OCEAN MORTALITY AND MATURITY SCHEDULES OF KARLUK RIVER SOCKEYE SALMON AND SOME COMPARISONS OF MARINE GROWTH AND MORTALITY RATES

By R. A. FREDIN, *Fishery Biologist (Research)*

BUREAU OF COMMERCIAL FISHERIES, Biological Laboratory, Seattle, Wash.

ABSTRACT

Four population models representing different temporal distributions of natural mortality during the ocean life of Karluk sockeye salmon (*Onchorhynchus nerka*) are developed and discussed. The first model simulates a constant monthly instantaneous mortality rate throughout ocean life of sockeye. In the second model, the monthly instantaneous mortality rate is greatest during the first month of ocean residence and decreases arithmetically in each succeeding month. In the third model, the monthly instantaneous mortality rate decreases geometrically during the first 6 months of ocean life and remains constant thereafter. The fourth model simulates a "catastrophic", age-specific first-month instantaneous mortality rate and a constant, age-independent mortality rate in the second and succeeding months of ocean life.

Data collected on the releases and returns of marked Karluk sockeye in the late 1920's and early 1930's are used to estimate ocean mortality rates of the different fresh-water age groups of fish. The rates vary with the population model used, year of ocean life and fresh-water age. Mortality of the smaller, 3-fresh-water smolts is greater than for the larger, 4-fresh-water fish during at least a part of ocean residence.

Maturity schedules are estimated for 3- and 4-fresh-water smolts in each population model. Depending on the distribution of ocean mortality, from 53 to 62 percent of the 3-fresh-water fish and 74 to 80 percent of the 4-fresh-water sockeye achieve maturity by the end of their second year at sea.

The estimated instantaneous ocean mortality rates are compared with available estimates of Karluk sockeye ocean growth rates (weighted by the proportions of fish that mature as 1-, 2-, 3- and 4-ocean sockeye) on a monthly and annual basis to determine the net increase or decrease in weight during ocean residence. Except during the last year of ocean life of the relatively small fraction of Karluk sockeye that spend 4 years at sea, and then only for the first of 4 mortality distributions considered, ocean growth exceeds natural mortality.

The ranges of the estimated increases in bulk of Karluk sockeye during the first, second, and third years of ocean life, respectively, are 609 to 1,035 percent, 54 to 144 percent, and 26 to 84 percent. During the fourth year of ocean life, the bulk of Karluk sockeye is estimated to decrease by 8 to 10 percent under the first population model, and increase by 11 to 38 percent under the other 3 models.

The estimated percentage changes in bulk show that, except for the relatively scarce 4-ocean fish under the first population model, any capture of Karluk sockeye before the end of their ocean life causes a loss of potential yield, provided there exists an inshore fishery capable of catching the fish not needed for reproduction of the stock.

Information on the distribution and magnitude of ocean mortality of salmon and their maturity schedules is useful for comparing marine growth and mortality rates to determine the changes in bulk (net increase or decrease in weight) of a year class during ocean residence. Knowledge of changes in bulk, in turn, is useful for comparing salmon yields obtained by a pelagic fishery with the potential yields available to an inshore fishery.

Among the data available for studying the natural mortality of salmon during their ocean

NOTE.—Approved for publication Dec. 31, 1963.

life are those reported by Barnaby (1944), who gives the details of a number of experiments involving the marking of sockeye smolts at Karluk River during the late 1920's and early 1930's and the enumeration of returns of marked fish to that river system after 1–4 years of ocean residence. These experiments provide an impressive array of population data that are particularly useful for estimating ocean mortality of salmon, because they were obtained before the development of a large-scale pelagic salmon fishery west of longitude 175° W. in the North Pacific Ocean and likely are free of the confounding effects of high seas fishing.

Ricker (1962) utilized certain data from the Karluk marking experiments in his excellent analysis of the ocean growth and mortality of sockeye salmon during their last 2 years at sea. Parker (1962) also used the Karluk data in his unique study of the ocean mortality of Pacific salmon. Much of Barnaby's experimental population data are used here in an ocean mortality analysis that differs from the analyses and results presented by Ricker and Parker, respectively, in that (a) a somewhat different mathematical model is used to estimate ocean mortality for the case where the mortality rate is assumed to be constant throughout ocean residence, and (b) estimates of ocean mortality are made for three situations where the rate is considered to vary during ocean residence.

The portion of Barnaby's experimental population data used in this paper consists of the releases and returns of smolts that were marked by the removal of the adipose and one or both of the ventral fins. This analysis will be primarily concerned with the two fresh-water age groups of Karluk sockeye that, according to Rounsefell (1958, table 17), account for over 95 percent of the annual run to that system. These are the 3- and 4-fresh-water smolts, or fish that migrate to sea in their third and fourth years of life respectively.[1]

For each of the four temporal distributions of ocean mortality considered in this study, I will estimate the percentages of 3- and 4-fresh-water smolts that mature after 1, 2, 3, and 4 years of ocean residence.

The estimates of ocean mortality presented here are compared with available growth rate data to determine changes in bulk of Karluk sockeye during ocean life. A number of such determinations are given in the last section of the paper. On the basis of these determinations, some inferences are drawn regarding the effects of high-seas fishing on the potential yield in weight of Karluk sockeye.

DURATION OF OCEAN RESIDENCE OF KARLUK SOCKEYE

Barnaby (1944) states that the major part of the seaward migration of Karluk sockeye takes place during the last week of May and the first 2 weeks of June each year. He also notes that the older smolts, that is, 4- and 5-fresh-water fish, migrate to sea earlier within the 3-week period of seaward migration than the younger smolts, that is, the 2- and 3-fresh-water fish. On the basis of these observations, I will assume for purposes of this study that 5-fresh-water smolts begin ocean life on June 1, 4-fresh-water smolts on June 5, 3-fresh-water smolts on June 10, and 2-fresh-water smolts on June 15.

From Rounsefell (1958, appendix table A–4) we can estimate the nearest dates ending in 5 or 0 on which 50 percent of the sockeye of different fresh-water and ocean ages return to the Karluk River. These estimates are given in table 1.

Using the dates of return given in table 1 as end points of ocean residence, the estimated duration of ocean life for each of 15 age groups of Karluk River sockeye is as shown in table 2.

For purposes of this study, it is assumed that the maximum ocean residence of 2- and 3-fresh-water smolts is 47.83 months, the maximum ocean residence of 4-fresh-water smolts is 48.17 months, and the maximum ocean residence of 5-fresh-water smolts is 36.50 months.

TABLE 1.—*Estimated dates on which 50 percent of the sockeye of different fresh-water and ocean ages return to Karluk River*

Fresh-water age group	Ocean age group[1]			
	1	2	3	4
2	July 15	June 30	June 15	June 10
3	Aug. 15	July 20	June 10	June 5
4	Sept. 5	Aug. 25	June 10	June 10
5	Sept. 10	Aug. 30	June 15	---------

[1] Ocean age is designated here as the nearest number of full years the fish spend in the ocean. A fish that spends, say, 26 months in the ocean is referred to as a 2-ocean fish.

[1] Ricker (1962) refers to these two groups as 2- and 3-fresh-water sockeye respectively; Parker (1962) refers to them as 2- and 3-annuli smolts; Rounsefell (1958) refers to them as 3- and 4-year-old seaward migrants.

TABLE 2.—*Estimated duration of ocean residence, in months, of 15 age groups of Karluk River sockeye*

Fresh-water age group	Ocean age group 1	2	3	4
2	13.00	24.50	36.00	47.83
3	14.17	25.33	36.00	47.83
4	15.00	26.67	36.17	48.17
5	15.33	27.00	36.50	

RELEASES AND RETURNS OF MARKED KARLUK SOCKEYE SMOLTS

Barnaby (1944, tables 33–35, 37, 39, 41, and 43) reports the numbers of smolts of each fresh-water age group that were marked by the removal of the adipose and one or both of the ventral fins in seven different marking experiments between 1929 and 1933 at the Karluk River. He also shows the estimated returns of marked fish by ocean age for each experiment. Except for the correction of a few minor errors in the estimated returns and an added estimate of a return of 17 4-ocean fish from the 3-fresh-water smolts marked in the second experiment in 1930, Barnaby's data on releases and returns are shown in table 3.

EFFECT OF MARKING ON OCEAN SURVIVAL

The extent to which the removal of adipose-ventral fins affected the percentage returns of marked Karluk smolts cannot be determined from the Karluk sockeye data, since the entire smolt run was not counted in any year of marking and comparative survival rates of marked and unmarked smolts are not available. That the removal of adipose and ventral fins probably caused a differential mortality among marked Karluk smolts is indicated by results of experiments in other systems in which sockeye smolts were marked by the removal of adipose-ventral fin combinations. Ricker (1962), using data from Cultus Lake sockeye marking studies (Foerster, 1934, 1936, 1937), estimated that on a day-to-day basis, marked sockeye were about 27 percent more vulnerable to the causes of death in operation than unmarked fish. This means that the instantaneous ocean mortality rate of marked sockeye was about 1.27 times the instantaneous natural mortality rate encountered by unmarked sockeye during their ocean life.

For purposes of this study, I will use the factor 1.27 in estimating the instantaneous ocean mortal-

TABLE 3.—*Estimated releases and returns of Karluk River sockeye smolts marked by the removal of the adipose and one or both ventral fins.*

[Barnaby, 1944, tables 33–35, 37, 39, 41, and 43]

Year of release	Experiment number	Fresh-water age group	Group number	Estimated release (N_o)	Estimated returns: 1-ocean (R_1)	2-ocean (R_2)	3-ocean (R_3)	4-ocean (R_4)	Total (ΣR)	Estimated total percentage returns $(\Sigma R)/(N_o)$
				Number	*Number*	*Number*	*Number*	*Number*	*Number*	*Percent*
1929	1	3	1	21,858	656	2,882	450		3,988	18.24
		4	2	28,041	1,002	5,362	783		7,147	25.49
		5	3	162		22			22	13.58
1930	1	2	4	252			12		12	4.76
		3	5	14,676	28	1,730	725		2,483	16.92
		4	6	9,773	146	2,237	235		2,618	26.79
		5	7	299	5	62			67	22.41
	2	2	8	237						
		3	9	14,923	42	1,587	808	17	2,454	16.44
		4	10	9,554	208	2,396	160		2,764	28.93
		5	11	286		123			123	43.01
1931	1	2	12	84		23	23		46	54.76
		3	13	41,403	39	3,845	4,857	46	8,787	21.22
		4	14	8,145	119	2,349	339		2,807	34.46
		5	15	368		150			150	40.76
1932	1	3	16	6,275	13	833	339	11	1,196	19.06
		4	17	8,593	109	1,212	412	23	1,756	20.44
		5	18	132			4		4	3.03
	3	3	19	9,381		1,256	926	45	2,227	23.74
		4	20	5,580	50	594	306	12	962	17.24
		5	21	39						
1933	1	2	22	250		15	32		47	18.80
		3	23	25,394	7	3,208	1,441		4,656	18.34
		4	24	13,692	45	2,423	941		3,409	24.90
		5	25	664		77	29		106	15.96
Totals		2		823		38	67		105	12.76
		3		133,910	785	15,341	9,546	119	25,791	19.26
		4		83,378	1,679	16,573	3,176	35	21,463	25.74
		5		1,950	5	434	33		472	24.20

ity rates of unmarked Karluk sockeye from the release and return data given in table 3.

POPULATION MODEL 1

In this population model, the assumption is carried that the instantaneous ocean mortality rate of Karluk sockeye is constant throughout their ocean life. Notation is as follows:

N_o = The number of marked smolts of a given fresh-water age.

M = The monthly instantaneous mortality rate of unmarked sockeye during their ocean life.

1.27—A factor to adjust for the effects of marking on ocean survival.

t_1+k_1 = The number of full months (t_1) plus the additional fraction of a month (k_1) elapsing between the time of seaward migration and the return of mature 1-ocean fish to the Karluk River.

N_1 = The number of 1-ocean sockeye surviving at the end of t_1+k_1 months of ocean residence.

p_1 = The proportion of the surviving 1-ocean sockeye that mature and return to the Karluk River at the end of t_1+k_1 months.

R_1 = The number of 1-ocean sockeye that return to the Karluk River at the end of t_1+k_1 months of ocean residence.

$1-p_1$ = The proportion of the surviving 1-ocean sockeye that do not mature at the end of t_1+k_1 months of ocean residence.

N'_1 = The number of the surviving, immature 1-ocean sockeye at the end of t_1+k_1 months at sea.

t_2+k_2 = The number of full months (t_2) plus the additional fraction of a month (k_2) elapsing between the time of seaward migration and the return of mature 2-ocean fish to the Karluk River.

N_2 = The number of 2-ocean sockeye surviving at the end of t_2+k_2 months of ocean residence.

p_2 = The proportion of the surviving 2-ocean sockeye that mature and return to the Karluk River at the end of t_2+k_2 months.

R_2 = The number of 2-ocean sockeye that return to the Karluk River at the end of t_2+k_2 months of ocean residence.

$1-p_2$ = The proportion of the surviving 2-ocean sockeye that do not mature at the end of t_2+k_2 months of ocean residence.

N'_2 = The number of surviving, immature 2-ocean sockeye at the end of t_2+k_2 months at sea.

t_3+k_3 = The number of full months (t_3) plus an additional fraction of a month (k_3) elapsing between the time of seaward migration and the return of mature 3-ocean sockeye to the Karluk River.

N_3 = The number of 3-ocean sockeye surviving at the end of t_3+k_3 months of ocean residence.

p_3 = The proportion of the surviving 3-ocean sockeye that mature and return to the Karluk River at the end of t_3+k_3 months. (In the case of the 5-fresh-water smolts, t_3+k_3 is equal to 36.50 months, and p_3 is assumed to be equal to one.)

R_3 = The number of 3-ocean sockeye that mature and return to the Karluk River at the end of t_3+k_3 months of ocean residence.

$1-p_3$ = The proportion of the surviving 3-ocean sockeye that do not mature at the end of t_3+k_3 months of ocean residence.

N'_3 = The number of surviving, immature 3-ocean sockeye at the end of t_3+k_3 months of ocean residence.

t_4+k_4 = The number of full months (t_4) plus the additional fraction of a month (k_4) elapsing between the time of seaward migration and the return of mature 4-ocean sockeye to the Karluk River.

N_4 = The number of 4-ocean sockeye surviving at the end of t_4+k_4 months of ocean residence.

p_4 = The proportion of the surviving 4-ocean sockeye that mature and return to the Karluk River at the end of t_4+k_4 months of ocean residence. (In this study, it is assumed that the maximum ocean residence of 2-, 3- and 4-fresh-water smolts is t_4+k_4 months. Hence p_4 is assumed to be equal to one for these fresh-water age groups.)

R_4 = The number of 4-ocean sockeye that mature and return to the Karluk River at the end of t_4+k_4 months of ocean residence.

Identities among the foregoing quantities are as follows:

$$N_1=N_0e^{-1.27M(t_1+k_1)} \tag{1}$$

$$R_1=p_1N_1=p_1N_0e^{-1.27M(t_1+k_1)} \tag{2}$$

$$N'_1=(1-p_1)N_1=N_1-p_1N_1=N_1-R_1 \tag{3}$$

$$\begin{aligned} N_2&=N'_1e^{-1.27M[(t_2+k_2)-(t_1+k_1)]} \\ &=N_1e^{-1.27M[(t_2+k_2)-(t_1+k_1)]} \\ &\qquad -R_1e^{-1.27M[(t_2+k_2)-(t_1+k_1)]} \\ &=N_0e^{-1.27M(t_2+k_2)}-R_1e^{-1.27M[(t_2+k_2)-(t_1+k_1)]} \end{aligned} \tag{4}$$

$$\begin{aligned} R_2&=p_2N_2 \\ &=p_2N_0e^{-1.27M(t_2+k_2)} \\ &\qquad -p_2R_1e^{-1.27M[(t_2+k_2)-(t_1+k_1)]} \end{aligned} \tag{5}$$

$$N'_2=(1-p_2)N_2=N_2-p_2N_2=N_2-R_2 \tag{6}$$

$$\begin{aligned} N_3&=N'_2e^{-1.27M[(t_3+k_3)-(t_2+k_2)]} \\ &=N_2e^{-1.27M[(t_3+k_3)-(t_2+k_2)]}-R_2e^{-1.27M[(t_3+k_3)-(t_2+k_2)]} \\ &=N_0e^{-1.27M(t_3+k_3)}-R_1e^{-1.27M[(t_3+k_3)-(t_1+k_1)]} \\ &\qquad -R_2e^{-1.27M[(t_3+k_3)-(t_2+k_2)]} \end{aligned} \tag{7}$$

$$\begin{aligned} R_3=p_3N_3&=p_3N_0e^{-1.27M(t_3+k_3)} \\ &\qquad -p_3R_1e^{-1.27M[(t_3+k_3)-(t_1+k_1)]} \\ &\qquad -p_3R_2e^{-1.27M[(t_3+k_3)-(t_2+k_2)]} \end{aligned} \tag{8}$$

$$N_3' = (1-p_3)N_3 = N_3 - p_3N_3 = N_3 - R_3 \qquad (9)$$

$$\begin{aligned} N_4 = R_4 &= N_3' e^{-1.27M[(t_4+k_4)-(t_3+k_3)]} \\ &= N_3 e^{-1.27M[(t_4+k_4)-(t_3+k_3)]} - R_3 e^{-1.27M[(t_4+k_4)-(t_3+k_3)]} \\ &= N_0 e^{-1.27M(t_4+k_4)} - R_1 e^{-1.27M[(t_4+k_4)-(t_1+k_1)]} \\ &\quad - R_2 e^{-1.27M[(t_4+k_4)-(t_2+k_2)]} \\ &\quad - R_3 e^{-1.27M[(t_4+k_4)-(t_3+k_3)]} \end{aligned} \qquad (10)$$

Equation (10), which is analogous to equation (11) of Parker (1962), can be used to estimate the monthly instantaneous ocean mortality rates for 2-, 3-, and 4-fresh-water smolts by entering observed or assumed quantities for N_0, R_1, R_2, R_3, R_4, t_1+k_1, t_2+k_2, t_3+k_3, and t_4+k_4 in the equation, and inserting trial values for M until one which results in a balanced expression is obtained. In a similar manner, equation (8) can be used to estimate M for 5-fresh-water smolts, since p_3 is assumed to be equal to one for this fresh-water age group.

Estimates of Monthly Instantaneous Mortality Rates

Of the 25 groups of marked sockeye smolts (table 3), there were 11 in which the numbers of fish released were small. These were the four groups of 2-fresh-water smolts and seven groups of 5-fresh-water smolts. The returns from each of these groups were also small in mumber, and they occurred in only 1 or 2 years following seaward migration. Because of the small numbers of fish involved, the instantaneous mortality rates are not estimated for the individual groups of 2- and 5-fresh-water smolts. Instead, the data for the four groups of marked 2-fresh-water smolts are combined, as are the data for the seven groups of marked 5-fresh-water smolts, for estimating the instantaneous ocean mortality rates for these two fresh-water age groups.

An estimate of the monthly instantaneous mortality rate can be obtained for each of the remaining 14 groups of marked sockeye, consisting of seven groups of 3-fresh-water smolts and seven groups of 4-fresh-water smolts.

Substitution of the appropriate t- and k-values in equations (10) and (8) yields the following expressions for estimating the monthly instantaneous ocean mortality rates for the four fresh-water age groups:

2-fresh-water smolts:

$$R_4 = N_0e^{-60.74M} - R_1e^{-44.23M} - R_2e^{-29.63M} - R_3e^{-15.02M}$$

3-fresh-water smolts:

$$R_4 = N_0e^{-60.74M} - R_1e^{-42.75M} - R_2e^{-28.58M} - R_3e^{-15.02M}$$

4-fresh-water smolts:

$$R_4 = N_0e^{-61.18M} - R_1e^{-42.13M} - R_2e^{-27.30M} - R_3e^{-15.24M}$$

5-fresh-water smolts:

$$R_3 = N_0e^{-46.36M} - R_1e^{-26.89M} - R_2e^{-12.06M}$$

The estimates of monthly instantaneous ocean mortality rates, as derived from the appropriate equations and release and return data, are given in table 4. The marked group numbers associated with the estimates are shown in parentheses.

TABLE 4.—*Estimated instantaneous ocean mortality rates of Karluk River sockeye, population model 1*

[Effects of marking adjusted by factor of 1.27]

Fresh-water age group	Monthly instantaneous ocean mortality rate (M)	Mean M for 3- and 4-fresh-water smolts	Standard deviation of mean M
2	0.0496 (Groups 4, 8, 12, and 22 combined).		
3	0.0520 (1); 0.0480 (5); 0.0477 (9); 0.0381 (13); 0.0445 (16); 0.0365 (19); 0.0455 (23).	0.0446	0.0021
4	0.0402 (2); 0.0380 (6); 0.0366 (10); 0.0303 (14); 0.0426 (17); 0.0456 (20); 0.0369 (24).	.0386	.0018
5	0.0402 (Groups 3, 7, 11, 15, 18, 21, and 25 combined).		

Relation Between Monthly Instantaneous Mortality Rate and Age and Size of Smolts

The estimates of monthly instantaneous ocean mortality rates shown in table 4 indicate a general decrease with an increase in the fresh-water age of smolts: 0.0496 for 2-fresh-water smolts; an average of 0.0446 for 3-fresh-water smolts; an average of 0.0386 for 4-fresh-water smolts; and 0.0402 for 5-fresh-water smolts. Since the estimates for the 2- and 5-fresh-water smolts are based on relatively small numbers of fish, they should, in a comparison of ocean mortality rate with age at time of outmigration, be considered as rough approximations. Each of the estimated average mortality rates for the 3- and 4-fresh-water smolts on the other hand are based on seven groups of marked sockeye. Each group contained large numbers of marked fish. Six of seven paired groups, that is, two groups of smolts marked in the same way in the same year, showed a higher ocean mortality rate for 3-fresh-water smolts than for 4-fresh-water smolts. The standard deviations of the means show that the difference between the mean mortality rates for 3- and 4-fresh-water smolts is significant at about the 85 percent confidence level.

735-722 O—64——5

From Barnaby (1944, table 27), we can estimate the average body length of fish in each of the four fresh-water age groups of smolts in the seaward migration through the week ending June 14 for the years 1929 to 1933 combined. The average lengths for the 2-, 3-, 4-, and 5-fresh-water smolts were 108, 131, 143, and 146 millimeters, respectively. Plotting the estimated monthly instantaneous mortality rates for the four fresh-water age groups against average lengths of smolts at time of seaward migration, as in figure 1, we see a general decrease in ocean mortality as size of smolts increases.

Mortality Rates of 3- and 4-Fresh-Water Smolts by Ocean Age and Ocean Year

The mortality rates for the different ocean age groups and ocean years of life of 3- and 4-fresh-water smolts, the two fresh-water age groups which account for practically the entire run of Karluk sockeye, can be estimated from the average monthly instantaneous ocean mortality rates (table 4) and estimates of the duration of ocean residence of different ocean age groups (table 2).

For sockeye of a given fresh-water age that mature at ocean age x, the total ocean mortality rate is estimated from the expression:

$$a_x = 1 - e^{-M(t_x + k_x)}$$

where t_x is the number of full months of ocean residence and k_x is the fraction of an additional month (if any) of ocean residence.

The annual ocean mortality rates during the first, second, third, and fourth years of ocean residence of sockeye of a given fresh-water age are obtained from the following expression:

$$a'_x = 1 - e^{-M[(t_x + k_x) - (t_{x-1} + k_{x-1})]}$$

where the quantity $[(t_x + k_x) - (t_{x-1} + k_{x-1})]$ represents the number of months elapsing between the time that one ocean age group returns to the Karluk River and the time that the next ocean age group returns to the Karluk River. This quantity generally is not equal to 12 months, hence the annual ocean mortality rates usually apply to periods of time other than 12 months. For example, table 2 shows for 3-fresh-water smolts that 1-ocean mature sockeye spend an average of 14.17 months at sea, 2-ocean mature sockeye spend an additional 11.16 months at sea, and so forth. Only in the case of 4-ocean mature sockeye of the 4-fresh-water smolts do the fish spend 12 months more in the ocean than sockeye that mature in the preceding year.

Table 5 shows the total ocean mortality rates for each ocean age group and the annual mortality rates for each ocean year of life for 3- and 4-fresh-water smolts.

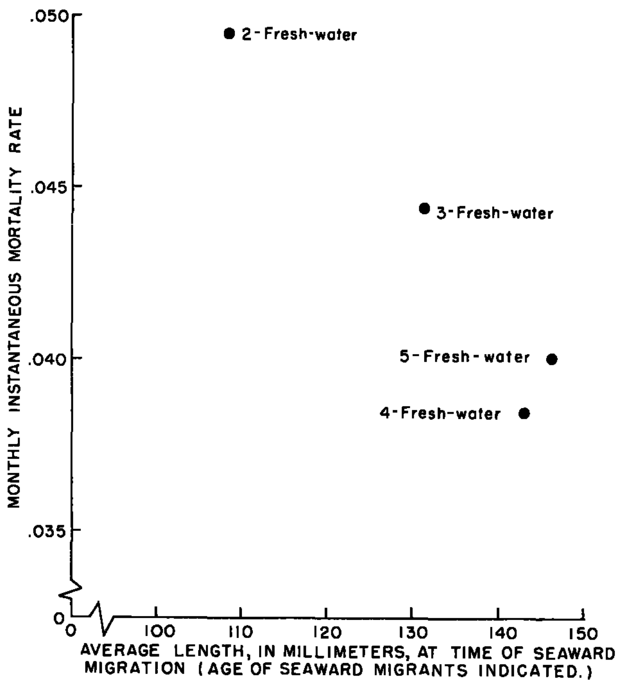

FIGURE 1.—Estimates of monthly instantaneous ocean mortality rates for Karluk sockeye of different lengths at time of seaward migration. (Data from table 4, and Barnaby, 1944, table 27).

TABLE 5.—*Estimated mortality rates for each ocean age group and ocean year, 3- and 4-fresh-water smolts, Karluk River sockeye, population model 1*

Fresh-water age group	Average monthly instantaneous ocean mortality rate, M	Ocean age	Duration of ocean residence	Total instantaneous mortality rate	Total ocean mortality rate (a_x)	Duration of ocean year	Instantaneous ocean mortality rate during year	Annual ocean mortality rate (a'_x)
		Years	*Months*		*Percent*	*Months*		*Percent*
3	0.0446	1	14.17	0.6320	46.8	14.17	0.6320	46.8
		2	25.33	1.1297	67.7	11.16	.4977	39.2
		3	36.00	1.6056	79.9	10.67	.4759	37.9
		4	47.83	2.1332	88.2	11.83	.5276	41.0
4	.0386	1	15.00	.5790	44.0	15.00	.5790	44.0
		2	26.67	1.0295	64.3	11.67	.4505	36.3
		3	36.17	1.3962	75.2	9.50	.3667	30.7
		4	48.17	1.8594	84.4	12.00	.4632	37.1

The estimated total ocean mortality rates for 3-fresh-water smolts range from 46.8 percent for those sockeye that mature as 1-ocean fish to 88.2 percent for those that mature as 4-ocean fish. Corresponding estimates for 4-fresh-water smolts are 44.0 and 84.4 percent, respectively.

The annual mortality rates generally decreased with the progression of ocean years. This is due, of course, to a general decrease in the number of months elapsing between the times that one ocean age group matured and the next older ocean age group matured. If the durations of ocean residence were 12, 24, 36, and 48 months for the four ocean age groups, the annual ocean mortality rates would be approximately 41.4 percent for 3-fresh-water smolts and 37.1 percent for 4-fresh-water smolts.

Maturity Schedules of 3- and 4-Fresh-Water Smolts

The maturity schedules of the 3-and 4-fresh-water smolts, that is, the proportions of a given population of seaward migrants that mature after 1, 2, 3, and 4 years of ocean residence, can be roughly estimated from the ratios, $R_1/\Sigma R$, $R_2/\Sigma R$, $R_3/\Sigma R$, and $R_4/\Sigma R$, which can be obtained from table 3. Such ratios, however, do not account for the mortality that occurs among immature sockeye from one year to the next during their ocean life. As a result, the ratios, $R_1/\Sigma R$, and $R_2/\Sigma R$, are generally overestimates of the proportions of a given smolt migration that mature as 1- and 2-ocean fish. Conversely, $R_3/\Sigma R$ and $R_4/\Sigma R$ are generally underestimates of the proportions of a given smolt migration that mature as 3- and 4-ocean fish.

The factors, p_1, p_2, p_3, and p_4, in equations (2), (5), (8), and (10) represent the proportions of surviving 1-, 2-, 3-, and 4-ocean sockeye that mature at the end of the first, second, third, and fourth years of ocean residence. The equivalents of p_1, p_2, and p_3 are as follows:

$$p_1=R_1/N_0e^{-1.27M(t_1+k_1)} \quad (11)$$

$$p_2=R_2/\{N_0e^{-1.27M(t_2+k_2)}-R_1e^{-1.27M[(t_2+k_2)-(t_1+k_1)]}\} \quad (12)$$

$$p_3=R_3/\{N_0e^{-1.27M(t_3+k_3)}-R_1e^{-1.27M[(t_3+k_3)-(t_1+k_1)]}-R_2e^{-1.27M[(t_3+k_3)-(t_2+k_2)]}\} \quad (13)$$

The factor, p_4, is assumed to be equal to one. Except for p_1, these factors do not reflect the maturity schedules of a given smolt migration, because they do not account for the proportions of fish that matured in the preceding year or years.

Denoting the proportions of a given smolt migration that mature as 1-, 2-, 3-, and 4-ocean sockeye by p'_1, p'_2, p'_3, and p'_4, where $p'_1+p'_2+p'_3+p'_4=1$, we see that $p_1=p'_1$; $p_2=p'_2/(1-p'_1)$; $p_3=p'_3/(1-p'_1-p'_2)$; and $p_4=p'_4/(1-p'_1-p'_2-p'_3)$. Transposing we obtain the following expressions for p'_1, p'_2, p'_3, and p'_4:

$$p'_1=p_1 \quad (14)$$

$$p'_2=p_2(1-p'_1) \quad (15)$$

$$p'_3=p_3(1-p'_1-p'_2) \quad (16)$$

$$p'_4=1-p'_1-p'_2-p'_3 \quad (17)$$

Substitution of the appropriate values for (t_1+k_1), (t_2+k_2), and (t_3+k_3) in equations (11), (12), and (13) provides the following expressions for p_1, p_2, and p_3:

3-fresh-water smolts:

$$p_1=R_1/\{N_0e^{-18.00M}\}$$
$$p_2=R_2/\{N_0e^{-32.17M}-R_1e^{-14.17M}\}$$
$$p_3=R_3/\{N_0e^{-45.72M}-R_1e^{-27.72M}-R_2e^{-13.55M}\}$$

4-fresh-water smolts:

$$p_1=R_1/\{N_0e^{-19.05M}\}$$
$$p_2=R_2/\{N_0e^{-33.87M}-R_1e^{-14.82M}\}$$
$$p_3=R_3/\{N_0e^{-45.94M}-R_1e^{-26.89M}-R_2e^{-12.06M}\}$$

Using data from tables 3 and 4 to estimate p_1, p_2, and p_3 for each group of marked 3- and 4-fresh-water smolts, and inserting these estimates in equations (14) to (17), we can obtain the average percentages of 3- and 4-fresh-water smolts that mature as 1-, 2-, 3-, and 4-ocean fish. These are shown in table 6.

TABLE 6.—*Estimated average percentages of 3- and 4-fresh-water Karluk River sockeye smolts that mature at different ocean ages, population model 1*

[Each average is based on seven groups of marked fish; effects of marking adjusted by factor of 1.27]

Fresh-water age group	Percent maturing at ocean age:			
	1	2	3	4
	(p'_1)	(p'_2)	(p'_3)	(p'_4)
3	1.35	51.41	45.77	1.47
4	3.34	71.04	24.61	1.01

Approximately one-half of the 3-fresh-water smolts mature by the end of 2 years in the ocean, with most of the remainder maturing after 3 years in the ocean. Nearly 75 percent of the 4-fresh-water smolts mature by the end of the second year of ocean residence.

Total Ocean Mortality Rate For a Given Outmigration

The total ocean mortality rate for a given outmigration of sockeye smolts depends upon the magnitude of the mortality rates for the different ocean age groups and the proportions of seaward migrants that mature after 1, 2, 3, and 4 years of ocean residence. The rate is represented by the expression:

$$a=1-p'_1(1-a_1)-p'_2(1-a_2)-p'_3(1-a_3)-p'_4(1-a_4) \qquad (18)$$

where a_1, a_2, a_3, and a_4 are as shown in column 6 of table 5, and p'_1, p'_2, p'_3, and p'_4 are as shown in table 6. For 3-fresh-water smolts, the average total ocean mortality rate is 73.3 percent, and for 4-fresh-water smolts, the average total ocean mortality rate is 66.5 percent.

POPULATION MODEL 2

Data presented by Ricker (1962), as well as the data shown in figure 1 of this paper, strongly suggest that the ocean mortality of sockeye salmon is greater while the fish are small than it is when they become larger. Accordingly, it seems that a population model that accounts for a decreasing monthly instantaneous natural mortality rate with increasing size of fish, or cumulative time spent in the ocean, probably represents the actual survival conditions of sockeye salmon during their ocean life far better than a population model in which a constant natural mortality rate is assumed. In this section, we will consider a population model in which the monthly instantaneous natural mortality rate is a function of the number of months spent in the ocean by 3- and 4-fresh-water smolts.

The quantities N_0, R_1, R_2, R_3, R_4, p_1, p_2, p_3, p_4, t_1+k_1, t_2+k_2, t_3+k_3, and t_4+k_4 are as defined in Population Model 1. The factor 1.27 is used to adjust for the effects of marking. During the first month of a maximum of t_4+k_4 months of ocean residence, the instantaneous ocean mortality rate is represented by M_1. The instantaneous mortality rate during the second month of ocean residence is represented by M_2 and is assumed to be equal to $(1-d)M_1$, where d is equal to $1/(t_4+k_4)$. The instantaneous mortality rate during the third month of ocean residence is represented by M_3 and is assumed to be equal to $(1-2d)M_1$. In each succeeding month of ocean life, the instantaneous mortality rate is assumed to decrease by the quantity dM_1. The sequence of monthly instantaneous mortality rates is an arithmetic progression.

During month t_x of ocean life, the instantaneous mortality rate, M_{t_x}, is equal to $[M_1-(t_x-1)dM_1]$ or $M_1[1-(t_x-1)d]$. The instantaneous mortality rate for the fraction k_x of month (t_x+1) is $k_xM_1[1-(t_x)d]$. The rate for the remaining fraction $(1-k_x)$ of the month is $(1-k_x)M_1[1-(t_x)d]$. The sum of the monthly instantaneous mortality rates from the first month of ocean life through month t_x is $(t_x/2)(M_1+M_{t_x})$. Upon substitution for M_{t_x} and factoring, this sum is equivalent to $M_1(t_x/2)[2-(t_x-1)d]$. The sum of the monthly instantaneous ocean mortality rates from, say, month (t_1+2) through month t_2 is given by $[(t_2-t_1-1)/2][M_{t_1+2}+M_{t_2}]$. Upon substitution for M_{t_1+2} and M_{t_2} and factoring, this sum is equal to $M_1[(t_2-t_1-1)/2][2-(t_1+t_2)d]$. Thus, the returns of sockeye of different ocean ages are as shown by the following equations:

$$R_1=p_1N_0e^{-1.27M_1\left\{\frac{t_1}{2}[2-(t_1-1)d]+k_1[1-(t_1)d]\right\}} \qquad (19)$$

$$R_2=p_2N_0e^{-1.27M_1\left\{\frac{t_2}{2}[2-(t_2-1)d]+k_2[1-(t_2)d]\right\}} -p_2R_1e^{-1.27M_1\left\{(1-k_1)[1-(t_1)d]+\frac{t_2-t_1-1}{2}[2-(t_1+t_2)d]+k_2[1-(t_2)d]\right\}} \qquad (20)$$

$$R_3=p_3N_0e^{-1.27M_1\left\{\frac{t_3}{2}[2-(t_3-1)d]+k_3[1-(t_3)d]\right\}}-p_3R_1e^{-1.27M_1\left\{(1-k_1)[1-(t_1)d]+\frac{t_3-t_1-1}{2}[2-(t_1+t_3)d]+k_3[1-(t_3)d]\right\}} -p_3R_2e^{-1.27M_1\left\{(1-k_2)[1-(t_2)d]+\frac{t_3-t_2-1}{2}[2-(t_2+t_3)d]+k_3[1-(t_3)d]\right\}} \qquad (21)$$

$$R_4=N_0e^{-1.27M_1\left\{\frac{t_4}{2}[2-(t_4-1)d]+k_4[1-(t_4)d]\right\}}-R_1e^{-1.27M_1\left\{(1-k_1)[1-(t_1)d]+\frac{t_4-t_1-1}{2}[2-(t_1+t_4)d]+k_4[1-(t_4)d]\right\}} -R_2e^{-1.27M_1\left\{(1-k_2)[1-(t_2)d]+\frac{t_4-t_2-1}{2}[2-(t_2+t_4)d]+k_4[1-(t_4)d]\right\}}-R_3e^{-1.27M_1\left\{(1-k_3)[1-(t_3)d]+\frac{t_4-t_3-1}{2}[2-(t_3+t_4)d]+k_4[1-(t_4)d]\right\}} \qquad (22)$$

Equation (22) can be used to solve for M_1 for the 3- and 4-fresh-water smolts by the trial method used in Population Model 1. Values for t_1, k_1, t_2, k_2, t_3, k_3, t_4, and k_4 can be obtained from table 2, and the values for N_0, R_1, R_2, R_3, and R_4 from table 3. For 3-fresh-water smolts, d is equal to 1/47.83 or 0.020907; for 4-fresh-water smolts, d is equal to 1/48.17 or 0.020760. Substitution of the appropriate t-, k-, and d-values in equation (22) yields the following expressions for estimating M_1:

3-fresh-water smolts:

$$R_4 = N_0 e^{-31.00 M_1} - R_1 e^{-15.49 M_1} - R_2 e^{-7.02 M_1} - R_3 e^{-2.01 M_1}$$

4-fresh-water smolts:

$$R_4 = N_0 e^{-31.22 M_1} - R_1 e^{-14.99 M_1} - R_2 e^{-6.38 M_1} - R_3 e^{-2.06 M_1}$$

Estimates of Monthly Instantaneous Mortality Rates

Each of the seven groups of marked 3-fresh-water smolts provides an estimate of the first-month instantaneous ocean mortality rate of Karluk sockeye that migrate to sea in their third year of life. Seven groups of marked 4-fresh-water smolts provide estimates of the first-month instantaneous ocean mortality rate of Karluk sockeye that migrate to sea in their fourth year of life. These estimates, their averages, and the standard deviations of the means are shown in table 7. The marked group numbers associated with the estimates are shown in parentheses.

Using the averages in table 7 as the instantaneous mortality rates of 3- and 4-fresh-water smolts during their first month of ocean residence, we can estimate the mortality rates in any ocean month, m, as follows:

$$M_m = M_1[1-(m-1)d] \qquad (23)$$

TABLE 7.—*Estimates of first-month instantaneous ocean mortality rates for 3- and 4-fresh-water smolts, Karluk River sockeye, population model 2*

[Effects of marking adjusted by factor of 1.27]

Fresh-water age group	First-month instantaneous ocean mortality rate, M_1	Average	Standard deviation of mean
3	0.0720 (1); 0.0695 (5); 0.0700 (9); 0.0575 (13); 0.0648 (16); 0.0545 (19); 0.0660 (23).	0.0649	0.0025
4	0.560 (2); 0.0529 (6); 0.0504 (10); 0.0424 (14); 0.0619 (17); 0.0673 (20); 0.0534 (24).	.0549	.0030

Table 8 gives the instantaneous mortality rates for each month of ocean residence for the two fresh-water age groups.

Mortality Rates of 3- and 4-Fresh-Water Smolts by Ocean Age and Ocean Year

From the estimated monthly instantaneous ocean mortality rates given in table 8, we obtain estimates of the mortality rates for each ocean age group and ocean year as shown in table 9.

The estimated total ocean mortality rates for 3-fresh-water smolts range from 54.7 percent for those fish that mature as 1-ocean sockeye to 79.5 percent for those fish that mature as 4-ocean sockeye. Corresponding estimates for the 4-fresh-water smolts are 50.5 and 74.1 percent respectively.

Under this population model, the annual ocean mortality rates for 3-fresh-water smolts decrease from 54.7 percent during the first year (14.17 months) of ocean residence to 9.8 percent during the fourth year (11.83 months) of ocean residence. For 4-fresh-water smolts, the annual mortality rate decreases from 50.5 percent during the first year of ocean residence to 8.5 percent during

TABLE 8.—*Estimated monthly instantaneous ocean mortality rates for 3- and 4-fresh-water smolts, Karluk River sockeye, population model 2*

Month at sea (m)	Instantaneous mortality rate, fresh-water age group		Month at sea (m)	Instantaneous mortality rate, fresh-water age group		Month at sea (m)	Instantaneous mortality rate, fresh-water age group		Month at sea (m)	Instantaneous mortality rate, fresh-water age group	
	3	4		3	4		3	4		3	4
1	0.0649	0.0549	13	0.0486	0.0412	25	0.0323	0.0275	37	0.0160	0.0139
2	.0635	.0538	14	.0473	.0401	26	.0310	.0264	38	.0147	.0127
3	.0622	.0526	15	.0459	.0389	27	.0296	.0253	39	.0133	.0116
4	.0608	.0515	16	.0445	.0378	28	.0283	.0241	40	.0120	.0104
5	.0595	.0503	17	.0432	.0367	29	.0269	.0230	41	.0106	.0093
6	.0581	.0492	18	.0418	.0355	30	.0256	.0218	42	.0093	.0082
7	.0568	.0481	19	.0405	.0344	31	.0242	.0207	43	.0079	.0070
8	.0554	.0469	20	.0391	.0332	32	.0228	.0196	44	.0066	.0059
9	.0540	.0458	21	.0378	.0321	33	.0215	.0184	45	.0052	.0048
10	.0527	.0446	22	.0364	.0310	34	.0201	.0173	46	.0038	.0036
11	.0513	.0435	23	.0350	.0298	35	.0188	.0161	47	.0025	.0025
12	.0500	.0424	24	.0337	.0287	36	.0174	.0150	48	.0011	.0013
									49		.0002

TABLE 9.—*Estimated ocean mortality rates for each ocean age group and ocean year, 3- and 4-fresh-water smolts, Karluk River sockeye, population model 2*

[Effects of marking adjusted by factor of 1.27]

Fresh water age group	Ocean age	Duration of ocean residence	Total instantaneous mortality rate	Total ocean mortality rate (a_x)	Duration of ocean year	Instantaneous mortality rate during year	Annual ocean mortality rate (a'_x)
	Years	*Months*		*Percent*	*Months*		*Percent*
3	1	14.17	0.7929	54.7	14.17	0.7929	54.7
	2	25.33	1.2255	70.6	11.16	.4326	35.1
	3	36.00	1.4815	77.3	10.67	.2560	22.6
	4	47.83	1.5843	79.5	11.83	.1028	9.8
4	1	15.00	.7038	50.5	15.00	.7038	50.5
	2	26.67	1.0739	65.8	11.67	.3701	30.9
	3	36.17	1.2606	71.6	9.50	.1867	17.0
	4	48.17	1.3494	74.1	12.00	.0888	8.5

the fourth year of ocean residence. Most of the ocean mortality takes place during the first 14 or 15 months of ocean residence according to the estimates given in table 9.

MATURITY SCHEDULES

The maturity schedules for 3- and 4-fresh-water smolts under Population Model 2 are estimated by the procedure described under Population Model 1. Factorization and transposition of terms in equations (19) to (21) and substitution of appropriate values for the terms and sums of the arithmetic progressions in the exponents of these equations provide the following expressions for the proportions of surviving 1-, 2-, and 3-ocean sockeye that mature at the end of the first, second, and third years of ocean life:

3-fresh-water smolts:

$$p_1 = R_1/[N_0 e^{-15.52M_1}]$$
$$p_2 = R_2/[N_0 e^{-23.98M_1} - R_1 e^{-8.47M_1}]$$
$$p_3 = R_3/[N_0 e^{-28.99M_1} - R_1 e^{-13.48M_1} - R_2 e^{-5.01M_1}]$$

4-fresh-water smolts:

$$p_1 = R_1/[N_0 e^{-16.28M_1}]$$
$$p_2 = R_2/[N_0 e^{-24.84M_1} - R_1 e^{-8.56M_1}]$$
$$p_3 = R_3/[N_0 e^{-29.16M_1} - R_1 e^{-12.83M_1} - R_2 e^{-4.32M_1}]$$

Using data from tables 3 and 7 in the above expressions to obtain estimates of p_1, p_2, and p_3 for each group of marked 3- and 4-fresh-water smolts and inserting the resulting p-values in equations (14) to (17), we can obtain the average percentages of 3- and 4-fresh-water smolts that mature as 1-, 2-, 3-, and 4-ocean sockeye under Population Model 2. The average percentages are shown in table 10.

Under Population Model 2, slightly higher proportions (approximately 4 to 7 percent) of the

TABLE 10.—*Estimated average percentages of 3- and 4-fresh-water Karluk River sockeye smolts that mature at different ocean ages, population model 2*

[Each average is based on seven groups of marked fish; effects of marking adjusted by factor of 1.27]

Fresh-water age group	Percent maturing at ocean age:			
	1	2	3	4
	(p'_1)	(p'_2)	(p'_3)	(p'_4)
3	1.63	57.74	39.83	0.80
4	3.89	74.48	21.14	.49

3- and 4-fresh-water smolts mature by the end of 2 years of ocean life than under Population Model 1. The differences between the maturity schedules under Population Models 1 and 2 result from differences in the distribution of ocean mortality.

Total Ocean Mortality Rate for a Given Outmigration

The ocean mortality rate for a given outmigration of sockeye is the same under Population Model 2 as it was under Population Model 1. This rate is fixed, in our estimates, by the ratios of marked fish returning to those released. Redistribution of the monthly instantaneous ocean mortality rates does not affect it.

POPULATION MODEL 3

Population Models 1 and 2 deal with what might be considered as two extreme situations with regard to the temporal distribution of ocean mortality of Karluk sockeye. In one case we considered ocean mortality to be constant throughout the period of ocean residence. In the other case we considered ocean mortality to decrease continually throughout the period of ocean residence, becoming zero at the end of 4 years. In view of the evidence which suggests that the ocean mortality rate of sockeye is greater while they are small than it is when they become larger and in view of the lack of evidence that the ocean mortality rate continually decreases and becomes zero after an extended period of time, it seems worthwhile to examine what is intended to be an intermediate situation, one that we will consider under Population Model 3.

In this model it is assumed that the monthly instantaneous mortality rate decreases geometrically during the first 6 months of ocean residence such that M_2, the second-month mortality rate, is equal to $0.5M_1$, where M_1 is the first-month mortality rate; M_3, the third-month mortality rate, is equal to $0.5M_2$ or $0.25M_1$; M_4, the fourth-month mortality rate, is equal to $0.5M_3$ or $0.125M_1$; M_5, the fifth-month mortality rate, is equal to $0.5M_4$ or $0.0625M_1$; and M_6, the sixth-month mortality rate, is equal to $0.5M_5$ or $0.03125M_1$. It is further assumed that the instantaneous mortality rate during the seventh and each succeeding month of ocean residence is equal to M_6 or $0.03125M_1$.

The sum of the monthly instantaneous mortality rates during the first 6 months of ocean residence is $M_1+0.5M_1+0.25M_1+\ldots+0.03125M_1$, or $1.96875M_1$. The sum of the monthly instantaneous mortality rates during any number of months after the sixth month of ocean residence is the product of the number of months involved and $0.03125M_1$.

The quantities N_0, R_1, R_2, R_3, R_4, p_1, p_2, p_3, p_4, t_1+k_1, t_2+k_2, t_3+k_3, and t_4+k_4 are as defined in the previous models. The factor 1.27 is used to adjust for the effects of marking. Thus, the returns of sockeye of different ocean ages are as shown by the following equations:

$$R_1=p_1N_0e^{-1.27M_1[1.96875+(t_1+k_1-6)(0.03125)]} \quad (24)$$

$$R_2=p_2N_0e^{-1.27M_1[1.96875+(t_2+k_2-6)(0.03125)]} - p_2R_1e^{-1.27M_1[(t_2+k_2)-(t_1+k_1)](0.03125)} \quad (25)$$

$$R_3=p_3N_0e^{-1.27M_1[1.96875+(t_3+k_3-6)(0.03125)]} - p_3R_1e^{-1.27M_1[(t_3+k_3)-(t_1+k_1)](0.03125)} - p_3R_2e^{-1.27M_1[(t_3+k_3)-(t_2+k_2)](0.03125)} \quad (26)$$

$$R_4=N_0e^{-1.27M_1[1.96875+(t_4+k_4-6)(0.03125)]} - R_1e^{-1.27M_1[(t_4+k_4)-(t_1+k_1)](0.03125)} - R_2e^{-1.27M_1[(t_4+k_4)-(t_2+k_2)](0.03125)} - R_3e^{-1.27M_1[(t_4+k_4)-(t_3+k_3)](0.03125)} \quad (27)$$

Equation (27) is used to solve for M_1 for the 3- and 4-fresh-water smolts by the trial method mentioned previously. Substitution of the appropriate t- and k-values in equation (27) yields the following expressions for estimating M_1:

3-fresh-water smolts:

$$R_4=N_0e^{-4.16M_1}-R_1e^{-1.34M_1}-R_2e^{-0.89M_1}-R_3e^{-0.47M_1}$$

4-fresh-water smolts:

$$R_4=N_0e^{-4.17M_1}-R_1e^{-1.32M_1}-R_2e^{-0.85M_1}-R_3e^{-0.48M_1}$$

TABLE 11.—*Estimates of first-month instantaneous ocean mortality rates for 3- and 4-fresh-water smolts, Karluk River sockeye, population model 3*

[Effects of marking adjusted by factor of 1.27]

Fresh-water age	First-month instantaneous ocean mortality rate, M^1	Average	Standard deviation of mean
3	0.5224 (1); 0.5230 (5); 0.5279 (9); 0.4410 (13); 0.4870 (16); 0.4140 (19); 0.4976 (23).	0.4876	0.0167
4	0.4138 (2); 0.3953 (6); 0.3746 (10); 0.3181 (14); 0.4669 (17); 0.5114 (20); 0.4063 (24)	.4123	.0236

Estimates of Monthly Instantaneous Ocean Mortality Rates

Each of the seven groups of marked 3-fresh-water smolts and the seven groups of marked 4-fresh-water smolts (table 3) provides an estimate of the first-month instantaneous ocean mortality rate of Karluk sockeye that migrate to sea in their third and fourth years of life. These estimates, their averages, and the standard deviations of the means, are shown in table 11. The marked group numbers associated with the estimates are shown in parentheses.

Using the averages in table 11 as the instantaneous mortality rates of 3- and 4-fresh-water smolts during their first month of ocean residence, we can obtain estimates of the mortality rates during the second through sixth months of ocean residence under Population Model 3 by multiplying M_1 by 0.5, 0.25, 0.125, 0.0625, and 0.03125, respectively. Table 12 gives the instantaneous mortality rates for each month of ocean residence for the two fresh-water age groups.

Mortality Rates of 3- and 4-Fresh-Water Smolts by Ocean Age and Ocean Year

From the estimated monthly instantaneous ocean mortality rates given in table 12, we obtain estimates of the mortality rates for each ocean age group and ocean year as shown in table 13.

TABLE 12.—*Estimated monthly instantaneous ocean mortality rates 3- and 4-fresh-water smolts, Karluk River sockeye, population model 3*

Month at sea	Instantaneous mortality rate	
	3-fresh-water fish	4-fresh-water fish
1st	0.4876	0.4123
2d	.2438	.2062
3d	.1219	.1031
4th	.0610	.0515
5th	.0305	.0258
6th and each succeeding month	.0152	.0129

TABLE 13.—*Estimated ocean mortality rates for each ocean age group and ocean year, 3- and 4-fresh-water smolts, Karluk River sockeye, population model 3.*

[Effects of marking adjusted by factor of 1.27]

Fresh water age group	Ocean age	Duration of ocean residence in months	Total instantaneous mortality rate	Total ocean mortality rate (a_x)	Duration of ocean year	Instantaneous mortality rate during year	Annual ocean mortality rate (a'_x)
	Years	*Months*		*Percent*	*Months*		*Percent*
3	1	14.17	1.0842	66.2	14.17	1.0842	66.2
	2	25.33	1.2538	71.4	11.16	.1696	15.6
	3	36.00	1.4160	75.7	10.67	.1622	15.0
	4	47.83	1.5958	79.7	11.83	.1798	16.4
4	1	15.00	.9279	60.5	15.00	.9279	60.5
	2	26.67	1.0784	66.0	11.67	.1505	14.0
	3	36.17	1.2010	69.9	9.50	.1226	11.5
	4	48.17	1.3558	74.2	12.00	.1548	14.3

The estimated total ocean mortality rates for 3-fresh-water smolts range from 66.2 percent for those fish that mature as 1-ocean sockeye to 79.7 percent for those fish that mature as 4-ocean sockeye. Corresponding estimates for the 4-fresh-water smolts, under this model, are 60.5 and 74.2 percent, respectively.

The annual ocean mortality rates for 3-fresh-water smolts decrease from 66.2 percent during the first year of ocean residence to 16.4 percent during the fourth year of ocean life. For 4-fresh-water smolts, the annual ocean mortality rate decreases from 60.5 percent during the first year of ocean life to 11.5 percent during the third year of ocean life and then increases to 14.3 percent during the longer fourth year of ocean residence.

Under this model, most of the ocean mortality takes place during the first 6 months of ocean residence.

Maturity Schedules

Factorization and transposition of terms in equations (24) to (26) and substitution of appropriate *t*- and *k*- values in the exponents of these equations provide the following expressions for the proportions of surviving 1-, 2-, and 3-ocean sockeye that mature at the end of the first, second, and third years of ocean life:

3-fresh-water smolts:

$$p_1 = R_1/[N_o e^{-2.82M_1}]$$
$$p_2 = R_2/[N_o e^{-3.27M} - R_1 e^{-0.44M_1}]$$
$$p_3 = R_3/[N_o e^{-3.69M_1} - R_1 e^{-0.87M_1} - R_2 e^{-0.42M_1}]$$

4-fresh-water smolts:

$$p_1 = R_1/[N_o e^{-2.86M_1}]$$
$$p_2 = R_2/[N_o e^{-3.32M_1} - R_1 e^{-0.46M_1}]$$
$$p_3 = R_3/[N_o e^{-3.70M_1} - R_1 e^{-0.84M_1} - R_2 e^{-0.38M_1}]$$

Using data from tables 3 and 11 in the foregoing expressions to obtain estimates of p_1, p_2, and p_3 for each group of marked 3- and 4-fresh-water smolts and inserting the resulting *p*-values in equations (14) to (17), we can obtain the average percentages of 3- and 4-fresh-water smolts that mature as 1-, 2-, 3-, and 4-ocean sockeye under Population Model 3. The average percentages are shown in table 14.

TABLE 14.—*Estimated average percentages of 3- and 4-fresh-water Karluk River sockeye smolts that mature at different ocean ages, population model 3*

[Each average is based on seven groups of marked fish; effects of marking adjusted by factor of 1.27]

Fresh-water age group	Percent maturing at ocean age:			
	1	2	3	4
	(p'_1)	(p'_2)	(p'_3)	(p'_4)
3	2.35	59.78	37.05	0.82
4	5.15	74.75	19.62	.48

Under this population model, approximately 2 or 3 percent more of the 3- and 4-fresh-water smolts mature by the end of the second year of ocean life than under Population Model 2.

POPULATION MODEL 4

It might be hypothesized that the difference between the ocean mortality rates of 3- and 4-fresh-water sockeye smolts is caused by some survival condition which operates differentially on small (3-fresh-water) and large (4-fresh-water) smolts early in the ocean lives of these fish, say, during the first month of ocean residence and that the mortality rate during succeeding months of ocean life is the same for the two fresh-water age groups. If this is the case, it would seem to follow that the first-month ocean mortality rates for both fresh-water age groups would be great in comparison with the mortality rates during the second and succeeding months of ocean life. In this section, we will consider a population model that simulates these survival conditions.

It is assumed that the first-month instantaneous ocean mortality rate of 4-fresh-water smolts, M_{1_4}, is 20 times M_{2_4}, their instantaneous mortality rate during the second and each succeeding month of ocean residence. The first-month instantaneous ocean mortality rate of 3-fresh-water smolts is represented by M_{1_3} or cM_{1_4}, where c measures the differential mortality caused by some survival condition. The mortality rate of 3-fresh-water smolts during the second and each succeeding month of ocean residence is assumed to be the same as for 4-fresh-water smolts, that is M_{2_4}, or 0.05 M_{1_4}.

The quantities N_0, R_1, R_2, R_3, R_4, p_1, p_2, p_3, p_4, t_1+k_1, t_2+k_2, t_3+k_3, and t_4+k_4 are as previously defined. The factor 1.27 is used to adjust for the effects of marking. Hence, the returns from the 4-fresh-water smolt migrations are as shown by the following expressions:

$$R_1=p_1N_0e^{-1.27M_{1_4}[1+(t_1+k_1-1)(0.05)]} \quad (28)$$

$$R_2=p_2N_0e^{-1.27M_{1_4}[1+(t_2+k_2-1)(0.05)]} - p_2R_1e^{-1.27M_{1_4}(0.05)[(t_2+k_2)-(t_1+k_1)]} \quad (29)$$

$$R_3=p_3N_0e^{-1.27M_{1_4}[1+(t_3+k_3-1)(0.05)]} - p_3R_1e^{-1.27M_{1_4}(0.05)[(t_3+k_3)-(t_1+k_1)]} - p_3R_2e^{-1.27M_{1_4}(0.05)[(t_3+k_3)-(t_2+k_2)]} \quad (30)$$

$$R_4=N_0e^{-1.27M_{1_4}[1+(t_4+k_4-1)(0.05)]} - R_1e^{-1.27M_{1_4}(0.05)[(t_4+k_4)-(t_1+k_1)]} - R_2e^{-1.27M_{1_4}(0.05)[(t_4+k_4)-(t_2+k_2)]} - R_3e^{-1.27M_{1_4}(0.05)[(t_4+k_4)-(t_3+k_3)]} \quad (31)$$

The returns of 1-, 2-, 3-, and 4-ocean fish from the 3-fresh-water smolt migrations are represented by equations identical to (28) through (31) respectively except that c, rather than 1, appears as the first term inside the bracketed portion of the first exponent of each equation. Thus, the returns of 4-ocean fish from the 3-fresh-water smolts migrations are represented as follows:

$$R_4=N_0e^{-1.27M_{1_4}[c+(t_4+k_4-1)(0.05)]} - R_1e^{-1.27M_{1_4}(0.05)[(t_4+k_4)-(t_1+k_1)]} - R_2e^{-1.27M_{1_4}(0.05)[(t_4+k_4)-(t_2+k_2)]} - R_3e^{-1.27M_{1_4}(0.05)[(t_4+k_4)-(t_3+k_3)]} \quad (32)$$

Equation (31) is used to solve for the first-month instantaneous ocean mortality rate for the 4-fresh-water smolts by the trial method used in previous population models. Substitution of appropriate t- and k-values from table 2 reduces equation (31) to the following expression:

$$R_4=N_0e^{-4.26M_{1_4}}-R_1e^{-2.11M_{1_4}} - R_2e^{-1.36M_{1_4}}-R_3e^{-0.76M_{1_4}}$$

Estimates of Monthly Instantaneous Ocean Mortality Rates

Each of seven groups of marked 4-fresh-water smolts (table 3) provides an estimate of the first-month instantaneous ocean mortality rate of Karluk sockeye that migrate to sea in their fourth year of life. These estimates, their average, and the standard deviation of the mean are shown in table 15. The marked group numbers associated with the estimates are given in parentheses.

TABLE 15.—*Estimates of first-month instantaneous ocean mortality rates for 4-fresh-water Karluk River sockeye smolts, population model 4*

[Effects of marking adjusted by factor of 1.27]

First-month instantaneous ocean mortality rate, M_{1_4}	Average, $\overline{M}_{1_4}$	Standard deviation of mean
0.4734 (2); 0.4501 (6); 0.4290 (10); 0.3608 (14); 0.5212 (17); 0.5656 (20); 0.4522 (24).	0.4646	0.0248

Based on the average first-month instantaneous ocean mortality rate of 0.4646, the estimated mortality rate of 4-fresh-water (and 3-fresh-water) smolts during the second and each succeeding month of ocean residence is 0.05 times 0.4646 or 0.0232.

Inserting the estimate of $\overline{M}_{1_4}$ and appropriate t- and k-values in equation (32), we obtain the following expression for the returns of 4-ocean fish from the seaward migrations of 3-fresh-water smolts:

$$R_4=N_0e^{-0.59c}e^{-1.38}-R_1e^{-0.99}-R_2e^{-0.66}-R_3e^{-0.35}$$

Transposing terms and taking logarithms, we obtain the following expression for c:

$$c=\ln\{[R_4+R_1e^{-0.99}+R_2e^{-0.66}+R_3e^{-0.35}]/N_0e^{-1.38}\}/-0.59$$

Each of seven groups of marked 3-fresh-water smolts (table 3) provides an estimate of c. Each estimate of c, in turn, can be multiplied by M_{1_4} to furnish an estimate of M_{1_3}, the first-month instantaneous ocean mortality rate for 3-fresh-water sockeye smolts. Table 16 shows the estimates of c and M_{1_3} for each marked group, the average first-month instantaneous ocean mortality rate, and the standard deviation of the mean mortality rate.

TABLE 16.—*Estimates of first-month instantaneous ocean mortality rates of 3-fresh-water Karluk River sockeye smolts, population model 4*

[Effects of marking adjusted by factor of 1.27]

Marked group No.	Coefficient of differential mortality, c	First-month instantaneous ocean mortality rate, M_{13}
1	1.67	0.7759
5	1.62	.7526
9	1.65	.7666
13	1.09	.5064
16	1.41	.6551
19	.95	.4414
23	1.47	.6830
Averages	1.41	0.6544
Standard deviation of mean mortality rate		.0500

Based on the averages given in table 16, the first month instantaneous ocean mortality rate of 3-fresh-water smolts is approximately 40 percent greater than the corresponding rate for 4-fresh-water smolts and about 28 times (1.41×20 or 0.6544/0.0232) greater than the instantaneous mortality rate during the second and each succeeding month of ocean residence for 3- and 4-fresh-water smolts.

Mortality Rates of 3- and 4-Fresh-Water Smolts by Ocean Age and Ocean Year

From the average first-month instantaneous ocean mortality rates given in tables 15 and 16, we obtain estimates of the mortality rates for each ocean age group and ocean year as shown in table 17.

TABLE 17.—*Estimated ocean mortality rates for each ocean age group and ocean year, 3- and 4-fresh-water smolts, Karluk River sockeye, population model 4*

[Effects of marking adjusted by factor of 1.27]

Fresh water age group	Ocean age	Duration of ocean residence	Total instantaneous mortality rate	Total ocean mortality rate (a_x)	Duration of ocean year	Instantaneous mortality rate during year	Annual ocean mortality rate (a'_x)
	Years	*Months*		*Percent*	*Months*		*Percent*
3	1	14.17	0.9599	61.7	14.17	0.9599	61.7
	2	25.33	1.2189	70.4	11.16	.2589	22.8
	3	36.00	1.4664	76.9	10.67	.2475	21.9
	4	47.83	1.7408	82.5	11.83	.2745	24.0
4	1	15.00	.7894	54.6	15.00	.7894	54.6
	2	26.67	1.0601	65.4	11.67	.2707	23.7
	3	36.17	1.2805	72.2	9.50	.2204	19.8
	4	48.17	1,5589	79.0	12.00	.2784	24.3

The estimated total ocean mortality rates range from 61.7 percent for those 3-fresh-water smolts that mature as 1-ocean fish to 82.5 percent for those that mature as 4-ocean sockeye. Corresponding estimates for the 4-fresh-water smolts are 54.6 and 79.0 percent, respectively.

The annual ocean mortality rates for 3-fresh-water smolts decrease from 61.7 percent during the first year of ocean life to about 22 to 24 percent during each of the last 3 years of ocean residence. For 4-fresh-water smolts, the annual ocean mortality rate decreases from 54.6 percent during the first year of ocean life to about 20 to 24 percent during each of the succeeding years.

Under this model, of course, most of the ocean mortality takes place during the first month of ocean residence.

Maturity Schedules

Expressions for the proportions of surviving 1-, 2-, and 3-ocean sockeye that mature at the end of the first, second, and third years of ocean life can be obtained from equations (28) to (30) for 4-fresh-water smolts and from analogous equations (not shown in the text) for 3-fresh-water smolts. These expressions, after substitution of appropriate t- and k-values, are as follows:

3-fresh-water smolts:

$$p_1 = R_1/[N_0 e^{-1.27M_{14}(c+0.6585)}]$$
$$p_2 = R_2/[N_0 e^{-1.27M_{14}(c+1.2165)} - R_1 e^{-0.7087M_{14}}]$$
$$p_3 = R_3/[N_0 e^{-1.27M_{14}(c+1.7500)} - R_1 e^{-1.3862M_{14}} - R_2 e^{-0.6775M_{14}}]$$

4-fresh-water smolts:

$$p_1 = R_1/[N_0 e^{-2.1590M_{14}}]$$
$$p_2 = R_2/[N_0 e^{-2.9000M_{14}} - R_1 e^{-0.7410M_{14}}]$$
$$p_3 = R_3/[N_0 e^{-3.5033M_{14}} - R_1 e^{-1.3443M_{14}} - R_2 e^{-0.6032M_{14}}]$$

Using data from tables 3, 15, and 16 in the above expressions to obtain estimates of p_1, p_2, and p_3 for each group of marked 3- and 4-fresh-water smolts, and inserting the resulting p-values in equations (14) to (17), we can obtain the average percentages of 3- and 4-fresh-water smolts that mature as 1-, 2-, 3-, and 4-ocean sockeye under Population Model 4. The average percentages are shown in table 18.

TABLE 18.—*Estimated average percentages of 3- and 4-fresh-water Karluk River sockeye smolts that mature at different ocean ages, population model 4*

[Each average is based on seven groups of marked fish; effects of marking adjusted by factor of 1.27]

Fresh-water age group	Percent maturing at ocean age: 1 (p'_1)	2 (p'_2)	3 (p'_3)	4 (p'_4)
3	2.11	57.30	39.59	1.00
4	4.34	73.36	21.61	.69

The maturity schedules of 3- and 4-fresh-water smolts under this population model are very similar to those under Population Model 2.

COMPARISON OF OCEAN MORTALITY RATES

The estimated average monthly instantaneous mortality rates during the different years of ocean life of 3- and 4-fresh-water Karluk sockeye smolts under the four population models are compared in figures 2 and 3. Similar comparisons of the annual ocean mortality rates are given in figures 4 and 5.

The mortality rates obtained under Population Model 1 are lower during the first year of ocean life than those obtained under the other three models. The situation is reversed in the second year. In the third and fourth years of ocean residence, the mortality rates under Population Models 2, 3, and 4 are considerably lower than those obtained under Population Model 1. The

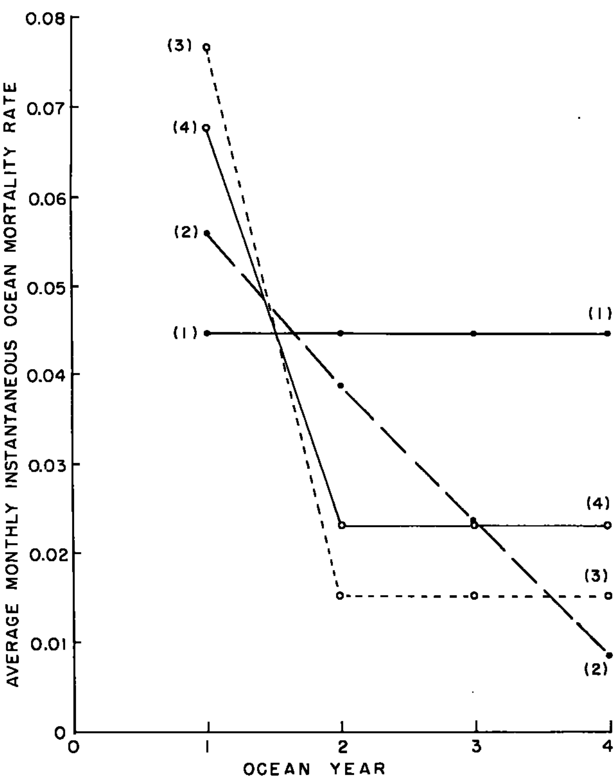

FIGURE 2.—Estimated average monthly instantaneous ocean mortality rates of 3-fresh-water Karluk River sockeye smolts under Population Models 1, 2, 3, and 4. (Data from tables 5, 9, 13, and 17.)

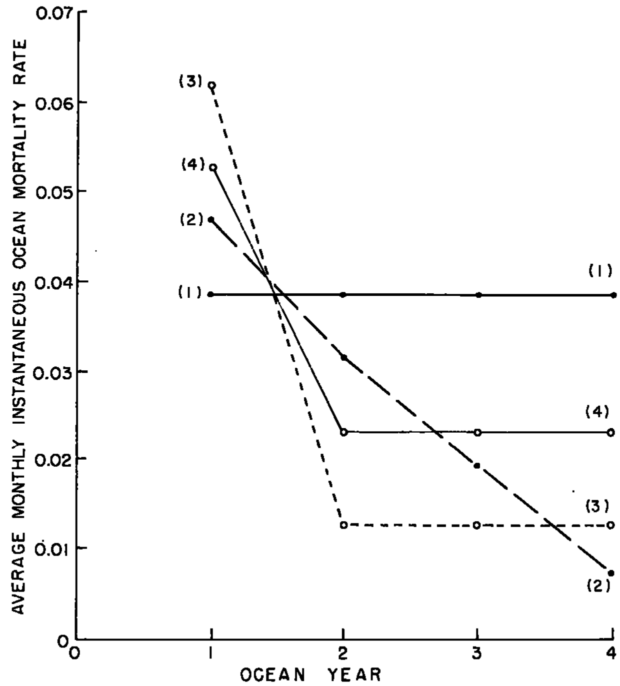

FIGURE 3.—Estimated average monthly instantaneous ocean mortality rates of 4-fresh-water Karluk sockeye smolts under Population Models 1, 2, 3, and 4. (Data from tables 5, 9, 13, and 17.)

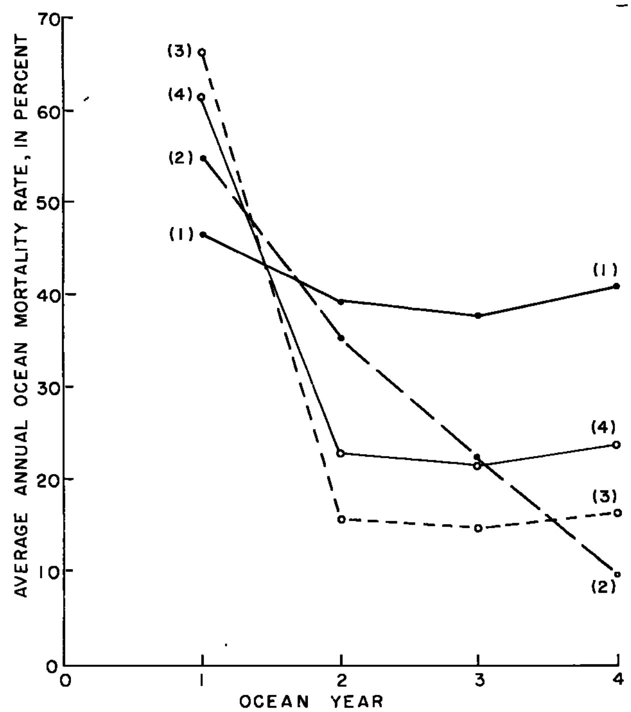

FIGURE 4.—Estimated average annual ocean mortality rates of 3-fresh-water Karluk sockeye smolts under Population Models 1, 2, 3, and 4. (Data from tables 5, 9, 13, and 17.)

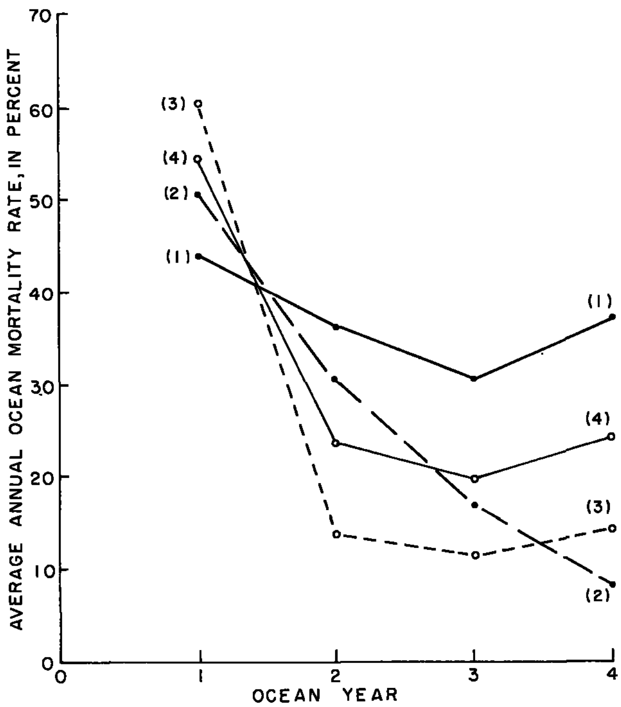

FIGURE 5.—Estimated average annual ocean mortality rates of 4-fresh-water Karluk sockeye smolts under Population Models 1, 2, 3, and 4. (Data from tables 5, 9, 13, and 17.)

mortality rates during the first 3 years of ocean life are of principal interest, since only a minor fraction of the sockeye spend 4 years in the ocean.

DISCUSSION OF OCEAN MORTALITY RATES

The accuracy of the ocean mortality rate estimates presented here depends on the accuracy of the basic data used in the four population models and the validity of certain assumptions carried in the different models.

The numbers of sockeye in each marked group released were determined by counting the individual fish from which fins were removed. Since each marked fish was handled in the process of fin excision, the counting errors can be considered negligible.

The age composition of the marked smolts was estimated for each day of marking. Judging from Barnaby's report (1944, p. 272 and table 26), from 65 to 200 fish were sampled each day for this purpose. Seasonal total sample sizes ranged from about 1,000 to 2,000 fish. From this it would appear that the percentage error in the estimated numbers of marked smolts of a given fresh-water age in any experiment was quite small, probably less than 2 or 3 percent.

In an attempt to minimize any bias caused, for example, by early-running smolts of a given fresh-water age returning as late-running adults in subsequent seasons (or, as another example, late-running smolts of a given fresh-water age returning as early-running adults in subsequent seasons), smolts were marked throughout the period of seaward migration, and sampling for returning marked adults was carried out rigorously. It was found that the percentage occurrence of returning marked fish of each age group was fairly constant throughout the season (Barnaby, 1944, p. 282). This indicates that proportionate numbers of early-, middle-, and late-running adults of a given fresh-water age had been marked as smolts.

Enumeration of returns of marked fish involved sampling as large a portion as possible of each day's catch taken near the mouth of the Karluk River by beach seine, a type of gear generally considered to be relatively nonselective with respect to age or size of fish. The numbers of sockeye of pertinent ocean ages that were examined for marks from 1930 to 1937, together with the sampling ratios, can be calculated from Barnaby's tables 33, 34, 37, 39, and 43 and are as follows:

Year of sampling for marked fish	Ocean age groups of marked fish occurring in indicated year of sampling (Year of smolt migration shown in parentheses)	Estimated fish of indicated ocean ages in total run in year of sampling	Estimated fish of indicated ocean ages examined for marks	Mark sampling ratio
		Number	*Number*	*Percent*
1930	1 (1929)	182,053	891	0.5
1931	1 (1930); 2 (1929)	1,501,886	210,920	14.0
1932	1 (1931); 2 (1930); 3 (1929)	1,412,179	159,279	11.3
1933	1 (1932); 2 (1931); 3 (1930); 4 (1929).	1,812,577	178,080	9.8
1934	1 (1933), 2 (1932), 3 (1931); 4 (1930).	2,064,190	311,730	15.1
1935	2 (1933); 3 (1932); 4 (1931)	1,407,551	151,321	10.8
1936	3 (1933); 4 (1932)	330,985	41,257	12.5
1937	4 (1933)	0	0	--------

Except for 1930, approximately 10 to 15 percent of each year's total run of sockeye of the pertinent ocean age groups was examined for marks. The low sampling ratio in 1930 might account for the relatively large numbers of marked 1-ocean sockeye that were estimated to have returned from the 1929 releases of 3- and 4-fresh-water smolts.

The number of marked fish returning to the Karluk River were estimated on a weekly basis from catch statistics, weir counts, age composition of sockeye in the catch and escapement, and the proportions of marked fish occurring in the catch samples examined.

Judging from the large numbers of fish examined for marks (except in 1930), it is likely that the statistical errors involved in applying the sample ratios of marked-to-unmarked fish to the total run are very small. A procedural error, however, might have been introduced by misallocation of sockeye catches made in waters along the northwest coast of Kodiak Island. Misallocation of Karluk sockeye to other river systems would result in underestimates of the numbers of marked fish returning to the Karluk River and overestimates of ocean mortality. Misallocation of sockeye of other systems to the Karluk runs, on the other hand, would result in overestimates of the numbers of marked fish returning to the Karluk River and underestimates of ocean mortality.

On the basis of a tagging experiment on the western shore of Uganik Bay on Kodiak Island in 1927 (Rich and Morton, 1929), Barnaby (1944) considered all sockeye caught along the Kodiak Island coast between Cape Karluk (about 3 miles west of the mouth of the Karluk River) and West Point (about 6 miles inside the western shore of Uganik Bay and about 75 miles northeasterly from the mouth of the Karluk River) to have been fish originating in the Karluk River. Rich and Morton's study shows that some of the sockeye tagged in Uganik Bay were destined to areas other than the Karluk River. This indicates that some sockeye were misallocated to the Karluk runs by Barnaby's procedure. The extent to which this probable misallocation is compensated for by the allocation of Karluk sockeye caught outside the Cape Karluk-West Point area to other river systems cannot be accurately assessed. There is, however, some information available on this matter from unpublished catch statistics, tagging studies conducted in the late 1940's (Bevan, 1962), and escapement counts.

Donald E. Power and I have made a compilation of sockeye catch statistics for the Cape Karluk-West Point area for the years from 1930 to 1936. This compilation showed that approximately 70 percent of the total sockeye catch assigned to the Karluk River from 1930 to 1936 was taken between Cape Karluk and Cape Uyak, about 8 miles northeast of the mouth of the Karluk River. Thus, the bulk of the sockeye catch assigned to the Karluk River was taken within a relatively short distance from the mouth of the river.

Bevan (1962) shows that only a relatively small proportion of sockeye tagged in the area between Cape Karluk and Cape Uyak in 1948 was recovered in areas other than the Karluk River or near its mouth. This indicates that the great majority of sockeye caught in the Cape Karluk-Cape Uyak area were Karluk fish.

During the years 1930–36, when marked sockeye were returning to the Karluk River, approximately 60 percent of the estimated total Karluk sockeye runs consisted of fish that passed through the counting weir in the Karluk River. Thus, if all of the sockeye caught between Cape Karluk and Cape Uyak are considered to have originated in the Karluk River, those catches plus the escapements would account for about 88 percent (60 percent plus 0.7 times 40 percent) of the estimated total Karluk sockeye runs between 1930 and 1936. Of the remaining portion of the estimated total runs, that is, the sockeye caught between Cape Uyak and West Point, Rich and Morton (1929) show that a large proportion of the fish taken inside the mouth of Uganik Bay are Karluk sockeye. Bevan (1962) also shows that large proportions of the sockeye taken in the Cape Uyak-West Point area originate in the Karluk River.

That Barnaby's procedure for allocating catches to the Karluk sockeye runs likely resulted in a misallocation of Karluk fish to other river systems is indicated by the results of tagging experiments reported by Bevan (1962). Those experiments showed that large proportions of sockeye tagged outside the Cape Karluk-West Point area, namely, off Afognak Island in 1948 and off Uganik, Raspberry, and Afognak Islands in 1949, were fish that originated in the Karluk River. Bevan reports that from sockeye tagging at a wide variety of locations along the northwest coast of Kodiak Island, the Karluk system accounted for about 90 percent of the stream recoveries made on that coast.

On the basis of the foregoing information, it is reasonable to conclude that relatively small proportions of the estimated total Karluk sockeye runs from 1930 to 1936 consisted of fish originating in other river systems and that these small proportions were offset or more than offset by misallocation of Karluk sockeye to other systems.

A source of mechanical error in the estimates of marked sockeye returning to the Karluk River is the failure to detect all of the marked fish in the catch samples that were examined. No measure of such error is available for the Karluk experiments. It is an error, however, that is generally recognized to occur in marking studies. Such an error results in underestimates of numbers of marked fish returning and overestimates of ocean mortality rates.

The estimated durations of ocean residence probably contain some error. The errors, however, cannot be great since the smolts migrate to sea within a matter of a few weeks, and the estimated dates on which 50 percent of the fish in the different age groups return to the Karluk River are based on data for 27 years. In any event, an error of 1 or 2 months in estimating the durations of ocean residence would not affect the estimates of mortality very much.

The factor used to adjust for the effects of marking on survival perhaps should be some quantity other than 1.27. Just what, if any, alternative factor should be used is difficult to say, although it is highly unlikely that it should be less than 1.0. If no adjustment is made for the effects of marking, the instantaneous ocean mortality rates would be 1.27 times those rates obtained in the four population models. If the adjustment for marking mortality is increased, the instantaneous ocean mortality rates obtained in the four population models would be reduced. As Ricker (1962) points out, there is no theoretical upper limit that the adjustment can have.

If it is assumed that mortality due to marking takes place within a very short period of time after the marked fish are released, an adjustment for such mortality can be obtained from the ratio of percentage returns of marked and unmarked smolts. Although a considerable amount of evidence indicates that marked sockeye smolts suffer practically no mortality while being held for observation (Barnaby, 1944, and Foerster, 1937), I have estimated, for comparative purposes, the average monthly instantaneous ocean mortality rates of 3- and 4-fresh-water Karluk sockeye smolts, assuming an initial marking mortality of 60 percent and a constant ocean mortality rate. The estimate of initial loss is taken from data presented by Foerster (1934, 1936, and 1937) and as shown by Ricker (1962, table E, Appendix II). The average monthly instantaneous ocean mortality rates for the two fresh-water age groups of Karluk sockeye are approximately 0.026 and 0.017 which are considerably lower than corresponding estimates obtained in Population Model 1.

With regard to Population Model 1, available evidence strongly suggests that ocean mortality of sockeye is greater when the fish are small than it is when they become larger. Accordingly, it seems likely that the assumption of a constant ocean mortality rate results in an underestimate of ocean mortality during the early period of ocean residence and an overestimate during the later period of ocean life.

Concerning Population Model 2, it is rather unlikely that the ocean mortality rate decreases uniformly from month to month. It is also doubtful that the mortality of sockeye becomes negligible during the last several months of the fourth year of ocean residence. As for the first point, an arithmetic progression not only is a convenient method of representing a decreasing mortality rate but it also provides reasonably satisfactory estimates of the average monthly instantaneous mortality rates during the different ocean years of life even though the mortality rate does not decrease uniformly. As for the second point, relatively few Karluk sockeye would benefit from the low ocean mortality rates in the fourth year following seaward migration, because practically all of them mature after 2 or 3 years in the ocean.

Ocean mortality could be represented as a function of fish length or weight rather than time spent in the ocean in Population Model 2.

As indicated previously, Population Model 3 is intended to represent an intermediate situation with respect to the distributions of ocean mortality assumed in Population Models 1 and 2. From the standpoint of annual mortality rates (figs. 2 to 5), it does not depict the best intermediate situation. A lower rate of decrease in mortality during the first 6 months of ocean residence, combined with a constant ocean mortality rate thereafter, would provide annual mortality rates that lie between the estimates obtained in Population Models 1 and 2.

I am not aware of any information at this time upon which to judge the validity of the assumptions concerning ocean mortality in Population Model 4. For a situation such as that depicted in this model to occur would require a short-term, selective, intensive removal of smolts by predators near the mouth of the river, or a similar effect due to such factors as water temperature or salinity changes.

Some mention should be made of the fact that none of the population models presented here deals with situations such as where the mortality rate is considered to increase throughout the ocean life of sockeye or to be greater during the last month or two of ocean life of maturing sockeye than in preceding months or years.

The possibility that the mortality rate increases throughout the ocean life of sockeye salmon can be ruled out, I believe, on the basis of evidence from the Karluk marking experiments and for other sockeye populations (Ricker, 1962) that ocean mortality is greater during the early part of ocean residence than it is in later months and years.

It is of course possible that ocean mortality is greater during the last month or two of ocean life of maturing sockeye than in preceding months or years. Just what factor or factors might cause this to happen is difficult to say. As far as temporal effects of predation are concerned, smolts are subjected to considerable predation as they leave the river and enter the ocean. The size of the smolts probably renders them vulnerable to a variety of predators which cause little harm to adult sockeye. And, as Ricker(1962) mentions, although maturing sockeye are subject to predation by harbor seals and sea lions as they return to fresh water, they are leaving waters where the much more numerous fur seals occur.

Density-associated causes of mortality would seem to be less severe among maturing sockeye than smolt populations which are concentrated in small areas as they migrate to sea, and no more severe than for immature sockeye at sea.

Sockeye smolts appear to undergo at least as severe physical and chemical changes in their environment during their seaward migration as maturing sockeye undergo in their return to fresh water from the ocean.

Perhaps some physiological change associated with maturation causes an increased mortality among sockeye returning to fresh water. If so, it is not reflected in the general appearance of the fish. Sockeye taken in coastal waters are similar to maturing sockeye caught on the high seas insofar as body brightness and firmness of flesh are concerned (personal communication with R. R. French). Nor does it result in a loss of body weight, according to data on growth rates given by Ricker (1962).

The foregoing considerations, of course, do not rule out the possibility that ocean mortality of maturing sockeye is greater during the last month or two of ocean life than in preceding months or years. In this connection, further investigation of the distribution and extent of ocean mortality of salmon is under way. For the time being, however, it should be noted, as Ricker (1962) notes with respect to his estimates of ocean mortality, that if the mortality during the last few months of ocean life of maturing salmon is greater than the estimates presented here, then the mortality rates during preceding months must be less than those estimated here, since the total mortality is fixed.

COMPARISON OF OCEAN GROWTH AND MORTALITY

Ricker (1962, Appendix tables A, B, and C), using data from Barnaby (1932), gives estimates of the instantaneous growth rates for nine Karluk sockeye fresh-water-ocean age groups during different years of ocean growth. These estimates, together with extrapolated estimates for some age groups not included in his tables, are shown in table 19.

The average instantaneous growth rates of 3- and 4-fresh-water sockeye during each of the 4 years of ocean growth can be estimated by weighting the individual estimates of g shown in table 19 by the proportions of sockeye that mature as 1-, 2-, 3-, and 4-ocean fish. Each of the four population models provides estimates of the weighted average annual growth rates of the two fresh-water age groups.

Using the maturity schedule obtained in Population Model 1 (table 6), the weighted average instantaneous growth rates of 3-fresh-water smolts during the first, second, third, and fourth years of ocean growth are estimated as follows:

$$\bar{g}_1 = [3.159(.0135) + 2.811(.5141) + 2.894(1.4577) + 2.650(.0147)]/1 = 2.8513$$

$$\bar{g}_2 = [1.262(.5141) + 1.053(.4577) + 0.964(.0147)]/0.9865 = 1.1606$$

$$\bar{g}_3 = [0.867(.4577) + 0.794(.0147)]/0.4724 = 0.8647$$

$$\bar{g}_4 = [0.434(.0147)]/0.0147 = 0.4340$$

TABLE 19.—*Estimated instantaneous growth rates of Karluk River sockeye during four ocean growth years*

[Data from Ricker (1962); see footnotes for details on estimates shown in parentheses]

Fresh-water age group	Ocean age	Growth rate (g) during ocean growth year:			
		1	2	3	4
	Years				
3	1	3.159			
	2	2.811	1.262		
	3	2.894	1.053	0.867	
	4	[1] (2.650)	[2] (0.964)	[3] (0.794)	[4] (0.434)
4	1	2.922			
	2	2.655	.974		
	3	[5] (2.548)	[6] (0.927)	[7] (0.763)	
	4	[8] (2.333)	[9] (0.849)	[10] (0.699)	[11] (0.382)

[1] $(2.650)=\frac{1}{4}\left[\frac{2.811}{3.159}+\frac{2.894}{2.811}+\frac{1.053}{1.262}+\frac{2.655}{2.922}\right](2.894)$

[2] $(0.964)=\frac{1}{4}\left[\frac{2.811}{3.159}+\frac{2.894}{2.811}+\frac{1.053}{1.262}+\frac{2.655}{2.922}\right](1.053)$

[3] $(0.794)=\frac{1}{4}\left[\frac{2.811}{3.159}+\frac{2.894}{2.811}+\frac{1.053}{1.262}+\frac{2.655}{2.922}\right](0.867)$

[4] $(0.434)=\frac{1}{3}\left[\frac{1.262}{2.811}+\frac{0.867}{1.053}+\frac{0.974}{2.655}\right][(0.794)]$

[5] $(2.548)=\frac{1}{3}\left[\frac{2.922}{3.159}+\frac{2.655}{2.811}+\frac{0.974}{1.262}\right](2.894)$

[6] $(0.927)=\frac{1}{3}\left[\frac{2.922}{3.159}+\frac{2.655}{2.811}+\frac{0.974}{1.262}\right](1.053)$

[7] $(0.763)=\frac{1}{3}\left[\frac{2.922}{3.159}+\frac{2.655}{2.811}+\frac{0.974}{1.262}\right](0.867)$

[8] $(2.333)=\frac{1}{4}\left[\frac{2.811}{3.159}+\frac{2.894}{2.811}+\frac{1.053}{1.262}+\frac{2.655}{2.922}\right][(2.548)]$

[9] $(0.849)=\frac{1}{4}\left[\frac{2.811}{3.159}+\frac{2.894}{2.811}+\frac{1.053}{1.262}+\frac{2.655}{2.922}\right][(0.927)]$

[10] $(0.699)=\frac{1}{4}\left[\frac{2.811}{3.159}+\frac{2.894}{2.811}+\frac{1.053}{1.262}+\frac{2.655}{2.922}\right][(0.763)]$

[11] $(0.382)=\frac{1}{3}\left[\frac{1.262}{2.811}+\frac{0.867}{1.053}+\frac{0.974}{2.655}\right][(0.699)]$

Using this procedure to estimate the weighted average growth rates of 4-fresh-water smolts during each year of ocean growth under Population Model 1 and to obtain corresponding estimates for the two fresh-water age groups under Population Models 2, 3, and 4, we obtain the set of weighted average instantaneous growth rates shown in table 20.

TABLE 20.—*Estimated weighted average instantaneous growth rates* $(\overline{g})$ *of 3- and 4-fresh-water Karluk River sockeye smolts during 4 years of ocean growth, under population models 1, 2, 3, and 4*

Fresh-water age group	Year of ocean growth	Population model			
		1	2	3	4
3	1	2.8513	2.8484	2.8486	2.8496
	2	1.1606	1.1749	1.1802	1.1744
	3	.8647	.8656	.8654	.8652
	4	.4340	.4340	.4340	.4340
4	1	2.6343	2.6412	2.6462	2.6412
	2	.9607	.9630	.9636	.9625
	3	.7605	.7615	.7615	.7610
	4	.3820	.3820	.3820	.3820

In estimating the growth rates shown in table 20, the greatest weight is given to the growth rates for sockeye that mature after 2 or 3 years in the ocean. This means that in most cases the extrapolated estimates given in table 19 do not greatly affect the weighted averages. Also, with regard to the estimating procedure, the weighted growth rates are generally minimal values, since they represent the growth between the time that sockeye leave fresh water and the time that the first ocean annulus is formed, or the time between the formation of successive ocean annuli. The relatively rapid rates of growth that take place between the time the last ocean annulus is formed and the time that mature sockeye return to the Karluk River are not included in the estimates.

It is presumed here that the growth rates in each of the years of ocean growth pertain to periods of 12 months. Thus the duration of an ocean-growth-year differs somewhat from the durations of the ocean-mortality-years used in estimating mortality rates. To obtain a set of growth rate estimates that pertain to the time periods for which mortality estimates have been made, it is necessary to estimate the average monthly instantaneous growth rates in each ocean-growth-year and combine the resulting averages for parts of two ocean-growth-years. For example, the duration of the first year of ocean residence of 3-fresh-water fish has been estimated to be 14.17 months. The total instantaneous growth rate of 3-fresh-water smolts, under Population Model 1, during the first 14.17 months of ocean residence is estimated to be [(12) (2.8513)/12]+[(2. 17)(1.1606)/12], or 3.0612. The average monthly instantaneous growth rate during this period is, in turn, estimated to be 3.0612/14.17, or 0.2160. Also, for example, the duration of the second year of ocean residence of 3-fresh-water fish is considered to be 11.16 months. The total instantaneous growth rate of these fish during this period under Population Model 1 is estimated to be [(9.83) (1.1606)/12] plus [(1.33) (0.8647)/12], or 1.0465. The average monthly instantaneous growth rate is estimated to be 1.0465/11.16, or 0.0938.

Table 21 shows the total and monthly instantaneous rates of growth and mortality for 3- and 4-fresh-water Karluk sockye during each ocean year of life for each population model. Estimates

Table 21.—*Estimated instantaneous rates of growth and mortality and changes in bulk of 3- and 4-fresh-water Karluk River sockeye during each year of ocean life, population models 1, 2, 3, and 4*

[Mortality rate data from tables 5, 9, 13, and 17; growth rate data from table 20, adjusted for duration of ocean year (see text)]

Population model	Fresh-water age group	Ocean year	Duration of ocean year	Instantaneous rates of growth and mortality						Changes in bulk [1]	
				Yearly basis			Monthly basis				
				Growth	Mortality	Difference	Growth	Mortality	Difference	Per ocean year	Per month
			Months							*Percent*	*Percent*
1	3	1	14.17	3.0612	0.6320	2.4292	0.2160	0.0446	0.1714	1,035.0	18.7
		2	11.16	1.0465	.4977	.5488	.0938	.0446	.0492	73.1	5.0
		3	10.67	.7689	.4759	.2930	.0721	.0446	.0275	34.0	2.8
		4	11.83	.4278	.5276	−.0998	.0362	.0446	−.0084	−9.5	−0.8
	4	1	15.00	2.8745	.5790	2.2955	.1916	.0386	.1530	893.0	16.5
		2	11.67	.8897	.4505	.4392	.0762	.0386	.0376	53.6	3.8
		3	9.50	.5972	.3667	.2305	.0629	.0386	.0243	25.9	2.5
		4	12.00	.3820	.4632	−.0812	.0318	.0386	−.0068	−7.8	−0.7
2	3	1	14.17	3.0609	.7929	2.2680	.2160	.0560	.1600	866.0	17.4
		2	11.16	1.0584	.4326	.6258	.0948	.0388	.0560	87.0	5.8
		3	10.67	.7697	.2560	.5137	.0721	.0240	.0481	67.1	4.9
		4	11.83	.4278	.1028	.3250	.0362	.0087	.0275	38.4	2.8
	4	1	15.00	2.8820	.7038	2.1782	.1921	.0469	.1452	783.0	15.6
		2	11.67	.8917	.3701	.5216	.0764	.0317	.0447	68.5	4.6
		3	9.50	.5980	.1867	.4113	.0629	.0196	.0433	50.9	4.4
		4	12.00	.3820	.0888	.2932	.0318	.0074	.0244	34.1	2.5
3	3	1	14.17	3.0620	1.0842	1.9778	.2161	.0765	.1396	622.7	15.0
		2	11.16	1.0627	.1696	.8931	.0952	.0152	.0800	144.3	8.3
		3	10.67	.7695	.1622	.6073	.0721	.0152	.0569	83.5	5.8
		4	11.83	.4278	.1798	.2480	.0362	.0152	.0210	28.1	2.1
	4	1	15.00	2.8871	.9279	1.9592	.1925	.0619	.1306	609.4	13.9
		2	11.67	.8921	.1505	.7416	.0764	.0129	.0635	109.9	6.6
		3	9.50	.5980	.1226	.4754	.0629	.0129	.0500	60.9	5.1
		4	12.00	.3820	.1548	.2272	.0318	.0129	.0189	25.5	1.9
4	3	1	14.17	3.0620	.9599	2.1021	.2161	.0677	.1484	718.3	16.0
		2	11.16	1.0579	.2589	.7990	.0948	.0232	.0716	122.3	7.4
		3	10.67	.7693	.2475	.5218	.0721	.0232	.0489	68.5	5.0
		4	11.83	.4278	.2745	.1533	.0362	.0232	.0130	16.6	1.3
	4	1	15.00	2.8818	.7894	2.0924	.1921	.0526	.1395	710.4	15.0
		2	11.67	.8912	.2707	.6205	.0764	.0232	.0532	86.0	5.5
		3	9.50	.5976	.2204	.3772	.0629	.0232	.0397	45.8	4.0
		4	12.00	.3820	.2784	.1036	.0318	.0232	.0086	10.9	.9

[1] Exponential of difference between growth and mortality, less 1.

of the changes in bulk of sockye during ocean life are also given.

Under Population Model 1, the estimated natural mortality rates for 3- and 4-fresh-water sockeye are less than the estimated growth rates during each of the first 3 years of ocean life. The bulk (poundage) of 3-fresh-water fish is estimated to increase by 1,035, 73 and 34 percent, respectively, during the first, second, and third ocean years. The bulk of 4-fresh-water fish is estimated to increase by 893, 54 and 26 percent, respectively, during their first, second, and third years of ocean residence.

The estimated natural mortality rates during the fourth year of ocean life for the very small proportions of Karluk sockeye that mature as 4-ocean fish exceed the estimated growth rates. Hence, under the first population model, the bulk of Karluk sockeye in their fourth year at sea is estimated to decrease by about 10 percent (3-fresh-water fish) or 8 percent (4-fresh-water fish).

In the second model, the estimated ocean mortality rates for both fresh-water age groups are exceeded by the estimated growth rates throughout ocean life. During the first, second, third, and fourth ocean years, the bulk of 3-fresh-water sockeye is estimated to increase by 866, 87, 67, and 38 percent, respectively. Corresponding estimated increases for 4-fresh-water sockeye are 783, 69, 51, and 34 percent, respectively.

Under Population Model 3, the bulk of 3- and 4-fresh-water Karluk sockeye is estimated to increase in each year of ocean life. Estimated percentage increases in bulk during the first, second, third, and fourth years of ocean life are 623, 144, 84, and 28, respectively, for 3-fresh-water fish, and 609, 110, 61, and 26, respectively, for 4-fresh-water fish.

In the fourth population model also, the estimated natural mortality rates of 3- and 4-fresh-

735-722 O—64——6

water fish are exceeded by the estimated growth rates in each ocean year. The bulk of 3-fresh-water sockeye is estimated to increase by 718, 122, 69, and 17 percent, respectively, during the first, second, third, and fourth years of ocean life. Increases in bulk of 4-fresh-water fish are estimated to be 710, 86, 46, and 11 percent, respectively, for the first through the fourth ocean years.

The percentage changes in bulk in table 21 show that, except for the relatively scarce 4-ocean fish under the first population model, any capture of Karluk sockeye before the end of their ocean life causes a loss of potential poundage yield, provided there exists an inshore fishery capable of catching the fish not needed for reproduction of the stock. The extent of the loss depends upon the distribution of ocean mortality and the year of ocean life in which the salmon would be captured by a high seas fishery. Computations of losses are not given here. It can be pointed out, however, that any mortality caused by net injury or inadvertent capture of Karluk sockeye during their first year of ocean life would result in an especially great loss of potential catch.

Attention is called to two matters relating to the estimated changes in bulk of Karluk sockeye during their ocean life. One, the estimates of net increase in bulk in table 21 are generally minimal due to the fact that the weighted average growth rates do not include the rapid growth that takes place during the last few months of ocean life of maturing sockeye. Secondly, if the distribution of ocean mortality is altered to reflect an increase in the mortality of maturing sockeye during their last month or two of ocean life, the bulk of the nonmaturing sockeye, as well as the loss in yield resulting from the capture of such fish, must also increase, because the total ocean mortality is fixed.

SUMMARY

Four population models simulating different temporal distributions of natural mortality during the ocean life of Karluk River sockeye salmon are developed. Assumptions employed in each of the models are discussed. Data collected in the late 1920's and early 1930's on the releases and returns of marked fish are used to estimate ocean mortality rates and maturity schedules of different fresh-water age groups of Karluk sockeye. The estimates primarily concern 3- and 4-fresh-water fish, the two fresh-water age groups that generally account for 95 percent or more of the annual runs to the Karluk system. The ocean mortality rate estimates are compared with available growth rate data to determine the changes in bulk (net increase or decrease in weight) of Karluk sockeye during ocean life.

In the first population model, natural mortality is assumed to be constant throughout ocean life. The estimates of monthly instantaneous ocean mortality rates obtained in this model generally decrease as the age and size of smolts increase: 0.0496 for 2-fresh-water smolts averaging 108 millimeters in length; 0.0446 for 3-fresh-water smolts averaging 131 millimeters in length; 0.0386 for 4-fresh-water smolts averaging 143 millimeters in length; and 0.0402 for 5-fresh-water smolts averaging 146 millimeters in length. These monthly instantaneous rates generate annual (12-month) ocean mortality rates of 44.8, 41.4, 37.1, and 38.3 percent, respectively.

Approximately 1.3, 51.4, 45.8, and 1.5 percent of the 3-fresh-water smolts are estimated to mature as 1-, 2-, 3-, and 4-ocean sockeye respectively. Corresponding percentages for 4-fresh-water smolts are about 3.3, 71.0, 24.6, and 1.0 percent.

The estimated natural mortality rates during the first 3 years of ocean life are less than the estimated ocean growth rates for both the 3-, and 4-fresh-water age groups of Karluk sockeye. During successive periods (called ocean years) of about 14, 11, and 11 months of ocean life, the bulk (poundage) of 3-fresh-water sockeye is estimated to increase by 1,035, 73, and 34 percent, respectively. During their first, second, and third ocean years (corresponding to periods of about 15, 12, and 10 months), 4-fresh-water sockeye are estimated to increase in bulk by 893, 54, and 26 percent, respectively.

The estimated natural mortality rates during the fourth year of ocean life for the very small proportions of 3- and 4-fresh-water fish that mature as 4-ocean fish exceed the estimated growth rates. Hence, under the first population model, the bulk of Karluk sockeye in their fourth year at sea is estimated to decrease by about 10 percent for 3-fresh-water fish and about 8 percent for 4-fresh-water fish.

In the second population model, the instantaneous natural mortality rate is assumed to be

greatest in the first month of ocean life and then decreases arithmetically in each of the following 47 or 48 months until it becomes zero. The first-month instantaneous mortality rates are estimated to be 0.0649 for 3-fresh-water sockeye and 0.0549 for 4-fresh-water sockeye. The instantaneous rates are estimated to decrease each month by about 0.0014 for 3-fresh-water fish and 0.0011 for 4-fresh-water fish.

The natural mortality rates during the first, second, third, and fourth ocean years for 3-fresh-water fish are 54.7, 35.1, 22.6, and 9.8 percent, respectively. Corresponding estimates for 4-fresh-water fish are 50.5, 30.9, 17.0, and 8.5 percent.

Under the second population model, about 1.6, 57.7, 39.8 and 0.8 percent of the 3-fresh-water smolts are estimated to mature as 1-, 2-, 3-, and 4-ocean sockeye, respectively. Corresponding percentages for the 4-fresh-water smolts are about 3.9, 74.5, 21.1, and 0.5.

For both the 3- and 4- fresh-water age groups, the estimated ocean mortality rates are exceeded by the estimated growth rates throughout ocean life. During the first, second, third, and fourth ocean years, the bulk of 3-fresh-water sockeye is estimated to increase by 866, 87, 67, and 38 percent, respectively, while the bulk of 4-fresh-water sockeye is estimated to increase by 783, 68, 51, and 34 percent, respectively.

In the third population model, the monthly instantaneous natural mortality rate is assumed to be greatest during the first month of ocean life, decreases geometrically by a factor of 0.5 in each of the next 5 months, and remains constant during the sixth and each succeeding month. First-month instantaneous mortality rates are estimated to be 0.4876 for 3-fresh-water sockeye and 0.4123 for 4-fresh-water sockeye. The instantaneous mortality rates in the sixth and each succeeding month are estimated to be 0.0152 for 3-fresh-water fish and 0.0129 for 4-fresh-water fish.

The natural mortality rates for 3-fresh-water fish during their first ocean year (approximately 14 months) is estimated to be 66.2 percent. The rate for succeeding 12-month periods is estimated to be 16.7 percent. The natural mortality rate for 4-fresh-water fish during their first ocean year (15 months) is estimated to be 60.5 percent. The rate for succeeding 12-month periods is estimated to be 14.3 percent.

About 2.4, 59.8, 37.0, and 0.8 percent of the 3-fresh-water smolts are estimated to mature as 1-, 2-, 3-, and 4-ocean sockeye, respectively, under the third population model. Corresponding estimates for the 4-fresh-water smolts are 5.2, 74.8, 19.6, and 0.5 percent.

The estimated natural mortality rates of 3- and 4-fresh-water fish are less than the estimated growth rates during each ocean year. The bulk of 3-fresh-water sockeye is estimated to increase by 623, 144, 84, and 28 percent during the first, second, third, and fourth ocean years, respectively. Corresponding estimates of percentage increases in bulk of 4-fresh-water fish are 609, 110, 61, and 26.

In the fourth population model, the instantaneous natural mortality rate is assumed to be greater for 3-fresh-water sockeye than for 4-fresh-water fish during the first month of ocean life, greater for both fresh-water age groups during the first month than during the second and succeeding months, and constant and the same for the two fresh-water age groups during each month of ocean residence following the first month.

Starting with the assumption that the first-month instantaneous ocean mortality rate of 4-fresh-water sockeye is 20 times the mortality rate of this fresh-water age group in each of the following months, the instantaneous mortality rates of sockeye of that fresh-water age group are estimated to be 0.4646 during the first month of ocean life and 0.0232 during each succeeding month. Under this model, 0.0232 is also the estimated monthly instantaneous natural mortality rate of 3-fresh-water sockeye after their first month in the ocean. The first-month instantaneous mortality rate of 3-fresh-water fish is estimated to be 0.6544, about 40 percent greater than the corresponding estimate for 4-fresh-water fish and about 28 times the mortality rate of 3-fresh-water fish during the second and succeeding months of ocean life.

The total ocean mortality rate for 3-fresh-water fish during their first ocean year is estimated to be 61.7 percent. The corresponding estimate for 4-fresh-water sockeye is 54.6 percent. For both fresh-water age groups the rate for succeeding 12-month periods is estimated to be 24.3 percent.

The maturity schedules of 3- and 4-fresh-water smolts are estimated to be about the same in the fourth population model as in the second model.

The estimated natural mortality rates of 3- and

4-fresh-water sockeye are exceeded by the estimated growth rates in each ocean year. The bulk of 3-fresh-water sockeye is estimated to increase by 718, 122, 68, and 17 percent, respectively, during the first, second, third and fourth years of ocean life. Corresponding estimates of increases in bulk of 4-fresh-water fish are 710, 86, 46, and 11 percent.

The estimated percentage changes in bulk show that, except for the relatively scarce 4-ocean fish under the first population model, any capture of Karluk sockeye before the end of their ocean life causes a loss of potential yield, provided there exists a coastal fishery capable of catching the fish not needed for reproduction of the stock.

ACKNOWLEDGMENTS

W. E. Ricker and R. R. Parker of the Nanaimo Station of the Fisheries Research Board of Canada, D. G. Chapman of the Department of Mathematics of the University of Washington, J. T. Barnaby, Bureau of Sport Fisheries and Wildlife, Fish and Wildlife Service, U.S. Department of the Interior, and C. J. DiCostanzo, G. Hirschhorn, R. H. Lander and R. P. Silliman of the Bureau of Commercial Fisheries, Fish and Wildlife Service, U.S. Department of the Interior all reviewed this paper and made many useful suggestions regarding its content.

LITERATURE CITED

BARNABY, JOSEPH T.

1932. The growth of the red salmon (*Oncorhynchus nerka* Walbaum) of the Karluk River and the growth of its scales. M.A. Thesis, Stanford University, 50 p.

1944. Fluctuations in abundance of red salmon *Oncorhynchus nerka* (Walbaum) of the Karluk River, Alaska. U.S. Fish and Wildlife Service, Fishery Bulletin 39, vol. 50, pp. 237–295.

BEVAN, DONALD EDWARD

1962. Estimation by tagging of the size of migrating salmon populations in coastal waters. *In* Studies of Alaska red salmon, edited by Ted S. Y. Kov, University of Washington (Seattle), Publications in Fisheries, new series, vol. 1, pp. 373–449. 34 figs.

FOERSTER, R. E.

1934. An investigation of the life history and propagation of the sockeye salmon (*Oncorhynchus nerka*) at Cultus Lake, British Columbia. No. 4. The life history cycle of the 1925 year class with natural propagation. Contributions to Canadian Biology and Fisheries, N.S., vol. 8, No. 27, pp. 345–355.

1936. An investigation of the life history and propagation of the sockeye salmon (*Oncorhynchus nerka*) at Cultus Lake, British Columbia. No. 5. The life history cycle of the 1926 year class with artificial propagation involving the liberation of free-swimming fry. Journal of the Biological Board of Canada, vol. 2, No. 3, pp. 311–333.

1937. The return from the sea of sockeye salmon (*Oncorhynchus nerka*) with special reference to percentage survival, sex proportions and progress of migration. Journal of the Biological Board of Canada, vol. 3, No. 1, pp. 26–42.

PARKER, ROBERT R.

1962. Estimations of ocean mortality rates for Pacific salmon (*Oncorhynchus*). Journal of the Fisheries Research Board of Canada, vol. 19, No. 4, pp. 561–589.

RICH, WILLIS H., and FREDERICK G. MORTON

1929. Salmon tagging experiments in Alaska, 1927 and 1928. Bulletin of the U.S. Bureau of Fisheries, 1929 (1930), vol. 45 (Doc. 1057; issued October 12, 1929), pp. 1–23.

RICKER, W. E.

1962. Comparisons of ocean growth and mortality of sockeye salmon during their last two years. Journal of the Fisheries Research Board of Canada, vol. 19, No. 4, pp. 531–560.

ROUNSEFELL, GEORGE A.

1958. Factors causing decline in sockeye salmon of Karluk River, Alaska. U.S. Fish and Wildlife Service, Fishery Bulletin 130, vol. 58, pp. 83–169.