late	Very Late	Early	Peak	Late	Very Late
Early	1957	Albion	—	2,448	2,471	—	—	2,406	2,325	—
Stuart		Ft. St. James	2,454	2,392	2,225	—	2,296	2,210	2,056	—
		Forfar Cr.-Spawned	2,261	2,133	2,091	—	1,935*	1,865*	1,813*	—
Adams	1958	Albion	2,802	2,750	2,560	2,630	2,561	2,547	2,403	2,419
River		Thompson Canyon	—	—	—	2,623	—	—	—	2,268
		Adams River Arrival	3,191	3,042	3,022	—	2,717	2,477	2,344	—
		Adams River Fresh Dead	—	2,480	—	2,461**	—	2,302*	—	2,087**

  * Corrected for loss of eggs.
** Died unspawned.

Weights of Components

Weights of the various organs or components of the sockeye are analysed here as percentage of total weight, and are calculated from sample mean weights, sexes separated.

FILLETS AND TRIMMINGS

The two components of the eviscerated sockeye, fillets and trimmings, were separated in most samples analysed in 1957 and 1958, but not in samples taken in 1956 or 1959. Only three runs of sockeye in the study were sampled for fillet and trimming weights at more than two stations, viz., the Early Stuart run of 1957 and the Adams and Early Stuart runs of 1958.

Sockeye left the open sea with nearly 2/3 of their weight in fillets and just under 1/3 in trimmings (FIGURE 2). At spawning, fillets comprised about 1/2 the body weight and trimmings approximately 40%. Egg expulsion altered the complementary changes which occurred in relative weight of fillets and trimmings of females (FIGURE 2). After spawning was complete, complementary changes again occurred between spent and dead samples of females as well as males. During migration, females showed greater decrease in fillet size and a smaller increase in trimming relative weight than males.

Possible racial differences may be found in relative weight of fillets and trimmings (FIGURE 2). Adams sockeye generally had relatively lighter fillets and heavier trimmings than Early Stuart.

Relative weights of fillets and trimmings through the various segments of a run at a given sampling station were examined for evidence of consistent change. There was a tendency for the earlier (and plumper) fish to have fillets composing a greater proportion of the total weight, but the tendency was not significant statistically.
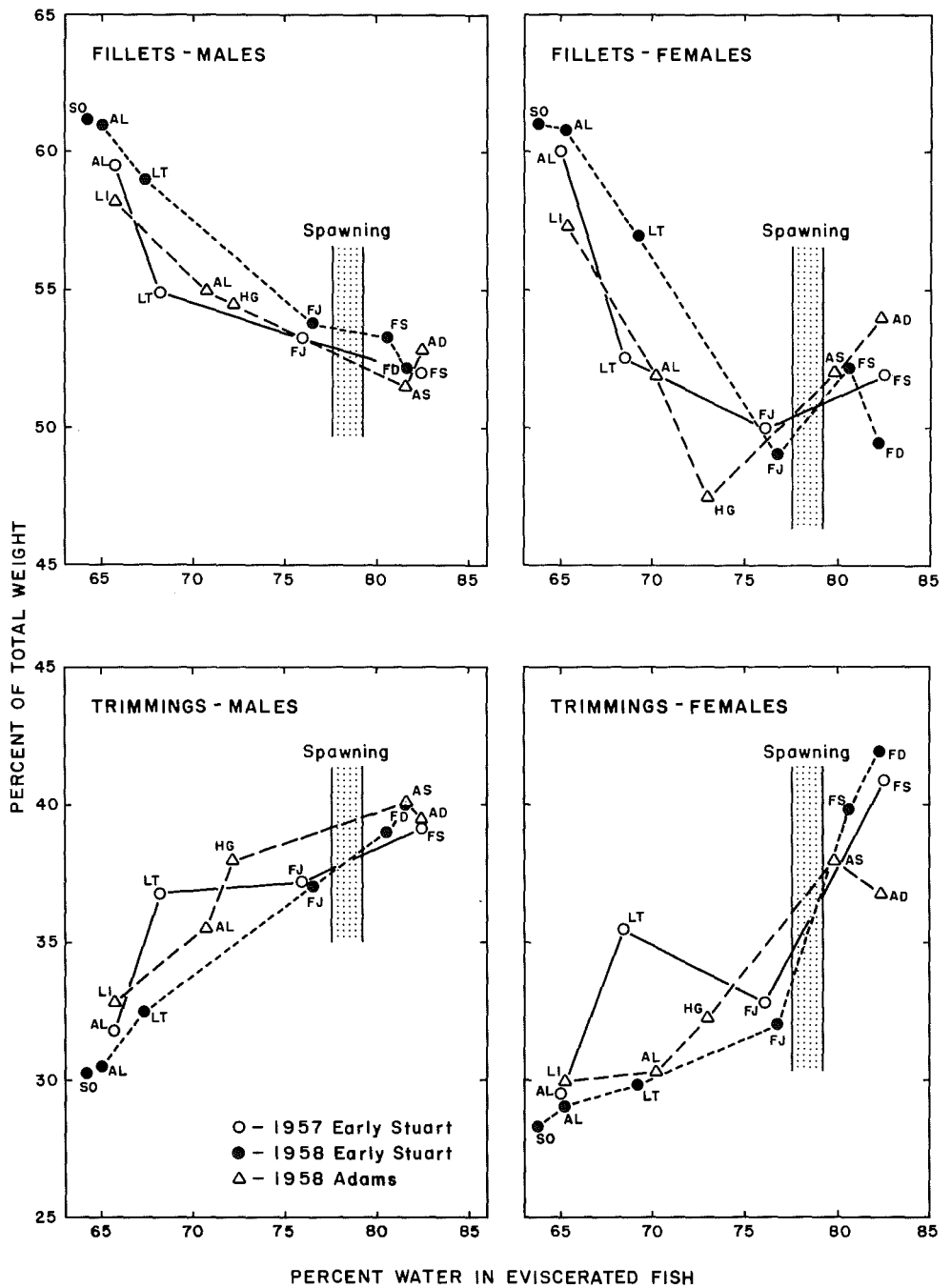
FIGURE 2—Mean relative weight of fillets and trimmings (as a percentage of total weight of fish) in samples of Early Stuart and Adams sockeye compared with mean percentage water in eviscerated fish. Peak samples except as noted in TABLES 2 and 3.

VISCERA EXCLUDING GONADS

Mean relative weight of male and female viscera (gonads omitted), from peak samples of the three races sampled extensively, varied from less than 4% to over 7% during the prespawning stages (FIGURE 3) with females having slightly higher values than males. Relative weight of female viscera less gonads increased during spawning because eggs were discharged.
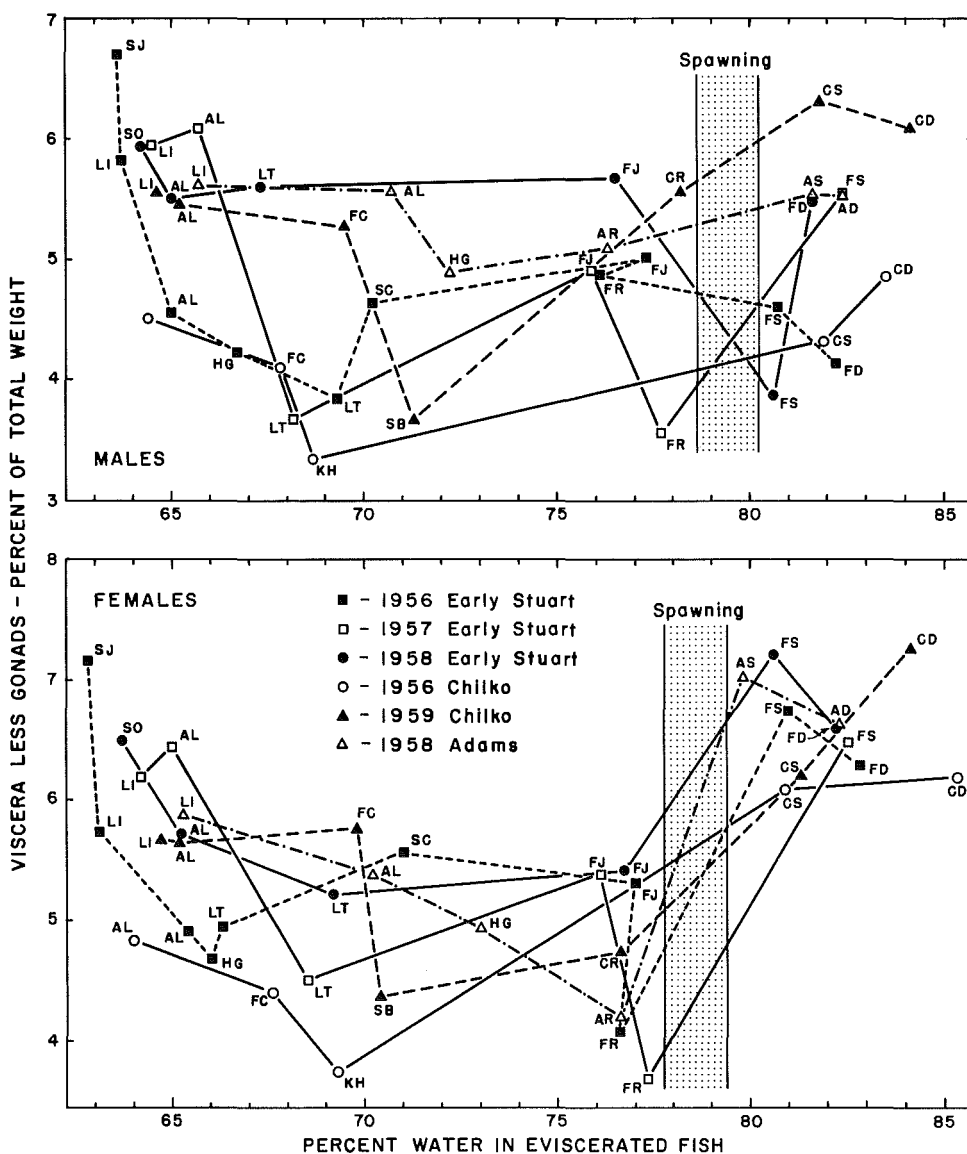

FIGURE 3—Mean weight of viscera excluding gonads in samples of sockeye (expressed as a percentage of mean total weight) compared with mean percentage water in eviscerated fish. Peak samples except as noted in TABLES 2 and 3.

The large, irregular variations in relative weights of viscera excluding gonads precluded any conclusions concerning racial differences or differences between segments of a run.

GONADS

Relative mean weight of testes in peak samples of sockeye ranged from 1% to 4% of body weight (FIGURE 4). Testicular growth in size was completed at or soon after arrival in the estuary. Ovary growth was approximately a linear function of percentage water in the eviscerated female during most of migration, ranging from about 3% of body weight prior to entering the river, to 11%-17% just before spawning. During spawning, ovaries were reduced to small remnants in successful spawners (data not shown) while testes were reduced to about half their former size.

There were racial differences in relative ovary weight in Fraser River sockeye (FIGURE 4). Adams River females had larger ovaries than those of other races and Chilko sockeye also appeared to have slightly larger ovaries than Early Stuart females at the same percentage water. Both Early Stuart and Chilko sockeye ovaries were at approximately the same relative size at the same percentage of water in the eviscerated fish on arrival in the estuary in different years, even though times of arrival were different.

Single sample means are also presented in FIGURE 4 for comparison of other races with the three races sampled in detail. Pitt females sampled in the lower Pitt River appeared to follow the ovary weight schedule of Adams females. Late Stuart females sampled at Fort St. James followed the same course as ovaries in Early Stuart fish. Horsefly ovaries sampled at Likely were on the schedule followed by Chilko females.

There also were racial differences in testicular development (FIGURE 4). Early Stuart sockeye entered coastal waters with testes forming about 2% of total weight, with an increase to over 3% before migration was half completed. However, Chilko and Adams males had testes weighing 3% or more of total weight when first sampled in salt water.

TABLE 11—Mean gonad weight expressed as percent of mean total sockeye weight for males and females of different segments of the 1957 Early Stuart and 1958 Adams River runs.

Race	Year	Location	Males				Females			
			Early	Peak	Late	Very Late	Early	Peak	Late	Very Late
Early Stuart	1957	Albion	—	2.6	2.9	—	—	4.0	4.1	—
		Ft. St. James Forfar Cr.	3.5	3.5	3.2	—	11.7	11.3	12.6	—
		Spawned	2.4	2.0	1.3	—	0.3*	0.2*	0.8*	—
Adams River	1958	Albion	2.9	2.9	2.5	2.3	12.0	11.5	15.5	15.4
		Thompson Canyon Adams River	—	—	—	2.3	—	—	—	17.4
		Arrival Adams River	2.8	3.0	2.7	—	17.3	16.7	18.3	—
		Fresh Dead	—	1.3	—	1.6	—	1.2*	—	—

* Ovary remnants are not comparable to other data due to variable egg retention.
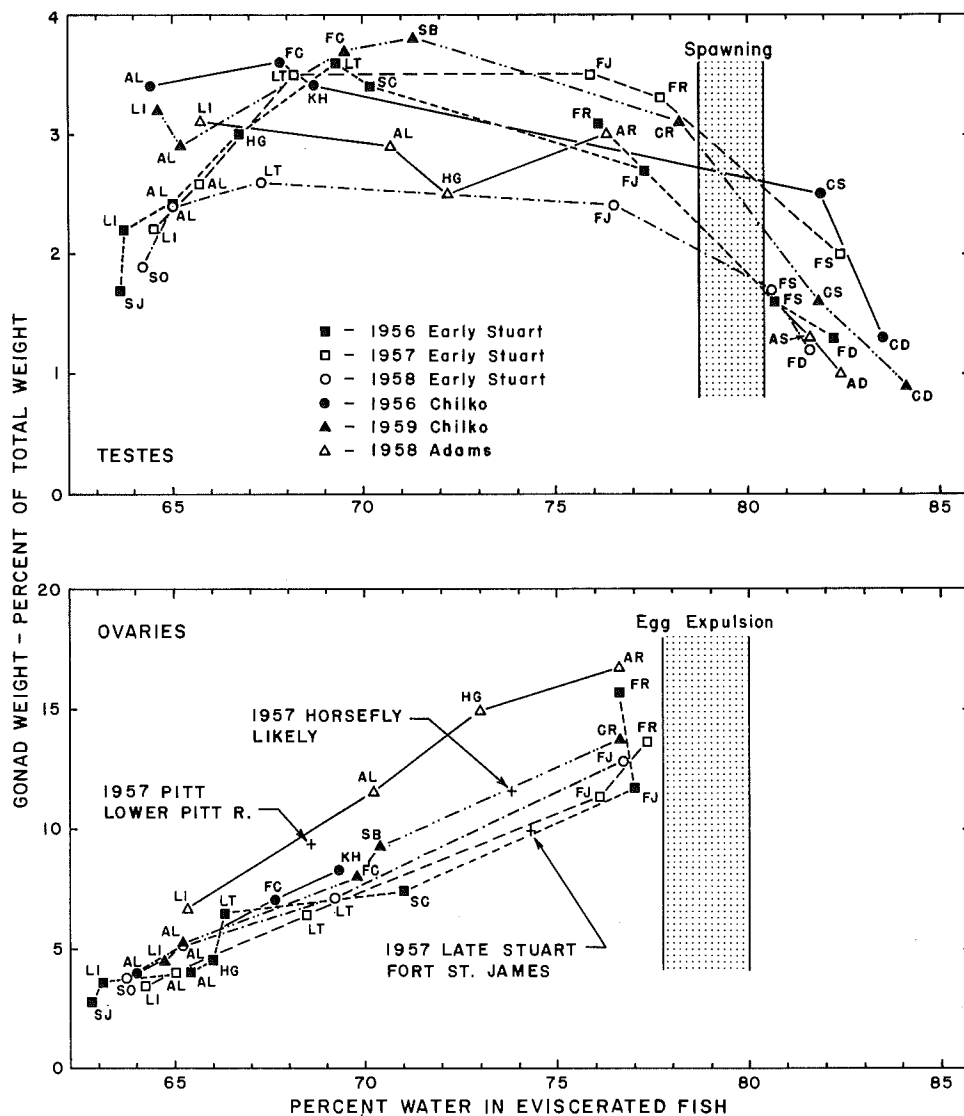
FIGURE 4—Mean weight of gonads in samples of sockeye (expressed as percentage of total weight) compared with mean percentage water in eviscerated fish. Peak samples except as noted in TABLES 2 and 3.

Relative gonad weight showed no consistent trend from earlier to later segments of a run at the same sampling station (TABLE 11). Because testes did not show large, steady changes in size, this result is not unexpected in males. The steady ovary growth during maturation suggests that later females should have larger percentage ovaries than earlier females. This was demonstrated for large samples of Horsefly sockeye taken in 1969 (Williams 1973) and Colgrove 1966 showed the same phenomenon for females of the 1964 Chilko sockeye run.

Specific Gravity

Specific gravity of the eviscerated fish was found to decrease from salt water samples to spawned and dead samples (FIGURE 5). Specific gravity of eviscerated sockeye generally decreased in a sockeye run as it passed a given sampling station (TABLE 12). In only two comparisons between one sample and the next later sample at the same station or stage (Adams River dead), did the specific gravity increase. However, in these samples of fresh dead sockeye from the Adams River the very late samples were dead unspawned and therefore may not have advanced to the low specific gravities of spawned sockeye.

TABLE 12—Mean specific gravity values for samples of eviscerated sockeye from different segments of the 1957 Early Stuart and 1958 Adams River runs.

Race	Year	Location	Males				Females			
			Early	Peak	Late	Very Late	Early	Peak	Late	Very Late
Early Stuart	1957	Albion	—	1.022	1.020	—	—	1.022	1.020	—
		Ft. St. James Forfar Creek	1.023	1.019	1.011	—	1.024	1.023	1.016	—
		Spawned	1.014	1.005	1.002	—	1.015	1.009	1.003	—
Adams River	1958	Albion	1.028	1.028	1.021	1.017	1.030	1.029	1.022	1.018
		Thompson Canyon	—	—	—	1.021	—	—	—	1.027
		Adams River Ripe	1.023	1.019	1.013	—	1.029	1.027	1.018	—
		Adams River Fresh Dead	—	1.005	—	1.009*	—	1.007	—	1.011*

* Died unspawned.

Summary

Physical measurements demonstrated changes occurring during migration to the spawning ground, with some racial differences and differences between segments being shown. Total weight decreased during migration and spawning. Total weight and specific gravity also decreased from early to late segments of a run.

The relative weight of various components of the sockeye body reflected the changes accompanying energy expenditure and maturation. Fillets decreased considerably in weight indicating that a large part of the energy supply was stored there. Viscera excluding gonads also decreased in weight.

Racial differences were found in gonad development, wherein the earlier migrating races studied generally had less developed ovaries and testes at arrival at the river mouth. Early Stuart sockeye had the smallest ovaries and testes at entry into fresh water. Chilko and Adams sockeye had the largest percentages of testes at this stage and Adams and Pitt had the largest percentage of ovaries.
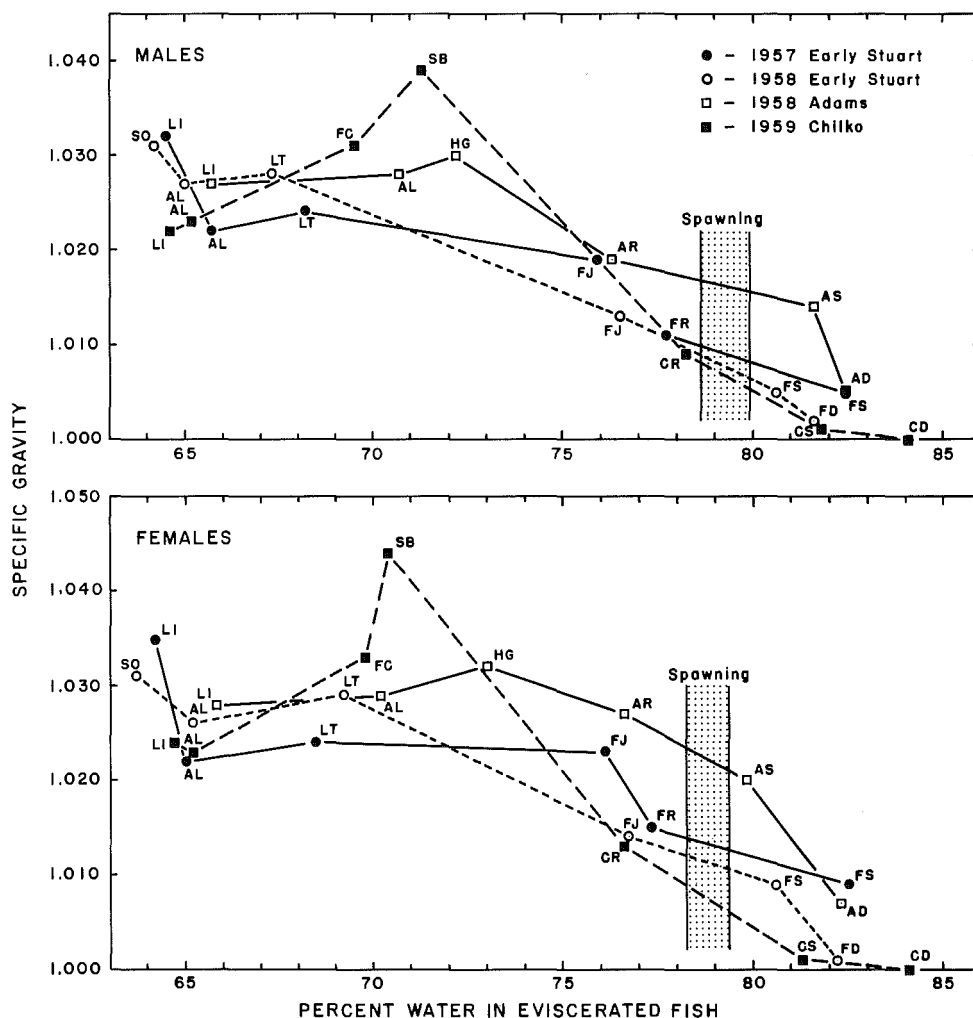
FIGURE 5—Mean specific gravity values for eviscerated male and female sockeye compared with percentage water in the eviscerated fish. Peak samples except as noted in TABLES 2 and 3.

CONSTITUENT ANALYSES

Eviscerated Sockeye

Mean percentages of fat, protein and water in the eviscerated carcass of sockeye in samples from the races studied are given in TABLES 13, 14, 15 and 16. Mean percentages of fat and protein in samples from the peak of the runs changed uniformly over the period of sampling in relation to the percentage of water (FIGURES 6 and 7). Fat and protein changes were similar from year to year and from race to race with the possible exception of the 1956 Chilko run.

Percentage water in the eviscerated fish provides a useful index of maturation. All races of Fraser sockeye studied appeared to enter coastal waters with 63% to 65% water in

TABLE 13—Mean percentages of protein, fat, and water in samples of eviscerated Early Stuart sockeye in 1956, 1957 and 1958 by sex and location. Samples comprise 4 or more fish for each sex at each station.

PROTEIN

	1956		1957						1958			
	♂	♀	♂			♀			♂		♀	
Station	Peak	Peak	Early	Peak	Late	Early	Peak	Late	Early	Peak	Early	Peak
Port San Juan	19.7	19.5	—	—	—	—	—	—	—	—	—	—
Sooke	—	—	—	—	—	—	—	—	20.3	—	20.4	
Lummi Island	19.5	19.9	—	19.8	—	—	19.9	—	—	—	—	—
Albion	19.4	19.9	—	20.2	20.6	—	20.4	20.7	20.6	—	20.5	—
Hell's Gate	20.3	19.7	—	—	—	—	—	—	—	—	—	—
Lillooet	19.1	20.2	—	18.7	—	—	19.2	—	20.5	—	20.3	—
Soda Creek	19.7	19.2	—	—	—	—	—	—	—	—	—	—
Fort St. James	16.9	17.0	19.4	18.6	18.7	19.3	18.5	19.0	—	18.5	—	18.6
Forfar Cr.-Arrival	17.7	17.9	—	16.4	—	—	17.1	—	—	—	—	—
Forfar Cr.-Live, Spent	15.5	15.8	16.9	14.9	15.0	17.2	15.4	16.0	—	17.0	—	17.1
Forfar Cr.-Dead, Fresh	15.4	14.3	—	—	—	—	—	—	—	15.7	—	15.6

FAT

	1956		1957						1958			
	♂	♀	♂			♀			♂		♀	
Station	Peak	Peak	Early	Peak	Late	Early	Peak	Late	Early	Peak	Early	Peak
Port San Juan	14.7	15.9	—	—	—	—	—	—	—	—	—	—
Sooke	—	—	—	—	—	—	—	—	14.1	—	14.7	—
Lummi Island	14.6	15.1	—	13.3	—	—	14.7	—	—	—	—	—
Albion	13.8	13.4	—	12.4	12.3	—	13.4	13.0	13.7	—	14.0	—
Hell's Gate	11.5	12.3	—	—	—	—	—	—	—	—	—	—
Lillooet	10.0	11.7	—	9.4	—	—	9.5	—	10.5	—	9.3	—
Soda Creek	8.4	8.6	—	—	—	—	—	—	—	—	—	—
Fort St. James	3.9	4.0	5.1	4.3	3.6	4.5	3.4	3.7	—	3.5	—	3.4
Forfar Cr.-Arrival	4.3	3.4	—	3.9	—	—	3.5	—	—	—	—	—
Forfar Cr.-Live, Spent	1.9	1.4	2.1	1.2	1.2	1.3	0.9	1.1	—	1.8	—	1.2
Forfar Cr.-Dead, Fresh	1.4	1.0	—	—	—	—	—	—	—	1.5	—	0.9

	WATER											
	1956		1957						1958			
	♂	♀	♂			♀			♂		♀	
Station	Peak	Peak	Early	Peak	Late	Early	Peak	Late	Early	Peak	Early	Peak
Port San Juan	63.6	62.8	—	—	—	—	—	—	—	—	—	—
Sooke	—	—	—	—	—	—	—	—	64.2	—	63.7	—
Lummi Island	63.7	63.1	—	64.5	—	—	64.2	—	—	—	—	—
Albion	65.0	65.4	—	65.7	65.9	—	65.0	65.3	65.0	—	65.2	—
Hell's Gate	66.7	66.0	—	—	—	—	—	—	—	—	—	—
Lillooet	69.3	66.3	—	68.2	—	—	68.5	—	67.3	—	69.2	—
Soda Creek	70.2	71.0	—	—	—	—	—	—	—	—	—	—
Fort St. James	77.3	77.0	74.0	75.9	76.5	74.4	76.1	75.9	—	76.5	—	76.7
Forfar Cr.-Arrival	76.1	76.6	—	77.7	—	—	77.3	—	—	—	—	—
Forfar Cr.-Live, Spent	80.7	81.0	79.4	82.4	82.6	80.1	82.5	81.7	—	80.6	—	80.6
Forfar Cr.-Dead, Fresh	82.2	82.8	—	—	—	—	—	—	—	81.6	—	82.2

TABLE 14—Mean percentages of protein, fat and water in samples of eviscerated Chilko sockeye in 1956 and 1959, by sex and location. Samples comprise 11 or more fish for each sex at each location.

	PROTEIN						FAT						WATER					
	1956		1959				1956		1959				1956		1959			
	♂	♀	♂		♀		♂	♀	♂		♀		♂	♀	♂		♀	
Station	Peak	Peak	Early	Peak	Early	Peak	Peak	Peak	Early	Peak	Early	Peak	Peak	Peak	Early	Peak	Early	Peak
Lummi Island	—	—	—	20.7	—	20.8	—	—	—	12.4	—	13.6	—	—	—	64.6	—	64.7
Albion	19.0	19.4	—	20.3	—	20.0	14.3	14.8	—	13.0	—	12.7	64.4	64.0	—	65.2	—	65.2
Farwell Canyon	19.4	19.5	—	20.1	—	20.0	10.6	10.6	—	8.7	—	9.0	67.8	67.6	—	69.5	—	69.8
Siwash Bridge	—	—	—	20.2	—	20.0	—	—	—	6.7	—	6.2	—	—	—	71.3	—	70.4
Keighley Holes	19.2	19.5	—	—	—	—	9.6	9.3	—	—	—	—	68.7	69.3	—	—	—	—
Chilko R. Spawning Ground: Nearly Ripe	—	—	16.5	—	17.8	—	—	—	3.8	—	3.8	—	—	—	78.2	—	76.6	—
Live-Spent	12.8	14.2	15.0	—	15.3	—	3.5	2.7	2.0	—	1.6	—	81.9	80.9	81.8	—	81.3	—
Dead-Fresh	11.8	11.4	13.8	—	12.9	—	3.4	1.9	1.3	—	0.9	—	83.5	85.6	84.1	—	84.1	—

TABLE 15—Mean percentages of protein, fat and water in samples of eviscerated Pitt, Horsefly and Late Stuart sockeye in 1957 by sex and location. Samples comprise 7 or more fish for each sex at each location.

Station	PROTEIN		FAT		WATER	
	♂	♀	♂	♀	♂	♀
Pitt						
Lower Pitt River	21.7	21.2	8.4	9.3	68.8	68.6
Spawning Grounds-						
Fresh Dead	16.9	17.5	1.7	2.3	80.6	79.3
Horsefly						
Quesnel River at Likely	18.8	18.8	5.0	5.9	74.5	73.8
Horsefly River-Fresh Dead	14.1	14.0	1.0	0.9	84.0	83.9
Late Stuart						
Fort St. James	19.4	19.3	5.1	4.5	74.2	74.3
Middle River-Fresh Dead	15.3	16.3	2.0	1.1	80.7	81.4

the eviscerated fish (FIGURES 6 and 7), and water percentage increased continuously to death at from 79.3% to 85.6% water in means of samples. Ripe sockeye contained from 76.1% to 78.2% water, while spent sockeye ranged from 79.8% to 82.5% water in peak sample means. Clearly, spawning occurred over a restricted water proportion in eviscerated fish. The close inverse correlation between fat and water percentages (FIGURES 6 and 7) indicates a similar connection between maturation and proportion of fat.

Not only were the means of fat percentages in samples of eviscerated fish inversely related to percent water but the percentages of fat for individual fish were similarly related within most samples (FIGURE 8). Males, not shown in FIGURE 8, were similar to females. Large deviations from the trend of regression of constituent percentages in FIGURE 8 are found in a few individual sockeye. Some fish which diverge from the constituent trend had totals of fat, protein and water percentages which exceeded 100% or were less than 98%. Other fish with anomalous percentages had very high or very low weights. Not all divergent constituent percentages could be explained by these anomalies, however. Comparison between protein and water percentages for individual eviscerated fish produced the same scatter along the trend of sample mean values as found for fat.

Correlations between various constituents in individual eviscerated sockeye at each station are presented in TABLES 17 and 18. Largest and most consistent correlations were found between fat and water percentages.

Percentage fat in eviscerated sockeye decreased gradually during migration and spawning (FIGURES 6 and 7), but the rate of decrease slowed during and after spawning. Protein percentage was stable during the first part of maturation and then fell gradually during the latter part of migration and spawning. Although the limited data for the 1957 Horsefly and Late Stuart sockeye migrations are not presented graphically, the percentage composition of eviscerated fish fell very close to the values shown in FIGURES 6 and 7. Pitt sockeye, although of a short migration race, also showed no significant deviations from the three sockeye races studied in detail. While the paths followed by constituent concentrations were along a common trend, percentages often were not similar at the same sampling station for the same race in different years.

TABLE 16—Mean percentages of protein, fat, and water in samples of eviscerated Adams River sockeye in 1958 by sex and location. Samples comprise 18 or more fish for each sex at each station.

| | PROTEIN | | | | | | | |
| | Males | | | | Females | | | |
Station	Early	Peak	Late	Very Late	Early	Peak	Late	Very Late
Lummi Island	—	20.7	—	—	—	19.7	—	—
Albion	19.7	19.6	18.5	17.5	19.0	19.2	18.8	17.6
Hell's Gate	—	19.9	—	—	—	19.4	—	—
Thompson R. Canyon	—	—	—	18.6	—	—	—	18.7
Adams R. Spawning Grounds: Arrival	18.0	17.3	16.3	—	18.5	17.6	17.6	—
Live, Spent	—	16.5	—	—	—	17.3	—	—
Dead, Spent	—	14.8	—	—	—	14.9	—	—
Dead, Unspawned	—	—	—	16.0	—	—	—	15.8
	FAT							
Lummi Island	—	11.6	—	—	—	11.9	—	—
Albion	9.4	8.4	5.8	5.3	9.4	9.3	5.7	5.2
Hell's Gate	—	6.6	—	—	—	6.3	—	—
Thompson R. Canyon	—	—	—	2.9	—	—	—	2.6
Adams R. Spawning Grounds: Arrival	3.9	3.8	2.4	—	3.8	3.5	2.2	—
Live, Spent	—	1.1	—	—	—	1.7	—	—
Dead, Spent	—	1.3	—	—	—	1.4	—	—
Dead, Unspawned	—	—	—	1.5	—	—	—	1.6
	WATER							
Lummi Island	—	65.7	—	—	—	65.3	—	—
Albion	69.5	70.7	73.5	74.3	70.0	70.2	72.1	74.5
Hell's Gate	—	72.2	—	—	—	73.0	—	—
Thompson R. Canyon	—	—	—	77.2	—	—	—	75.2
Adams R. Spawning Grounds: Arrival	76.7	76.3	79.4	—	75.9	76.6	77.6	—
Live, Spent	—	81.6	—	—	—	79.8	—	—
Dead, Spent	—	82.4	—	—	—	82.3	—	—
Dead, Unspawned	—	—	—	81.2	—	—	—	81.4

A slight difference in composition between sexes was evident (FIGURES 6 and 7). Females began migration with slightly higher fat percentages and slightly less water percentages than males. Females also ended their lives with a lower proportion of fat and protein, and the final percentage of water was slightly higher in the females than in males.

Although mean percentage of constituents in eviscerated fish by race followed similar paths (FIGURES 6 and 7), there were racial differences in composition at equivalent distances caused by different schedules of migration (FIGURE 9). Percentage fat (used as an example) for runs of the six sockeye races studied showed that Adams River and Pitt River sockeye had lower fat content than the other two races at equivalent distances. The delay of Adams sockeye off the Fraser River mouth is shown as a vertical section (position estimated) near the seaward end of the fat trend line, and is a racial character not usually shared by the other races studied. Rate of change of fat percentage by distance was similar during migration for the three races with long migrations that were sampled extensively. The single samplings of the Horsefly and Late Stuart
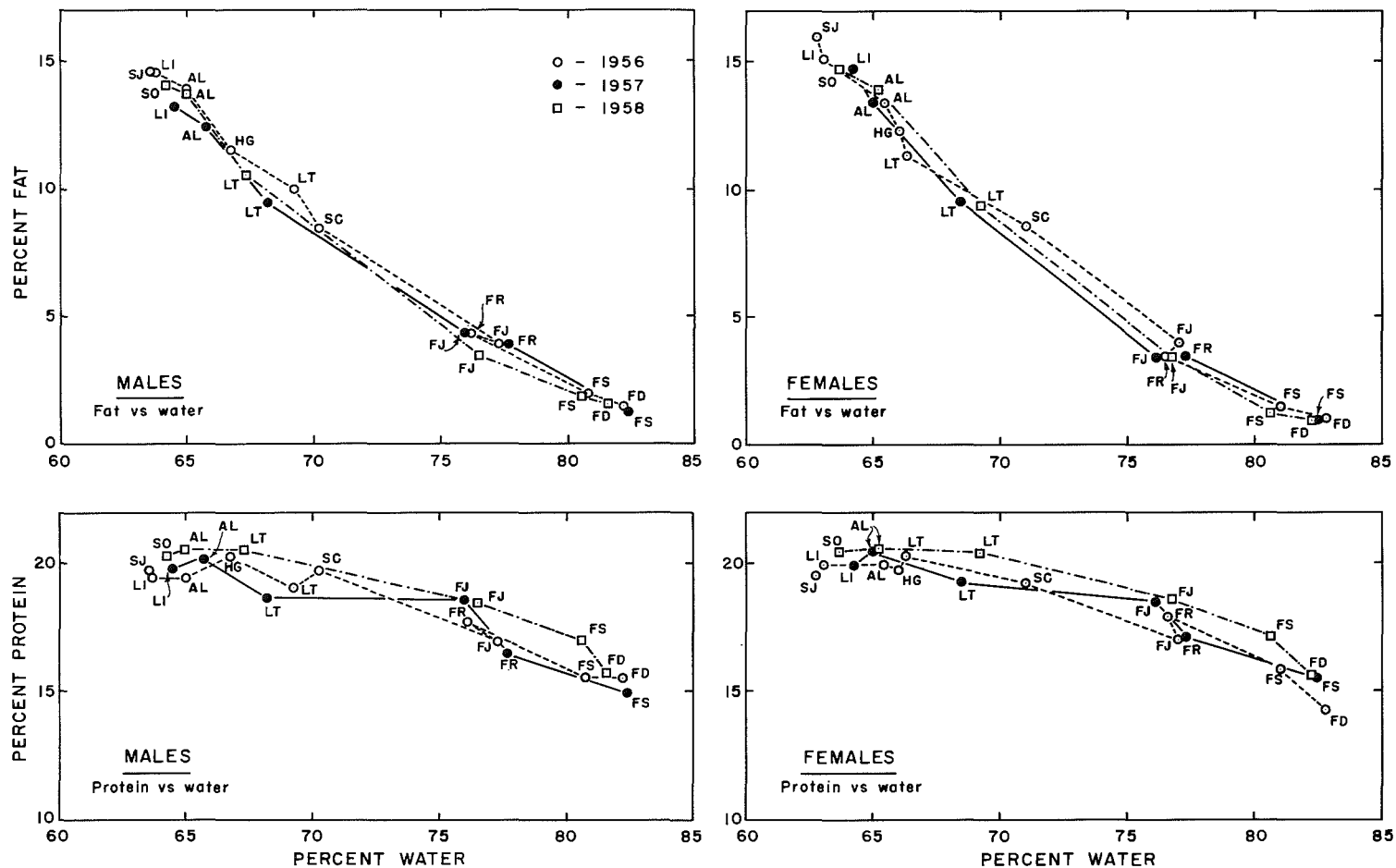
FIGURE 6—Mean fat and protein percentages plotted on mean percentage of water for eviscerated sockeye during migration and spawning of the Early Stuart race.
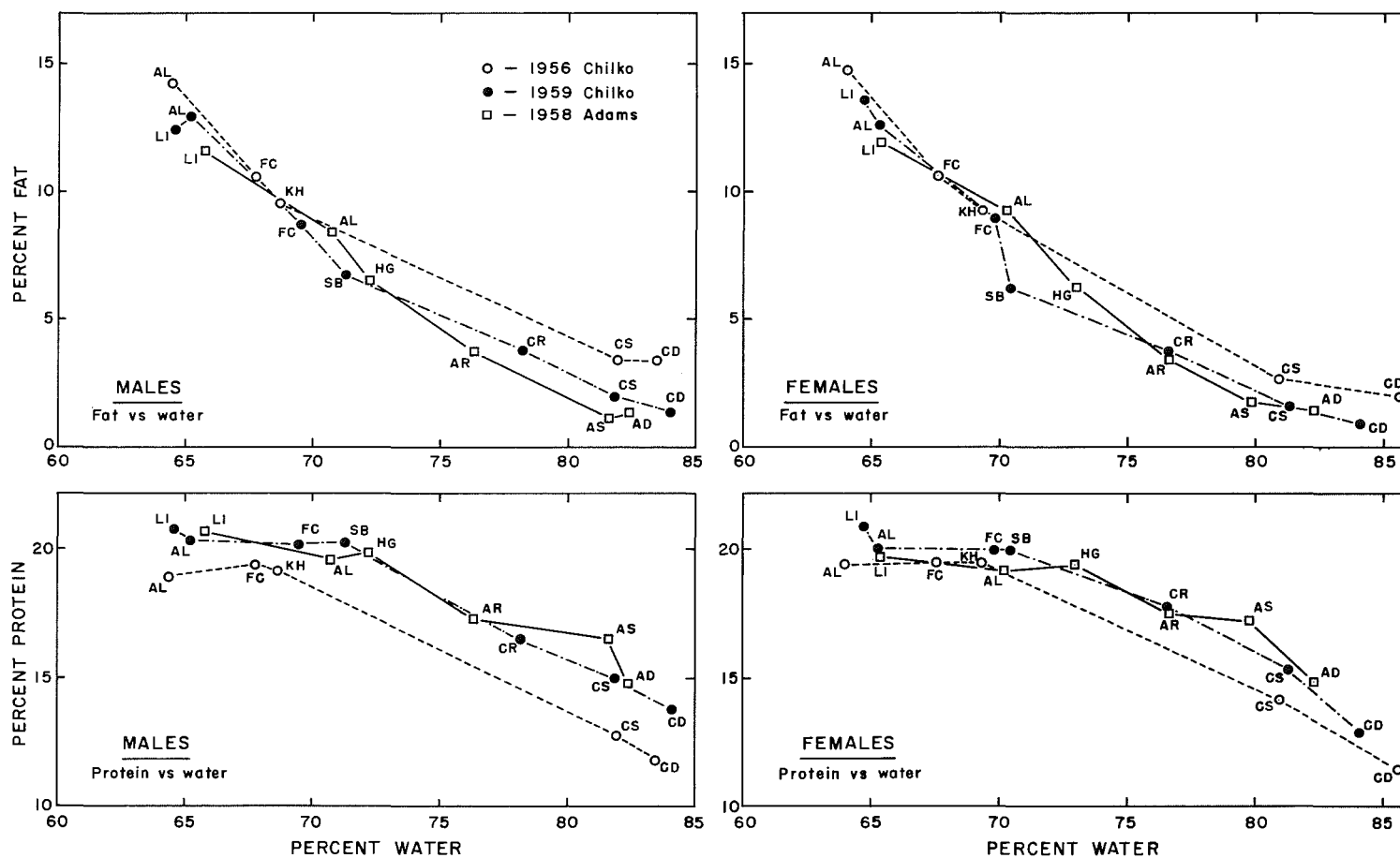
FIGURE 7—Mean fat and protein percentages plotted on mean percentage of water for eviscerated sockeye during migration and spawning of the Chilko and Adams races.

migrations indicate that these races probably followed about the same fat use schedule as the Early Stuart race. There is a statistically significant difference between fat percentages of the 1956 and 1959 Chilko migrations.

There were generally consistent changes in mean composition of eviscerated sockeye between different segments of a run at the same location (TABLES 13 and 16). Of 20 comparisons between successive adjacent samples at the same station, 16 showed a decrease in fat percentage, 3 showed an increase, and one showed no change. Percentage water showed the opposite trend, increasing in successive samples at the same sampling station. In the same 20 comparisons, water proportion showed an increase in 17 cases and a decrease in 3 instances. The probability of these frequencies occurring in samples from a
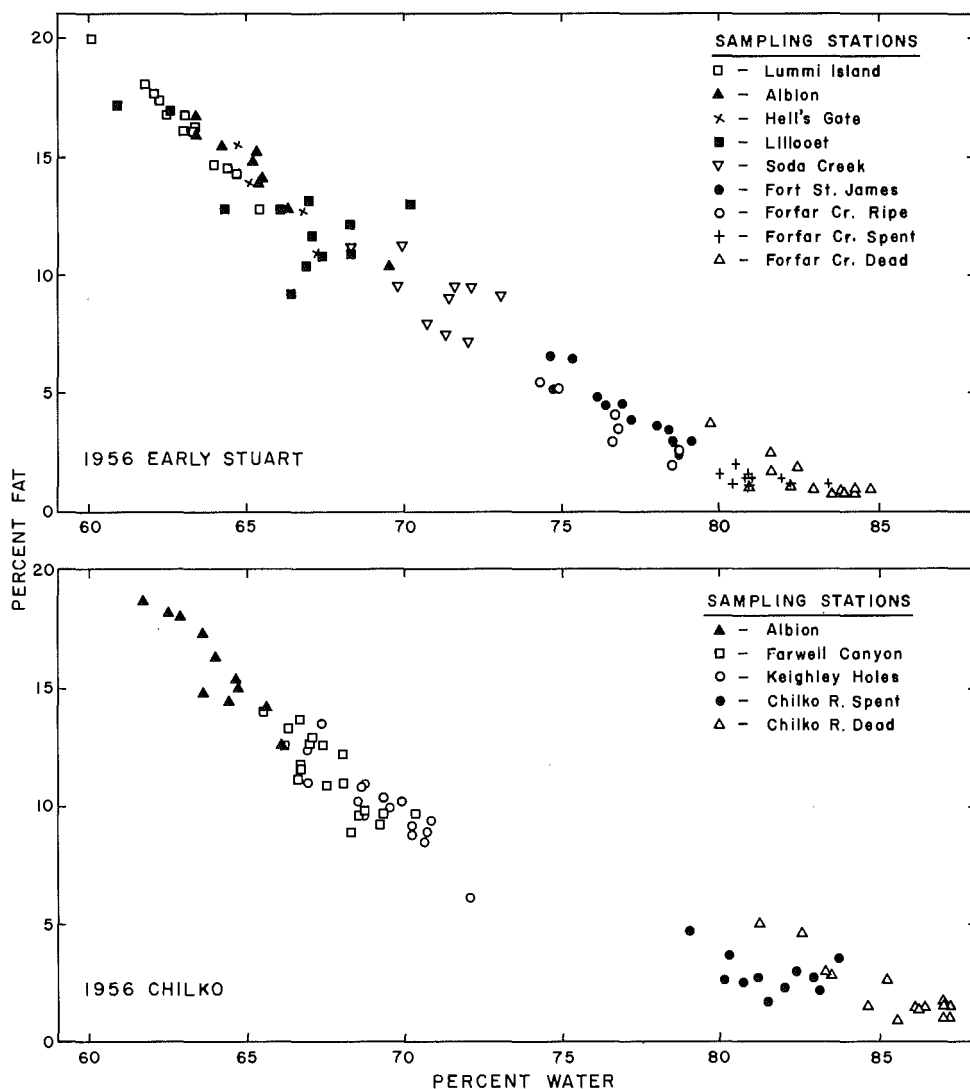

FIGURE 8—Relationship between percentage fat and water in individual eviscerated sockeye females of peak samples from the 1956 Early Stuart run (upper graph) and the 1956 Chilko run (lower graph).
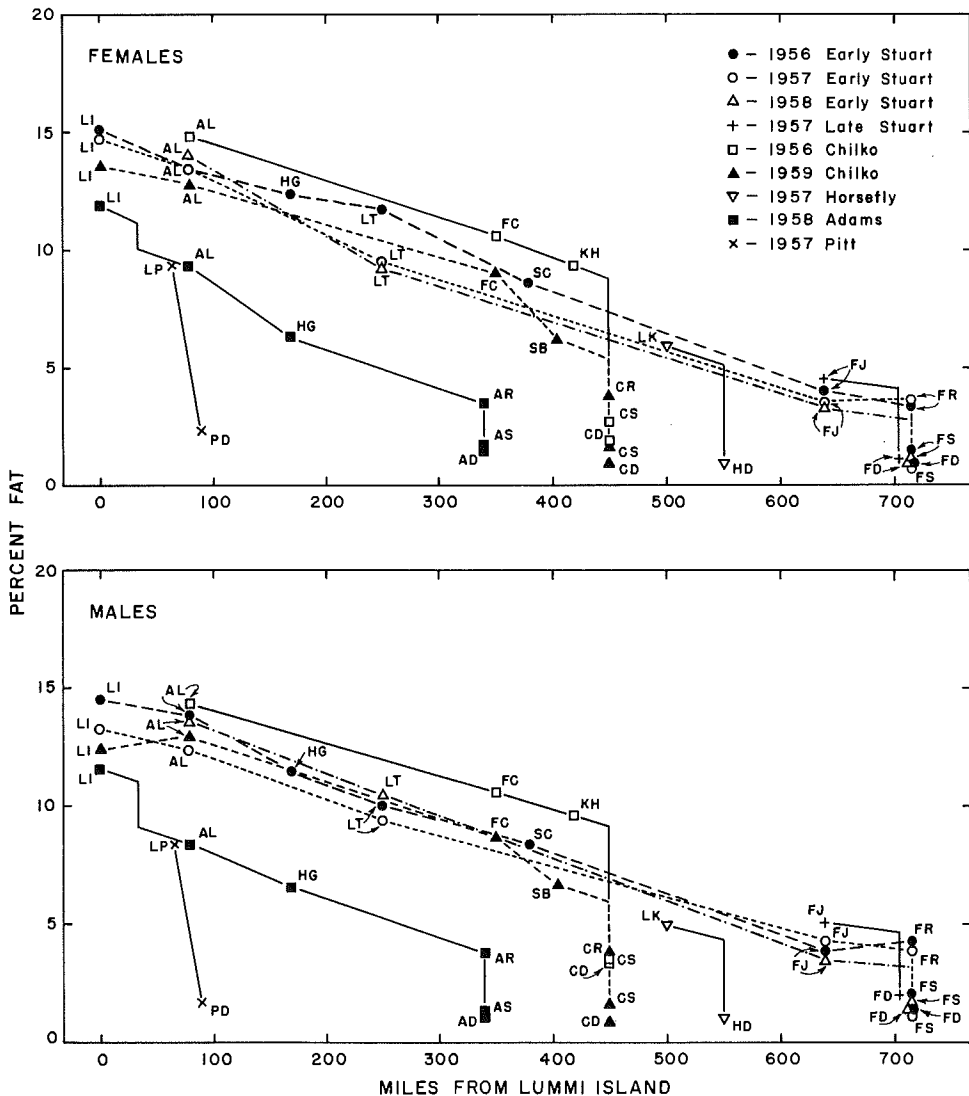
FIGURE 9—Mean percentage fat in samples of eviscerated male and female sockeye of the six races studied vs. the distance of the sampling station from Lummi Island. Peak samples except as noted in TABLES 2 and 3.

migration with no changes in fat or water percentage at a single sampling station is less than 0.01. Protein showed a less consistent change. In the 20 comparisons, 12 showed a decrease and 7 an increase in protein percentage.

Sockeye spawning, which occurs between arrival (or ripe) and spent samples also appeared to follow the composition differences between segments of the run (TABLES 13 and 16). This is most evident in late segment ripe and spent samples, which had generally lower fat and higher water percentages than equivalent early or peak samples within the same sex. Early samples of ripe and spent sockeye showed less consistent differences from peak samples.

TABLE 17—Correlations between percent protein, fat and water within samples of 1956 Early Stuart sockeye, individual fish determinations.

EVISCERATED MALES

Location of Sample	No. of Fish	Correlation Coefficients		
		Protein vs Fat	Protein vs Water	Fat vs Water
Lummi Island	7	-0.267	0.161	-0.897**
Albion	9	-0.423	0.367	-0.883**
Hell's Gate	9	-0.540	0.443	-0.934**
Lillooet	7	-0.311	-0.392	-0.633
Soda Creek	4	-0.426	-0.713	-0.311
Ft. St. James	9	0.669*	-0.790*	-0.891**
Forfar Creek:				
Arrival	7	0.144	-0.525	-0.887**
Spent	12	0.536	-0.760**	-0.907**
Fresh Dead	10	0.009	-0.483	-0.478

EVISCERATED FEMALES

Lummi Island	13	-0.773**	0.783**	-0.988**
Albion	9	-0.103	0.136	-0.969**
Hell's Gate	4	-0.216	0.223	-0.936
Lillooet	13	-0.044	-0.561*	-0.704**
Soda Creek	10	-0.298	-0.260	-0.583
Ft. St. James	13	0.642*	-0.817**	-0.935**
Forfar Creek:				
Arrival	7	0.673	-0.790*	-0.945**
Spent	12	0.315	-0.615*	-0.706**
Fresh Dead	12	0.379	-0.813**	-0.753**

* Significant at the 5% probability level.
** Significant at the 1% probability level.

TABLE 18—Correlations between percent protein, fat and water within samples of 1956 Chilko sockeye, individual fish determinations.

EVISCERATED MALES

Location of Sample	No. of Fish	Correlation Coefficients		
		Protein vs Fat	Protein vs Water	Fat vs Water
Albion	13	-0.625*	0.502	-0.901**
Farwell Canyon	9	-0.432	0.174	-0.904**
Keighley Holes	13	-0.306	0.302	-0.971**
Chilko Spawning Grounds:				
Spent	15	0.147	-0.761**	-0.643**
Fresh Dead	14	-0.183	-0.671**	-0.506

EVISCERATED FEMALES

Albion	11	-0.484	0.475	-0.921**
Farwell Canyon	19	-0.345	0.016	-0.816**
Keighley Holes	16	-0.341	0.002	-0.876**
Chilko Spawning Grounds:				
Spent	11	-0.042	-0.493	-0.394
Fresh Dead	15	0.552*	-0.726**	-0.895**

* Significant at the 5% probability level.
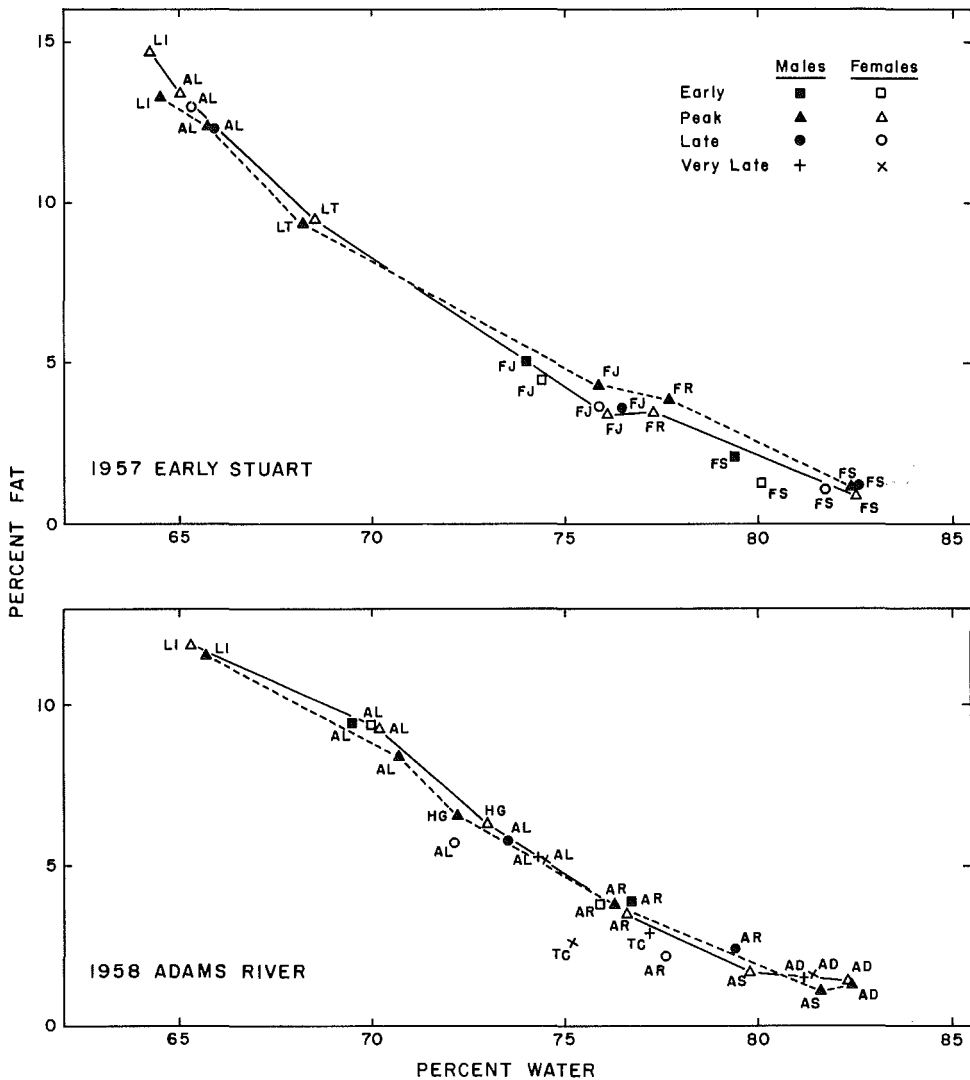** Significant at the 1% probability level.

FIGURE 10—Relationship between mean percentages of fat and water in eviscerated fish from early, peak, late, and very late samples from the 1957 Early Stuart and 1958 Adams River sockeye runs.

Although the constituent composition of successive samples of eviscerated sockeye at a given sampling station was different, early and late segment samples followed a similar relation to percent water as the samples from the peak of the run (FIGURE 10).

Because sockeye of successive segments of a run decreased in weight (TABLE 10) while length did not decrease (TABLE 8), and because mean composition of eviscerated fish changed from early to late segments (TABLE 16), the possibility that composition might vary with condition factor was examined. Correlation analysis of condition factor versus fat percentage in individual eviscerated fish showed a positive relationship in most of the 26 samples of 1956 Early Stuart and Chilko sockeye having seven or more fish per sample (FIGURE 11). The combined correlation coefficient (0.317) for fat percentage
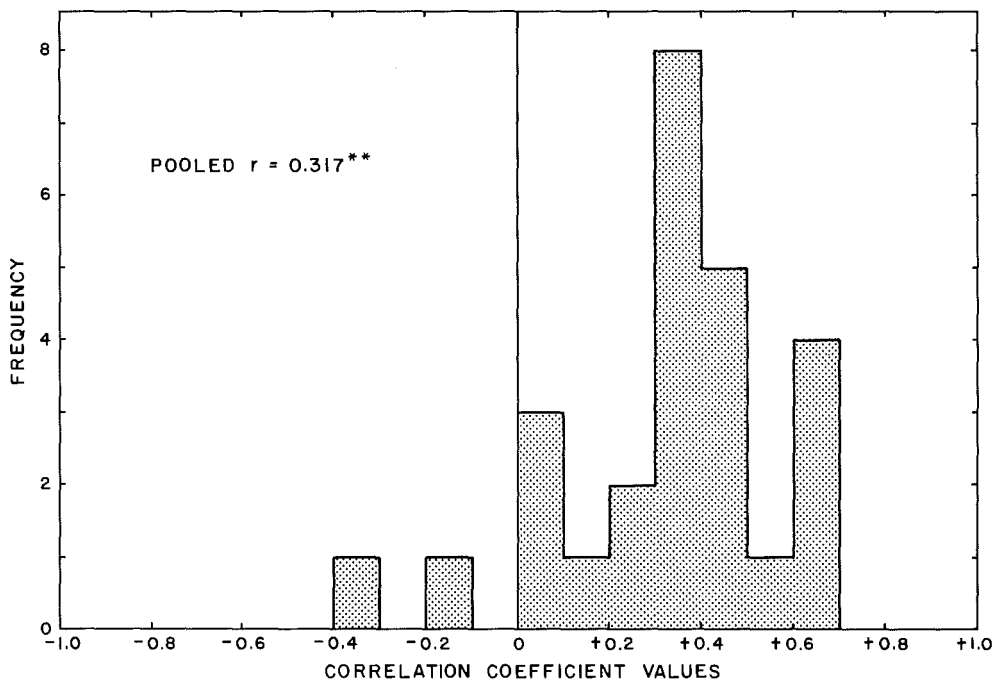
FIGURE 11—Values of 26 correlation coefficients between percentage fat and condition factor in data for individual eviscerated fish in samples of Early Stuart and Chilko sockeye taken in 1956.

(analysis of covariance, Snedecor 1956) is highly significant although not of large value. Because fat and water percentages in individual eviscerated fish have an inverse relationship (TABLES 17 and 18), percent water will be negatively correlated with condition.

Fillets and Trimmings

The composition of fillets and of trimmings from the 1958 Early Stuart peak samples of male sockeye were different at the same sampling station (FIGURE 12). The structural role of trimmings was indicated by the protein determinations. Percentage protein in trimmings remained nearly constant or possibly decreased slightly during migration and spawning, while protein in fillets fell by a third during the latter part of life. Trimmings appeared to have a larger mineral or ash content than fillets because the sum of mean protein, fat and water percentages in trimmings in all samples totaled less than the sum for fillets. Presumably this consistent difference arose from materials included in bones and fin rays.

No essential differences were noted between the 1958 Early Stuart run and the 1957 Early Stuart or 1958 Adams run in the changes followed by fat, protein and water percentages. Also, no consistent differences between sexes were found in these three runs. Too few samples of sockeye from successive segments of a run passing a given sampling station were dissected into fillets and trimmings to demonstrate consistent differences between segments.
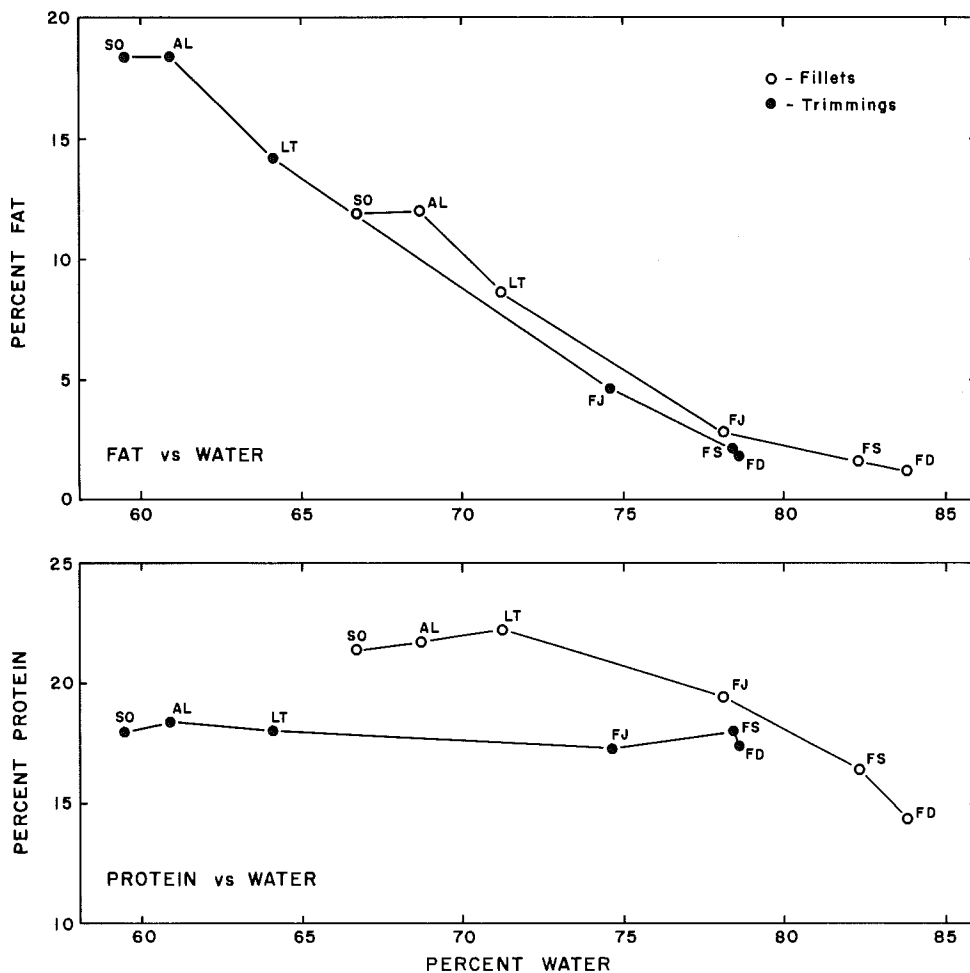
FIGURE 12—Mean percentages of fat and protein related to mean percentage water in fillets and trimmings of samples of male sockeye of the 1958 Early Stuart run. Peak samples except as noted in TABLE 2.

Viscera Excluding Gonads

Viscera are the internal organs lying in the body cavity, and as defined here, exclude the gonads. Viscera provide a small store of energy for the sockeye whereas the gonads take up material that could otherwise be used for energy. Composition data for viscera was available for the samples of 1957, 1958 and 1959, but not for 1956 samples.

Composition of viscera (FIGURE 13) was similar to that of the eviscerated fish. The fat versus water percentages for Chilko sockeye (FIGURE 13) fell approximately along the right hand end of the same curves in FIGURE 7. Similarly, the protein versus water percentages curve of FIGURE 13 approximated the right hand end of the equivalent curves for eviscerated fish. The viscera had lower fat and protein concentrations, and higher water proportion than the eviscerated fish at the same sampling stations.

Most racial comparisons of viscera composition showed no obvious differences from the data for the 1959 Chilko sockeye shown in FIGURE 13. Races sampled at or near entry into fresh water had visceral composition similar to the 1959 Chilko sockeye at Lummi Island or Albion, with the exception of Pitt and Adams sockeye. The Adams fish apparently entered the estuary with viscera in a more mature condition, since their viscera in the Lummi Island samples were equivalent in composition to Chilko viscera at Farwell Canyon.
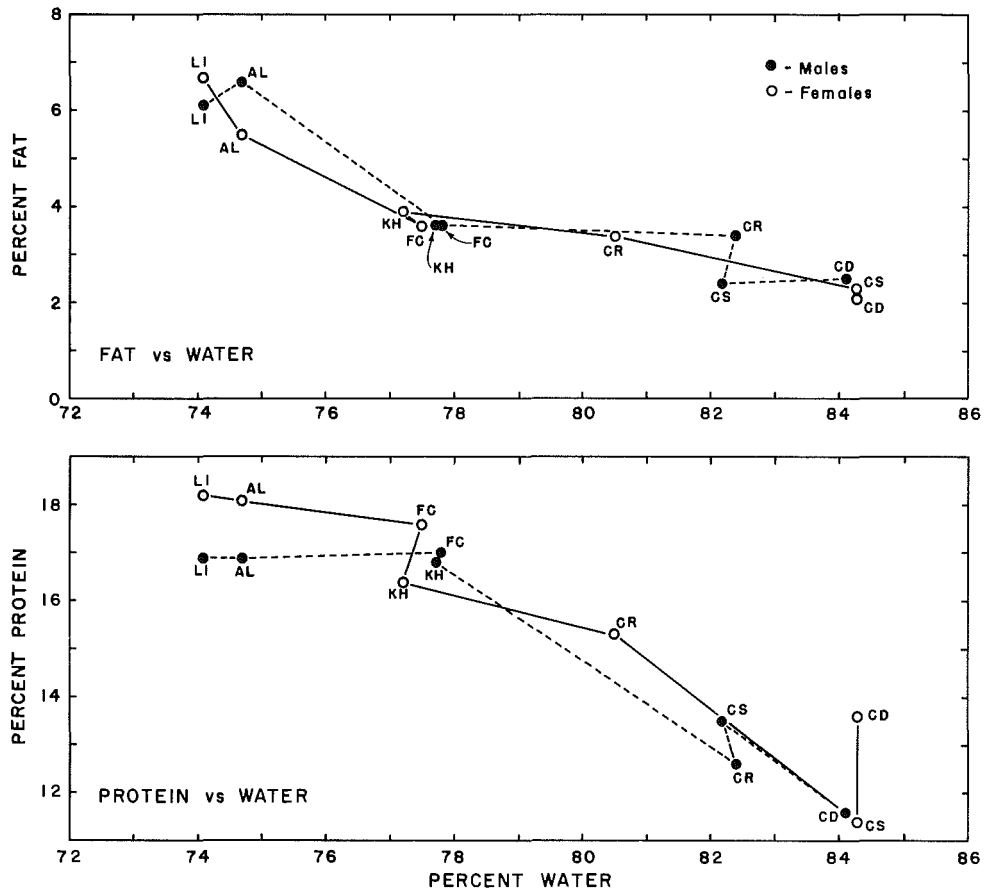

FIGURE 13—Mean percentages of fat and protein related to mean percentage of water in viscera excluding gonads from samples of the 1959 Chilko sockeye run. Peak samples except as noted in TABLE 3.

Constituent percentages in viscera showed some evidence of increasing maturity from earlier to later segments of a run at a single sampling station. The percentage of water showed a consistent increase from earlier to later segments of a run, but fat and protein did not show consistent changes.

Gonads

Gonad composition data for individual fish in 1956 are not available because gonads were combined with viscera in that year. Composition of gonads in the three succeeding

years was obtained only for combinations of these organs from several fish, therefore mean composition only was examined.

Percentages of fat, protein and water were markedly different between testes and ovaries (FIGURE 14). Testes had a greater water concentration and lower fat proportion than ovaries. Fat percentages in testes remained almost constant at a level near the minimum for any of the organs studied. Ovaries had higher percentages of protein at a given location than other organs or tissues analysed.
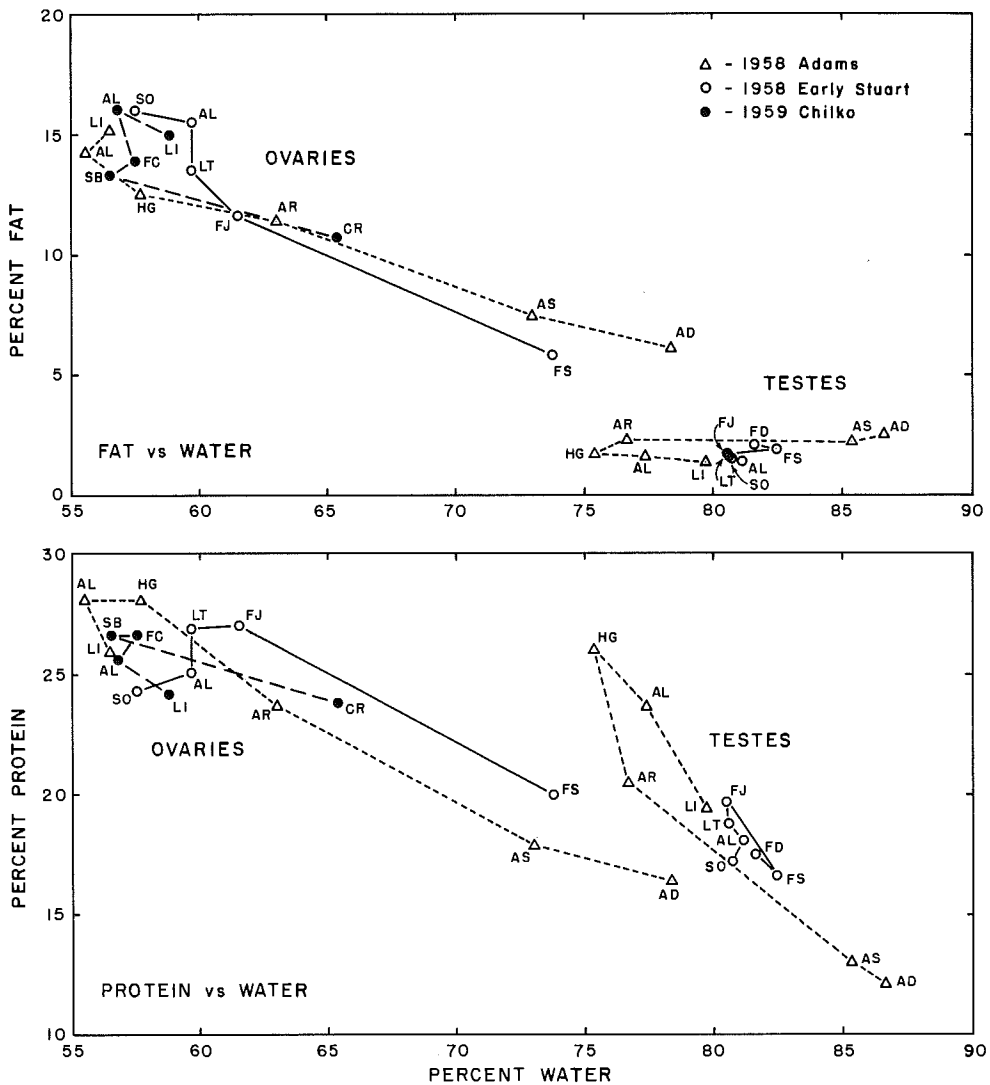

FIGURE 14—Mean percentages of fat and protein for gonads related to mean percentage water in samples from Fraser River sockeye. Ovary composition from Early Stuart and Adams runs of 1958 and Chilko run of 1959. Testicular composition for Early Stuart and Adams runs of 1958 only. Peak samples except as noted in TABLES 2 and 3.

None of the variations in ovary composition could be ascribed to racial differences (FIGURE 14). Constituent percentages in ovaries varied irregularly through most of maturation. As spawning neared, percentages of fat and protein fell and water percentage rose. Composition of ovary remnants in spent and dead females varied and tended toward that of viscera less gonads. Composition of ovaries of the 1957 Early Stuart run did not differ significantly from the runs depicted in FIGURE 14. The Pitt, Horsefly and Late Stuart sockeye runs, which were sampled at only two stations, were likewise similar in ovary composition to the races shown in FIGURE 14.

Testicular development followed a peculiar reflex path of protein and water percentage (FIGURE 14). During the first part of migration, protein percentage rose and water proportion decreased accordingly, since fat remained essentially constant. During the last stages of migration this process was reversed and continued past spawning.

Mean constituent percentages in testes from peak samples showed apparent racial differences (FIGURE 14). Percentages of protein and water in testes of Adams sockeye varied over a much wider range than those in Early Stuart males. Testicular composition in the 1957 Early Stuart run was much like that of the 1958 Early Stuart males. Constituent percentages in testes of the 1959 Chilko samples also fell into the trend of variation of Adams testes. However, the range of variation of protein and water was intermediate between that of Adams and of Early Stuart fish. The Pitt, Horsefly and Late Stuart runs appeared to follow a schedule of testicular composition more like that of Adams or Chilko sockeye than like the Early Stuart runs. The reason for the racial differences is not apparent.

Percentage composition data for ovaries and testes for the various segments of the run at the same station did not show consistent trends.

Summary

Changing percentages of fat, protein and water in sample means of eviscerated fish of all races studied followed similar courses during migration and spawning in the eviscerated fish, and in the two main subdivisions, fillets and trimmings. All races studied entered the estuary with about the same percentages of fat and protein, and spawning occurred in a narrow range of constituent percentages. Water percentage in eviscerated fish provided a useful index of maturation.

Slight differences in composition were noted between sexes in eviscerated fish, and racial differences occurred in composition of testes, but not in ovaries or other viscera. Sockeye in a later segment of a run appeared to be more mature than fish in a preceding segment based on constituent percentages in eviscerated fish. Analyses of individual eviscerated fish showed a significant positive correlation between condition factor and percent fat.

ENERGY EXPENDITURE

The use of body energy stores in a migrating sockeye after it stops feeding follows several courses. Protein and fat are consumed for swimming or metabolic energy (TABLE 19). Part of the original stores of protein and fat become incorporated into the gonads with an unknown efficiency (TABLE 20). Calculated energy expenditure for migration therefore contains swimming energy, basic metabolic energy, and the energy required to transfer material to the gonads.

TABLE 19—Mean amounts (gm) of fat and protein used in migration by three sockeye races.

			Stations or Stages			
Race	Year	Constituent	Lummi Id. to Albion	Albion to Arrival	Albion to Dead	Arrival to Dead
MALES						
Early Stuart	1956	Fat	14	240	—	84
	1957	Fat	25	190	—	—
	1958	Fat	—	—	298	—
	1956	Protein	-3	23	—	150
	1957	Protein	-3	69	—	—
	1958	Protein	—	—	175	—
Chilko	1956	Fat	—	—	252	—
	1959	Fat	-9	199	—	55
	1956	Protein	—	—	157	—
	1959	Protein	15	97	—	99
Adams	1958	Fat	94	111	—	76
	1958	Protein	66	10	—	145
FEMALES						
Early Stuart	1956	Fat	28	237	—	39
	1957	Fat	28	212	—	—
	1958	Fat	—	—	273	—
	1956	Protein	-14	123	—	99
	1957	Protein	-20	106	—	—
	1958	Protein	—	—	196	—
Chilko	1956	Fat	—	—	305	—
	1959	Fat	9	178	—	49
	1956	Protein	—	—	241	—
	1959	Protein	3	80	—	115
Adams	1958	Fat	43	124	—	45
	1958	Protein	-20	54	—	84

Between the estuary or river mouth and arrival at the spawning ground, the gonads take up fat and protein, which are not available for migrational use (TABLE 20). Between spawning ground arrival and death, testes shrink and ovaries all but disappear. Loss of fat and protein from the gonads between spawning ground arrival and death was assumed to be entirely due to expulsion of sex products. Any error from resorption of fat and protein from the testes is minor, since the maximum decrease in testicular constituents was 15 grams of protein and a gram of fat (Adams males), most of which must have gone into milt. Ovary remnants were too small to provide significant energy amounts.

Energy derived from the eviscerated body of the sockeye forms more than 95% of the total energy put into migration and gonad enlargement (TABLE 21). The viscera excluding gonads provided more protein than fat due to the low fat content of viscera, but visceral contribution to total protein expenditure was less than a third that of the eviscerated body in the most extreme case (Adams males). The eviscerated body provided more than 97% of energy once the fish reach the spawning grounds.

TABLE 20—Mean amounts (gm) of fat and protein used in gonad enlargement, or lost as sex products (last column) by three sockeye races.

			Stations or Stages		
			Lummi Id.	Albion	Arrival
Race	Year	Constituent	to Albion	to Arrival	to Dead
MALES					
Early Stuart	1956	Fat	0	1	1
	1957	Fat	0	1	—
	1958	Fat	—	1	1
	1956	Protein	1	6	12
	1957	Protein	2	5	—
	1958	Protein	—	6	11
Chilko	1956	Fat	—	1	1
	1959	Fat	0	0	1
	1956	Protein	—	3	12
	1959	Protein	-1	1	11
Adams	1958	Fat	0	1	1
	1958	Protein	1	-1	15
FEMALES					
Early Stuart	1956	Fat	3	19	35
	1957	Fat	3	18	—
	1958	Fat	—	19	35
	1956	Protein	4	51	76
	1957	Protein	5	47	—
	1958	Protein	—	45	71
Chilko	1956	Fat	—	13	30
	1959	Fat	4	10	28
	1956	Protein	—	41	65
	1959	Protein	5	34	62
Adams	1958	Fat	17	5	46
	1958	Protein	40	16	95

Not all fat and protein is transformed to energy (TABLE 22). Between 40% and 70% of the protein and from 5% to 26% of the fat was retained in dead sockeye. Males used less of the fat and protein complements than females. The 1956 Chilko run also used a smaller portion of its fat complement, which was higher throughout the migration (FIGURE 9).

Conversion of constituent amounts in TABLE 19 to energy units for fat and protein separately demonstrates that fat provided from 72.5% to as high as 81% of the energy expenditures for river migration and spawning (TABLE 23). Predominance of fat as an energy source results largely from its use throughout migration whereas protein use was minor until migration was almost completed (FIGURES 6 and 7).

Males expended more total energy than females with the exception of the 1956 Chilko run (TABLE 23). This was due to the larger size of males which was not completely offset by the generally greater percentage decrease in energy stores in females (TABLES 13, 14 and 15).

The data indicate that transfer of constituents within energy stores occurred to a small extent between fillets and trimmings (TABLE 24). The calculated protein content of

TABLE 21—Total amounts (gm) of fat and protein contributed by eviscerated body and by viscera excluding gonads to (A) migration and gonad enlargement and to (B) spawning activity, plus the energy equivalent (kcal) of these amounts.

A — ALBION TO RIPE

| | | | Constituent Use (gm) | | | | Equivalent Energy (kcal) | | |
| | | | Eviscerated Body | | Viscera Exclud. Gonads | | Eviscer. | Viscera Exclud. | % from Eviscer. |
Race	Year	Sex	Fat	Protein	Fat	Protein	Body	Gonads	Body
Early Stuart	1956	M	238	26	3	3	2,320	40	98.3
Early Stuart	1956	F	252	204	4	10	3,180	78	97.6
Early Stuart	1957	M	186	62	5	12	1,984	96	95.4
Early Stuart	1957	F	225	137	5	16	2,654	112	96.0
Chilko	1959	M	195	92	4	6	2,191	62	97.2
Chilko	1959	F	184	106	4	8	2,146	70	96.8
Adams	1958	M	112	7	0	2	1,070	8	99.3
Adams	1958	F	127	60	2	10	1,427	60	96.0

B — RIPE TO DEAD

Early Stuart	1956	M	83	144	1	6	1,362	34	97.6
Early Stuart	1956	F	39	98	0	1	764	4	99.5
Chilko	1959	M	54	97	1	2	900	18	98.0
Chilko	1959	F	48	114	1	1	914	13	98.6
Adams	1958	M	75	141	1	4	1,276	26	98.0
Adams	1958	F	44	86	1	-2	762	1	99.9

TABLE 22—Mean energy stores in the whole sockeye excluding gonads, at Albion and dead on the spawning grounds.

| | | | Albion | | Dead at Spawning Grounds | | | |
Race	Year	Sex	Fat (gm)	Protein (gm)	Fat (gm)	% Fat Remaining	Protein (gm)	% Protein Remaining
Early Stuart	1956	M	358	516	33	9.2	337	65.3
Early Stuart	1956	F	313	478	18	5.8	205	42.9
Early Stuart	1958	M	329	489	30	9.1	308	63.0
Early Stuart	1958	F	307	464	15	4.9	223	48.1
Chilko	1956	M	340	465	87	25.6	305	65.6
Chilko	1956	F	349	470	31	8.9	188	40.0
Chilko	1959	M	279	445	25	9.0	248	55.7
Chilko	1959	F	250	405	13	5.2	176	43.5
Adams	1958	M	221	511	33	14.9	357	69.9
Adams	1958	F	200	445	26	13.0	271	60.9

TABLE 23—Energy amounts (kcal) derived from fat and protein for river migration (gonad enlargement omitted) and spawning (egg or milt loss excluded), calculated separately for each constituent.

Race	Year	Sex	Fat		Protein		Total
			Energy	%	Energy	%	Energy
Early Stuart	1956	M	3,013	81.0	709	19.0	3,722
Early Stuart	1957	M	2,492*	75.2	820*	24.8	3,312*
Early Stuart	1958	M	2,771	79.4	717	20.6	3,488
Chilko	1956	M	2,344	78.4	644	21.6	2.988
Chilko	1959	M	2,362	74.6	804	25.4	3,166
Adams	1958	M	1,739	73.3	635	26.7	2,374
Early Stuart	1956	F	2,567	73.8	910	26.2	3,477
Early Stuart	1957	F	2,409*	75.7	775*	24.3	3,184*
Early Stuart	1958	F	2,539	75.9	804	24.1	3,343
Chilko	1956	F	2,837	74.2	988	25.8	3,825
Chilko	1959	F	2,111	72.5	799	27.5	2,910
Adams	1958	F	1,739	75.4	566	24.6	2,305

* Values for 1957 Early Stuart on spawning grounds estimated.

trimmings increased at the expense of fillet protein apparently at least until the spawning ground was reached. This change was much larger in males than in females, suggesting that an excess of protein is taken up for secondary sexual development in males whereas in females most of this protein is required for ovary development.

Variation in energy use per kg of sockeye between sexes and years was generally large (TABLES 25 and 26). Females used more kcal per kg per mile and per day between Albion and the spawning grounds than males, except for 1959 Chilko. Chilko sockeye expended more kcal/kg per mile of river migration, while Early Stuart sockeye used more kcal/kg per day. Early Stuart sockeye used more kcal/kg per day during spawning, possibly because the time between spawning and death was shorter than for the other two races. This suggests that the daily use of energy decreases rapidly after spawning is completed.

Summary

Energy expenditure was determined for total river migration in three sockeye races. Separation of energy for basal metabolism and for transfer of constituents to the gonads was not attempted, but constituents and energy acquired by the gonads prior to spawning were differentiated.

The eviscerated body of the sockeye provided more than 95% of the total energy expenditure during migration and spawning. Between 40% and 70% of the protein and 5% to 26% of the fat was retained in dead sockeye. Males used less of their constituent complements than females. Females transferred protein from the fillets to the ovaries whereas males transferred little protein to the testes but more to the trimmings. Females generally used more energy per kg of fish during river migration, and races differed in specific energy use per mile or per day of migration.

TABLE 24—Mean total weight (gm) and mean weights of fat, protein and water in fillets and trimmings, and of protein in gonads in samples of sockeye of the 1957 and 1958 Early Stuart run, and of the 1958 Adams run. Peak samples except as noted in TABLE 2.

| | | MALES | | | | | | | | Gonad Protein |
| | | Fillets | | | | Trimmings | | | | |
Race/Year	Station	Total	Fat	Prot.	H₂0	Total	Fat	Prot.	H₂0	
Early Stuart	Albion	1,460	137	315	1,000	778	142	138	471	11
1957	Lillooet	1,302	66	267	921	871	137	138	562	14
	Ft. St. James	1,290	37	253	997	901	56	155	667	17
	Spent	1,112	11	156	936	837	13	134	670	—
Early Stuart	Sooke	1,492	178	319	995	734	135	132	437	8
1958	Albion	1,510	181*	328*	1,037*	755	139	139	460	10
	Lillooet	1,497	129*	332*	1,066*	825	117	149	529	12
	Ft. St. James	1,382	39*	268*	1,079*	955	44	165	712	13
	Spent	1,169	19*	192*	962*	856	18	154	671	—
Adams	Lummi	1,699	160	369	1,160	957	148	182	585	18
1958	Albion	1,509	100*	302*	1,111*	979	117	185	652	19
	Hell's Gate	1,537	77	309	1,147	1,069	94	207	734	19
	Spent	1,355	15	202	1,138	1,056	12	197	816	—
		FEMALES								
Early Stuart	Albion	1,447	149	315	982	713	138	126	424	24
1957	Lillooet	1,135	64	239	806	765	116	126	496	37
	Ft. St. James	1,106	25	211	862	722	36	130	532	68
	Spent	809	6	116	684	636	6	106	509	—
Early Stuart	Sooke	1,420	175	307	936	664	130	118	393	21
1958	Albion	1,449	174*	313*	984*	695	126	126	436	26
	Lillooet	1,340	95*	289*	966*	703	96	128	454	46
	Ft. St. James	1,107	29*	211*	873*	723	33	130	536	78
	Spent	872	10*	147*	724*	664	9	117	522	—
Adams	Lummi	1,405	133	281	961	733	121	139	438	42
1958	Albion	1,320	92	256	969	773	103	145	500	82
	Hell's Gate	1,154	52	225	875	786	71	152	540	102
	Spent	1,043	14	167	857	762	16	145	583	—

* Constituents total more than total weight due to slight errors in constituent analyses.

DISCUSSION

Sockeye as a species are adapted to a long non-feeding migration, either by distance or time, using stored energy. This characteristic is shared with other species of Pacific salmon (genus *Oncorhynchus*), and with steelhead trout and Atlantic salmon (both genus *Salmo*). The nature of the migration and spawning fast, with its complex use of energy storing materials, has been gradually disclosed over the last 100 years.

Previous Work on Salmon

In the years 1877 to 1880, Miescher-Rüsch (1880) examined size and chemical constituents of the Atlantic salmon of the Rhine River in the vicinity of the spawning grounds in Switzerland, about 700 miles from the sea. Although he did not use Kjeldahl

protein analysis, and he determined composition of body muscle only from a selected part on the back, he found constituent changes with maturation similar to those in sockeye. He concluded that material required for gonad growth was taken from the body muscle.

Atlantic salmon from the east coast of Scotland were carefully examined by Paton (1898) and collaborators. Paton recognized two types of salmon, an early migrating, smaller sized variety which spawned in or near the headwaters of the rivers, and a late migrating stock of larger fish which spawned nearer the coast at a later time. Fat percentage was higher in the early type at the beginning of river migration, whereas protein did not differ between stocks. Progressive decrease in fat and increase in water percentages in body muscle followed a course close to that of sockeye fillets (FIGURE 12), and spawning appeared to occur at 3-4% fat and 75-80% water. Depletion of energy stores thus appeared to be less than for sockeye, probably related to subsequent survival of some spent Atlantic salmon. A large surplus of energy was shown to be expended from fat and protein of body muscles above that necessary for gonad development. This was recognized as necessary to raise the salmon to the elevation of the spawning ground and to "overcome the friction of the stream".

Chinook salmon of the Columbia River, according to data presented by Greene (1926), showed composition changes in muscles and in internal organs similar to sockeye of the Fraser River during the spawning migration. Columbia River chinook salmon of

TABLE 25—Specific energy use in kcal/kg, kcal/kg/mi, and kcal/kg/day during migration and spawning for sockeye of Early Stuart, Chilko and Adams runs.

		MALES			
				Stations or Stages	
Race	Year	Measurement	Lummi Id. to Albion	Albion to Arrival	Arrival to Dead
Early Stuart	1956	kcal/kg	43	829	551
		kcal/kg/mile	0.5	1.4	—
		kcal/kg/day	17	37	79
	1957	kcal/kg	89	818	—
		kcal/kg/mile	1.1	1.3	—
		kcal/kg/day	22	34	—
	1958	kcal/kg	—	881	551
		kcal/kg/mile	—	1.4	—
		kcal/kg/day	—	30	58
Chilko	1956	kcal/kg	—	666	455
		kcal/kg/mile	—	1.8	—
		kcal/kg/day	—	17	30
	1959	kcal/kg	-10	1,004	455
		kcal/kg/mile	-0.1	2.7	—
		kcal/kg/day	-5	25	30
Adams	1958	kcal/kg	407	374	476
		kcal/kg/mile	5.1	1.4	—
		kcal/kg/day	15	21	24

TABLE 26—Specific energy use in kcal/kg, kcal/kg/mile and kcal/kg/day during migration and spawning for sockeye of Early Stuart, Chilko and Adams runs.

| | | | FEMALES | | |
| | | | Stations or Stages | | |
Race	Year	Measurement	Lummi Id. to Albion	Albion to Arrival	Arrival to Dead
Early Stuart	1956	kcal/kg	82	1,190	442
		kcal/kg/mile	1.0	1.9	—
		kcal/kg/day	33	51	63
	1957	kcal/kg	74	1,055	—
		kcal/kg/mile	0.9	1.7	—
		kcal/kg/day	19	44	—
	1958	kcal/kg	—	1,165	442
		kcal/kg/mile	—	1.8	—
		kcal/kg/day	—	39	47
Chilko	1956	kcal/kg	—	1,125	567
		kcal/kg/mile	—	3.0	—
		kcal/kg/day	—	28	38
	1959	kcal/kg	45	978	567
		kcal/kg/mile	0.6	2.6	—
		kcal/kg/day	23	24	38
Adams	1958	kcal/kg	128	553	355
		kcal/kg/mile	1.6	2.1	—
		kcal/kg/day	4.7	31	18

the summer season generally began river migration with a higher fat proportion in muscles and developed larger ovaries in proportion to total weight than Fraser sockeye. Earlier races entering the Columbia River had higher fat content than later races.

Pentegov et al. (1928) investigated the autumn chum salmon of the Amur River over the 700 mile migration from saltwater to spawning grounds. Their data, reviewed by Idler and Clemens (1959) showed considerable similarity to Early Stuart sockeye. Pentegov et al. analysed the chum body after discarding the head and tail, hence their determinations were probably equivalent to fillet composition. Protein percentages were higher and fat lower than for Stuart sockeye fillets at equivalent distances on migration but chums had exhausted their protein and fat stores to a greater degree after spawning was completed.

Davidson and Shostrom (1936) did a great number of constituent determinations on pink salmon (*O. gorbuscha*) in central and southeastern Alaska, at three stations (salmon traps) in saltwater throughout a migration season, and on fish entering a coastal spawning stream throughout the spawning migration. Constituent analysis was confined to a section cut across the body near the middle by canning machinery, with composition probably equivalent to sockeye fillets. Pink salmon stood apart from the other species, apparently having greater protein and lower fat proportion for a given percentage of water. Pinks caught in saltwater varied from 4% to 10% fat and from 67% to 72% water. The low fat store is in harmony with spawning in coastal streams requiring a small reserve of energy. Samples from traps showed indications of increasing maturity only near the end of the season. Fish entering the spawning stream showed a definite increase in

maturity during the latter half of the arrival period, i.e., water percentage increased and percent fat fell. Racial differences, if any, were much less than in sockeye.

Previous work on changes in constituent composition and in related features of sockeye during migration and spawning had been fragmentary except for that done by Kizevetter (1948). Kizevetter presented results which indicated that Paratunka sockeye were quite similar in size, constituent composition, and other characteristics to Fraser River sockeye. Depletion of fat and protein, and increase in water percentage in sockeye between saltwater and freshwater, and between the river mouth and spawning ground was clearly shown. Sockeye entering the river were demonstrated to become more mature as the migration season progressed. Composition of ovaries and testes were generally comparable to Fraser sockeye at various stages of energy store depletion.

Various constituent determinations have been made on sockeye and other salmon in more recent years but usually in small, isolated samples for specialized purposes. Brett (1964) found complementary gradients of fat and water percentages in fingerling sockeye of 20-100 grams total weight. Brett (1973) determined fat and protein in adult female sockeye entering Great Central Lake (British Columbia) before and after forced exercise to determine energy extraction from fat and protein stores. The unexercised females (ovaries analysed separately from the rest of the fish) were closely equivalent in composition to eviscerated Pitt River sockeye sampled at the Lower Pitt River (TABLE 15). Protein was about 20% and fat close to 9%. Ovary water proportion was within the range of Fraser sockeye early in migration (FIGURE 14) but the fat percentage was generally higher and protein lower than in Fraser ovaries.

Fraser River Sockeye Studies

The studies reported here demonstrate (1) the amount and distribution of energy stores within an individual Fraser River sockeye, (2) the way the stores are used by individual male and female sockeye and by different segments of a run within a year, (3) differences in energy expenditure between years by a single race, and (4) differences in energy expenditure between races in general. Measurements necessary to the studies also allowed analysis of other attributes of sockeye energy stores as related to fish size.

GRADIENTS IN ENERGY STORES

A complex relationship was found between length, weight, and energy stores of individual sockeye relative to timing within a run and to progress up the river. Several gradients in energy stores were found. First and most obvious is the decrease in fat and protein percentages in the eviscerated fish (TABLES 13, 14, 15 and 16) in peak samples taken at successive times and distances during the migration of a single race. Constituent percentages in eviscerated fish can be interpreted as energy stores because the preponderance of total energy stores is found in the eviscerated fish (TABLE 21).

Second, quite variable constituent percentages were found within a sample of sockeye from a station on the migration path or stage on the spawning grounds (FIGURE 8), with correlated gradients in the percentages (TABLES 17 and 18). Since fat percentage is correlated with condition factor (FIGURE 11), part of the variation is attributable to differences of condition within each sample. The variation suggests that constituent percentages should not be based on a single fish sample, but should be based on the mean of several fish.

Third, gradients in mean constituent percentages and in mean specific gravities in eviscerated sockeye occur between successive samples at a single sampling station (TABLES 12, 13 and 16). Earlier sockeye of a race have higher percentages of fat and protein. Because the earlier fish weigh more (TABLE 10) and have a higher condition factor on the average, the gradient must be due in part to the changing condition of the fish. Furthermore, earlier sockeye appear to spawn with larger fat and protein stores than later fish (TABLES 13 and 16), consequently it is necessary to know what segment of a run is being sampled. These findings support other evidence (Killick 1955) that sockeye maintain their chronological order during migration and spawning.

Finally, differences may occur between years for a given race. Eviscerated sockeye of the 1956 Chilko run had consistently higher fat percentages than did the 1959 Chilko samples throughout the run (FIGURE 9). However, no significant differences in constituent composition were found between the three successive Early Stuart runs (FIGURE 9).

Variation in time of migration of the Early Stuart run in different years did not affect the constituent composition. Although the 1958 Early Stuart sockeye migration was approximately 10 days later than the normal 1956 and 1957 runs (Henry 1961), the 1958 eviscerated sockeye had about the same constituent composition as in 1956 and 1957 at each station (FIGURES 6 and 9).

On the other hand the 1956 Chilko run appeared to be several days earlier than the 1959 run (TABLE 3), and had slightly higher fat and slightly lower protein constituents in relation to proportion of water throughout migration (FIGURES 7 and 9). No other explanation has been found for the difference between the two Chilko runs.

The findings concerning energy store gradients indicate that careful planning of sampling is required. Either catching gear or time of sampling may cause a sample to be non-representative of a whole population. Racial differences must also be considered where mixed races are sampled.

ENERGY CHANGES IN INDIVIDUAL SOCKEYE

Sockeye must maintain structural integrity while drawing heavily on body materials for energy to migrate and spawn. Protein plays the predominant structural role, with a large remainder at death, while fat plays a minor structural role (TABLE 24). A greater weight of fat is contributed to energy production than protein (TABLES 19 and 20) and, in addition, fat has more than twice the energy content per unit weight. Stored protein seems to be needed only for gonad enlargement, yet a relatively large amount is used as well for energy (TABLE 19).

Protein use is confined mainly to the latter part of the migration (FIGURES 6, 7 and 13). Between spawning ground arrival and death, protein use may be more than twice that of fat by weight (TABLE 19), but in these cases (1956 Early Stuart and 1959 Chilko females) the difference in energy is small due to the higher energy content of fat. FIGURES 6 and 7 indicate that as sockeye near the spawning ground, the rate of protein decrease may reach or slightly exceed that of fat.

Duncan and Tarr (1958) found that the quantity of the non-protein nitrogen portion of Early Stuart sockeye muscle changed very little from Lummi Island to Forfar Creek arrival, although the total nitrogen amount decreased considerably. Many of the compounds found within the non-protein nitrogenous fraction (Wood 1958) are involved

in the energy producing machinery of the muscles and thus would be expected to be maintained at a constant amount during migration. After spawning ground arrival, the non-protein nitrogenous components could decrease since the need for maximum swimming ability is past.

Fat is stored both within the muscle cells and in the intercellular spaces of chinook salmon muscle (Greene 1926) and sockeye fat storage may be similar. Withdrawal of intercellular fat probably explains the gradual shrinkage of fillets (FIGURE 2, TABLE 24). Since fat and water changes are complementary in muscles (fillets, FIGURE 12) the intracellular fat withdrawn is apparently replaced by water to maintain cell volume. Protein replacement by water is also indicated once protein use begins.

The burning of fat and protein for energy produces metabolic water in about the same amount by weight as the fat but less than half the protein (Hoar 1966). However, it seems unlikely that only metabolic water is involved in the inverse fat-water relationship because fat is replaced by water in the trimmings (FIGURES 2 and 12) where metabolism of fat would be negligible.

During maturation, male sockeye develop an enlarged head with an elongated and hooked snout to a much greater extent than females. Protein is required for these changes and in females there is less expendable protein for this development than in males because more protein is required for maturing the ovaries than the testes (TABLE 24). Transfer of protein to the trimmings is less in females than in males.

Female sockeye allocate more stored material to gonad enlargement than males and transport this larger organ with less muscle (FIGURE 2). Males have testes of almost mature size before river migration begins while ovary development continues throughout migration (FIGURE 4).

Specific gravity changes parallel the reduction of energy stores during migration and spawning. The greatest decrease in specific gravity of eviscerated sockeye occurred after much of the migration was completed, when protein use increased. Since protein has a specific gravity of about 1.33 (Hoar 1966) while fat has a specific gravity of about 0.93 (estimated from Bailey et al. 1952), protein changes would provide a qualitative explanation of specific gravity trends.

ENERGY EXPENDITURE BY RACE

Stores of fat in sockeye are a requirement of both migration distance and of time spent between cessation of feeding and death after spawning. Pitt and Chilko sockeye migrate earlier than necessary and spend the extra time in the vicinity of the spawning grounds waiting to mature (FIGURE 9). Stuart, Horsefly and Adams sockeye begin river ascent with little time to spare and arrive at the spawning grounds with fat stores near maximum depletion.

Increased protein stores do not appear to be an important requirement for the longer migrations. Protein stores are similar in all races on arrival at the estuary (TABLES 13, 14, 15 and 16). Indeed, eviscerated Pitt River sockeye had the highest percentage protein, and therefore the largest protein stores, even though they were sampled within a few miles of their spawning grounds (TABLE 1).

Prediction of degree of vulnerability to delays to migration can be made only very approximately from the energy stores data (TABLES 13, 14, 15 and 16). Chilko and Pitt sockeye have more fat remaining in energy stores at spawning ground arrival than other

races studied (FIGURE 9) and therefore could accommodate an equivalent delay on the migration route in terms of the energy budget. The other races studied had generally smaller fat reserves remaining at arrival at the spawning grounds (FIGURE 9) and therefore would be able to accommodate shorter delays during migration. These inferences fit observations of time between arrival and spawning at the various spawning grounds.

Survivable delays have been observed for certain sockeye races. Talbot (1950) recorded delays survived by sockeye tagged immediately below Hell's Gate in the Fraser Canyon. Maximum estimated sustained delay was 14 days. Since he could not apportion the tagged sockeye to known fractions of the runs involved, Talbot could not estimate delays survived by a majority of fish. Cooper and Henry (1962) observed delays to groups of Early Stuart sockeye in the Fraser Canyon at or downstream from Hell's Gate during extreme high water periods. Their data indicated low or no survival to spawning from delays of about a week, but good survival of sockeye delayed only 3 or 4 days.

The possibility of differential effects of delays to migration on the different segments of a sockeye run were mentioned by Idler and Clemens (1959). The data obtained from the 1957 Early Stuart run and the 1958 Adams River run suggest that earlier sockeye in a run have higher percentages of fat and protein in the eviscerated fish (TABLES 13 and 16) and therefore larger energy stores than later segment fish. However, earlier fish also end spawning with larger percentages of fat and protein remaining. Later segment fish use a smaller amount of fat on migration and arrive at the spawning ground with less fat remaining than earlier fish. The significance of these differences with respect to the effect of delay of early and late segment fish is not clear. Because early segment fish tend to have higher prespawning mortality, no conclusions about differential effects of delay appear warranted from the data presented.

Evidence of ability to delay spawning past the normal time has not been found in sockeye. Use of energy stores, ripening of gonads, spawning time and spawning behaviour must be largely under the control of biochemical mechanisms which appear to impose an inflexible schedule. Time schedules must be basically photoperiodic (Gilhousen 1960). Another factor is the histopathological changes accompanying maturation found by Colgrove (1966) which predispose sockeye to a limited lifespan as maturity approaches.

TABLE 27—Mean total energy used by three races of sockeye during river migration, and proportion used for gain in elevation.

Race	Total Energy (kcal)		Energy for Altitude Change (percent)	
	Males	Females	Males	Females
Early Stuart	2,227	2,562	0.18	0.15
Chilko	1,968	2,343	0.33	0.26
Adams	1,073	1,374	0.24	0.17

Total energy used during river migration of Fraser sockeye is dissipated predominantly as heat in water friction. The energy required to lift a sockeye to the respective spawning grounds is a very small percentage of total migration energy (TABLE 27). Energy

expended ranged from 1,073 kilocalories for Adams males to 2,562 kilocalories for Early Stuart females.

Energy expenditure (kcal/kg/day) between Albion and the spawning ground for the Early Stuart runs of 1957 and 1958 was lower than in 1956 (TABLES 25 and 26), for unknown reasons. River discharges were generally lower in 1956 than in the following two years. River temperatures in 1956 were generally intermediate between 1957 (lower) and 1958 (higher) although the estimated means were not much different (1958 higher than 1957 by about 6°F or 3½°C). The 1956 sockeye were slightly larger than in 1957 and 1958 (TABLE 9) but Brett and Glass (1973) indicate increasing efficiency for the same swimming speed with increasing size.

Average energy expenditure per kg per mile of river migration, sexes combined, was similar for Early Stuart and Adams sockeye, but the Chilko race used more kcal/kg/mile than the other two races (TABLES 25 and 26). Probably this is the result of the steeper Chilko migration path, which averages almost 10 ft rise per mile compared with 3.4 and 4 ft per mile for Early Stuart and Adams fish, respectively (TABLE 1). Average expenditure of energy per kg per mile for the three races is proportional to the 0.43 power of the average slopes (FIGURE 15).
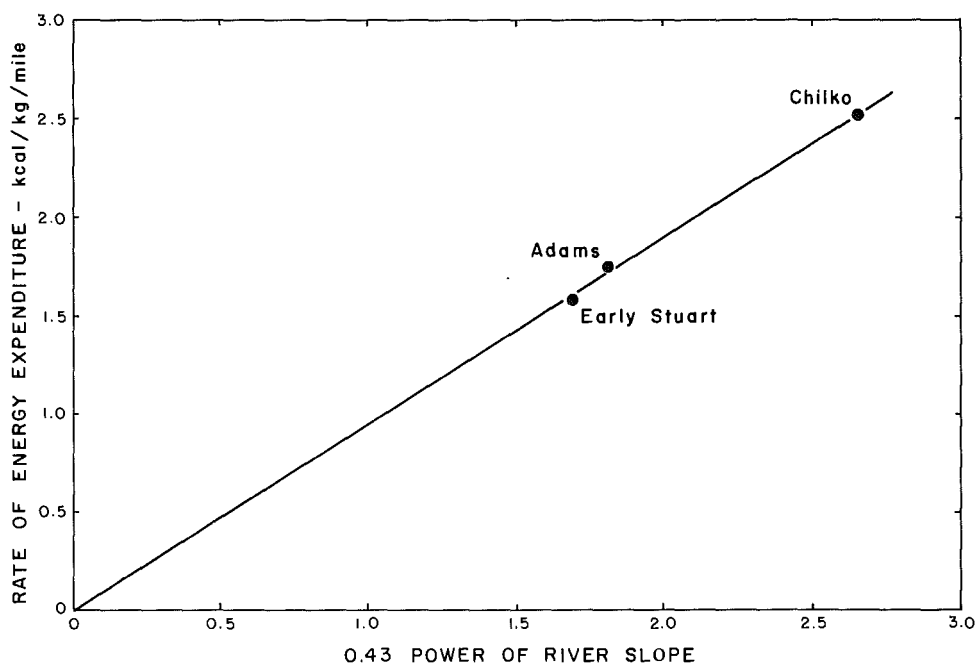

FIGURE 15—Relationship between mean rate of energy expenditure for sexes combined by race, and the average slope of the river migration path for each race.

Adams sockeye had about the same specific energy use per mile as Early Stuart sockeye (FIGURE 15), but the use per day was considerably less for Adams sockeye (TABLES 25 and 26). Average daily energy use for the two races is approximately in the ratio of the distances migrated per day, which in turn is approximately proportional to

the hours of daylight available for migration. This relationship is supported by observations (unpublished) indicating that sockeye migration during darkness is low relative to the migration during daylight.

Brett (1973) tested two groups of adult sockeye in a cage at the outlet of Great Central Lake, and obtained power outputs for swimming speeds of 2.14 and 2.55 ft/sec. Energy expenditures of 27 and 24 kcal/kg/day over 10 and 14 days reported for the Great Central Lake sockeye were close to the means for sexes combined in both Chilko and Adams sockeye, but were below that for Early Stuart sockeye. Migration rates for Fraser sockeye are estimated at between 1.6 and 2.2 ft/sec but since they migrate mainly in turbulent waters, their effective speed through the water is not known.

Migration rates of Fraser sockeye may be compared with calculated river currents. Studies have been made (unpublished calculations) of the mean travel time for water in the Chilko-Chilcotin River system from Chilko Lake to the Fraser River confluence. For the August river discharges in 1956 and 1959, the mean travel time of river water would have been about 25 hours or a velocity of 6.4 fps.

Clearly, none of the sockeye races examined in this study can migrate against the main river currents along the entire path of migration. A multitude of observations indicate that in difficult river reaches, the sockeye stay along the banks close to the surface. Back eddies and friction slowed currents are traversed whenever possible. Sockeye undoubtedly have specifically adapted to make long migrations to the spawning grounds with minimum expenditure of energy, and their energy stores are sufficient to accomplish this under normal conditions with little excess.

SUMMARY

1. Six races of Fraser River sockeye were sampled at 2 to 10 stations or stages during migration and spawning in 1 to 3 of the years 1956 through 1959. Physical and percentage constituent measurements were obtained.

2. Decreases in weight, specific gravity, and possibly length were found during migration and spawning. Weight and specific gravity decreased from early to late segments of a run at a sampling station.

3. Body muscles (fillets) lost weight and the remainder of the eviscerated fish (trimmings) gained weight during migration and spawning. Racial differences were found in relative body muscle size.

4. Ovaries increased markedly in size during estuary and river migration, while testes were near maximum size at estuary arrival. Racial differences in relative ovary size were found.

5. Fat and protein percentages decreased, and water increased in eviscerated sockeye during migration and spawning. Within samples, fat and water content were also inversely related. Mean percent water in samples of eviscerated fish formed a useful index of maturation.

6. Percentage fat, total weight, and specific gravity decreased, and percentage water increased from early to later segments of a racial run. Segments maintained this sequence through migration and spawning.

7. Correlations between length, weight, and constituent percentages in eviscerated fish showed higher fat and lower water proportion in heavier fish at a given length within samples, indicating the possibility of poorly representative samples arising from size selection. Variation precludes use of single fish to obtain a representative sample.

8. Racial differences occurred in composition of testes. Slight differences were found between sexes in eviscerated fish composition, wherein females began migration with slightly higher fat percentage and died with slightly lower percentage.

9. Within samples, fillets, trimmings, ovaries, testes and other viscera had generally distinctive constituent compositions.

10. Between 40% and 70% of total protein and 5% to 26% of fat remained in dead, spawned sockeye.

11. The eviscerated body contributed more than 95% of the total energy expenditure.

12. During migration, males apparently transferred protein from fillets to trimmings for secondary sexual development, while in females most of an equivalent amount was used for ovary development.

13. Energy stores were independent of year-to-year variations in time of migration.

14. Fat provided more than 70% of migration and spawning energy. Protein became a significant source of energy only very late in migration and during spawning.

15. Energy expenditure during river migration and spawning for three races varied between 2,374 and 3,722 kcal for males, and between 2,305 and 3,825 kcal for females. Males had higher values in 5 of the 6 runs studied. On a per kilogram basis, females had consistently greater energy expenditure during river migration.

16. Calculated energy use in kcal per kg per day of river migration for three years of sampling for the same race showed a variation of 30 to 37 for males and 39 to 51 for females. Energy use per day was in the ratio of distances migrated per day, which was in turn approximately proportional to hours of daylight available for migration. Energy use per kg per mile for three races varied as the 0.43 power of the river slope.

17. Sockeye have adapted to make the spawning migration with the least expenditure of energy and their energy stores are sufficient to accomplish this with little excess. Various data indicate that Fraser River sockeye cannot migrate against the main river current in the swifter parts of their river migration routes, and stay close to the bank under such conditions.

18. Comparison of results for Fraser River sockeye with data for other sockeye and other species of salmon indicate similar constituent relationships and changes during maturation. Differences were related to variations in the life cycles, which in general included a long non-feeding spawning migration.

ABBREVIATIONS OF SAMPLING STATION NAMES USED IN FIGURES

AL — Albion

AR — Adams River, ripe fish

AS — Adams River, spent fish

AD — Adams River, dead fish

CR — Chilko River, ripe fish

CS — Chilko River, spent fish

CD — Chilko River, dead fish

FC — Farwell Canyon

FJ — Fort St. James

FR — Forfar Creek, ripe fish

FS — Forfar Creek, spent fish

FD — Forfar Creek, dead fish

HD — Horsefly River, dead fish

HG — Hell's Gate

KH — Keighley Holes

LD — Late Stuart, dead fish

LI — Lummi Island

LK — Likely

LP — Lower Pitt River

PD — Pitt River, dead fish

SB — Siwash Bridge

SC — Soda Creek

SJ — Port San Juan

SO — Sooke

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