<u>Northwest and Alaska Fisheries Center Processed Report*</u>

SOME OBSERVATIONS ON THE BIOLOGY AND VARIATIONS OF

POPULATIONS OF SOCKEYE SALMON OF THE

NAKNEK AND UGASHIK SYSTEMS OF BRISTOL BAY, ALASKA

by

Jerome J. Pella and Herbert W. Jaenicke

September 1978

U.S. DEPARTMENT OF COMMERCE
National Oceanic and Atmospheric Administration
National Marine Fisheries Service
Northwest Fisheries Center
2725 Montlake Boulevard East
Seattle, Washington 98112

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*Northwest and Alaska Fisheries Center Auke Bay Laboratory
National Marine Fisheries Service, NOAA
P.O. Box 155, Auke Bay, AK 99821

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SOME OBSERVATIONS ON THE BIOLOGY AND VARIATIONS OF POPULATIONS OF SOCKEYE SALMON OF THE NAKNEK AND UGASHIK SYSTEMS OF BRISTOL BAY, ALASKA

by

Jerome J. Pella and Herbert W. Jaenicke[1]

INTRODUCTION

The Naknek and Ugashik river systems of southwestern Alaska lie on the Alaska Penninsula and enter the eastern side of Bristol Bay (Figure 1). Physically the Naknek system is the more complex, consisting of seven major interconnected basins of four lakes. Coville, Grosvenor, and Naknek lakes form a chain which drains into Bristol Bay through the Naknek River. Brooks Lake drains into the South Bay basin of Naknek Lake--one of four basins of that lake.

The Ugashik system comprises two interconnected lakes, Upper Ugashik Lake and Lower Ugashik Lake, which drain via the Ugashik River to Bristol Bay about 150 km to the southwest of the Naknek River mouth. The total surface area of these lakes, 385 km^2, is roughly one-half the 790 km^2 of the Naknek system.

Both systems support substantial populations of sockeye salmon, Oncorhynchus nerka. Escapements in the Naknek system averaged 902,000 fish between 1955 and 1974; in the Ugashik system the corresponding average is 430,000 fish (Table 1). Recent escapements to the Ugashik River are among the lowest of this 20-yr period. The 20 escapements to the Naknek system have shown eightfold variation, but the Ugashik system has had nearly sixtyfold variation.

The same age types of sockeye salmon, distinguished by lengths of freshwater and marine residence, occur in either system. Most individuals spend either one or two winters in fresh water before migrating to sea as age I or age II smolts, respectively; a few spend three winters in fresh water and migrate as age III smolts. Thereafter the fish spend 1-4 yr in the ocean before maturing and returning to spawn in fresh water as 1-, 2-, 3-, or 4-ocean fish; most spend either 2 or 3 yr at sea. Survival in both fresh water and the ocean is highly variable and freshwater and marine age compositions vary radically among broods. These factors are common to Bristol Bay stocks and make the determination of escapement goals and forecasting of future returns difficult.

As part of an effort to gain knowledge about sockeye salmon of Bristol Bay on which to base management and forecasting, the National Marine Fisheries Service (NMFS; formerly U.S. Bureau of Commercial Fisheries) began an intense long-term study of sockeye salmon of the Naknek and Ugashik systems in the 1950's. Included as major efforts were programs for monitoring smolt migrations, adult escapements, and catches.

The smolt monitoring program was initiated on a limited scale in 1955 by Dr. Richard R. Straty of NMFS's Auke Bay Laboratory (ABL). After 1958 a sampling program devised by Dr. C. J. DiCostanzo[2], also of ABL, allowed estimation of total numbers of smolts migrating from each system. Age composition samples further permitted estimation of total numbers by freshwater age and also numbers produced by each spawning.
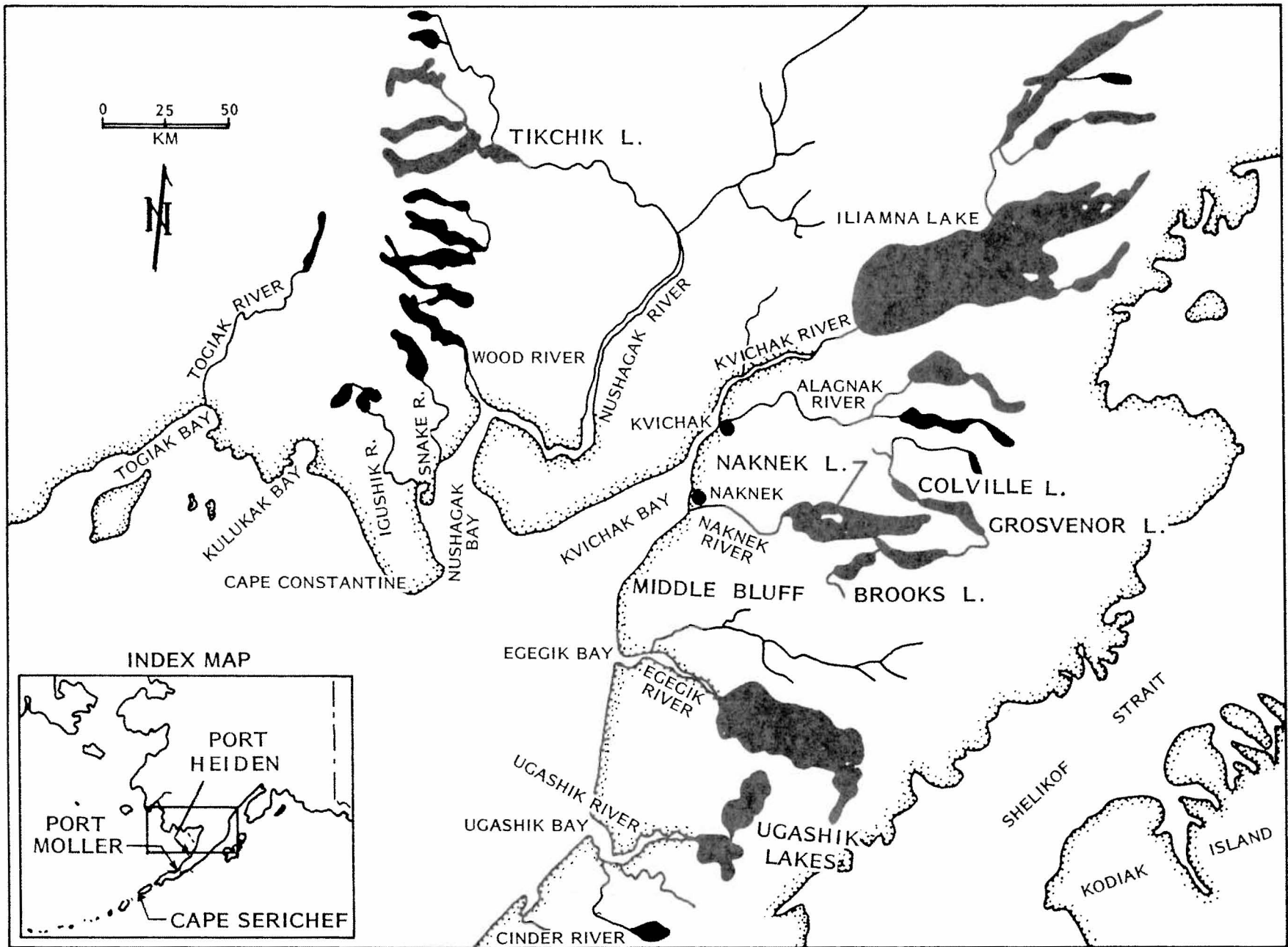
Figure 1.--Principal sockeye salmon river systems in Bristol Bay.

Table 1.--Estimates of sockeye salmon escapements (in thousands) to the Naknek and Ugashik river systems, 1955-74.[a]

Year	Naknek River	Ugashik River
1955	273	77
1956	1,773	425
1957	635	215
1958	278	280
1959	2,232	219
1960	828	2,304
1961	351	349
1962	723	255
1963	905	388
1964	1,350	473
1965	718	997
1966	1,016	704
1967	756	239
1968	1,023	71
1969	1,331	160
1970	733	735
1971	936	530
1972	587	79
1973	357	39
1974	1,241	62
Average	902	430

[a]Robert D. Paulus, Alaska Department of Fish and Game, Juneau, Alaska, personal communication.

Estimations of numbers in parental generations began in 1956 for both river systems. The escapements were sampled for sex, size, and age composition beginning in 1957 for the Naknek system and 1958 for the Ugashik system. In some years fecundity samples were taken for estimation of potential egg deposition.

Catches were also estimated and sampled for sex, size, and age composition in the Naknek and Ugashik catch districts beginning in 1958. This information together with that on adult escapement provided estimates of the numbers returning from broods of smolts.

Therefore the life history of sockeye salmon of these systems can be examined in two logical phases--freshwater and marine. Survival and age structure of sockeye salmon in each phase can be related to parameters of the populations. Some of this information has been examined previously (Burgner et al. 1969). In this paper we extend those analyses and incorporate additional information which has accumulated since NMFS terminated the field work in 1963 and the Alaska Department of Fish and Game (ADF&G) continued the monitoring programs.

The high quality of information on sockeye salmon of the Naknek and Ugashik systems is due in a large measure to Dr. C. J. DiCostanzo who dealt with this complex research problem both as an analyst and administrator; this report is dedicated to his memory.

The first sections of this report deal with potential egg deposition, smolt migrations, and returning adults. Fecundity samples from each system are analyzed to determine sources of variation and to eliminate these in computations of potential egg deposition. Potential egg deposition in either system is estimated for years from 1956 to 1969. Observations from the smolt sampling programs are used to estimate numbers, age composition, and size of smolts for each year of seaward migration from 1958 to 1972 in the Naknek system and from 1958 to 1970 except 1966 in the Ugashik system. An attempt to improve estimates of numbers of adults returning to the Naknek and Ugashik systems fails, but provides material for speculation on terminal migration routes of sockeye salmon in eastern Bristol Bay. Estimates of adult returns to the Naknek and Ugashik systems from another source are adopted. Estimates of potential egg deposition, smolt production, and adult returns form the basis for the subsequent analysis of population processes, especially as related to productivity of the stocks.

POTENTIAL EGG DEPOSITION

Individual Fecundity

The total number of eggs, or potential egg deposition, brought into a system by a spawning run can be estimated from the information on number of eggs per female, called fecundity, and number of females in the spawning escapement. Errors in potential egg deposition estimates can be reduced by partitioning females of spawning populations into strata among which there exist differences in mean fecundity. Obvious criteria for stratification are size and age type.

A continuous-time series of escapement estimates and age, sex, and length composition samples from the outlet rivers leading directly to Bristol Bay are available for the Naknek and Ugashik systems for the years after the late 1950's, starting in 1957 for Naknek and 1958 for Ugashik. Salmon in these rivers at the time of composition sampling are presumably mixtures of the spawning units of each system; in the Naknek River, at least, the spawning units are not segregated by date of entry (Straty 1966). Fecundity samples, too, were drawn in 1942, 1963, 1964, and 1965 for the Naknek system, and 1942, 1965, 1966, and 1971 for the Ugashik system. The egg count, or its estimate, age type, and length (mideye to fork of tail) of each female in the fecundity samples were determined. Next we used these samples to estimate the average fecundity of the escaping females, and then average fecundity to estimate the potential egg deposition.

Generally the number of eggs produced by a fish bears a direct curvilinear relationship to length. Females have increasing numbers of eggs at greater lengths, but numbers of eggs increase faster than length. Rounsefell (1957) concluded that over the small size range of mature Oncorhynchus, a linear relationship between fecundity and length is an adequate description. In analyses to be discussed now, we assume the number of eggs produced by a mature female is linearly related to her body length. Analysis of covariance is used to compare fecundity-length relationships estimated from these samples.

Females of the fecundity samples could be classified by year of return and ocean-age type. Rounsefell (1957) had found significant annual variation in fecundity of pink salmon (Oncorhynchus gorbuscha) and differences in fecundity among ocean ages of sockeye salmon. Initially the linear regression function relating fecundity and length was computed by least squares for each year, either ocean age, and either river system (Table 2; Figures 2 and 3). Length was significant in explaining variation in fecundity among females in all Naknek samples but in only three of the eight cases for Ugashik samples. Sample sizes from the Ugashik system were smaller, roughly one-half of those from the Naknek system. Further, in the three recent years for Naknek sampling, equal numbers were sampled in length strata covering the length range; in the Ugashik sampling, no attempt was made to distribute the sample numbers over the length range. As a result, the power to detect an underlying fecundity-length relationship would be reduced for the Ugashik.

Immediately evident from the fitted regression equations is another difference between rivers. Naknek River relationships have lower intercepts and greater slopes than Ugashik River relationships except for 2-ocean females in 1971. Also in that year, the relationship for 3-ocean females of Ugashik River had an improbable negative slope estimate; the regression was not significant, however.

At least some of the eight relationships within each system differ detectably (P<0.05 for Naknek samples; P<0.01 for Ugashik samples). Searching for an explanation, differences among years in the relationships for either ocean age could not be detected for the Naknek system. Apparently a difference between ocean ages exists at least in some years in the Naknek system; however, only in 1965 could a difference in the relationships for ocean ages be detected (P<0.05). We computed the regressions for 2- and 3-ocean females of the Naknek system after pooling the samples from the 4 yr (Figure 4). Over the range of sizes which occur, 2-ocean females have greater

Table 2.--Regression coefficients of the fecundity (Y)-length (X) relationships for female Naknek and Ugashik sockeye salmon by year of return and ocean age.

Year	2-ocean	3-ocean
Naknek River		
1942	Y = -3956 + 14.66X*	Y = -4224 + 14.57X**
1963	Y = -6973 + 20.64X**	Y = -7234 + 20.24X**
1964	Y = -5906 + 18.51X**	Y = -4163 + 14.89X**
1965	Y = -3362 + 13.30X**	Y = -7330 + 20.40X**
Ugashik River		
1942	Y = 1472 + 4.62X^{ns}	Y = 1713 + 4.20X^{ns}
1965	Y = -952 + 9.91X*	Y = 566 + 7.19X*
1966	Y = 1013 + 5.09X^{ns}	Y = -354 + 8.58X^{ns}
1971	Y = -3240 + 14.13X*	Y = 9889 - 9.93X^{ns}

^{ns}Regression not significant

*Regression significant at 5%.

**Regression significant at 1%.
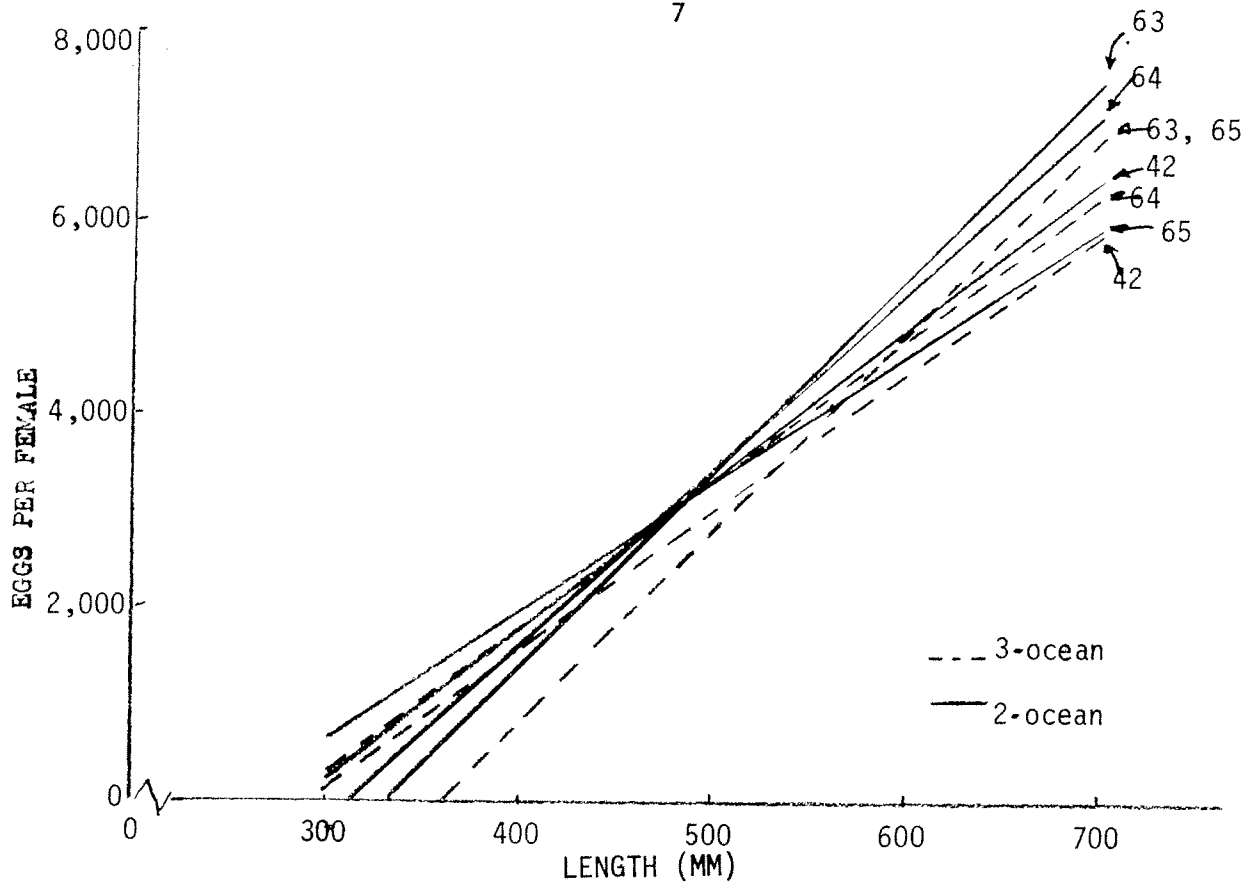
Figure 2.--Fecundity-length relationship by year and ocean age in the Naknek system.
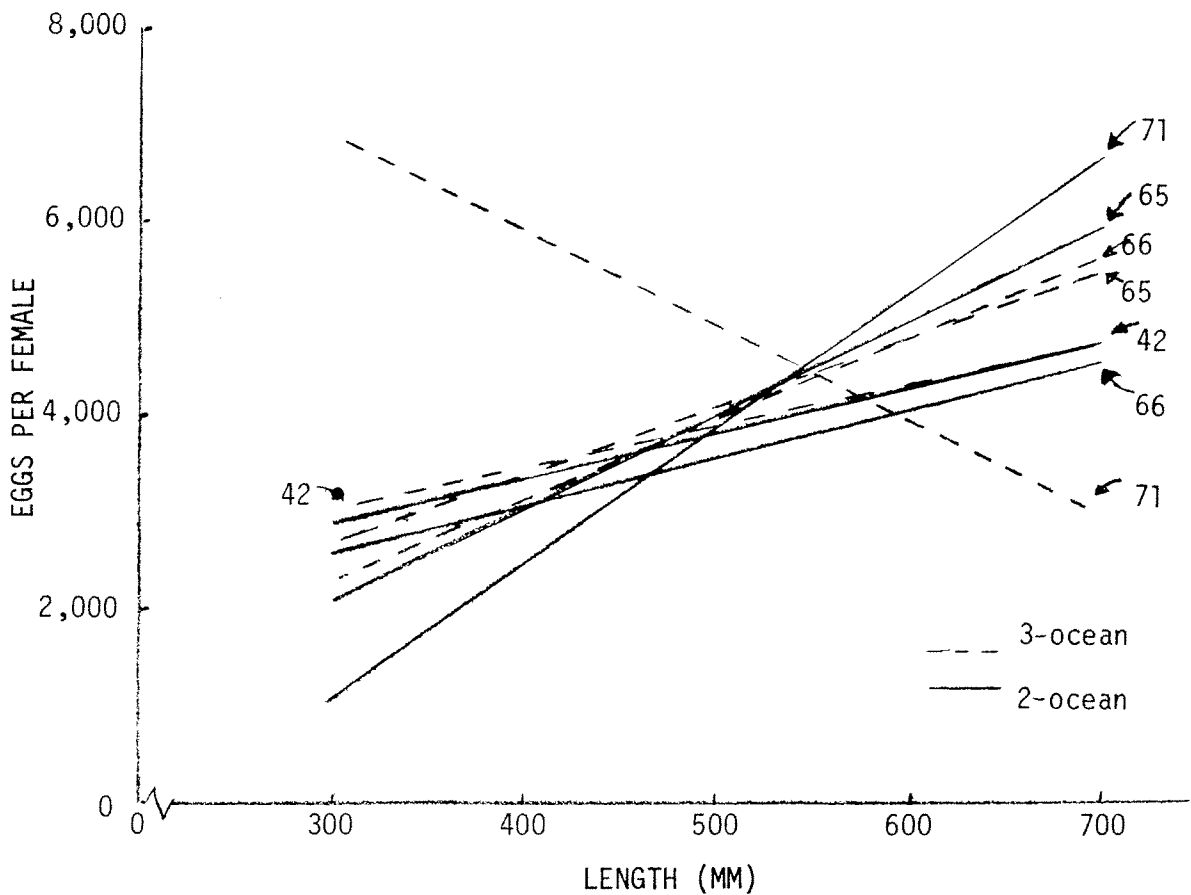
Figure 3.--Fecundity-length relationship by year and ocean age in the Ugashik system.
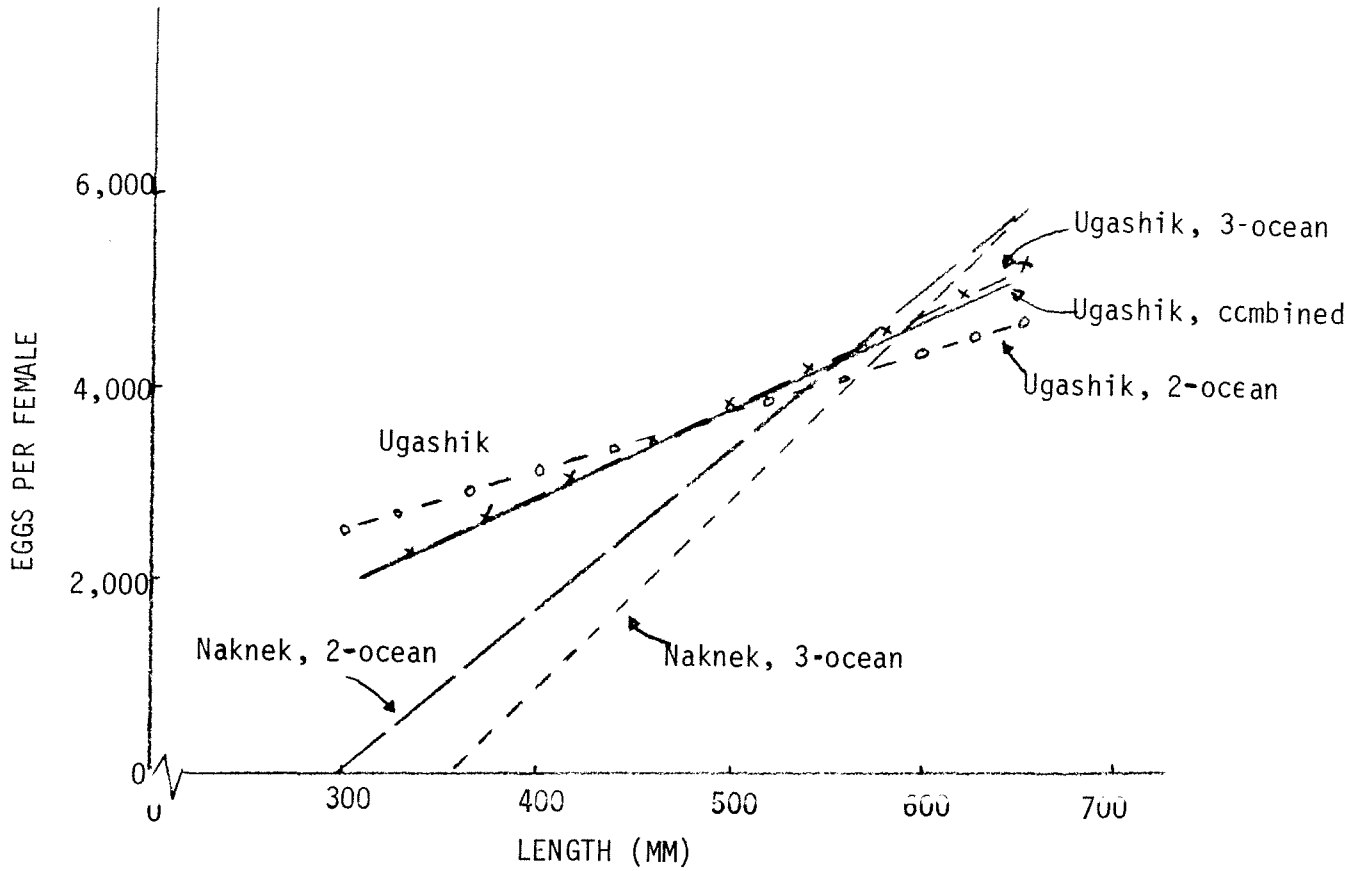
Figure 4.--Fecundity-length relationships used to compute potential egg deposition for Naknek and Ugashik systems.

average fecundity than 3-ocean females at a given length. Rounsefell (1957) discovered the same phenomenon held for Karluk sockeye salmon; for a given size, females which spend a shorter time in the ocean have greater fecundity.

In contrast to Naknek samples, differences among years for either ocean age could be detected in Ugashik samples ($P<0.05$ for 2-ocean females; $P<0.01$ for 3-ocean females). Differences between ocean ages were detectable only in 1971 ($P<0.05$). The fitted lines were conspicuous for that year (Figure 3), particularly for 3-ocean females. When 1971 was omitted from the analysis, annual variation was still detectable for 2-ocean but not 3-ocean females. The fitted relationships for these two ocean ages after omitting 1971 (Figure 4) intersect in the midrange of female length. A regression relationship (based on the pooled data of both ocean ages and 3 yr omitting 1971) indicates the average fecundity of Ugashik females exceeds that of Naknek females over much of their length range (Figure 4).

Total Egg Production of Spawners

Observations on escapements into the Naknek and Ugashik rivers include annual estimates for each system since 1956, and age, sex, and length composition sampling since 1957 for Naknek River and since 1958 for Ugashik River. Age, sex and length composition samples have been used to partition estimates into numbers in age, sex, and length categories; allocation was in proportion to numbers in the categories occurring in the samples. Numbers and lengths of 2-ocean and 3-ocean females have been used together with earlier-determined fecundity-length relationships to estimate potential egg depositions for the two systems for 1956 to 1969 (Table 3). Fecundity-length relationships used for the Naknek system were those for either ocean age (Figure 4); the combined relationship for both ocean ages based on fecundity samples of 1942, 1965, and 1966 was used for the Ugashik system (Figure 4).

Estimated potential egg deposition in the Naknek system ranged from 450 million to 3,610 million eggs; in the Ugashik system the range was greater, extending from 155 million to 4,488 million eggs (Table 3). The 14-yr average for the Naknek system, 1,877 million eggs, was roughly 1.65-fold the corresponding average potential egg deposition for the Ugashik system, namely, 1,139 million eggs. While average potential egg deposition in the Naknek system exceeded that of the Ugashik system, estimated potential egg deposition per spawner, either male or female, for the Ugashik system exceeded that of the Naknek system roughly 1.2-fold (Table 3). Potential egg deposition per spawner in the Ugashik system exceeds that of the Naknek system as a result of the greater average fecundity of Ugashik females at a given size (Figure 4), the greater average length of Ugashik females (Table 4), and the greater average proportion of females in Ugashik escapements (Table 5).

SMOLT MIGRATIONS

Estimation of Numbers

Estimation of smolt migrations measures output from the freshwater phase and input to the marine phase. Such information is patently desirable for understanding sockeye salmon dynamics.

Table 3.--Estimates of potential egg deposition (millions of eggs) and potential egg deposition per spawner (eggs/spawner) in the Naknek and Ugashik river systems, 1956-69.

Brood year	Potential egg deposition		Potential egg deposition per spawner	
	Naknek	Ugashik	Naknek	Ugashik
1956	3,360[a]	986[b]	1,896	2,318
1957	1,293	498[b]	2,037	2,318
1958	450	612	1,618	2,189
1959	3,610	563	1,618	2,568
1960	1,446	4,488	1,746	1,948
1961	712	1,039	2,028	2,980
1962	1,618	497	2,238	1,946
1963	1,941	903	2,144	2,326
1964	2,579	1,000	1,911	2,115
1965	1,307	2,453	1,821	2,461
1966	2,174	1,846	2,139	2,621
1967	1,523	575	2,016	2,408
1968	1,730	155	1,691	2,186
1969	2,532	325	1,902	2,026
Mean	1,877	1,139	1,915	2,315

[a] In 1956 the Naknek escapement was estimated, but its composition was not sampled. Average values for proportions and for lengths of 2-ocean and 3-ocean females in escapements of the years 1957-69 were used to estimate egg deposition.

[b] In 1956 and 1957 the Ugashik escapements were estimated, but their compositions were not sampled. Average values for proportions and for lengths of 2-ocean and 3-ocean females in escapements of the years 1958-69 were used to estimate egg depositions.

Table 4.--Estimated mean length (mideye to fork of tail) in millimeters of females of two ocean ages from the Naknek and Ugashik escapements, 1957-69.[a]

Year	Naknek		Ugashik	
	2-ocean	3-ocean	2-ocean	3-ocean
1957	490	546	___	___
1958	489	544	518	566
1959	506	561	518	570
1960	471	552	492	582
1961	471	554	531	571
1962	506	565	516	582
1963	510	574	518	576
1964	486	565	498	570
1965	490	549	486	540
1966	484	553	504	564
1967	498	560	513	574
1968	504	569	517	585
1969	504	568	509	545
Mean	493	558	510	569

[a] Donald E. Rogers, Fisheries Research Institute, University of Washington, Seattle, Wa., personal communication.

Table 5.--Estimated percentages of escapements to the Naknek and Ugashik systems that were female, 1956-69.[a]

Year	Naknek	Ugashik
1956	---	--
1957	54.23	--
1958	45.72	53.13
1959	45.91	61.25
1960	48.72	52.19
1961	51.45	67.34
1962	57.98	48.31
1963	54.54	56.43
1964	58.34	55.47
1965	51.56	66.27
1966	55.74	61.97
1967	53.01	57.04
1968	44.80	53.28
1969	52.92	52.02
Mean	51.92	57.06

[a]Robert D. Paulus, Alaska Department of Fish and Game, Juneau, Alaska, personal communication.

Sampling Design

At the beginning of smolt studies in the late 1950's, the numbers of smolts emigrating from Bristol Bay lakes were known to vary tremendously on diurnal and seasonal time scales as well as annually (DiCostanzo and Rietze 1957; Rietze and Spangler 1958; Kerns 1961; Burgner 1962). Further, the spatial distribution of the smolts across the width of a river at a given moment was known to be uneven, with the migrants favoring certain sections. In studies of the Naknek and Ugashik smolt migrations, scientists decided to stratify by days across the seasons of migration, by periods within the days, and by sections across the widths of the rivers in order to reduce the most obvious sources of variation in estimating smolt migrations. However, with the number of strata deemed necessary, not all could be sampled.

A sampling design was adopted in which only some of the strata were sampled, and for which the information gained could be used to estimate migration in all strata. The three classifications--season, day, and river width--were partitioned with an eye toward utilizing lattice sampling theory (Patterson 1954; Yates 1960). The season was simply partitioned into days. If the river width was partitioned into p sections, each day was subdivided into p+1 time periods. Width of the Ugashik River was partitioned into 5 sections and width of the Naknek River into 6-15 depending on the year. Sections within each river were of equal width.

Cubic lattice populations of p^3 sampling units--day, period of day, and river section cells--were defined and sampled by selecting from their p sampling days, p time periods, and p sections, p^2 units which included one unit from every combination of strata in two classifications, i.e., one unit was sampled from each day and time of day combination, each day and section combination, and each section and time of day combination. These lattice samples were obtained from an arbitrarily selected latin square, the rows and columns of which were randomized. The selected units to be sampled from the cubic lattice populations were given by the combinations of rows, columns, and letters in the squares.

The sampling program in most years on either river partitioned the season into three sequences: (1) a sequence of such lattice samples, the days of which are called lattice days, each supplemented by observations in one section chosen as an index; (2) a second sequence of index days interspersed among the lattice days, during which continuous sampling occurred over all p+1 periods comprising a day but only in the index section; and (3) a third sequence of days when no sampling occurred (Figure 5). Although the sampling schedule evolved over the years, it always included lattice samples with extra-lattice sampling to permit expanding lattice estimates to 24-h days for most days during which migrations occurred.

The primary sampling units--day, period of day, and section combinations-- were subsampled in two dimensions: section width and period of day. Fyke nets used for sampling fished the entire depth of a section from surface to river bed, but only a fraction of the width of a section (Straty 1960). The proportion of the section width fished differed between rivers in any year, and varied among years for Naknek River only. However, for a given river and year a constant proportion of each section width was sampled. In addition to subsampling the section width, the time period was subsampled

TIME PERIODS

	1	2	3	4	5	6
1	S_1/S_4	S_2/S_4	S_3/S_4	S_4	S_5/S_4	--
2	S_2/S_4	S_3/S_4	S_4	S_5/S_4	S_1/S_4	--
3	S_3/S_4	S_4	S_5/S_4	S_1/S_4	S_2/S_4	--
4	S_4	S_5/S_4	S_1/S_4	S_2/S_4	S_3/S_4	--
5	S_5/S_4	S_1/S_4	S_2/S_4	S_3/S_4	S_4	--
6	S_4	S_4	S_4	S_4	S_4	S_4
7	S_4	S_4	S_4	S_4	S_4	S_4
8	--	--	--	--	--	--

Figure 5.--Example of a sampling plan from a 5^3 lattice with two index days, one day with no sampling, and an extra-lattice period within days*.

*The sections of the stream, or net sites, are labelled S_1, S_2, ..., and S_5. The fourth site is the index site. Extra-lattice days six and seven are index days. The five lattice time periods within days together with the sixth extra-lattice period cover either the entire 24-h days or, in some cases, a portion of the days thought to include the major migration. The migration was sampled at the sites indicated for each day and time period. The lattice sample consists of the observations at the lattice days and periods at the nonindex sites, if the index net is fished simultaneously, and at the index net if it is fished alone.

irregularly. The net was generally fished for an entire period of a primary unit, but exceptions occurred when the net was fished for less than or more than the time period. In such cases, the observed catches were appropriately adjusted to estimate catches for the period. These catches in the primary sampling units, observed or estimated, form the basis for estimation of total migrations.

Lattice-Ratio Estimator

The approach we chose to estimate migration involves (1) estimation of migrants during days and periods covered by lattice samples and (2) expansion of these lattice estimates to extra-lattice days and periods. The first stage utilizes either a simple (Patterson 1954) or a modified lattice estimator; the second, ratio estimators.

The simple unbiased lattice estimator of migration during the days and periods covered by a lattice sample is

$$T = \frac{p^3 \bar{y}}{\theta} \qquad (1)$$

where $\bar{y}$ is the mean catch of smolts over the p^2 units sampled from the p^3 units of the lattice population, and θ is the proportion of the width of a river section sampled by the net. The property of unbiasedness follows immediately from the fact that $\bar{y}$ is an unbiased estimate of the average number of smolts through a net width over the p^3 units of the cubic lattice (e.g., see Patterson 1954), provided the net captures, on the average, a proportion θ of the total number of migrants in a primary unit. No estimate of the variance of T is possible from a single sample of p^2 primary units drawn in the manner we have described.

The estimator T ignores any additional sampling during lattice days and periods. Since the index site was usually fished continuously during all lattice periods of lattice days, and the index site was favored by smolts, loss of information results from using the simple lattice estimator (1). When the additional information at the index site was available, we modified our estimator to

$$T' = \frac{\tilde{y}}{\theta} + p^2 \frac{(p-1)}{\theta} \bar{y}' \qquad (2)$$

where $\tilde{y}$ is the total catch of smolts at the index site during the p lattice periods of the p lattice days and $\bar{y}'$ is the mean catch of smolts over the p (p-1) units sampled from the lattice population at the nonindex sites. The estimator T' is unbiased. Its variance cannot be estimated from our samples, but the estimator T' has a smaller variance than T.

We estimate the total migration during the lattice sampling days as

$$M_1 = \frac{X}{t} \qquad (3)$$

where X, obtained from T or T', is the estimated migration during the lattice periods of lattice days, and t is an estimate of proportion of the daily migration which occurs during lattice periods.

We estimate the total migration during index days as

$$M_2 = \frac{c}{r\theta} \qquad (4)$$

where c is the total catch on the index days during both lattice and extra-lattice periods and r is an estimate of the proportion of smolts which migrate through the index site.

Finally, if we are considering an interval of N days covering a lattice sample, one or more index days, and one or more days during which no sampling occurred, our estimate of the total migration during this interval is

$$M_3 = \frac{N}{n} (M_1 + M_2) \qquad (5)$$

where n is the number of days in the interval when either lattice or index sampling occurred. The estimator M_3 is appropriate if the selection of days within the interval at which sampling occurred can be considered as simple random. In view of the erratic daily migrations observed, we would expect the actual systematic selection of days to be equivalent to the simple random sampling of days.

In implementing the estimation procedure, we partitioned the sampling season into a number of intervals each enclosing a complete lattice sample together with any index days and unsampled days interspersed among the lattice days. The procedure has an unavoidable ambiguity--index days or unsampled days following the last lattice day of one lattice sample and preceding the first lattice day of the next sample can be assigned to an interval associated with either the first or second lattice sample. We attempted to allocate such days in equal numbers to each interval, but when an odd number of such days lay between two lattice samples, an arbitrary decision was made in assigning the odd day to one of the intervals.

Within such a lattice interval, estimates of the proportion using the index site and the proportion migrating during the lattice periods were computed using only information from the sampling within the interval because these proportions may change over the season. The proportion migrating during lattice periods within days was estimated by the ratio of the catches at the index site during the lattice periods to the total catch at the index site during an index day. If several index days lay within a lattice interval, the individual estimates of the days were averaged arithmetically.

The proportion migrating through the index site was estimated in one of two ways depending on the sampling program of the particular year. If a net was fished continuously at the index site during lattice sampling, the proportion using the index site in migration was estimated by the ratio of the total catch at the index site during the lattice sampling to the estimated total migration during the days and periods covered by the lattice sampling. On the other hand, if the index net was not fished continuously during the lattice sampling, the ratio of the total catch at the index net during lattice sampling to the total catch at all the sites during the lattice sampling was used as the estimate of the proportion using the index site. The ratio of the expected values of the numerator and denominator of each of these estimators equals the parameter.

Most estimates of total annual migrations of smolts from the Naknek system (Table 6) for 1958 to 1972 and from the Ugashik system for 1958 to 1970 (Table 7) were determined by the procedure described: exceptions are indicated in the tables. Migrations ranged nearly 6-fold from 3.4 million to 18.6 million from the Naknek system compared to a greater than 22-fold variation of 1.3 million to 29.5 million from the Ugashik system. The average migration from the Naknek system over 15 yr has been 10.5 million; from the Ugashik system, the average for 12 yr has been 10.8 million.

Size and Age of Smolts

Lengths, weights, and ages of migrants were estimated from samples collected every night or every other night. Hundreds of smolts were retained from catches at the index site or at all sites across the river, if index fishing was not being practiced. These fish were placed in a live pen and processed in the early morning. About 100 live smolts were blind-dipped from the live pen and their lengths recorded; weights and scales were taken from 20 to 40 of the fish. After ADF&G assumed the projects, greater numbers of smolts were measured for length during heavy migrations.

Fork length, from tip of snout to fork of tail, was measured to the nearest millimeter. Weights were recorded to the nearest 0.1 g. Scales were taken for aging the fish so as to determine age composition and brood year of the migrants. Scales were taken from a few rows just above and below the lateral line and in the area bounded by the dorsal and adipose fins where the scales first develop (Clutter and Whitesel 1956). Ages are designated as I, II, and III, corresponding to the number of winter annuli.

Age composition and mean length and weight of each age group were calculated from the sample for each day or group of days. Corresponding values for the entire season were obtained by weighing these values in proportion to the percentage of the total migration they represented (Tables 8, 9, and 10).

The age composition information was used to allocate the total migrations among the age groups (Tables 6 and 7). Then numbers originating from spawnings in years could be determined (Tables 11 and 12). Broods of Naknek smolts have ranged from 4.1 million to 18.4 million; of Ugashik smolts, from 3.6 million to 28.0 million. Numbers in a brood depend on escapement of the parent generation as we show later.

ADULT RETURNS

Mature sockeye salmon returning to Bristol Bay for spawning originate from a number of major river systems (Figure 1). Bristol Bay river systems can be classified into three geographic groups; in order from west to east these are Togiak Bay, Nushagak Bay, and eastern Bristol Bay. In eastern Bristol Bay the main sockeye salmon-producing systems are the Kvichak, Alagnak, Naknek, Egegik, and Ugashik rivers. Associated with these rivers are three fishing districts: Naknek-Kvichak (subdivided in 1962 into Naknek and Kvichak sections), Egegik, and Ugashik. The boundaries of these districts have varied over the years as government managers have attempted, among other things, to severally regulate the exploitation of the stocks bound for these rivers.

Table 6.--Estimated sockeye salmon smolt migrations (in thousands) from the Naknek River, 1958-72.

Year of seaward migration	Number of age--			Total
	I	II	III	
1958	9,967	372	--	10,339
1959	6,243	1,512	--	7,755
1960	2,817	2,472	16	5,305
1961	4,349	1,241	--	5,590
1962	8,302	8,780	Trace[a]	17,082
1963	5,462	7,870	121	13,453
1964	2,094	4,632	7	6,733
1965	9,913	6,653	67	16,633
1966	2,846	5,573	--	8,419
1967	4,039	5,218	28	9,285
1968	7,662	10,543	391	18,596[b]
1969	7,490	5,035	--	12,525
1970	1,880	1,520	--	3,400
1971	8,235	2,894	--	11,129
1972	709	10,193	--	10,902

[a]Trace is < 0.05% of total migration.

[b]McCurdy, Michael L. (editor). 1969. 1968 Bristol Bay sockeye salmon smolt studies. Alaska Department of Fish and Game Informational Leaflet 138, 95 p.

Table 7.--Estimated sockeye salmon smolt migrations (in thousands) from the Ugashik River, 1958-70.

Year of seaward migration	Number of age--			Total
	I	II	III	
1958	11,031	214	--	11,245
1959	5,221	759	--	5,980
1960	2,927	1,927	49	4,903
1961	703	2,745	--	3,448[a]
1962	12,199	2,917	--	15,116
1963	13,643	15,824	Trace[b]	29,467
1964	12,237	3,025	15	15,277
1965	1,730	4,278	--	6,008
1966[c]	--	--	--	--
1967	2,758	2,496	--	5,254[d]
1968	24,950	1,849	--	26,799
1969	3,014	2,035	--	5,049[a,d]
1970	751	555	--	1,306[e]
1971[c]	--	--	--	--

[a]An unknown proportion of the age II smolts were not sampled early in the outmigration.

[b]Trace is < 0.05% of total migration.

[c]Smolts not counted.

[d]An unknown proportion of the age I smolts were not sampled late in the outmigration.

[e]Russell, Philip A. (editor). 1972. 1970 Bristol Bay sockeye salmon smolt studies. Alaska Department of Fish and Game Technical Data Report No. 4, 60 p.

Table 8.--Estimated age composition (percent) of Naknek and Ugashik river sockeye salmon smolts.[a]

Year of seaward migration	Naknek			Ugashik		
	Age I	Age II	Age III	Age I	Age II	Age III
1958	96.4	3.6	--	98.1	1.9	--
1959	80.5	19.5	--	87.3	12.7	--
1960	53.1	46.6	0.3	59.7	39.3	1.0
1961	77.8	22.2	--	20.4	79.6	--
1962	48.6	51.4	Trace	80.7	19.3	--
1963	40.6	58.5	0.9	46.3	53.7	Trace[b]
1964	31.1	68.8	0.1	80.1	19.8	0.1
1965	59.6	40.0	0.4	28.8	71.2	--
1966	33.8	66.2	--	--	--	--
1967	43.5	56.2	0.3	52.5	47.5	--
1968	41.2	56.7	2.1	93.1	6.9	--
1969	59.8	40.2	--	59.7	40.3	--
1970	55.3	44.7	--	57.5	42.5	--
1971	74.0	26.0	--	--	--	--
1972	6.5	93.5	--	--	--	--

[a]Parker, Kenneth P. (editor). 1974. 1972 Bristol Bay sockeye salmon smolt studies. Alaska Department of Fish and Game Technical Data Report No. 13, 79 p.

[b]Trace is < 0.05% of total migration.

Table 9.--Estimated fork length in millimeters of Naknek and Ugashik river sockeye salmon smolts.[a]

Year of seaward migration	Naknek			Ugashik		
	Age I	Age II	Age III	Age I	Age II	Age III
1958	91	114	--	93	122[b]	--
1959	97	106	--	90	120	--
1960	99	109	(c)	90	108	--
1961	103	113	--	90	112	--
1962	105	112	(c)	88	112	--
1963	98	114	121[d]	90	104	--
1964	97	110	--	92	118	--
1965	99	114	130[e]	94	114	--
1966	106	118	--	--	--	--
1967	113	119	134[f]	88	113	--
1968	99	108	--	93	113	--
1969	100	112	--	97	121	--
1970	100	114	--	97	125	--
1971	102	120	--	--	--	--

[a]Parker, Kenneth P. (editor). 1974. 1972 Bristol Bay sockeye salmon smolt studies. Alaska Department of Fish and Game Technical Data Report No. 13, 79 p.

[b]Jaenicke, Herbert W. 1968. Sockeye salmon smolt investigations on the Ugashik River, Alaska, 1958-63. M.S. Thesis, Humboldt State College, California, 102 p.

[c]One only.

[d]Ten in sample.

[e]Five in sample.

[f]Three in sample.

Table 10.--Estimated average weight (grams) of Naknek and Ugashik river sockeye salmon smolts.[a]

Year of seaward migration	Naknek			Ugashik		
	Age I	Age II	Age III	Age I	Age II	Age III
1958	6.9	11.3	--	6.4	11.7	--
1959	8.2	10.1	--	6.1	13.5	--
1960	8.8	11.9	(b)	6.6	11.0	--
1961	10.8	13.8	--	6.7	12.2	--
1962	10.4	12.5	(b)	6.1	12.3	--
1963	8.1	12.8	17.2[c]	6.1	9.6	--
1964	7.7	11.0	--	6.9	12.7	--
1965	8.4	13.0	18.6[d]	6.9	12.5	--
1966	10.6	14.2	--	--	--	--
1967	13.1	14.7	17.9[e]	6.0	12.2	--
1968	8.4	11.1	--	6.5	10.7	--
1969	7.5	12.1	--	7.5	14.5	--
1970	9.0	12.1	--	7.7	15.9	--
1971	8.8	13.5	--	--	--	--

[a]Parker, Kenneth P. (editor). 1974. 1972 Bristol Bay sockeye salmon smolt studies, Alaska Department of Fish and Game Technical Data Report No. 13, 79 p.

[b]One only.

[c]Ten in sample.

[d]Five in sample.

[e]Three in sample.

Table 11.--Estimated Naknek River sockeye salmon smolt production (in thousands), 1956-70.

Brood year	Number of smolts produced			
	Age I	Age II	Age III	Total
1956	9,967	1,512	16	11,495
1957	6,243	2,472	--	8,715
1958	2,817	1,241	trace[a]	4,058
1959	4,349	8,780	121	13,250
1960	8,302	7,870	7	16,179
1961	5,462	4,632	67	10,161
1962	2,094	6,653	--	8,747
1963	9,913	5,573	28	15,514
1964	2,846	5,218	391	8,455
1965	4,039	10,543	--	14,582
1966	7,662	5,035	--	12,697
1967	7,490	1,520	--	9,010
1968	1,880	2,894	--	4,774
1969	8,235	10,193	--	18,428
1970	709	--	--	--

[a]Trace is <0.05% of total migration.

Table 12.--Estimated Ugashik River sockeye salmon smolt production (in thousands), 1956-67.

Brood year	Number of smolts produced			
	Age I	Age II	Age III	Total
1956	11,031	759	49	11,839
1957	5,221	1,927	--	7,148
1958	2,927	2,745	--	5,672
1959	703	2,917	Trace[a]	3,620
1960	12,199	15,824	15	28,038
1961	13,643	3,025	--	16,668
1962	12,237	4,278	--	16,515
1963	1,730	--	--	--
1964	--	2,496	--	--
1965	2,758	1,849	--	4,607
1966	24,950	2,035	--	26,985
1967	3,014	555	--	3,569

[a]Trace is < 0.05% of total migration.

Tagging of returning adults in coastal waters of Bristol Bay (Thompson et al. 1954; Straty 1975) demonstrates that at least some sockeye salmon bound for any one of the eastern systems migrate through fishing districts other than that proximate to the home river's entrance. Thompson (1962) was convinced that Nushagak Bay stocks are essentially separated from the other regions' stocks when exploited within Bristol Bay, but that eastern stocks from the Egegik and Kvichak rivers (and presumably the Alagnak River) were mixed in the coastal waters proximate to and between these rivers' entrances.

Straty's (1975) inshore taggings further describe migrations within upper Bristol Bay. Ugashik sockeye salmon were detected as far north along the east coast as Middle Bluff above the Egegik River entrance and as far west along the north coast as Nushagak Bay (Figure 1). Egegik fish were detected from the Naknek River entrance south along the east coast to below Ugashik Bay. Westward, Egegik sockeye salmon occurred in Nushagak Bay. Naknek sockeye salmon were detected from the upper reaches of Kvichak Bay above and to the west of the Naknek River entrance and south along the east coast nearly to the Ugashik River entrance. Kvichak fish were detected as far south as the Ugashik River entrance along the east coast and as far west along the north coast as Nushagak Bay. Although the range of detection was far reaching, percent returns to a river system from releases generally decreased sharply with distance of the river from the release sites. Limits of the ranges are sometimes based on only one recovery from substantial numbers released.

Straty's (1975) view of terminal migration routes of eastern stocks, based on offshore exploratory fishing, offshore tagging, and inshore tagging, is one of progressive segregation--Ugashik, Egegik, and Naknek stocks serially move from the migrating body of eastern stocks and concentrate in the vicinity of their respective rivers' entrances. Kvichak stocks remain offshore and eventually enter Kvichak Bay concentrated on the northwest side. Nonetheless, catches in each eastern fishing district must consist of mixtures of stocks bound for several river systems, although such mixing may be negligible. Because adults of unknown origins were tagged in the studies described, interpretation of results to quantify mixing is difficult or impossible since the destination of marked individuals is unknown unless they escape the fishery, migrate to their stream of origin, and are observed there. Numerical measures of mixing in catch districts based on escapees require unavailable knowledge of rates at which tagged members of individual stocks were exploited.

Since individuals, because of mixing in catch districts, cannot be identified to stream of origin, the total returns of salmon bound for individual river systems are unknown. This information is essential in analysis of stock dynamics, such as evaluation of productivity and ocean survival, at the level of individual river systems. If Straty's (1975) conception of terminal migration is correct, mixing in catch districts other than Naknek-Kvichak is negligible and can be ignored.

Additional information available with which to examine the mixing problem in eastern fishing districts consists of the estimates of catches in the districts and escapements to the rivers, together with samples selected from them to determine their age type, sex, and length compositions. Although we now attempt to resolve the mixing problem with these data, the analysis does not

provide a satisfactory quantification of mixing in the catch districts. The results, which we view with circumspection, indicate the problem may be negligible some years and more severe in others. Further, the outcome points to an intriguing model of terminal migration routes.

Since 1958 estimation and sampling of catches and escapements of eastern Bristol Bay sockeye salmon have been routinely conducted. Examinations of length-frequencies and proportions by age type and sex in catches and escapements sometimes are suggestive of the occurrence of mixing (e.g., see Thompson et al. 1954), but quantification of the extent requires relating the totality of observations to a suitable model of the fishing, escapement, and sampling processes. First we describe the model purported to be sufficient for this purpose. Next, the methodology for estimation of parameters of the model from data is described. Thereafter, results and implications of applications are discussed.

Stochastic Model of Escapement, Fishing, and Sampling Processes

We now propose a model to approximate the escapement, fishing, and sampling processes. The model is most clearly described through the vehicle of a mechanical device, the pinball machine. Consider a game board consisting of an enclosed, perforated, inclined plane, equipped with adjustable deflectors. Lead balls are poured in at the top and roll down the board. The balls may either fall through one of the holes and so be "caught" or leave at an exit at the bottom and so "escape". Actual paths taken by the balls are random in an obvious sense, with the mean path determined by the deflector settings. The plane is partitioned into three zones of arbitrary shapes, sizes, and positions. Each zone contains some perforations.

The random 4-tuple of catches of each of the three zones and of the escapement resulting from a release of N balls has the multinomial distribution for a given setup of the machine. The distribution has four parameters: N and θ_1, θ_2, and θ_3 where θ_i is the probability a pinball falls through a hole in the i-th zone. We note for later reference that each probability may be written as the product of the unconditional probability that a ball falls through a hole and the conditional probability that the ball falls through a hole in the i-th zone given that it falls through a hole in some zone. Next, suppose that several types, say colors, of pinballs are released independently of one another. The random array of zone catches and escaping pinballs of the j-th type then clearly has again the multinomial distribution with the obvious addition of a subscript j to the parameter N. Further suppose that when a ball drops through a hole in a zone, it activates a counter for that zone which cannot discriminate its type. Therefore, the number of pinballs caught in each of the zones is known, but the type composition is unknown. However, simple random samples of the pinballs caught in each zone are taken to estimate the composition. Pinballs reaching the exit activate a similar counter and again simple random samples are taken to estimate their type composition. If the number of j-type pinballs released, N_j, is large and the sampling fractions in the catch zones, ϕ_1, ϕ_2, ϕ_3, and of the escapement, ϕ_4, are small, the actual multinomial distribution of the random 4-tuple of numbers of j-type pinballs occurring in the samples from the three catch zones and from the escapement is well approximated by the multiple Poisson distribution (see Feller 1968) with parameters:

$$\lambda_{ij} = \theta_i \phi_i N_j; \quad i = 1, 2, 3; \text{ and}$$

$$\lambda_{4j} = (1 - \sum_{i=1}^{3} \theta_i) \phi_4 N_j . \tag{6}$$

As a final elaboration, four groups of pinballs are run through the machine. Each group is composed of one or more types. After each group has passed through the machine, the deflectors are set to new positions to cause new patterns of passage. The number and position of the holes remain fixed between runs. Numbers reaching the exit are recorded and sampled for composition after each group has passed through the machine. After this sampling, the pinballs at the exit are discarded, and the counter is reset. The catch of each zone accumulated from the four groups is enumerated and sampled for type composition at the completion of the experiment. If we let

N_{ij} = number of pinballs of the j-th type released on the i-th run,

ϕ_k = sampling fraction of the catch in the k-th zone,

ϕ_{i+3} = sampling fraction of the escapement of the i-th run,

θ_{ik} = probability of a pinball released on the i-th run falling through a hole in the k-th zone,

X_{ijk} = random number of pinballs of the j-th type from the i-th run in the sample from the k-th zone, and

X_{ij4} = random number of pinballs of the j-th type from the i-th run in the sample of the escapement,

the multiple Poisson distribution with parameters

$$\lambda_{ijk} = \theta_{ik} \phi_k N_{ij}$$

$$\lambda_{ij4} = (1 - \sum_{k=1}^{3} \theta_{ik}) \phi_{i+3} N_{ij}$$

$$i = 1, 2, 3, 4; \quad j = 1, \ldots, J; \text{ and } k = 1, 2, 3. \tag{7}$$

is a good approximation to the actual multinomial distribution of the random numbers occurring in the samples provided N_{ij} is large and the sampling fractions are small.

The random number of pinballs of the j-th type sampled from the k-th zone,

$$Z_{jk} = \sum_{i=1}^{4} X_{ijk} ,$$

is the sum of four independent Poisson random variables and hence Poisson-distributed again with parameter

$$\sum_{i=1}^{4} \lambda_{ijk} .$$

The X_{ij4}, the random numbers of pinballs of the j-th type in the sample from the escapement of the i-th run, are also Poisson random variables and are independent of the Z_{jk}. The random variables have the following mean values:

$$E(X_{ij4}) = (1 - \sum_{k=1}^{3} \theta_{ik}) \; \phi_{i+3} \; N_{ij}$$

and

$$E(Z_{jk}) = \sum_{i=1}^{4} \theta_{ik} \; \phi_k \; N_{ij} \tag{8}$$

$$i = 1, 2, 3, 4; \; j = 1, \ldots, J; \; \text{and} \; k = 1, 2, 3.$$

An obvious analogy can be drawn between the Bristol Bay catch, escapement, and sampling processes and the pinball experiment last described. Pinballs represent individual salmon. Holes represent fishing gear. Pinballs falling through holes are salmon caught by the gear. The three zones represent the Naknek-Kvichak, Egegik, and Ugashik fishing areas. The four groups of pinballs are returning salmon bound for each of four spawning rivers: (1) Naknek; (2) Kvichak and Alagnak, (3) Egegik, and (4) Ugashik. (The Kvichak and Alagnak rivers have been combined because age, sex, and length composition sampling and, in some years, enumeration of the Alagnak River escapements were not conducted preceding 1963. Usually the Alagnak River accounts for a small part of the total escapement to the Kvichak and Alagnak rivers.) The particular random pattern of movement over the board, determined in the mean by deflector settings in relation to zones, has its analogue in the pattern of passage of returning salmon of the four river systems through eastern Bristol Bay. Therefore, we implicitly assume that Nushagak stocks are essentially separate of eastern stocks in the fishery within Bristol Bay.

The analogy between the pinball experiment and the actual fishing, escapement, and sampling processes stops short of the selective properties of the fishery. Sockeye salmon of Bristol Bay are caught exclusively by gillnets. The gillnets are known to be selective for size of individuals. Probability of retention of an individual encountering the gear increases with the size of the individual (e.g., see Burgner 1965). Small salmon probably pass through the mesh. The retention rate must diminish if salmon are very large; but nylon gillnets, which account for nearly all the catches in the years of this study, stretch sufficiently to accommodate a wide range of sizes. Significant reduction in the retention rate of large salmon is not evident from the ratios of catch to catch plus escapement plotted against length for the years of this study for eastern Bristol Bay systems.

To account for size selectivity, salmon will be classified into length intervals. We assume that the selection curve for the gillnets can be approximated by the integrated normal ogive

$$s_m = \int_{-\infty}^{\ell_m} \frac{1}{\sigma\sqrt{2\pi}} \; e^{-\frac{(t-\mu)^2}{2\sigma^2}} \; dt \tag{9}$$

where ℓ_m = midpoint of the m-th length interval. The pair (μ, σ) are named the selection ogive parameters. The function is reasonably flexible, depends

on only two parameters, and is monotone-increasing. Catch length frequencies as compared to escapement plus catch length frequencies for eastern Bristol Bay suggest to us a monotone-increasing function may be adequate to describe selectivity. Therefore with a minimum expense in coefficients to be estimated, a rough description of size selection may be incorporated in the basic model. Undoubtedly, alternative functions could be adopted, but choice among such functions is impossible with the available information.

The basic model at (7) and (8) requires the addition of the length interval subscript m to all constants and random variables except the sampling fractions. The parameter θ_{ikm}, the probability that a salmon in length interval m originating from river system i is caught in fishing district k, can be expressed as

$$\theta_{ikm} = \alpha_{ik} \; f_i \; s_m \qquad (10)$$

where

α_{ik}, the mixing coefficient of system i in district k, is the conditional probability that a salmon bound for river system i is captured in fishing district k given it is caught in one of the districts;

f_i, the encounter rate coefficient of system i, is the probability a salmon from the i-th river system encounters fishing gear on its passage through Bristol Bay; and

s_m is the conditional probability that a salmon of length interval m is captured given it encounters fishing gear.

<div align="center">Estimation of Model Parameters</div>

General Theory

Estimates and samples of catches from the Naknek-Kvichak, Egegik, and Ugashik districts and of escapements to the Naknek, Kvichak, Egegik, and Ugashik rivers are available to use in estimation of the parameters of the model. To introduce our methodology, we will treat the observations from samples of the actual catches and escapements as though they arose from simple random sampling for composition as described in the pinball experiment, and estimates of catches and escapements as fixed known constants. Actually the samples were stratified by time, and the estimates, particularly of escapements, are subject to error. Errors in estimates are probably negligible in comparison to deviations from the model from other sources. Stratified samples are treated as simple random samples in order to roughly incorporate measures of the reliability of the observations, to reduce the quantity of information and expense required in the estimation process, and to simplify an involved discussion; this expedient will be elaborated upon when weighting observations for relative precision is discussed. Consequences will be examined when results of applications are described.

If we return to equation (8) and add the length interval subscript, we obtain

$$E(X_{ijm4}) = (1 - \sum_{k=1}^{3} \theta_{ikm}) \; \phi_{i+3} \; N_{ijm} \qquad (11)$$

and

$$E(Z_{jkm}) = \sum_{i=1}^{4} \theta_{ikm} \, \phi_k \, N_{ijm} \tag{12}$$

We note from (11) that

$$N_{ijm} = \frac{E(X_{ijm4})}{(1 - \sum_{k=1}^{3} \theta_{ikm}) \, \phi_{i+3}} \tag{13}$$

If we substitute (10) and (13) into (12), divide by ϕ_k, and subtract the right-hand side of the resulting equation from both sides, we obtain

$$\frac{E(Z_{jkm})}{\phi_k} - \sum_{i=1}^{4} \frac{\alpha_{ik} \, f_i \, s_m}{1 - \sum_{k=1}^{3} \alpha_{ik} \, f_i \, s_m} \frac{E(X_{ijm4})}{\phi_{i+3}} = 0. \tag{14}$$

Our equation (14) is central to the parameter estimation and deserves comment. The first term,

$$E(Z_{jkm})/\phi_k \, , \tag{15}$$

is seen to be the total expected catch in district k of the (jm) salmon. Further the ratio

$$E(X_{ijm4})/\phi_{i+3} \tag{16}$$

is the total expected escapement to river system i of the (jm) salmon. The sum

$$\sum_{k=1}^{3} \alpha_{ik} \, f_i \, s_m = f_i s_m \tag{17}$$

is the exploitation rate of salmon in length interval m from river system i. The complement,

$$1 - \sum_{k=1}^{3} \alpha_{ik} \, f_i \, s_m \, , \tag{18}$$

is the expected proportion of the (jm) salmon escaping. The ratio,

$$\frac{E(X_{ijm4})/\phi_{i+3}}{1 - \sum_{k=1}^{3} \alpha_{ik} \, f_i \, s_m} \, , \tag{19}$$

then is the total number of (jm) salmon from the ith river system. It is now easily seen that the second term of equation (14) can be written as

$$\sum_{i=1}^{4} \alpha_{ik} \, f_i \, s_m \, N_{ijm} \, . \tag{20}$$

Since $\alpha_{ik} f_i s_m$ is the expected proportion of salmon of length interval m from river system i which are caught in district k, the sum (20) is simply the total expected catch in district k of (jm) salmon. Thus the assertion (14), while cumbersome, is patently true.

Now for each (jm) or age, sex, and length category of salmon, we have a system of three equations from (14), corresponding to the three districts, k=1, 2, and 3. The expectations are unknown to us, but their most reasonable estimators are simply the observed values. If we replace the expectations by the observed values, then generally it is no longer true that the corresponding expression equals zero as it did at (14). The new system corresponding to the (jm) salmon, with the observations replacing the expectations and using (17), is explicitly

$$G_1^{(jm)} = \frac{Z_{j1m}}{\phi_1} - \sum_{i=1}^{4} \frac{\alpha_{i1} f_i s_m}{1 - f_i s_m} \frac{X_{ijm4}}{\phi_{i+3}}$$

$$(21)$$

$$G_2^{(jm)} = \frac{Z_{j2m}}{\phi_2} - \sum_{i=1}^{4} \frac{\alpha_{i2} f_i s_m}{1 - f_i s_m} \frac{X_{ijm4}}{\phi_{i+3}}$$

$$G_3^{(jm)} = \frac{Z_{j3m}}{\phi_3} - \sum_{i=1}^{4} \frac{(1 - \alpha_{i1} - \alpha_{i2}) f_i s_m}{1 - f_i s_m} \frac{X_{ijm4}}{\phi_{i+3}}$$

$$j = 1, 2, \ldots, J; \; m = 1, 2, \ldots, M.$$

The observed X_{ijm4} appear in each equation of (21). The observed Z_{jkm} appears only in the k-th equation, k = 1, 2, 3.

To estimate the 14 parameters of the model, viz., the two selection curve parameters, 8 mixing coefficients (linear constraints reduce the original 12 to 8), and 4 encounter rate coefficients, we shall minimize the sum of squares of the deviations $G_k^{(jm)}$ over the parameter space. Our situation falls into that discussed by Deming (1943) or Guest (1961) concerning general least-squares theory for functionally related variables. The method of Gauss is used to improve an initial guess of the least-squares solution; and a variance-covariance matrix may be calculated for the parameter estimates assuming the linearized model holds in a sufficiently large neighborhood of the solution. Practically speaking, the variances and covariances should only be considered as rough guides to the precision of the estimates.

In an unrestricted search for the least-squares solution to equation system (21), the solution usually led outside the feasible solution space--estimates of parameters representing probabilities assumed values less than 0 or greater than 1. Therefore the search would be restricted by requiring solutions to be feasible; if an improved guess (calculated above at some iteration) was not feasible, the correction vector used to obtain this guess was scaled by 1/2 before being added to the preceding guess. If the resulting new guess from this modification of the search again was not feasible, the correction vector was scaled by $(1/2)^2$ before being added to the preceding guess. Again the new guess was checked to determine whether it was feasible. This process

was repeated, scaling the correction vector by powers of 1/2 until a feasible new guess was obtained.

The search, restricted or unrestricted, was continued until a satisfactory solution was obtained. Our criterion for acceptability is described later.

Statistical Weights

To apply the method, knowledge of the variances of the random variables in equation system (21) is needed to determine the efficient, weighted least-squares estimator; on the other hand, the less efficient, unweighted least-squares estimator can be developed without knowing the underlying variances. In fact the underlying variances are unknown, and must be replaced by estimates in the weighted estimator. Statistical properties of this modified, weighted least-squares estimator are unclear, but this estimator should be more efficient for a given set of data than the unweighted estimator. The procedure for the estimation of the variances will now be described.

We restrict our attention to the age groups which constitute nearly the entire sockeye salmon returns to eastern Bristol Bay: ages 4_2, 5_2, 5_3, and 6_3. Further, we include in our analysis only length intervals of an age and sex type for which we expect at least some minimal number in all samples from catches and escapements; the criterion is described momentarily. Therefore, the variances are greater than zero. We have seen that the random number of individuals of an age, sex, and length class in a sample from a catch district or escapement system is Poisson-distributed; therefore, the variance and expected number are equal. Our sample sizes from a catch district or escapement system are usually substantial, but the expected number falling in some length intervals may be small, and an actual absence of individuals falling in a class may occur. An estimate of the expected number and of the variance of the number occurring in such a class is the observed number. This estimate of the variance is unsatisfactory for two reasons: (1) it will produce many zero-valued estimates which we know are incorrect, and (2) our procedure cannot tolerate zero values for variances. As a result, age, sex, and length classes for which one or more of the variances were estimated as zero would have to be omitted from the analysis. Therefore we reasoned that an alternative estimate of the variances should be devised which would permit greater use of the data.

In computing statistical weights, we assumed the length frequency distribution of an age and sex type in the catch or escapement was normal. This assumption is probably invalid; however, as an approximation it seems reasonable for our purpose and later in this report we are careful to evaluate the effect of weighting. Using the sample mean and variance, we estimated the proportion of individuals in the corresponding population which occurred in a length interval by integrating the normal density over the interval. An adjusted number occurring in a length class in the sample was computed by redistributing the observed number of an age and sex type in the sample over the length intervals in proportion to the number expected on the basis of the normal distribution. This adjusted number was our estimate of the variance of the number occurring in a length class in the sample.

Results

Catch and escapement samples for the years 1958 to 1969 (excluding 1965 for which some of the information was incomplete) have been fitted to the model. A 10-mm length interval was used. Estimated numbers of each sex of the four major age types--4_2, 5_2, 4_3, and 6_3--were allocated to the length intervals in proportion to sample numbers in the intervals; these were taken as the

$$\frac{Z_{jkm}}{\phi_k} \quad \text{and} \quad \frac{X_{ijm4}}{\phi_{i+3}} \quad \text{of equation system (21).}$$

Alagnak and Kvichak numbers and samples were pooled.

Fittings were performed repeatedly. Parameters were estimated both using and omitting weighting; both cases were computed twice, using different initial guesses of the parameters (Table 13). Fittings were constrained to search over feasible values of the parameter space after an initial attempt was made to permit unrestricted searching with the high-mix guess. In this unrestricted search, weighting was used; in only one year, 1968, was the unrestricted solution within the feasible parameter space. Sampling was most intense that year in all catch districts and escapements; the more accurate determinations of the compositions of catches and escapements may be at least partially responsible for the feasible unrestricted fit.

Searching for a solution for any given year is expensive in computer time--a massive sequence of computations is required for each iteration. Therefore, the number of iterations was limited. Weighted fittings with the high-mix guess resulted after ten iterations. Judging from the rate of approach of intermediate solutions to the tenth, five iterations seemed adequate. Therefore the unweighted fittings with high- and low-mix guesses and the weighted fittings with low-mix guess were computed with five iterations. The variances of estimates were computed for the weighted estimates; such calculations are inappropriate for the unweighted fittings.

Initial guesses for the parameters were the same for all years (Table 13). The probability of encountering fishing gear was taken as one-half for stocks of each system. The parameters of the selection ogive, (μ,σ) were taken to be (495,28) for each system and run. These values were rough guesses obtained from inspection of various plots comparing ratios of catch to catch and escapement as related to length. Initial guesses for mixing coefficients were chosen to represent two conditions--complete mixing (high-mix guess) and virtually complete separation of stocks (low-mix guess). Under high mixing, the conditional probability of a fish of system i being caught in district k was taken intially as one-third. Under low mixing the conditional probability of a fish of system i being caught in the district proximate to this river mouth is 0.95 and in either of the two remaining districts is 0.025.

Outcomes of this analysis are inadequate for estimation of total returns by river system through allocation of catch to river of origin. However, results are not without merit in that circumstantial evidence is provided which indicates that interception of stocks outside the proximate catch districts for eastern systems may be severe in some years. As a case to study, we will discuss the results for 1968 in detail.

Table 13.--Initial guesses of parameters of adult returns model.[a]

Parameters	High-mix guess	Low-mix guess
f_1	0.5	0.5
f_2	.5	.5
f_3	.5	.5
f_4	.5	.5
α_{11}	.333	.95
α_{21}	.333	.95
α_{31}	.333	.025
α_{41}	.333	.025
α_{12}	.333	.025
α_{22}	.333	.025
α_{32}	.333	.95
α_{42}	.333	.025
μ	495	495
σ	28	28

[a]For f_i and α_{ij}, i refers to river system and j refers to fishing district as follows:

$i = $ 1 Naknek
2 Kvichak
3 Egegik
4 Ugashik

$j = $ 1 Naknek-Kvichak
2 Egegik
3 Ugashik

Analysis of 1968 catch and escapement samples for eastern Bristol Bay by any of five fitting procedures--combinations of restricted or unrestricted search, weighted or unweighted least squares, and high- or low-mixing guess-- produces identical qualitative results and very similar numerical results (Table 14). First, Egegik and Ugashik sockeye salmon were more likely to encounter gear than Naknek or Kvichak fish. Kvichak fish had the smallest estimates, 0.26 or 0.27, of encounter rate. A small return was anticipated for the Kvichak system and state managers kept the Kvichak section of the Naknek-Kvichak district closed to fishing until 11 July; by the time the Kvichak section was opened, 97% of the catch of 1.2 million sockeye salmon in the Naknek-Kvichak district had been taken.

Of special interest are the estimates of mixing coefficients. If the estimates have any validity, Ugashik sockeye salmon were heavily intercepted in both the Naknek-Kvichak district (necessarily the Naknek section) and the Egegik district; Egegik fish were heavily intercepted in the Naknek-Kvichak district; and both Naknek and Kvichak fish were intercepted in the Egegik district. That interceptions occurred is not surprising; the estimated magnitude is. While these interpretations are tenuous in view of results from the remaining years analyzed, they are consistent with two important observations. First, waters from the Egegik and Ugashik rivers are carried above their mouths toward the head of the bay (See Figures 6 and 7). Waters from the Naknek and Kvichak rivers are swept to the southwest during ebb tide and must encounter the Egegik and Ugashik waters somewhere above the entrance of the Egegik River, the general region considered by Thompson et al. (1954) as an area of mixing of stocks. The distances and directions these waters move and the places of encounter depend on tide stage and probably in part on wind conditions. If returning salmon key on odors of river waters in the coastal area, the potential for mixing of stocks as indicated by the 1968 analysis occurs, as well as annual variation in mixing. Second, the Ugashik run is usually later than the other eastern systems. Differences in timing of runs are difficult to ascertain, but the lag of Ugashik sockeye salmon is common knowledge in Bristol Bay. Searching by these fish far above their home stream entrance could cause the delay.

Catch and escapement samples and enumerations have been fitted by restricted search (R), weighted (W) and unweighted (U) least squares, and initial guess of high (H) or low (L) mixing for each year (Appendix Tables 1-12). Averages of annual estimates for each coefficient have been calculated for each fitting method (Tables 15-17). Weighted estimates are considered by us to be most reliable because weighted estimators should be most efficient. Average encounter rate estimates are reasonably consistent among methods (Table 15); Naknek and Kvichak stocks appear to be less likely to encounter gillnets than Egegik or Ugashik stocks. Only the high-mix guess under weighted fitting produced an average encounter rate which differed substantially from estimates by the remaining procedures, and this case was for Naknek stock. The averages of encounter rates suggest roughly 10% more of the Egegik and Ugashik stocks encounter gear than do stocks of the Kvichak or Naknek systems.

Exploitation rates depend not only on the encounter rates but also on the size-selective characteristics of the gillnets and the size-frequency distributions of the stocks. The exploitation rates must be less than or equal to the encounter rates. Of course, errors in estimation of encounter rates or

Table 14.--Parameter estimates of adult returns model for 1968 under unrestricted (U) or restricted (R) search, weighted (W) or unweighted (U) least squares, and initial guess of high (H) or low (L) mixing.

Method and river system	Encounter rate coefficients				Selection parameters	
	Naknek	Kvichak	Egegik	Ugashik	μ	σ
UWH	0.40	0.27	0.66	0.79	495.6	18.3
RWH	.40	.27	.68	.65	495.4	18.3
RWL	.40	.27	.68	.65	495.3	18.3
RUH	.44	.26	.70	.74	494.9	24.27
RUL	.44	.26	.70	.74	494.8	24.19

	Mixing coefficients		
	Naknek-Kvichak	Egegik	Ugashik
UWH			
Naknek	0.80	0.18	0.02
Kvichak	.86	.13	.01
Egegik	.28	.67	.05
Ugashik	.33	.56	.11
RWH			
Naknek	.79	.19	.02
Kvichak	.85	.13	.02
Egegik	.29	.67	.04
Ugashik	.32	.44	.24
RWL			
Naknek	.79	.19	.02
Kvichak	.86	.13	.01
Egegik	.29	.67	.04
Ugashik	.32	.44	.24

Table 14. Continued

Method and river system	Mixing coefficients		
	Naknek-Kvichak	Egegik	Ugashik
RUH			
Naknek	0.82	0.17	0.01
Kvichak	.84	.14	.02
Egegik	.22	.70	.08
Ugashik	.54	.28	.18
RUL			
Naknek	.82	.17	.01
Kvichak	.84	.14	.02
Egegik	.21	.71	.08
Ugashik	.55	.27	.18

Table 15. Average encounter rate coefficients by fitting procedure for stocks of four river systems.

Method[a]	Naknek	Kvichak	Egegik	Ugashik
RWH	0.35	0.50	0.60	0.61
RWL	.44	.48	.59	.59
RUH	.46	.48	.58	.62
RUL	.50	.48	.55	.59

[a] R = restricted search, W or U = weighted or unweighted least squares, and H or L = high or low mixing initial guess.

Table 16.--Average ogive parameters by fitting procedure.

Method[a]	μ	σ
RWH	495.0	23.93
RWL	495.4	24.70
RUH	494.6	23.02
RUL	495.4	26.24

[a] R = restricted search, W or U = weighted or unweighted least squares, and H or L = high or low mixing initial guess.

Table 17.--Average mixing coefficients by fitting procedure for stocks of four river systems in three fishing districts.

Method and river system	Naknek-Kvichak	Egegik	Ugashik
RWH[a]			
Naknek	0.72	0.12	0.16
Kvichak	.77	.14	.09
Egegik	.28	.58	.14
Ugashik	.36	.23	.41
RWL[a]			
Naknek	.94	.04	.02
Kvichak	.93	.05	.02
Egegik	.25	.71	.04
Ugashik	.23	.16	.61
RUH[a]			
Naknek	.66	.20	.14
Kvichak	.74	.14	.12
Egegik	.26	.54	.20
Ugashik	.35	.28	.37
RUL[a]			
Naknek	.92	.06	.02
Kvichak	.93	.04	.03
Egegik	.14	.81	.05
Ugashik	.21	.12	.67

[a]R = restricted search, W or U = weighted or unweighted least squares, and H or L = high or low mixing initial guess.
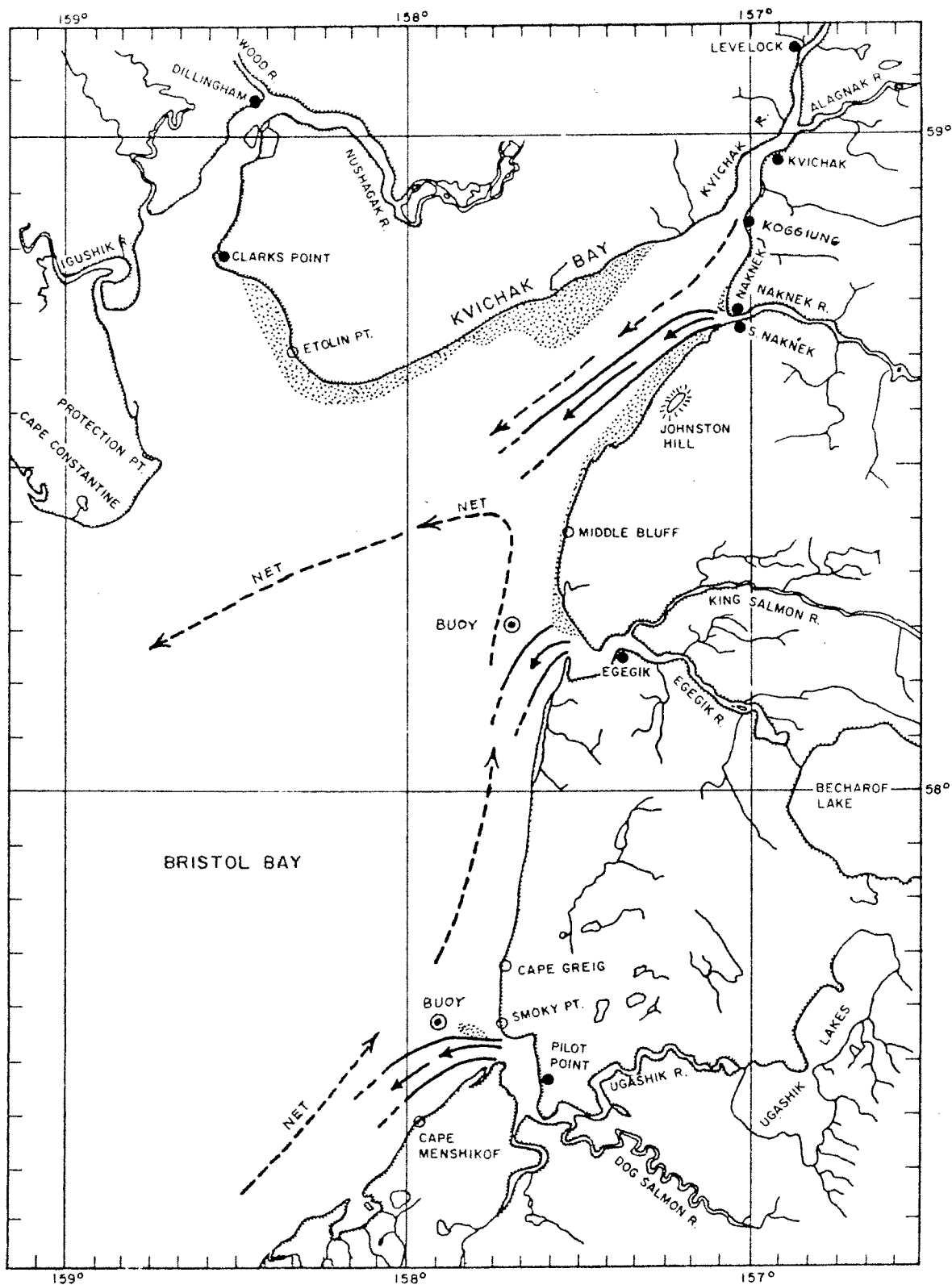
Figure 6.--General course of river waters in Bristol Bay during ebb tide as determined from dye tracking (Reproduced from Straty 1977).
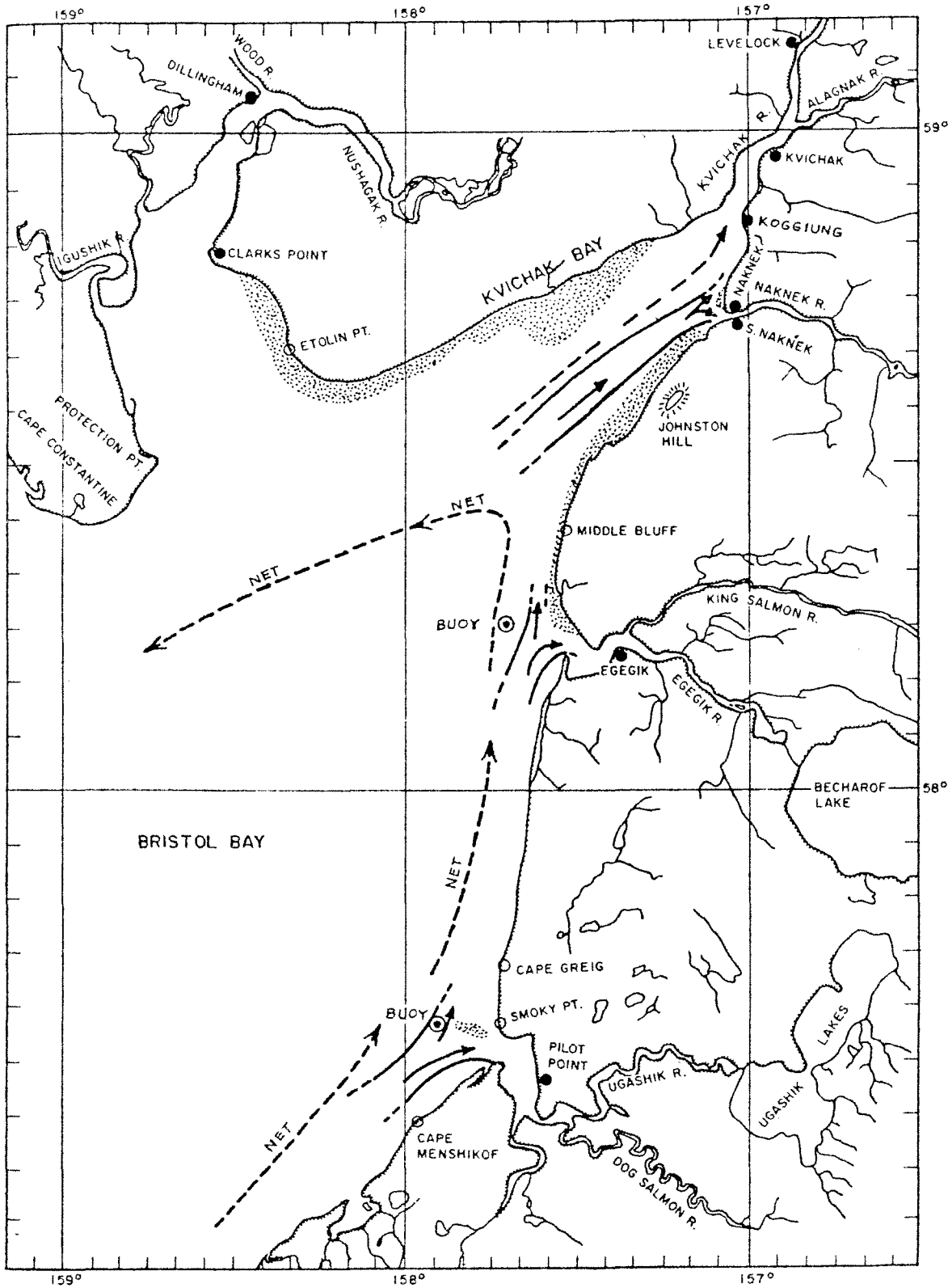
Figure 7.--General course of river waters in Bristol Bay during flood tide as determined from dye tracking (Reproduced from Straty 1977).

exploitation rates could violate the condition. Annual exploitation rates for these stocks calculated from escapements and ADF&G catch allocations (Robert D. Paulus, personal communication) for the same years are as follows: Naknek, 0.42; Kvichak, 0.40; Egegik, 0.56; and Ugashik, 0.48. In nearly all cases, averages of estimates of encounter rates (Table 15) exceed averages of estimates of exploitation rates calculated from the ADF&G information as expected from theory. Therefore, regardless of the approach, Egegik and Ugashik stocks are more heavily exploited than Naknek and Kvichak stocks.

The averages for selection ogive parameters are quite similar among methods of fitting (Table 16). The estimates lie close to our original guess. Probably the method is insensitive in estimating these parameters.

The averages of mixing coefficients tend to agree more closely among fits under the same mixing guess, high or low, than under the same fitting criterion, weighted or unweighted least squares. The high-mix guess resulted in coefficient estimates of greater interception of all stocks in districts not immediately adjoining their river of origin. However, for either low- or high-mix guesses the averages of mixing coefficients imply that greater proportions of Egegik and Ugashik stocks stray than Naknek or Kvichak stocks. In terms of absolute numbers, however, the straying may not be greater in these streams, particularly comparing the larger Kvichak stock with the other stocks.

Although the averages of coefficient estimates support the hypothesis of terminal migration of spawning runs to eastern Bristol Bay outlined under the discussion of the 1968 fittings, the results must be viewed circumspectly. First, restriction of estimates to the feasible parameter space should cause bias. Next, differences in estimates among fitting methods are often great (Appendix Tables 1-12). Nonetheless, close examination of the tables reveals other instances in addition to 1968 for which subsets of estimates are reasonably consistent between at least pairs of methods, e.g., encounter rates and mixing coefficients of Kvichak, Egegik, and Ugashik stocks in 1961 by weighted analysis with either high or low mixing guesses.

Consistency in estimates among methods provides greater confidence in qualitative implications of the coefficient values. In addition to the study of mean estimates of parameters, a measure of the consistency with which two methods estimate a particular coefficient is the correlation between their paired annual estimates of that coefficient. Such correlations have been computed for all pairwise combinations of methods and all coefficients (Tables 18-20). Generally, correlations are higher for encounter rates and ogive parameters than for many of the mixing coefficients. Comparisons of encounter rates and ogive parameters from high and low mixing guesses of weighted fittings show high positive correlations except for the Ugashik encounter rate. (Weighted fittings are considered best by us.) However, mixing coefficients from the two guesses under weighted fitting are not highly correlated except for those for Egegik stocks to the Naknek-Kvichak and Egegik districts and Ugashik stocks to the Egegik district. A definitive determination of terminal migration routes and exploitation rates of eastern stocks awaits either a tagging program--smolts tagged in the rivers with recoveries as adults in the fishing districts--or methodology to identify origins of individuals in catches.

Table 18. Correlations between encounter rate coefficients estimated by paired fitting procedures for stocks of four river systems.

Fittings and methods[a]	Naknek	Kvichak	Egegik	Ugashik
RWH-RWL	0.77	0.87	0.87	0.58
RWH-RUH	.50	.87	.86	.74
RWH-RUL	.24	.83	.68	.51
RWL-RUH	.19	.80	.76	.33
RWL-RUL	.32	.96	.72	.62
RUH-RUL	.84	.77	.83	.79

[a]R = restricted search, W or U = weighted or unweighted least squares, and H or L = high or low mixing initial guess.

Table 19.--Correlations between ogive parameters estimated by paired fitting procedures.

Fittings and methods[a]	μ	σ
RWH-RWL	0.87	0.88
RWH-RUH	.90	.57
RWH-RUL	.77	.59
RWL-RUH	.74	.55
RWL-RUL	.78	.74
RUH-RUL	.77	.77

[a]R = restricted search, W or U = weighted or unweighted least squares, and H or L = high or low mixing initial guess.

Table 20.--Correlations between mixing coefficients estimated by paired fitting procedures for stocks of four river systems.

Fittings and methods[a]	Naknek			Kvichak			Egegik			Ugashik		
	α_{11}	α_{12}	α_{13}	α_{21}	α_{22}	α_{23}	α_{31}	α_{32}	α_{33}	α_{41}	α_{42}	α_{43}
RWH-RWL	-0.03	0.38	0.56	-0.10	0.17	0.16	0.90	0.81	0.39	-0.03	0.87	0.59
RWH-RUH	.75	.15	.63	.86	.85	.55	.96	.82	.83	-.38	.62	.78
RWH-RUL	-.05	.12	.02	-.01	.22	.48	.73	.52	.04	.24	.33	.42
RWL-RUH	-.25	.20	-.05	-.21	.14	.16	.90	.73	.19	-.41	.49	.47
RWL-RUL	.81	.63	-.04	.87	.87	.18	.87	.86	.30	.45	.62	.53
RUH-RUL	-.26	.44	.37	-.17	.31	.63	.78	.52	.11	.76	.04	.76

[a]R = restricted search, W or U = weighted or unweighted least squares, and H or L = high or low mixing initial guess.

POPULATION PROCESSES

We begin an examination of information about escapements, smolt production, and adult returns with a view toward assessing productivity of the Naknek and Ugashik stocks and feasibility of the forecasting of future returns. Our efforts are concentrated on age composition and survival of sockeye salmon generations. Historical time series of observations at several life stages--egg, smolt, and mature adult--are the basis of the analysis.

Historical Time Series

Escapements to the Naknek system have usually equalled or exceeded those to the Ugashik system (Figure 8). The greatest escapements for either system during this time occurred in different years--1959 for the Naknek system and 1960 for the Ugashik system. Regular recurrence of the varying levels of escapements appears in either system. Local maxima occurred in 1959 and each 5 yr thereafter in the Naknek system; in the Ugashik system, this sequence lagged behind that of the Naknek system by 1 yr. In the Naknek system two additional local maxima occurred in 1966 and 1971.

The freshwater and marine age compositions of escapements for the years in which sampling was conducted have been estimated (Figures 9 and 10). Freshwater age composition is represented by the proportion of spawners which spent 2 yr in fresh water as juveniles; nearly all other spawners will have spent 1 yr. The freshwater age compositions of spawners in the two systems between 1958 and 1974 varied in close synchrony (Spearman rank correlation coefficient r_s = +0.87, P < 0.01). Marine age composition is represented by the proportion of spawners which spent 2 yr in the ocean; nearly all other spawners will have spent 3 yr. The marine age composition of spawners in the two systems for the same period also varied in close synchrony (r_s = +0.73, P < 0.01) and showed quasi-periodic variation with minima at 5 yr intervals--1961, 1966, and 1971. Probably a minimum occurred in 1957 for the Naknek system at least, making a 4-yr interval to the next minimum in 1961.

The total numbers of smolts produced from these escapements (Figure 11) were estimated earlier (Tables 11 and 12). Survivors of these smolts, total returns of the broods (Figure 12) including estimates of escapement, inshore Bristol Bay catch, and Japanese high seas catch, have been estimated by others (Paulus, personal communication). The estimated production of smolts from the Ugashik system peaked in the broods of 1960 and 1966; these maxima are reflected in total returns of the broods. The estimated production of smolts from the Naknek system peaked in 1960, 1963, and 1965; only the 1960 peak is clearly reflected in the total returns. Discrepancies between the smolt and total returns series may be caused by variations in ocean survival and unmeasurable sampling errors in smolt estimates. Ocean survival is examined later.

The age compositions of these progeny generations at the smolt stage can be estimated from both the smolt migrations and the total returns. This freshwater age composition is represented by the holdover rate, or proportion of individuals of a brood which migrate to the ocean after spending either 2 or, rarely, 3 yr in the lakes. The other members of the brood migrate after 1 yr. Holdover rates based on smolt migrations vary in good agreement with
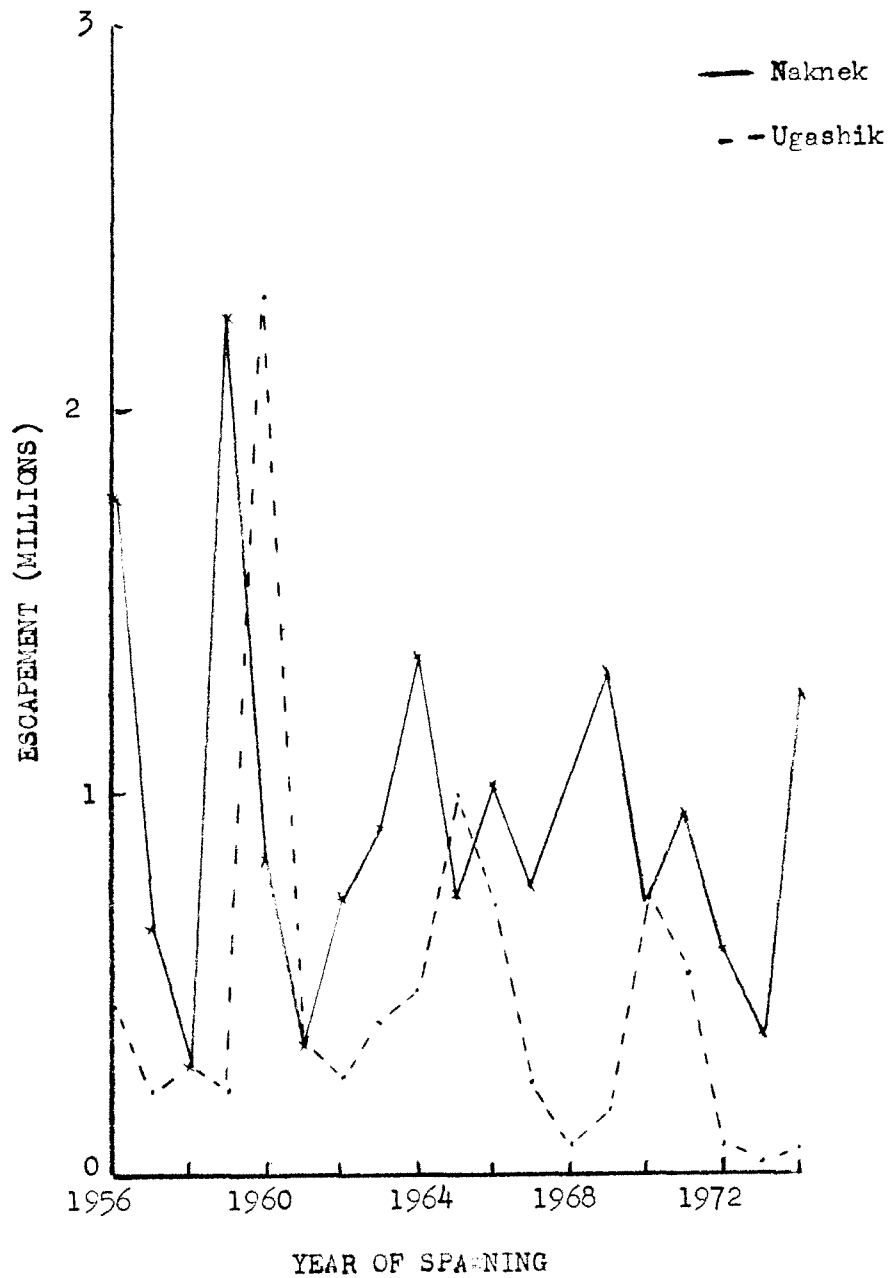
Figure 8.--Escapement (millions) to the Naknek and Ugashik systems by year (Source: Robert D. Paulus, Alaska Department of Fish and Game, Juneau, Alaska, personal communication).
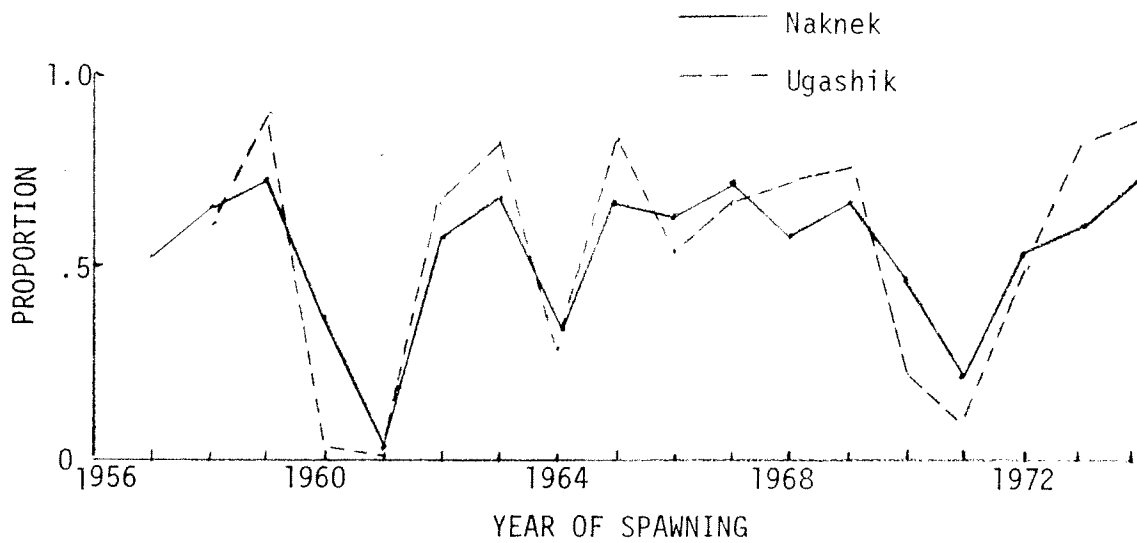
Figure 9.--Proportion of spawners which had remained 2 years in fresh water in Naknek and Ugashik systems (Source: Robert D. Paulus, Alaska Department of Fish and Game, Juneau, Alaska, personal communication).
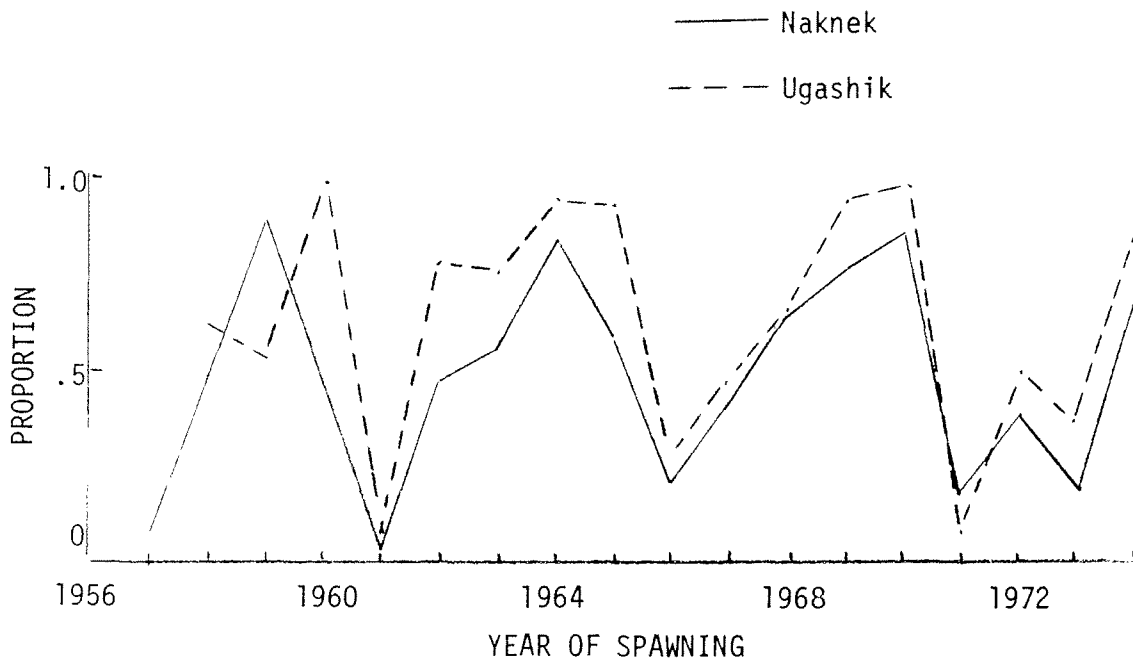
Figure 10.--Proportion of spawners which remained 2 years in the ocean before returning to the Naknek and Ugashik systems (Source: Robert D. Paulus, Alaska Department of Fish and Game, Juneau, Alaska, personal communication).
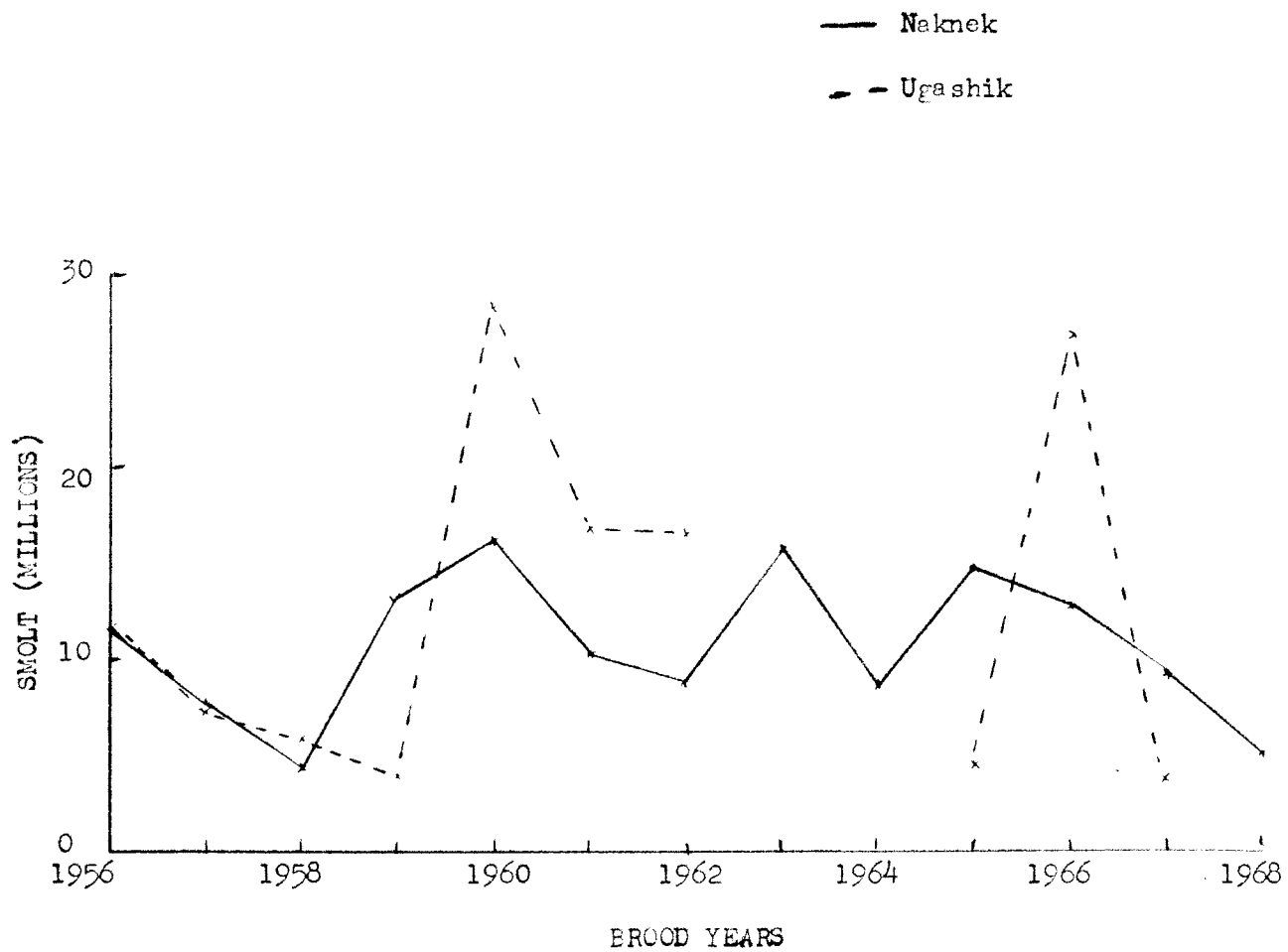
Figure 11.--Smolt produced (millions) in Naknek and Ugashik systems by brood year.
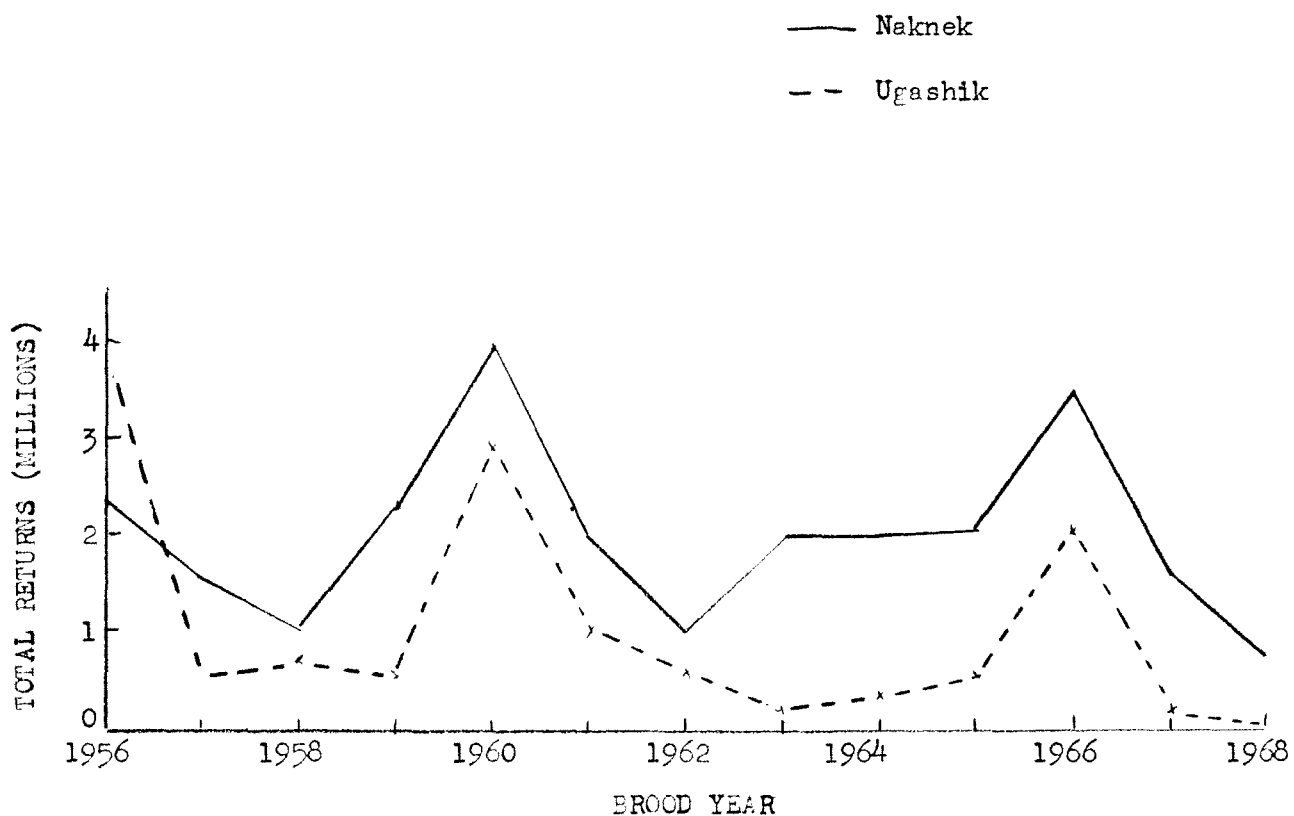
Figure 12.--Total returns (millions) to Naknek and Ugashik systems from spawnings in 1956 to 1968. (Source: Robert D. Paulus, Alaska Department of Fish and Game, Juneau, Alaska, personal communication).

corresponding values from total returns in the Ugashik (Spearman rank correlation coefficient r_s = +0.88, P < 0.01, Figure 13) but not the Naknek system (r_s = +0.31, P > 0.10, Figure 14). For the Ugashik system, holdover rates estimated from smolt migrations are generally much smaller than those estimated from total returns; this agrees with the lower apparent marine survival of age I smolts as compared to age II smolts in a later section. For the Naknek system the difference in apparent survival rates of the two age groups will be seen to be less consistent among broods, corresponding to the lower correlation between holdover rates from the two sources.

Variations of holdover rates in the two systems seem temporally related; those based on total returns are more highly correlated (Spearman rank correlation coefficient r_s = +0.76, P < 0.01) than those from smolt migrations (r_s = +0.54, P ∿ 0.05). Enhancement of the correlation could occur if marine survival rates of either age group are positively correlated between systems; such appears plausible from intuition and later analysis. Regular temporal variation of holdover rates is evident from estimates based on total returns (Figures 13 and 14). In both systems, minima occurred at 5-yr intervals--1956, 1961, and 1966. Holdover rates based on smolt migrations in Ugashik vary regularly with a 5-yr period (Figure 13); but in the Naknek system, cycling of estimates from smolt migrations is not evident (Figure 14). The discrepancy in the Naknek system may have occurred because of errors in estimates of smolts; or else the aperiodic time series of holdover rates at the smolt stage is actually transformed to the quasi-periodic series at the adult stage. We can find no reason why greater inaccuracies in the holdover rate estimates from the Naknek system should have occurred. One further indication of greater errors in Naknek smolt estimates is provided by later analysis of age compositions of parent and progeny generations. On the other hand, consistencies in variations in ocean survival rates between systems support their accuracy. We examine these ocean survival rates later and observe some indications of temporal regularity. Conceivably such temporal patterns in ocean survival rates could induce the periodicity in holdover rates at the adult stage.

The marine age compositions of progeny can be computed only from the total returns of broods. Nearly all individuals return after either 2 or 3 yr at sea. The proportions of Naknek broods returning after 2 yr show a tendency to 5-yr periodicity (Figure 15); minima occurred in 1956, 1961, and 1966. The proportions of Ugashik broods returning after 2 yr had minima in 1961 and 1966 as did Naknek broods; however, the 1956 brood in the Ugashik system had a high proportion of 2-ocean returns in contrast to the same brood from the Naknek system. Although similarities in the time series of ocean age compositions of Naknek and Ugashik broods are evident, the proportions of broods returning after 2 yr at sea from the two systems are not closely related (Spearman rank correlation coefficient r_s = +0.25, P > 0.20).

In addition to the time series on numbers and age compositions, average weights of smolts of the two freshwater ages are known for the years sampled (Figures 16 and 17). Clearly the weights of age I and age II Naknek smolts emigrating in a year are positively related (simple correlation coefficient r = +0.73, P < 0.01). The two age groups emigrating the same year are of two broods. If the weights of age I and age II smolts of the same brood are compared, evidence of a relation is not strong (r = +0.37, P > 0.10). Therefore, variations in the size of Naknek smolts are probably caused primarily by environmental variation.
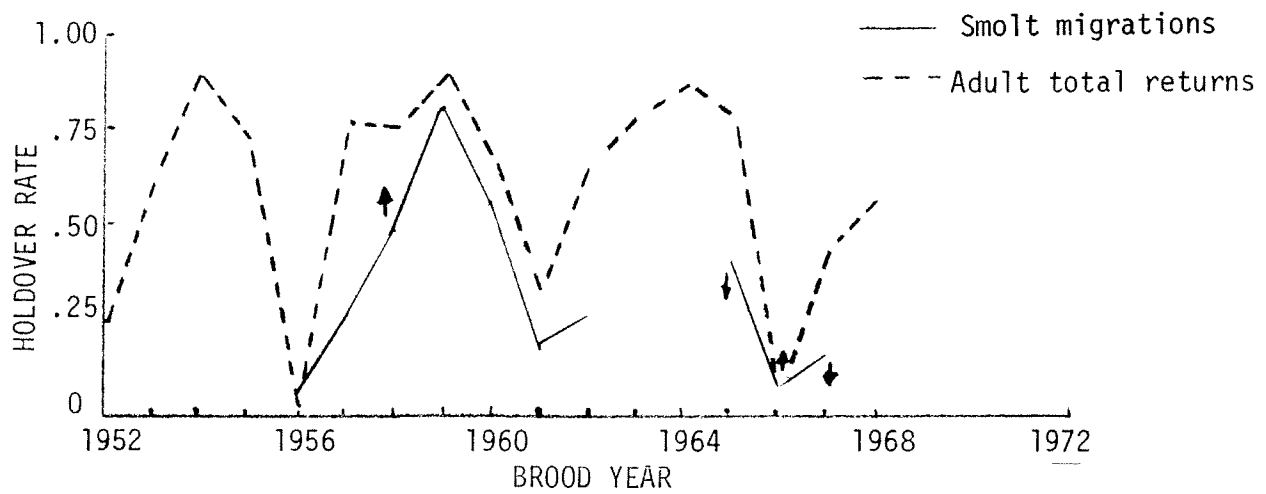
Figure 13.--Holdover rate versus brood year in the Ugashik system (Arrows indicate direction of corrections for possible bias because of suspected incomplete sampling of smolt migrations).
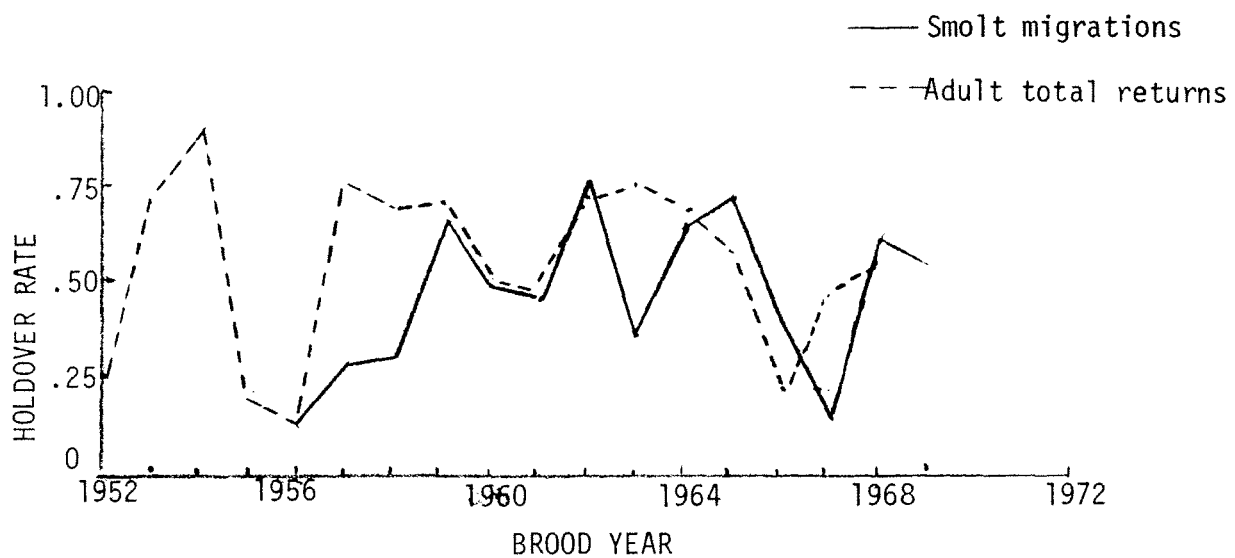
Figure 14.--Holdover rate versus brood year in the Naknek system.
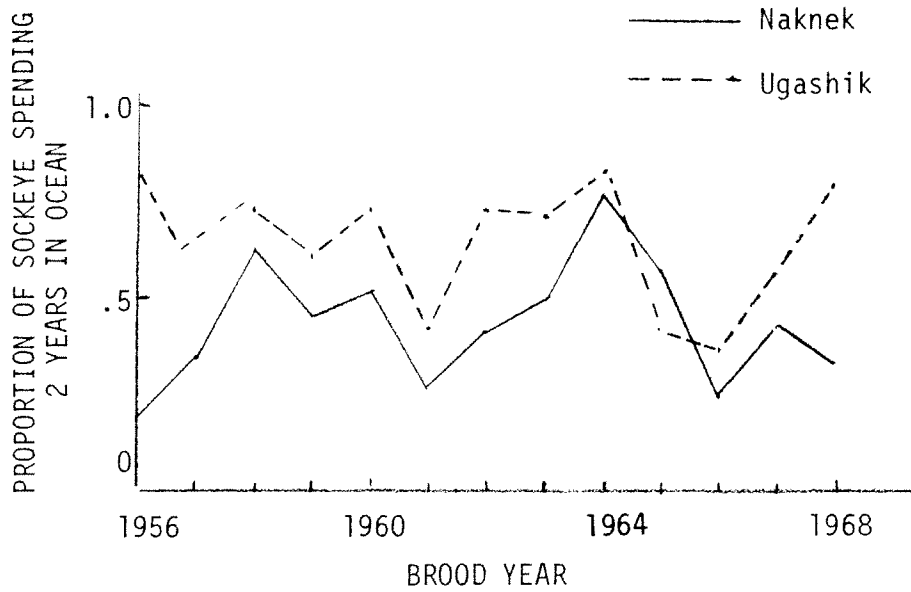
Figure 15.--Proportion of broods of the Naknek and Ugashik systems which spent 2 years in the ocean (Source: Robert D. Paulus, Alaska Department of Fish and Game, Juneau, Alaska, personal communication).

Figure 16.--Average weight (gm) of seaward migrants from Naknek system by freshwater age and year of migration.
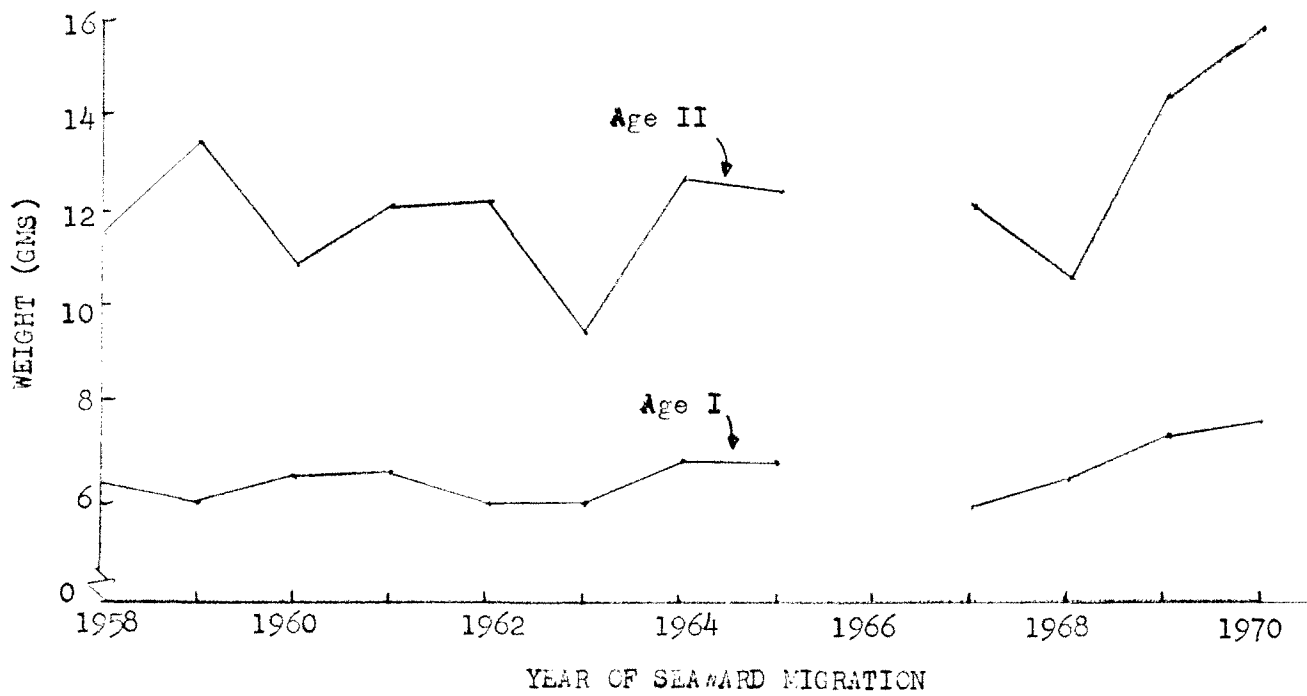
Figure 17.--Average weight (gm) of seaward migrants from Ugashik system by freshwater age and year of migration.

The average weights of age I Ugashik smolts vary only slightly (Figure 17) and these smolts are small compared to their Naknek counterparts. The average weights of age II Ugashik smolts are variable (Figure 17) and these smolts are comparable in size to age II Naknek smolts. The weights of the two ages of the same year of migration from the Ugashik system are significantly correlated (simple correlation coefficient $r = +0.70$, $P < 0.01$) but so are those of the same brood ($r = +0.75$, $P < 0.01$). If environmental influences are responsible for variations in the weights of Ugashik smolts, these factors either are not common to or exert different influences on freshwater growth in the two lake systems. The average weights of either age I or age II smolts from the Naknek and Ugashik systems emigrating in the same year are not correlated (age I, simple correlation coefficient $r = -0.34$, $P > 0.50$; age II, $r = -0.12$, $P > 0.50$). Local influences within lake systems induced by varying densities of sockeye salmon seem unimportant. In the Ugashik system the average weights of neither age I nor age II smolts are significantly correlated with potential egg deposition (age I, Spearman rank correlation coefficient $r_s = +0.20$, $P > 0.50$; age II, $r_s = -0.25$, $P > 0.20$) or number of smolts of the brood (age I, $r_s = -0.12$, $P > 0.25$; age II, $r_s = -0.37$, $P > 0.10$). Similarly, for the Naknek system the average weights of age I and age II smolts are not significantly correlated with potential egg deposition (age I, $r_s = +0.09$, $P > 0.50$; age II, $r_s = +0.15$, $P > 0.50$) or number of smolts of the brood (age I, $r_s = +0.20$, $P > 0.50$; age II, $r_s = -0.29$, $P > 0.10$).

Much of the variation in size of smolts at the time of seaward migration is caused by growing conditions in the lakes just before the smolts emigrate (Burgner et al. 1969). Naknek smolts emigrate roughly 2 wk later than Ugashik smolts as measured by median date of migration; also, the period of migration from the Naknek system is more extended (Hartman et al. 1967). Variations in springtime growing conditions would be better reflected by Naknek smolts. Age I Ugashik smolts are expected to be small and show small variation if they migrate before springtime growth occurs. Local differences in lacustrine springtime growing conditions between the systems and especially the differences in migration times probably account for the poor correspondence in time series of smolt weights between systems.

Associations Between Generational Age Compositions

A summary of studies on freshwater and marine ages of sockeye salmon indicates that both heredity and environment play roles in determining age at seaward migration and ocean age at maturity (Ricker 1972). In this section of the report we seek indications of these influences on Naknek and Ugashik sockeye salmon by comparing age compositions of parent and progeny generations and weight of smolts.

We have used correlation theory extensively. Significant correlations do not demonstrate cause and effect between variables. Rather, correlation coefficients measure the degree to which two variables are associated. Other variables may actually influence both variables significantly correlated, causing the association. This well-worn caveat in interpretation of associations is especially pertinent to variations in age compositions. Most time series examined appear quasi-periodic. Even if correlations occur between parents and progeny, the initiation and maintenance of the periodicity must be sought elsewhere. The merit of this correlation analysis

is the indication of rules of age inheritance if a genetic basis exists. Further, the flexibility of such rules in responding to environmental variation can be evaluated in relation to freshwater growth.

In this analysis we seek relationships between the freshwater and marine age compositions of progeny and the corresponding parental age compositions. The freshwater age composition of progeny generations can be determined from smolt migrations or adult returns. Information from smolt migrations, if accurate, is preferable because marine mortality varies between the years the freshwater age groups of a brood emigrate to sea, thereby adding environmental variation to a possible genetic basis for age at seaward migration. We represent the freshwater age composition of progeny by the proportion of a brood which emigrated at age II. The freshwater age composition of the parental generation is represented by the proportion of spawners which migrated to sea as juveniles at age II. The marine age compositions of progeny and parents are represented by the proportions of adult returns from a brood and of spawners, respectively, which were 2-ocean fish.

The freshwater age of progeny appears poorly related to that of the parent generation in the Naknek system (Table 21). Values of rank correlation coefficients for the Ugashik comparison are relatively large and positive. The outcome is consistent with our earlier speculation that Naknek smolt migration estimates may contain greater errors if an underlying correspondence exists. The correlations are not statistically significant in either case. Our expectation, if freshwater age is inherited and smolt sampling age composition estimates are accurate, is for greater correlation from smolt sampling than from adult returns; however, the correlations based on adult returns exceed those from smolt sampling for either system. This result is inexplicable if freshwater age is heritable unless the smolt estimates are seriously in error; such errors seem improbable, at least for the Ugashik system.

Comparisons of freshwater age compositions of progeny with marine age compositions of parents indicate correspondence in both systems (Table 21). The lack of statistical significance for the Ugashik system from smolt sampling is probably due to the fewer years (eight) for which data are available and the associated reduced power of the test as compared to the corresponding significant test from adult returns of 12 broods. The lack of statistical significance for Naknek freshwater age composition estimated from adult returns might easily be explained by variations in marine survival of the two freshwater ages of broods, particularily in view of the significance of the corresponding test from smolt sampling based on fewer broods.

Ocean age at maturity of parent and progeny generations is significantly correlated in both systems (Table 21). On the other hand, the ocean age of progeny seems unrelated to the freshwater age of parents (Table 21).

Among the four predominant age types, only the proportions of 5_2 fish in parent and progeny generations are significantly correlated (Table 22). The 6_3 fish of either river as well as the 4_2 fish of the Naknek River show no tendency to reproduce their kind. The 5_3 fish are intermediate, the correlations indicating the possibility of genetic inheritance of this age.

If a genetic basis exists for the associations between parent and progeny age compositions, the preceding correlation analysis shows the following rules

Table 21. Spearman rank correlation coefficients between freshwater (proportion of brood emigrating seaward at age II) and marine (proportion of brood returns of 2-ocean age) age compositions of progeny generations and corresponding age compositions of parent generations[a].

Proportion of parents		Proportion of progeny			
		Age II		2-ocean	
		Naknek	Ugashik	Naknek	Ugashik
Age II	A	-0.06^{ns}	0.36^{ns}	--	--
	B	0.15^{ns}	0.45^{ns}	0.16^{ns}	-0.13^{ns}
2-ocean	A	0.57^{*}	0.62^{ns}	--	--
	B	0.31^{ns}	0.53^{*}	0.62^{*}	0.58^{*}

[a]Freshwater age composition of progeny is based on smolt sampling information (A) and adult returns (B).

*Correlation significant at 5%.

ns Correlation not significant.

Table 22. Spearman rank correlation coefficients between proportions of dominant age types (4_2, 5_2, 5_3, and 6_3) in parental and progeny generations. Range of proportions of the age type among parental generations is indicated in parentheses.[a]

Age type	System	
	Naknek	Ugashik
4_2	-0.01^{ns} (.04-.56)	0.21^{ns} (.01-.95)
5_2	$.55^{*}$ (.06-.93)	$.90^{**}$ (.00-.92)
5_3	$.37^{ns}$ (.00-.68)	$.41^{ns}$ (.03-.81)
6_3	$-.40^{ns}$ (.01-.47)	$-.11^{ns}$ (.01-.38)

[a]Age composition of progeny determined from total returns.

ns Correlation not significant.

*Correlation significant at 5%.

**Correlation significant at 1%.

must apply. Parents with the 2-ocean age tend to produce 5_3 progeny; parents with the 3-ocean age tend to produce 5_2 progeny. Restated with specific age types, 4_2 and 5_3 parents tend to produce 5_3 progeny. Further, 5_2 and 6_3 parents tend to produce 5_2 progeny. Numerical measures of these particular associations have been computed from compositions of escapements and total adult returns of brood years from 1958 to 1969. In both river systems, the proportions of parents of the 3-ocean age are correlated with the proportions of their progeny of age 5_2 (Naknek, Spearman rank correlation coefficient $r_s = +0.72$, P < 0.01; Ugashik, $r_s = +0.76$, P < 0.01). Also, the proportions of parents of the 2-ocean age are correlated to a lesser degree with the proportions of their progeny of age 5_3 (Naknek, $r_s = +0.58$, P < 0.05; Ugashik, $r_s = +0.53$, P < 0.05).

Growth is thought to affect both the age at seaward migration of juvenile sockeye salmon and the duration of ocean residence. The length of stay of individuals of a brood in either the lakes or the ocean appears to be reduced among those realizing greatest growth in the respective environment (Foerster 1968).

The average length of stay of broods (as opposed to individuals) in fresh water at least seems associated with growth there. The proportions of broods holding over for an additional year in fresh water beyond a certain age have been observed to be associated with the size of migrants at that age; the associations can be positive or negative, depending on the particular stock (Ricker 1972). Therefore, among individuals both within broods and between broods, variation in growth of sockeye salmon seems to be associated with variation in age types.

In view of this association between growth and age, we present some results from a partial correlation analysis of growth of progeny and age compositions of parent and progeny generations. The partial correlation coefficient for a pair of variables measures the degree of their association when the remaining variables in the analysis are held fixed. Associations between the growth of progeny and their age composition can be estimated with the age compositions of parents held fixed. We examined two associations for each river system: (1) duration of freshwater residence and weight of age I migrants, and (2) duration of ocean residence and initial size of smolts. In the first case, four variables were included in the partial correlation analysis with broods as observations: holdover rate, average weight of age I smolts, proportion of parents which were freshwater age II, and proportion of parents which were 2-ocean. In the second case, four variables were also used: proportion of returns from a smolt cohort which matured as 2-ocean fish, initial average weight of the individual smolt, proportion of parents which were freshwater age II, and proportion of parents which were 2-ocean. Computations were performed twice for the Ugashik system, first using the weights of Ugashik smolts and next using the weights of their Naknek counterparts. Naknek smolt weights may better reflect variation in springtime growing conditions and are used in place of Ugashik weights . No statistical testing of the partial correlation coefficients was conducted; the probability distribution of the coefficients is unknown and is not reasonably assumed to be approximated from correlation theory based on normal random variables. Our analysis merely indicates the direction and degree of associations if they exist.

If the average duration of freshwater residence is associated with growth as reflected by age I smolts at time of migration, the direction of the relationship differs between systems (Table 23, line 1). However, when Naknek smolt weights are substituted for Ugashik weights, the directions agree. If the general climate of Bristol Bay influences holdover rates in both systems similarly, it does so before early spring growth in the year of migration of age I smolts occurs. Then duration of residence increases with conditions associated with better growth later.

If duration of ocean residence is associated with weight of the smolt, the association is closest for Naknek smolts and negligible for Ugashik smolts of either age (Table 23). However, when Naknek smolt weights are substituted for Ugashik weights the partial correlation coefficients become more comparable in magnitude to those of Naknek. Early growing conditions in the estuary may be correlated with those of the lakes. These growing conditions are probably better reflected by Naknek smolts. If so, the average stay in the ocean of smolts in either system declines when springtime growing conditions, either in the lakes or the ocean, are favorable.

The initiation and maintenance of quasi-periodic variations in the age compositions of these stocks and the fairly regular environmentally-induced variation in weight of Naknek age I smolts may possibly be related to temperature variations in the ocean habitat. Orderly, transpacific movements of large areas of anomalous warm and cold surface waters seem to occur around the North Pacific gyre, roughly $180°$ out of phase, with periods of 5 to 6 yr (Favorite and McLain 1973). These environmental features may have existed long enough for genotypes to have evolved with certain advantageous durations of freshwater and marine residences depending on the particular stock, the brood year, and stage of the environmental cycle. On the other hand, variations in age compositions may reflect the direct or immediate effect of the environment on sockeye salmon age schedules. The ocean temperatures may also influence the growing conditions in fresh water if they affect the general Bristol Bay climate.

Survival

Ricker Dependence, Duration of Residence, and Lognormal Variation

Knowledge of survival is fundamental in managing and forecasting sockeye salmon stocks. Studies of salmon survival must consider density dependence of survival (e.g., Ricker 1954); results are critical for setting escapement goals and for forecasting future returns. When analyzing for density dependence of survival, we used the Ricker form

$$R = \alpha S e^{-\gamma S} \varepsilon \qquad (22)$$

where
    R is the number of survivors,
    S is the initial number of individuals,
    α and γ are constants, and
    ε is a random multiplier.
Survival rate, R/S, then, is exponentially related to initial numbers according to the model

$$R/S = \alpha e^{-\gamma S} \varepsilon. \qquad (23)$$

Transforming to logarithms establishes a linear relation between the logarithm of survival rate and initial numbers:

Table 23. Partial correlation coefficients relating progeny growth and age composition with parent age composition held fixed for either river system[a].

Variables	Naknek	Ugashik
Freshwater holdover rate and average weight of age I smolts	+0.36	-0.25(+0.43)
Proportion of 2-ocean returns and average weight of age I smolts	+.67	+.01(+.34)
Proportion of 2-ocean returns and average weight of age II smolts	+.31	+.04(+.74)

[a]Coefficients in parentheses under Ugashik were obtained by using weights of Naknek smolts in place of the corresponding weights of Ugashik smolts.

$$y = \beta_0 + \beta_1 X_1 + \delta \qquad (24)$$

where

$y = \ln(R/S)$,

$X_1 = S$,

$\beta_0 = \ln \alpha$,

$\beta_1 = -\gamma$, and

$\delta = \ln \varepsilon$.

This version of the Ricker model ascribes explainable variation in survival rate to initial numbers alone. In the Naknek and Ugashik studies, considerable effort was directed toward determination of age structure in both fresh water and the ocean. We know proportions of broods holding over in fresh water vary widely, as do the proportions of broods which remain in the ocean for, say, 3 yr or longer rather than returning after 1 or 2 yr. The total survival rate of a cohort would be affected in fresh water or the ocean by duration of residence. Two broods with equal initial numbers under identical environmental conditions but differing in intrinsic holdover rates in fresh water presumably would have different total freshwater survival rates. Likewise, two smolt cohorts differing in intrinsic duration of ocean residence would have different total ocean survival rates. Longer residence would reduce survival rate in either case.

Since we have knowledge of holdover rates in fresh water and ocean ages of returns, variation in survival rate due to variation in duration of residence can be reduced or eliminated. To accomplish this end, we introduced an unspecified function f(h) into the right-hand side of expression (22), where h refers either to the freshwater holdover rate or the proportion of an ocean cohort returning after 3 or more yr at sea, depending on the particular phase being analyzed. Corresponding to (24) we developed the expression

$$y = \beta_0 + \beta_1 X_1 + \beta_2 X_2 + \delta \qquad (25)$$

where

$y = \ln(R/S)$,

$X_1 = S$,

$X_2 = h$,

$\beta_0 = \ln(\alpha f(h_0)) - \dfrac{h_0}{f(h_0)} \dfrac{df(h_0)}{dh}$

$\beta_1 = -\gamma$,

$\beta_2 = \dfrac{1}{f(h_0)} \dfrac{df(h_0)}{dh}$, and

$\delta = \ln \varepsilon$.

Derivation of (25) involves the addition of the multiplier f(h) to the right hand sides of (22) and (23), and the expansion to the first two terms of $\ln(f(h))$ in a Taylor's series about an arbitrary value, h_0, after the logarithm transformation corresponding to that between (23) and (24) is performed.

We made one further assumption--that the random multipliers ε are lognormally distributed such that their logarithms are normally distributed with mean zero and variance σ^2. The lognormal assumption is open to revision at a later time, if necessary, when sufficient observations are available to test its validity. Lognormal variation is consistent with both (1) observation--for roughly equal spawning populations, returns usually vary moderately about an

average but occasionally an extremely large return occurs; and (2) theory--survivors from an initial number of individuals, each exposed to a gauntlet of risks with probabilities of survival at each risk being drawn from an associated arbitrary probability distribution, will be approximately lognormally distributed under fairly general conditions (e.g., see Aitchison and Brown [1969], Chapter 3).

The independence of random multipliers is moot. Some of the evidence presented indicates that temporal cycling of some survival rates occurs. If the errors are not independent or do not share common variance, (24) or (25) are not efficiently estimated; however, the estimates of β_0, β_1, and β_2 are unbiased. Statistical testing should be considered circumspectly in such situations, although the procedures used are generally robust to violations of underlying assumptions.

The assumption that survival rate is related to density by (23) is clearly suspect; however, the form (23) may be a reasonable approximation to actual reduction in survival rate with increasing densities as has been repeatedly observed for salmon. Anyway our information is not sufficiently at odds with the model to warrant selection of an alternative.

The adequacy of the Taylor's series expansion of f(h) truncated after the first two terms is uncertain. We expect f(h) to be monotone decreasing; longer residence should reduce survival rates, other things being equal. By using the Taylor's series expansion, f(h) is approximated by a linear function; such may reasonably approximate the monotone-decreasing function.

The main attraction of the assumptions beyond their consistency or, more accurately, lack of inconsistency with observation and theory, is the linear model (25) which translates the problem of estimation and hypothesis testing into the well-developed theory of linear statistical models and the normal distribution. We performed regression analyses relating survival rate to initial numbers and duration of residence using (25) as the underlying model. Average survival rate as related to initial numbers and duration of residence was computed using estimates of regression coefficients and underlying variance (see Bradu and Mundlak [1970] for general methodology). Confidence bounds on average survival rate and survival rate of individual cohorts were established using standard methods from regression analyses (e.g., Chapter 4 of Goldberger [1964]). The standard methods were applied to the logarithm transform of survival rate to obtain confidence bounds on the average logarithm of survival rate and the logarithm of individual brood survival rate; these bounds were converted to bounds in the original scale of measurement by exponentiation. Products of such converted bounds with initial numbers are corresponding bounds for survivors.

Freshwater Phase

We estimated the survival rate from potential egg deposition to smolt migration for Naknek and Ugashik stocks from our previous results (Table 24). In the Naknek system, the freshwater survival rate ranged from less than 0.003 to more than 0.014, a greater than fivefold variation. In the Ugashik system, the survival rate ranged from less than 0.002 to more than 0.033, a greater than seventeenfold variation. Over a 14-yr period, the freshwater survival rate averaged 0.007 in the Naknek system. In the Ugashik system, the

Table 24. Potential egg deposition (millions of eggs) (PED), total smolt production (millions) and survival (s) from egg deposition to smolt migration by brood year, Naknek and Ugashik systems.

Brood	Naknek			Ugashik		
Year	PED	Smolts	s	PED	Smolts	s
1956	3,360	11.5	0.00342	986	11.8	0.01197
1957	1,293	8.7	.00673	498	7.1	.01426
1958	450	4.1	.00911	612	5.7	.00931
1959	3,610	13.2	.00366	563	3.6	.00639
1960	1,446	16.2	.01120	4,488	28.0	.00624
1961	712	10.2	.01433	1,039	16.7	.01607
1962	1.618	8.7	.00538	497	16.5	.03319
1963	1,941	15.5	.00799	903	--	--
1964	2,579	8.5	.00330	1,000	--	--
1965	1,307	14.6	.01117	2,453	4.6	.00188
1966	2,174	12.7	.00584	1,846	27.0	.01463
1967	1,523	9.0	.00591	575	3.6	.00626
1968	1,730	4.8	.00277	155	--	--
1969	2,532	18.4	.00727	325	--	--
Average	1,877	11.2	.00701	1,139	12.5	.01202

freshwater survival rate averaged 0.012 for the 10 yr for which information is available; the average survival rate in the Naknek system for the same 10 yr is between 0.007 and 0.008. The survival rate from potential egg deposition to smolt migration has averaged higher, over 1.5-fold, in the Ugashik system than the Naknek system. However, the survival rate varied more in the Ugashik system.

Variation in the freshwater survival rate may be caused by variation in the average length of freshwater residence among broods, density-related factors, and both physical and biological environments. We now examine the influence of length of residence and density.

The average freshwater survival rate should decline as length of residence increases. Evidently, this expectation does not hold for Naknek stocks (Figure 18), but is suggested by the same comparison of holdover rates estimated from smolt migrations and freshwater survival rates of Ugashik broods (Figure 19; Spearman rank correlation coefficient r_s = -0.47, 0.10 < P < 0.50). Other important sources of variation in freshwater survival must obscure the average relationships.

If the holdover rate is density-dependent, freshwater survival might vary with density in the Ugashik system (at least) indirectly, through dependence of survival and holdover. However, the holdover rate in either system appears poorly related to potential egg deposition (Figures 20 and 21; Naknek, Spearman rank correlation coefficient r_s = +0.15, P > 0.50; Ugashik, r_s = +0.01, P > 0.50) or numbers of smolts in the broods (Figures 22 and 23; Naknek, r_s = +0.10, P > 0.50; Ugashik, r_s = -0.23, P > 0.50).

Evidently the survival from egg to smolt of freshwater ages combined is inversely related to the initial seeding density for the Naknek system (Figure 24). The relationship for the Ugashik system, if one exists at observed seeding densities, is much more diffuse (Figure 25); it is difficult to determine any relationship because (1) high egg depositions are rare, and (2) survival at very similar seeding densities is highly variable. Nonetheless, survival rates at the two highest seeding densities are the lowest. An inverse relationship between average survival and egg deposition is suggested.

The survival rates were subjected to regression analysis utilizing equation (25) in stepwise regression with potential egg deposition and holdover rates as covariates (Tables 25 and 26). In these analyses the covariate which reduced the sum of squares of unexplained variation by the greatest amount was entered into the regression first; then the additional reduction in sum of squares of unexplained variation by the remaining covariate was determined.

In both the Naknek and the Ugashik systems, potential egg deposition entered the analysis first. However, only for the Naknek system is potential egg deposition statistically significant (P < 0.01) in explaining variation in survival rates; about 48% of the variation in survival above that explained by the mean, i.e., total variation, is accounted for by potential egg deposition. In the Ugashik system, potential egg deposition explains only about 19% of the total variation in survival. Although not statistically significant, we retained potential egg deposition in the Ugashik system as a covariate because the reduction in unexplained variation is substantial and the estimated average
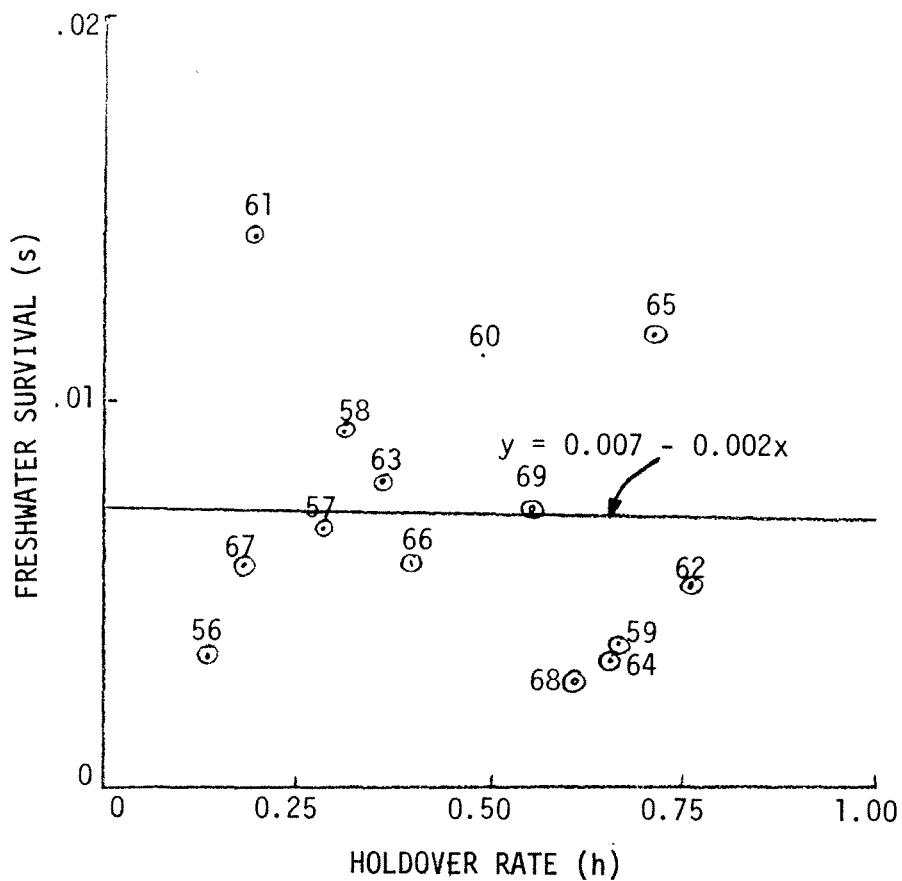
Figure 18.--Freshwater survival rate versus holdover rate for the Naknek system. (Brood years and least squares line are indicated.)
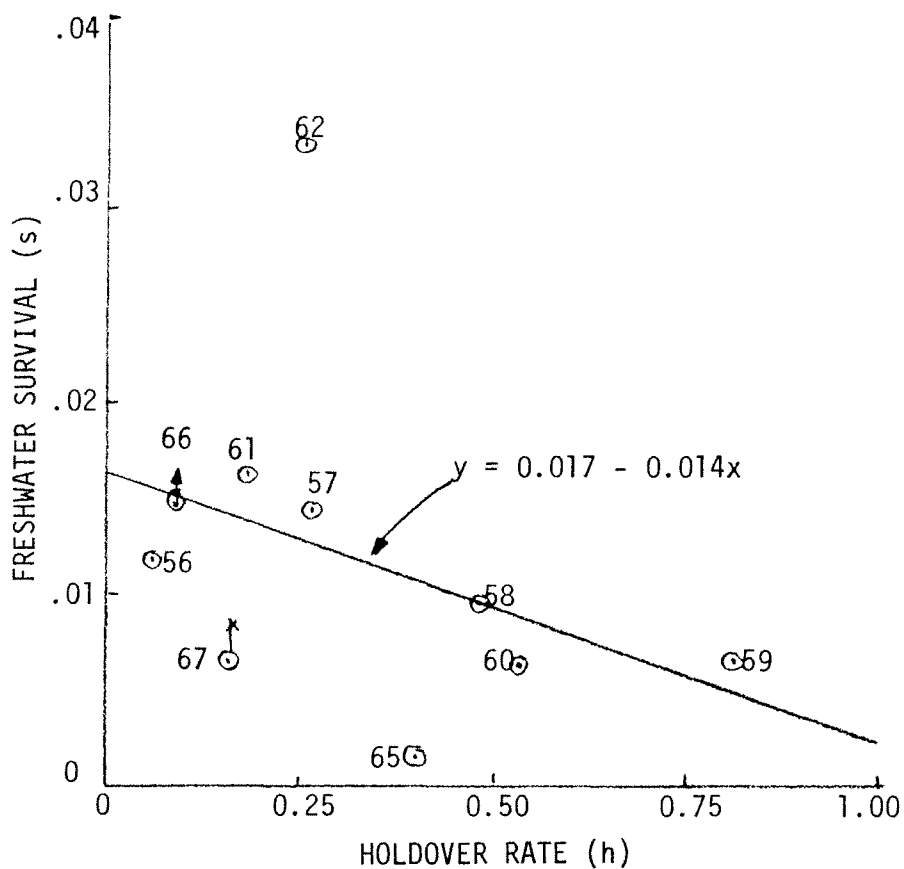
Figure 19.--Freshwater survival rate versus holdover rate for the Ugashik system. (Brood years and least squares line are indicated.)
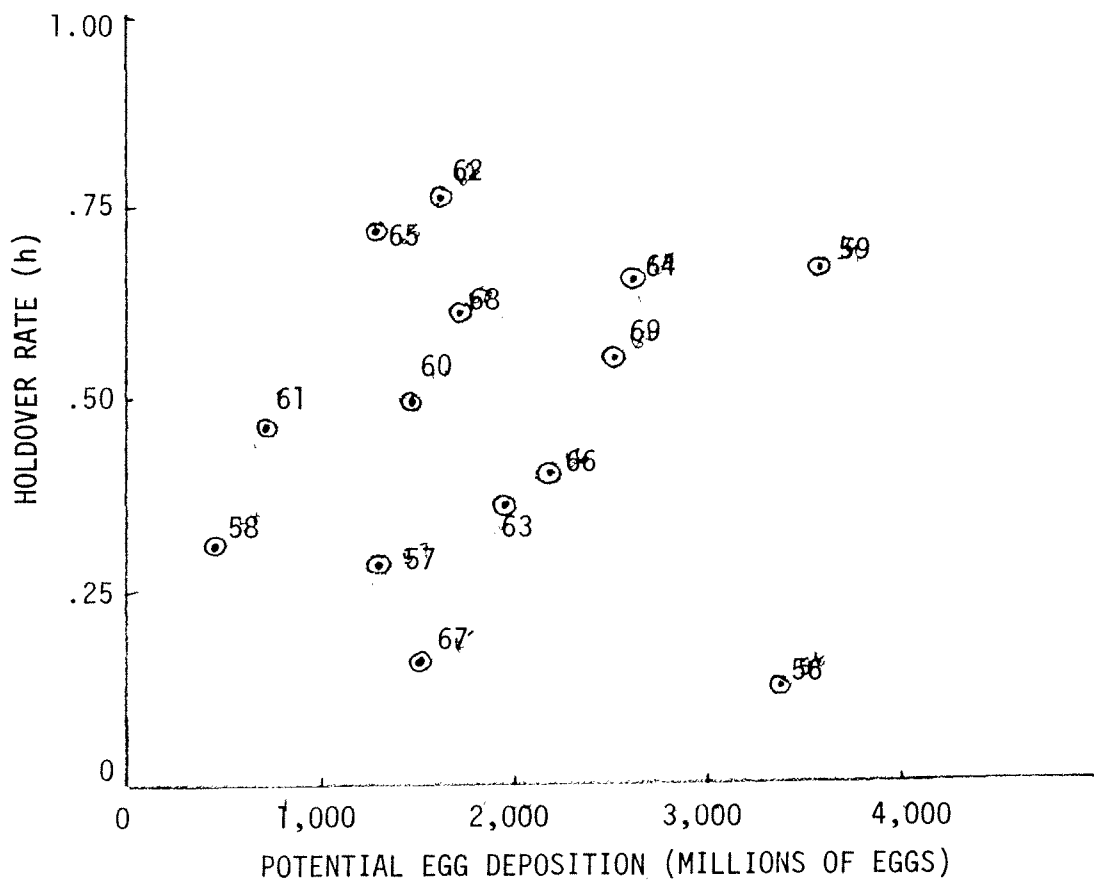
Figure 20.--Holdover rate versus potential egg deposition for Naknek system. (Brood years are indicated.)
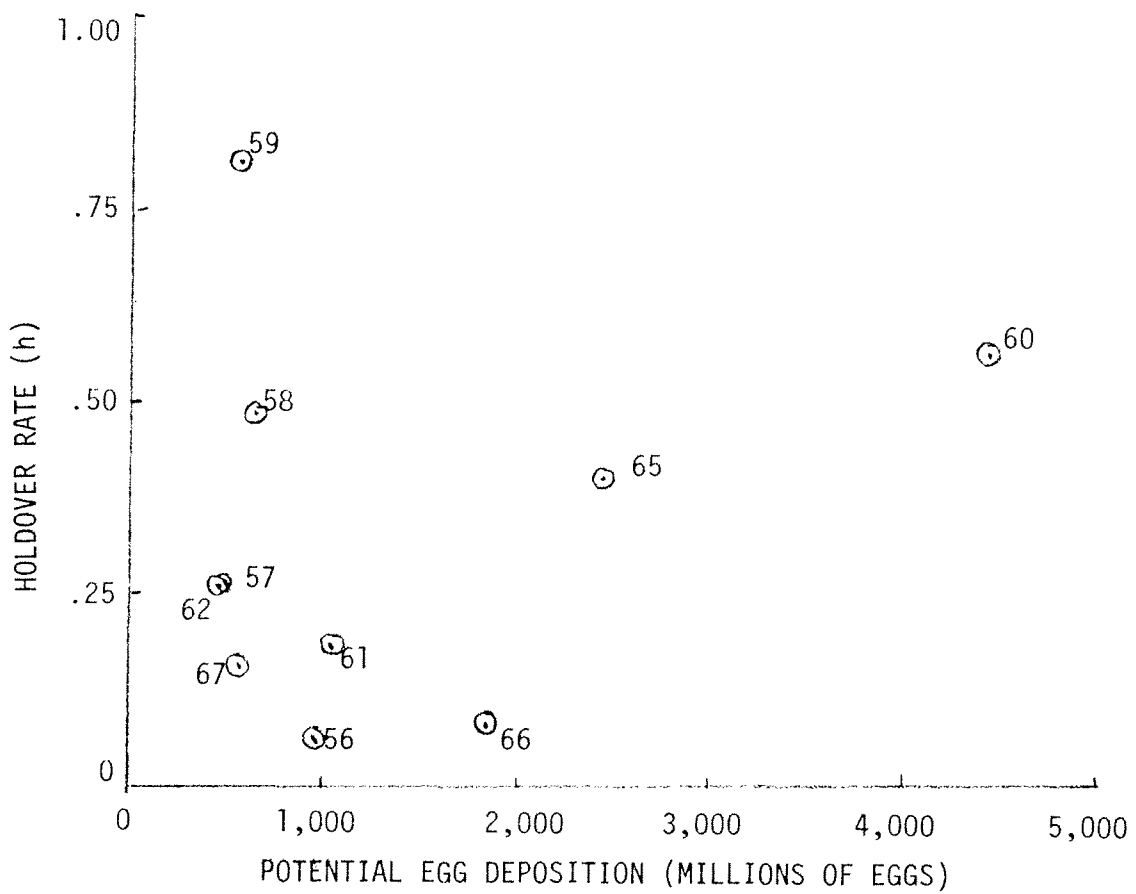
Figure 21.--Holdover rate versus potential egg deposition for Ugashik system. (Brood years are indicated.)
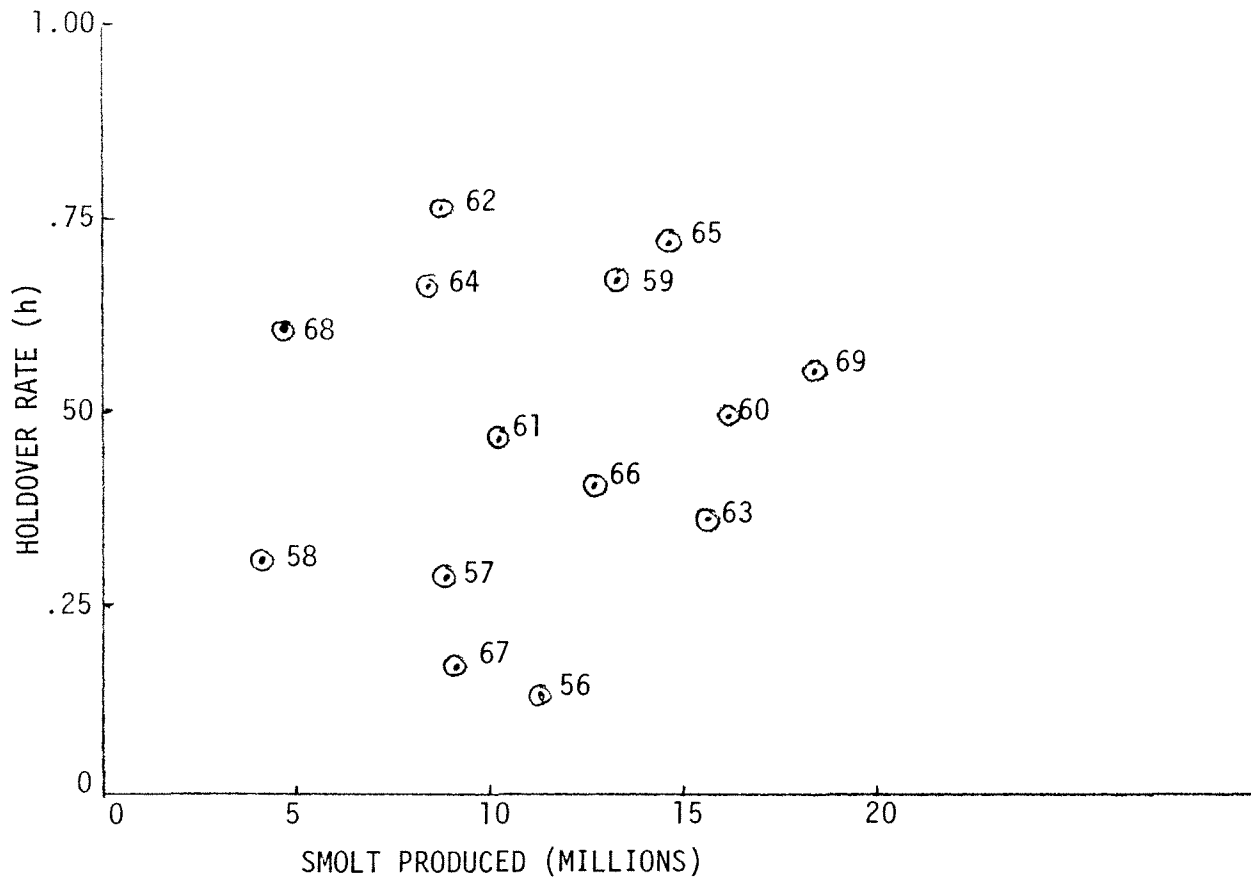
Figure 22.--Holdover rate versus brood size for the Naknek system. (Brood years are indicated.)
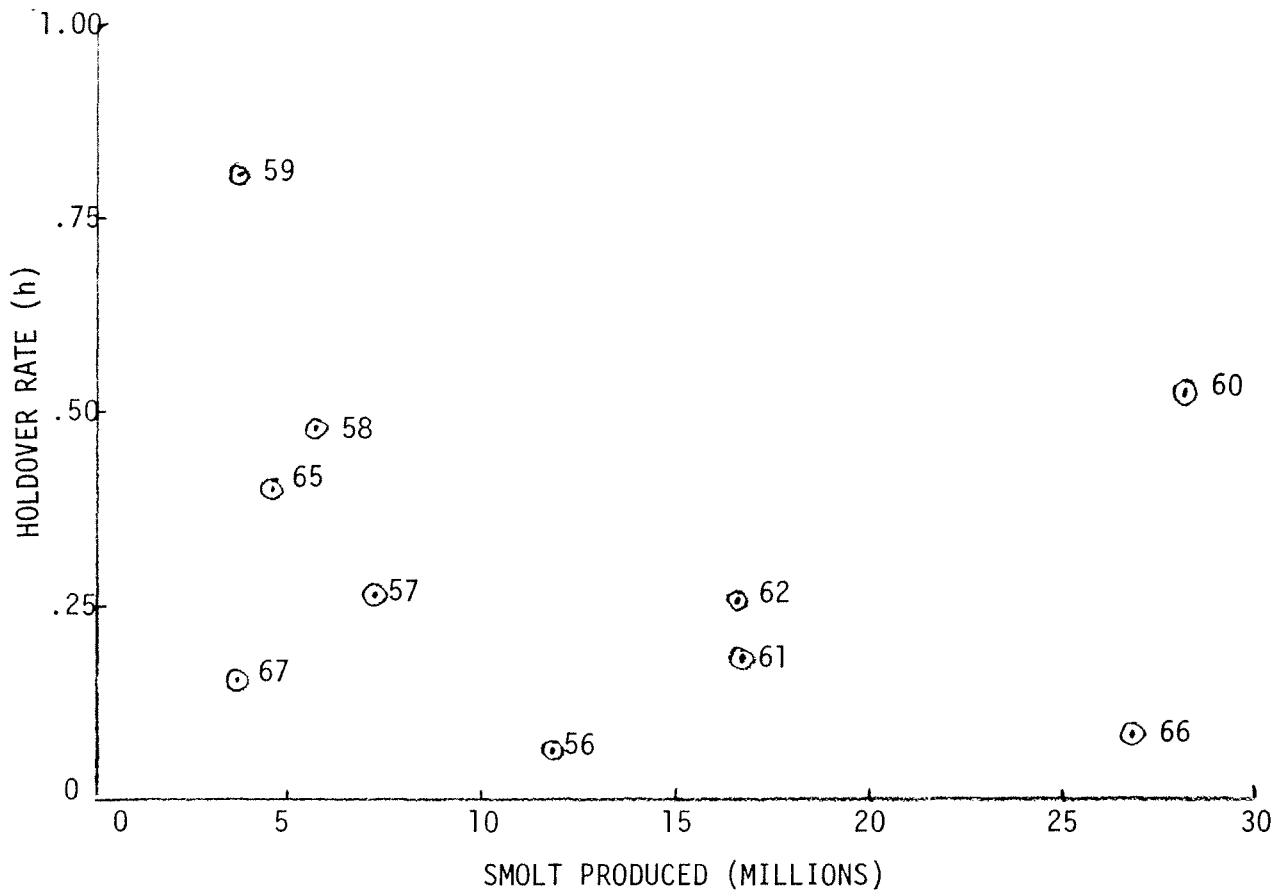
Figure 23.--Holdover rate versus brood size for the Ugashik system. (Brood years are indicated.)
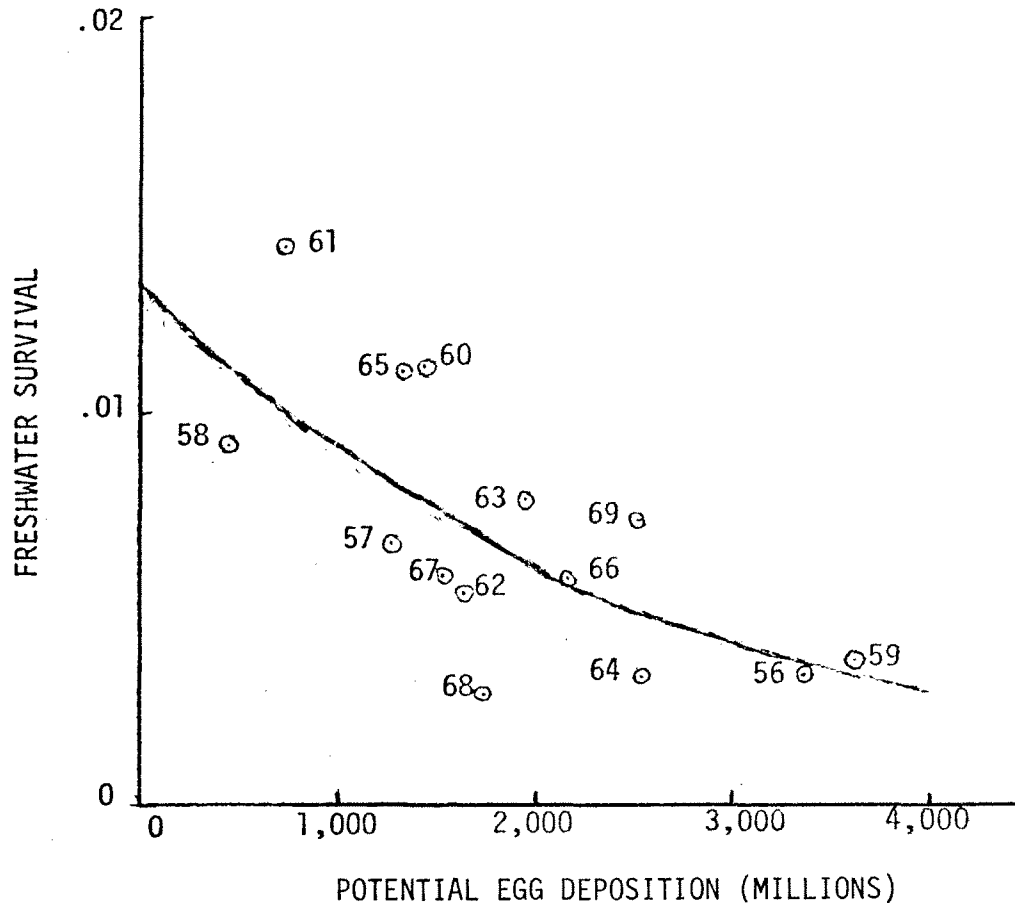
Figure 24.--Survival rate from potential egg deposition to smolt migration as related to potential egg deposition for the Naknek system. (Brood years and average survival rate are indicated.)
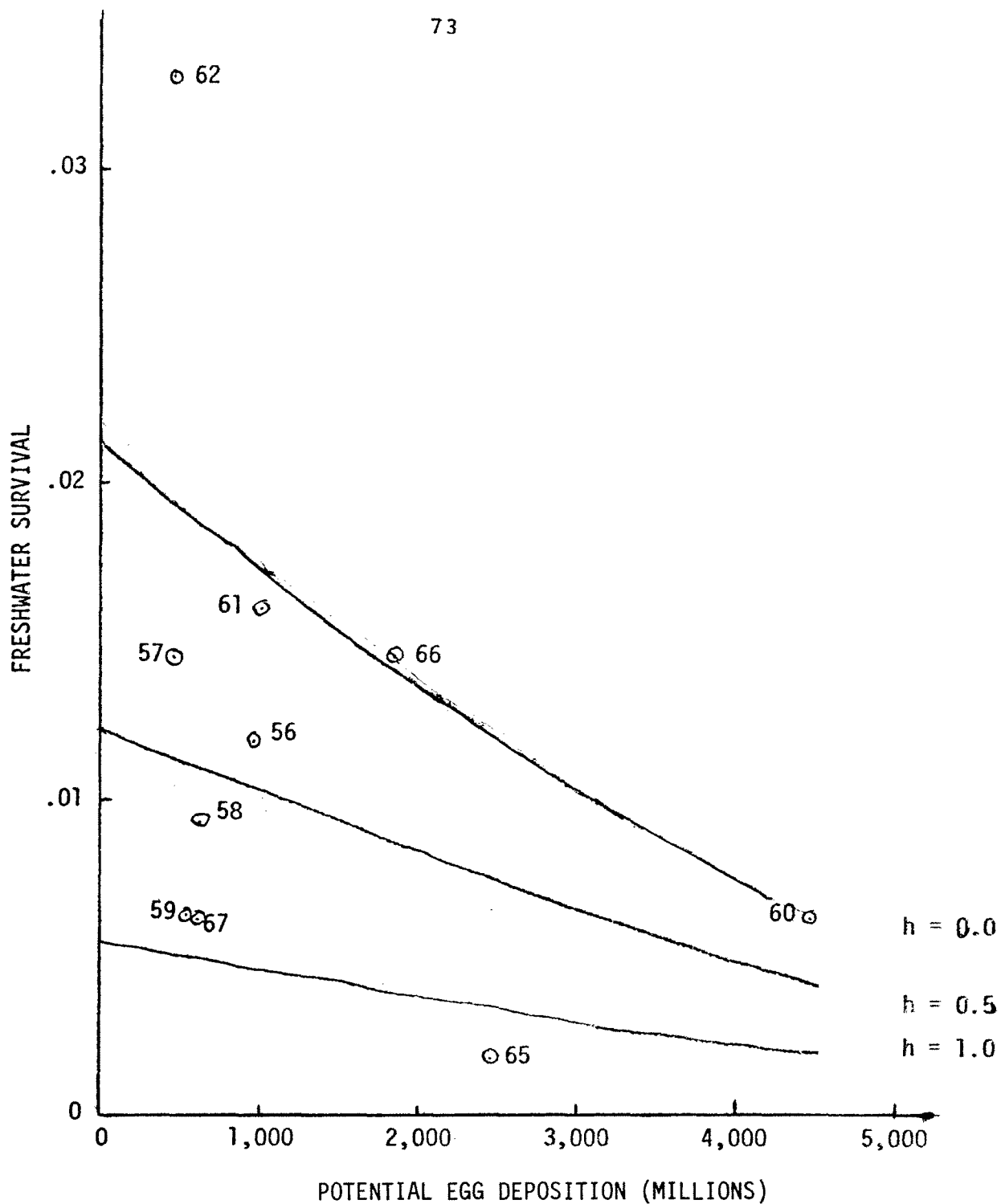
Figure 25.--Survival rate from potential egg deposition to smolt migration as related to potential egg deposition for the Ugashik system. (Brood years and average survival rate at several holdover rates (h) are indicated.)

Table 25. Stepwise regression analysis of freshwater survival rates as related to potential egg deposition and holdover rate in the Naknek system.

Source	df	SS	MS	F
Potential egg deposition	1	1.59537	1.59537	10.02**
Holdover rate	1	0.00065	0.00065	$< 1^{ns}$
Potential egg deposition and holdover rate	2	1.59602	0.79801	5.01*
Residual	11	1.75066	0.15915	--
Total	13	3.34668	--	--

^{ns}Regression not significant.

*Regression significant at 5%.

**Regression significant at 1%.

Table 26. Stepwise regression analysis of freshwater survival rates as related to potential egg deposition and holdover rate in the Ugashik system.

Source	df	SS	MS	F
Potential egg deposition	1	1.03175	1.03175	1.93^{ns}
Holdover rate	1	0.61067	0.61067	1.14^{ns}
Potential egg deposition and holdover rate	2	1.64242	0.82121	1.54^{ns}
Residual	7	3.73631	0.53376	--
Total	9	5.37873	--	--

^{ns}Regression not significant.

relationship between survival rate and potential egg deposition is inverse, as the true relationship must be.

Another inverse relationship was estimated for the Ugashik system--between average survival and holdover rate--which agrees with theory and substantially reduces unexplained variation in survival. In the Ugashik system the holdover rate, though not statistically significant, accounted for an additional 16% of total variation in survival. However, the holdover rate is without merit in explaining variation in the freshwater survival of Naknek sockeye salmon, as it accounts for less than an additional 0.02% of total variation. We retained both holdover rate and potential egg deposition in modelling freshwater survival in the Ugashik system, but for the Naknek system only potential egg deposition was retained because of the lack of explanatory power of the Naknek holdover rate.

The average survival rate as related to potential egg deposition (for both systems) and holdover rate (for Ugashik system only) was computed from estimates of regression coefficients and the underlying variance of either equation (24) or (25) depending on whether the system considered was Naknek or Ugashik, respectively (Figures 24 and 25). In the case of the Ugashik system, the average survival as related to potential egg deposition was computed for three levels of the holdover rate, namely, for h = 0.0, 0.5, and 1.0.

In the Naknek system, the estimated average survival declines from a maximum of roughly 0.014 to about 0.003 at the highest observed seeding densities (Figure 24). In the Ugashik system, the estimated average survival declines most sharply when few fish hold over (Figure 25). Values of survival for h = 0.0 and h = 1.0 can be used to estimate survival in the Ugashik system during each year of freshwater residence. When h = 0.0, all fish leave after the first year; therefore, that average survival represents first-year survival, from egg to age I smolts. When h = 1.0, all fish remain in fresh water for 2 yr before leaving; therefore, that average survival represents first- and second-year survival, from egg to age II smolts. The ratio of first- and second-year survival to first-year survival represents the survival of juveniles during the second year of lake residence. The second-year survival rate so estimated is roughly 0.25 at any density of potential egg deposition. While the estimate is intuitively reasonable to us, we cannot place much confidence in it because of the poor fit of model (25) to Ugashik survival information.

Annual variations in the freshwater survival rates of Naknek and Ugashik broods do not seem related when the effects of potential egg deposition and holdover rate are removed. Freshwater survival rates could be estimated jointly for 10 broods of these systems. The sample partial correlation coefficient between logarithms of these paired estimates is negative. Variables included in addition to the survival rates were potential egg deposition for either system and holdover rate only for the Ugashik system (holdover rate was found to have no explanatory power for Naknek freshwater survival rate). If annual variations in the general climate of Bristol Bay influence freshwater survival rates in these systems, other factors also affecting freshwater survival but acting independently between systems are sufficiently important to conceal this effect.

Those young salmon which survive the freshwater phase migrate to sea as smolts. The marine phase of Bristol Bay sockeye salmon lasts 1-4 yr with nearly all survivors returning to spawn after two or three winters at sea. We now consider survival during this ocean residence.

Marine Phase

The timing of the migrations of smolts of the two main freshwater age groups differs with age and river system. Age II smolts begin migrating earlier in the summer than age I smolts (Hartman et al. 1967). At either age, Naknek smolts migrate roughly 2 wk later than Ugashik smolts and enter the estuary over 150 km behind the Ugashik smolts on the ocean migration route along the southeastern shore of Bristol Bay (Straty 1974). Migration of Bristol Bay smolts through inner Bristol Bay is rapid but slows beyond Port Heiden (see index map, Figure 1); the reduced rate of migration causes progressive mixing of stocks as the smolts continue to move along the southeastern shore of Bristol Bay (Straty 1974). Thereafter, over the subsequent 2 or 3 yr, the salmon make two or three circuits of an elongated east-west course in the Bering Sea and North Pacific Ocean, the number of circuits directly related to the number of years at sea before maturity (Royce, Smith, and Hartt 1968). The Naknek and Ugashik stocks probably experience similar environmental conditions over most of their oceanic life except during the earliest phase within inner Bristol Bay.

The ocean survival rates of broods of Naknek and Ugashik smolts from time of emigration from the rivers to their return as adults (Table 27) were estimated from our estimates of smolt emigration and those of total adult return (Robert D. Paulus, personal communication). The estimates of total adult return include estimated numbers of adults intercepted on the high seas by the Japanese. Methods used to arrive at these estimates were presented by Fredin and Worlund (1974).

In the Naknek system, brood survival of freshwater age groups combined has ranged from 0.12 to 0.27, over twofold variation. In the Ugashik system, comparable brood survival has ranged from less than 0.04 to nearly 0.34, over ninefold variation. Survival of age I smolts has averaged 0.16 in the Naknek system and 0.08 in the Ugashik. Survival of age II smolts has averaged 0.26 in the Naknek system and 0.14 in the Ugashik. Although survival in either system and either age group varies tremendously, Naknek smolts of either age survive, on the average, roughly twice as well as their Ugashik counterparts.

The ratio of the average survival of age II smolts to that of age I smolts in the Naknek system is 1.6; in the Ugashik system, age II smolts do even better, the corresponding ratio being 1.8. The larger age II smolts survive better than age I smolts in either system.

The greater survival of age II smolts than age I smolts in either system is probably due in large part to the greater size of age II smolts. Although differences in survival among smolts of the two age groups may occur because of size differences, other factors must be of greater importance. Among broods of either age group in the Ugashik system, no evident improvement in survival occurs with increasing size (Figure 26). Likewise, in the Naknek system only a small proportion of the variation in survival within age groups, if any, would be explained by smolt size (Figure 27).

Table 27. Ocean survival rates of smolts from Naknek and Ugashik systems by brood year and freshwater age.

Brood Year	Naknek			Ugashik		
	Age I	Age II	Total	Age I	Age II	Total
1956	0.209	0.205	0.209	0.351	0.146	0.336
1957	.062	.469	.178	.027	.228	.082
1958	.112	.561	.254	.056	.181	.117
1959	.155	.180	.170	.078	.158	.143
1960	.237	.245	.241	.077	.127	.105
1961	.194	.201	.197	.053	.118	.065
1962	.138	.109	.119	.016	.088	.035
1963	.049	.256	.124	.018	--	--
1964	.223	.253	.234	--	.108	--
1965	.212	.116	.143	.043	.225	.116
1966	.355	.146	.272	.079	.054	.078
1967	.112	.464	.171	--	--	--
1968	.169	.141	.152	--	--	--
1969	.043	--	--	--	--	--
Average	.162	.257	.190	.080	.143	.120
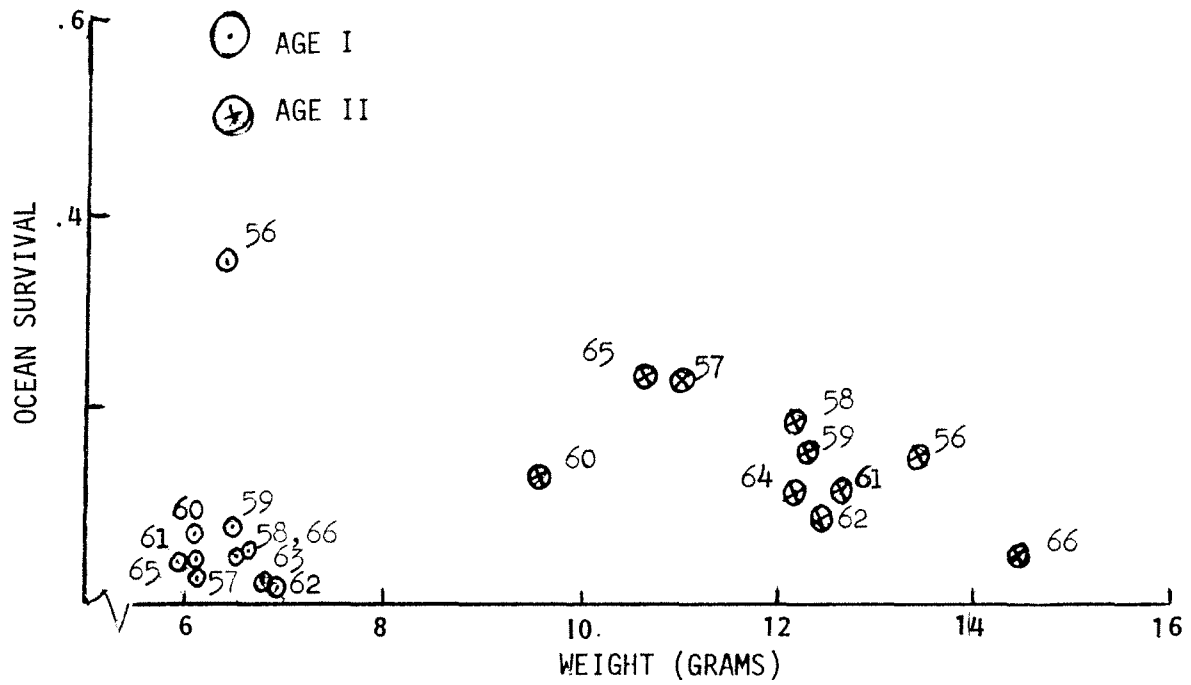
Figure 26.--Ocean survival rate of cohorts of smolts from the Ugashik system as related to their initial average weight (gm). (Brood years are indicated.)
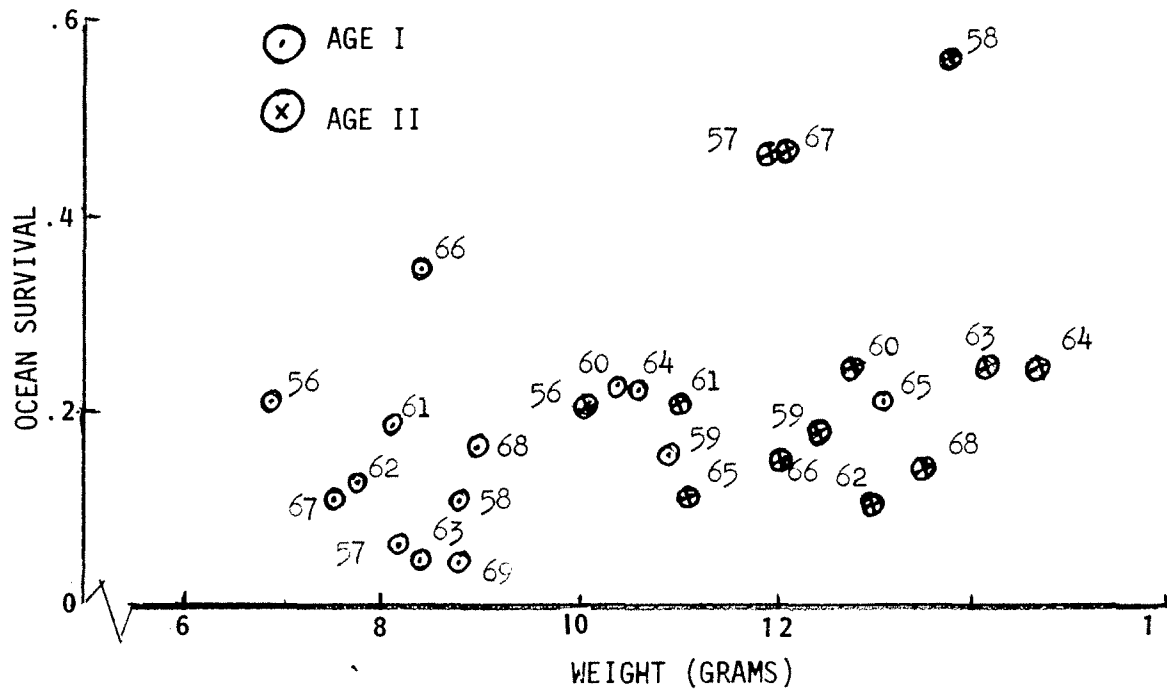
Figure 27.--Ocean survival rate of cohorts of smolts from the Naknek system as related to their initial average weight (gm). (Brood years are indicated.)

As in the case of variation in freshwater survival, variation in ocean survival could be related to variation in length of ocean residence of broods and density-related factors. As our measure of duration of ocean residence, we computed for each freshwater age group of each system the proportion of total survivors of each cohort of smolts which returned after 3 yr at sea. Nearly all survivors not returning after 3 yr did so after 2 yr. Then, to examine the variation in marine survival explained by variation in initial numbers of a cohort and in duration of ocean residence, we performed regression analyses using model (25). Stepwise regression was used as before when we analyzed freshwater survival.

Both the initial numbers of smolts and the proportion of 3-ocean returning adults are statistically significant (Table 28) in explaining variation in the ocean survival rate of age II Naknek smolts. Initial numbers accounted for 39% of the total variation in logarithm-transformed survival. Variation in the duration of ocean residence accounted for an addditional 20% of the total variation. Survival is inversely related to initial smolt numbers and to the proportion of 3-ocean-adult returns (Figure 28). We anticipated the reduced survival with longer ocean residence indicated by the relationship with 3-ocean proportion; however, the estimates of regression coefficients and underlying variance indicate the survival rate during the last year in the ocean for 3-ocean fish from Naknek age II smolts is only about 0.30 regardless of initial numbers. Our estimate of survival is low compared to previous assessments of Bristol Bay sockeye salmon survival during their third year at sea (Fredin 1965; Mathews 1968). Fredin obtained an estimate of 0.80 using data on year classes from 1950 to 1958 of Bristol Bay as a whole. Mathews found a lower value of 0.58 using data on the 1959, 1960, and 1961 year classes of Bristol Bay as a whole. Fredin's method using smolt counts was applied to our data for age II Naknek smolts and resulted in an even lower estimate of third year survival of 0.12. If the survival during the third year is as low as, say, 0.30, then the survival rate must drop sharply after the 2-ocean fish leave the cohorts; otherwise the total ocean survival of the age II Naknek smolts could not be as great as observed.

The inverse relationship with initial numbers indicates competition occurs. The waters of the inner bay are sparsely populated with plankton used as food by sockeye salmon and the fish undergo little or no growth for 4-6 wk after entry into Bristol Bay (Straty 1974). If competition occurs, we suspect it occurs at this period of ocean residence.

Evidence of competition immediately brings to mind the smolts of the Kvichak system which in many years dominate the numbers of smolts of the other systems of Bristol Bay. Their timing of migration (Hartman, Heard, and Drucker 1967) is such that they would probably precede the Naknek smolts along their common seaward migration route in Bristol Bay (Straty 1974); therefore the food supply of the Naknek smolts could be reduced by the feeding of Kvichak smolts. In fact, the correlation coefficient between logarithm-transformed ocean survival rates of age II smolts of Naknek broods of 1956 to 1968 and an index of numbers of Kvichak smolts (Paulus and Parker 1974) migrating seaward the same years is -0.53 (P < 0.05). However, that the postulated competition probably occurs within the cohorts of age II Naknek smolts rather than with Kvichak smolts, which covary to some degree with these Naknek smolts (r = +0.62, P < 0.05), is evinced by the following partial correlation analysis. The index of Kvichak smolt migrations has been added

Table 28. Stepwise regression analysis of ocean survival rates of age II smolts as related to initial numbers of smolts of the cohort and duration of ocean residence, Naknek system.

Source	df	SS	MS	F
Initial numbers	1	1.32818	1.32818	9.75*
Proportion of 3-ocean fish	1	0.68550	0.68550	5.03*
Proportion of 3-ocean fish and initial numbers	2	2.01368	1.00684	7.39*
Residual	10	1.36286	0.13629	—
Total	12	3.37654	—	—

*Regression significant at 5%
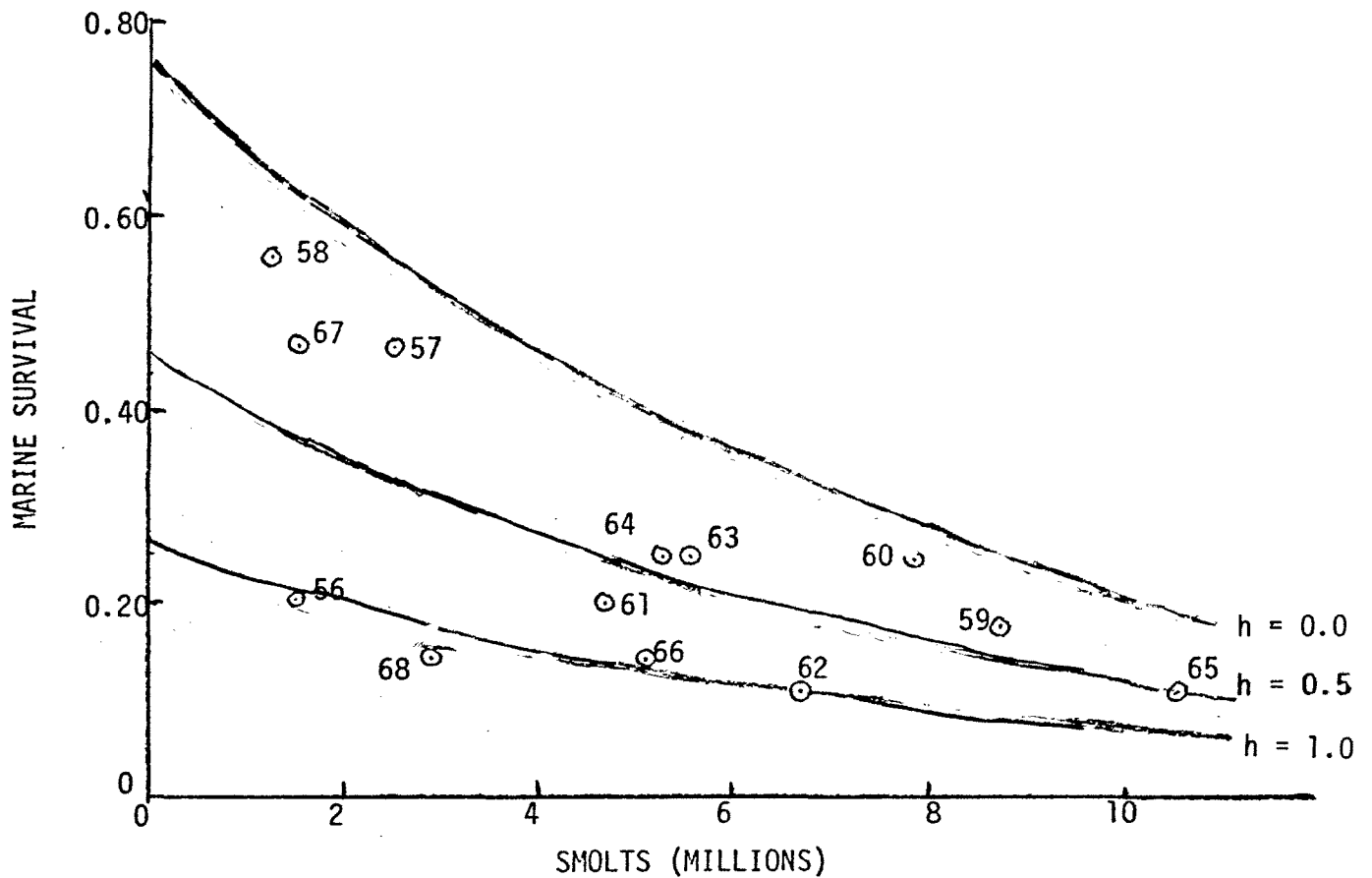
Figure 28.--Ocean survival rate of age II smolts of the Naknek system as related to initial number of migrants. (Brood years and average survival at three levels of duration of ocean residence (h) are indicated: h = 0.0, all fish mature after 2 years; h = 0.5, 50% of fish mature after 2 years and 50% mature after 3 years; h = 1.0, all fish mature after 3 years.)

to the variables used in the previous regression analysis of ocean survival rates of age II Naknek smolts. The partial correlation coefficient between logarithm-transformed ocean survival rates of age II Naknek smolts and the Kvichak index, controlling for number of age II Naknek smolts and their duration of ocean residence, is -0.15 (P > 0.30). The partial correlation coefficient between the same logarithm-transformed survival rates and numbers of age II Naknek smolts, controlling for duration of residence and Kvichak smolts, is -0.61 (P < 0.05). Therefore, the variation in survival of the age II Naknek smolts is more closely related to their numbers than to Kvichak smolt numbers, indicating the competition originates within the migrating cohorts of Naknek smolts.

Although both duration of ocean residence and initial numbers contribute to variation in the survival of age II Naknek smolts, neither factor is statistically significant for the remaining cases--age I Naknek smolts and age I or age II Ugashik smolts (Tables 29, 30, and 31). In each of these cases, duration of ocean residence entered the regression first and explains a considerably greater proportion of total variation of transformed survival. Ocean residence explains 32%, 26%, and 19% of total variation for age I Ugashik, age II Ugashik, and age I Naknek smolts, respectively; the initial numbers of smolts explain only 6%, less than 1%, and less than 1% of total variation, respectively.

Although the duration of ocean residence seems to explain substantial variation in ocean survival, the estimated relationship is positive for age II Ugashik smolts, contrary to that expected. The short range of variation in the proportion of 3-ocean returns and few observations, 10, is likely the cause. The other two estimated relationships between survival and duration of ocean residence are inverse as expected. However, all these relationships between survival and duration of ocean residence must be viewed with circumspection. We again used estimated regression coefficients and underlying variance to calculate survival over the ultimate year of ocean residence of 3-ocean fish from these smolts. The estimates are 0.06 and 0.23 for age I Ugashik and Naknek smolts, respectively. The estimate for age II Ugashik smolts is not feasible. If Fredin's method using smolt counts is employed, estimates of third-year survival are 0.18, 0.28, and 0.12 for age I and age II Ugashik smolts and age I Naknek smolts, respectively. Survival calculations include Japanese high seas catches as survivors, eliminating this exploitation as an explanation for the unanticipated low values. If the estimates are biased, the cause is unknown.

Initial numbers are relatively unimportant in explaining ocean survival of Ugashik smolts, either age I or age II, and age I Naknek smolts. Ugashik smolts are closest to outer Bristol Bay where food becomes abundant (Straty 1974); therefore food may not be as limiting for them as for Naknek smolts. However, the lack of explanatory power of the initial numbers of age I Naknek smolts is contradictory in view of earlier results for age II smolts.

Estimates of average ocean survival have been computed for all smolt groups under the assumption that duration of ocean residence has no influence. Undoubtedly, duration of ocean residence does affect survival, but the relationship is very poorly determined. As data accrue, the relationships will become more precisely known. The average survival rates of Ugashik smolts of either age and Naknek smolts of age I are computed as though independent

Table 29. Stepwise regression analysis of ocean survival rates of age I smolts as related to initial numbers of smolts of the cohort and duration of ocean residence, Naknek system.

Source	df	SS	MS	F
Proportion of 3-ocean fish	1	0.67941	0.67941	2.31^{ns}
Initial numbers	1	0.00229	0.00229	$< 1^{ns}$
Proportion of 3-ocean fish and initial numbers	2	0.68170	0.34085	1.16^{ns}
Residual	10	2.94671	0.29467	--
Total	12	3.62841	--	--

^{ns}Regression not significant.

Table 30. Stepwise regression analysis of ocean survival rates of age I smolts as related to initial numbers of smolts of the cohort and duration of ocean residence, Ugashik ststem.

Source	df	SS	MS	F
Proportion of 3-ocean fish	1	2.23810	2.23810	3.50^{ns}
Initial numbers	1	0.40670	0.40670	$<1^{ns}$
Proportion of 3-ocean fish and initial numbers	2	2.64480	1.32240	2.06^{ns}
Residual	7	4.47936	0.63991	__
Total	9	7.12416	__	__

^{ns}Regression not significant.

Table 31. Stepwise regression analysis of ocean survival rates of age II smolts as related to initial numbers of smolts of the cohort and duration of ocean residence, Ugashik system.

Source	df	SS	MS	F
Proportion of 3-ocean fish	1	0.44955	0.44955	2.44^{ns}
Initial numbers	1	0.00222	0.00222	$<1^{ns}$
Proportion of 3-ocean fish and initial numbers	2	0.45177	0.22588	1.22^{ns}
Residual	7	1.29108	0.18444	—
Total	9	1.74285	—	—

^{ns}Regression not significant.

of initial numbers, but the rate computed for age II Naknek smolts does account for this source of variation. The average survival of age II Ugashik smolts is estimated to be 0.144, about twice that of the age I smolts. However, age I Naknek smolts appear to have even greater survival then age II Ugashik smolts (Table 32). The relationship between average survival and initial numbers of age II Naknek smolts was obtained by refitting the survival data, including only initial numbers, in the regression analysis. The graph (not shown) of average survival resulting from this reevaluation follows closely that for the intermediate value of duration of ocean residence, h = 0.5, calculated earlier (Figure 28).

If large-scale oceanographic conditions in Bristol Bay and the North Pacific Ocean are responsible for substantial portions of the variations in ocean survival, we should anticipate good correspondence between the survival rates of cohorts of smolts migrating to sea in the same year. Relationships in survival among broods of the same freshwater age from the two river systems (Figure 29) or among broods of the two freshwater ages from the same river system (Figure 30) can be obscured for two principal reasons: (1) imprecision of survival estimates and (2) variable mortality induced by a patchy environment, most likely soon after smolts leave the rivers and before smolts of the systems become mixed in the estuary.

To examine the correspondence of survival rates for Naknek and Ugashik broods migrating to sea in the same year, survival rates were logarithm-transformed in an attempt to meet normality assumptions, and correlation coefficients were calculated and tested for statistical significance. Correlations were examined for four cases: (1) age I Naknek and Ugashik broods; (2) age II Naknek and Ugashik broods; (3) age I and age II Naknek smolts; and (4) age I and age II Ugashik smolts (Table 33 and Figures 29 and 30). In each case, the correlation coefficient is positive as expected if broods migrating the same year encounter similar environmental conditions determining survival. Correspondence between survival rates is statistically significant in only one case--survival of age I and age II Ugashik smolts migrating to sea in the same year. On the other hand, the two freshwater age groups of the Naknek system are poorly correlated.

Preceding analysis showed survival of age II smolts of the Naknek system is related to numbers migrating. We suspected that variation in the survival of age II smolts induced by variation in smolt numbers might possibly be responsible for the low correlation between survival of age II Naknek smolts and either survival of age I Naknek smolts or age II Ugashik smolts. Therefore, we computed partial correlation coefficients for these two cases, measures of the correlation of survival rates if smolt numbers of age II in the Naknek system were fixed. The partial correlation of Naknek and Ugashik brood survival rates of age II smolts is 0.49, or roughly the same as the simple correlation coefficient calculated before. The partial correlation of age I and age II Naknek smolt survival rates is 0.06, less than the correlation coefficient of 0.23 computed earlier (Table 33).

Ugashik smolts migrate to sea over a relatively short time interval; Naknek smolt migration is protracted with age II smolts preceding age I smolts as is typical for Bristol Bay stocks. Therefore, age I and age II smolts of the Ugashik system should experience more similar survival conditions than the Naknek freshwater age groups do during the early phase of ocean residence.

Table 32. Average ocean survival, 95% confidence bounds for average survival, and 95% confidence bounds for individual brood survival for Naknek age I and Ugashik age I and II smolts.[a]

River and age	Average	Bounds for average		Bounds for brood survival	
		Lower	Upper	Lower	Upper
Naknek, age I	0.166	0.096	0.199	0.034	0.562
Ugashik, age I	.075	.028	.100	.006	.435
Ugashik, age II	.144	.097	.181	.047	.376

[a]Computation based on logarithm-transformed survival rates.

Table 33. Sample sizes (n) and correlations (r) between log-transformed ocean survival estimates of smolts from the Naknek and Ugashik systems.

Between--	n	r
Naknek and Ugashik broods of age I	10	0.61^{ns}
Naknek and Ugashik broods of age II	10	$.45^{ns}$
Naknek age I and age II smolts emigrating the same year	13	$.23^{ns}$
Ugashik age I and age II smolts emigrating the same year	9	.72*

[ns]Correlation not significant.
*Correlation significant at 5%.
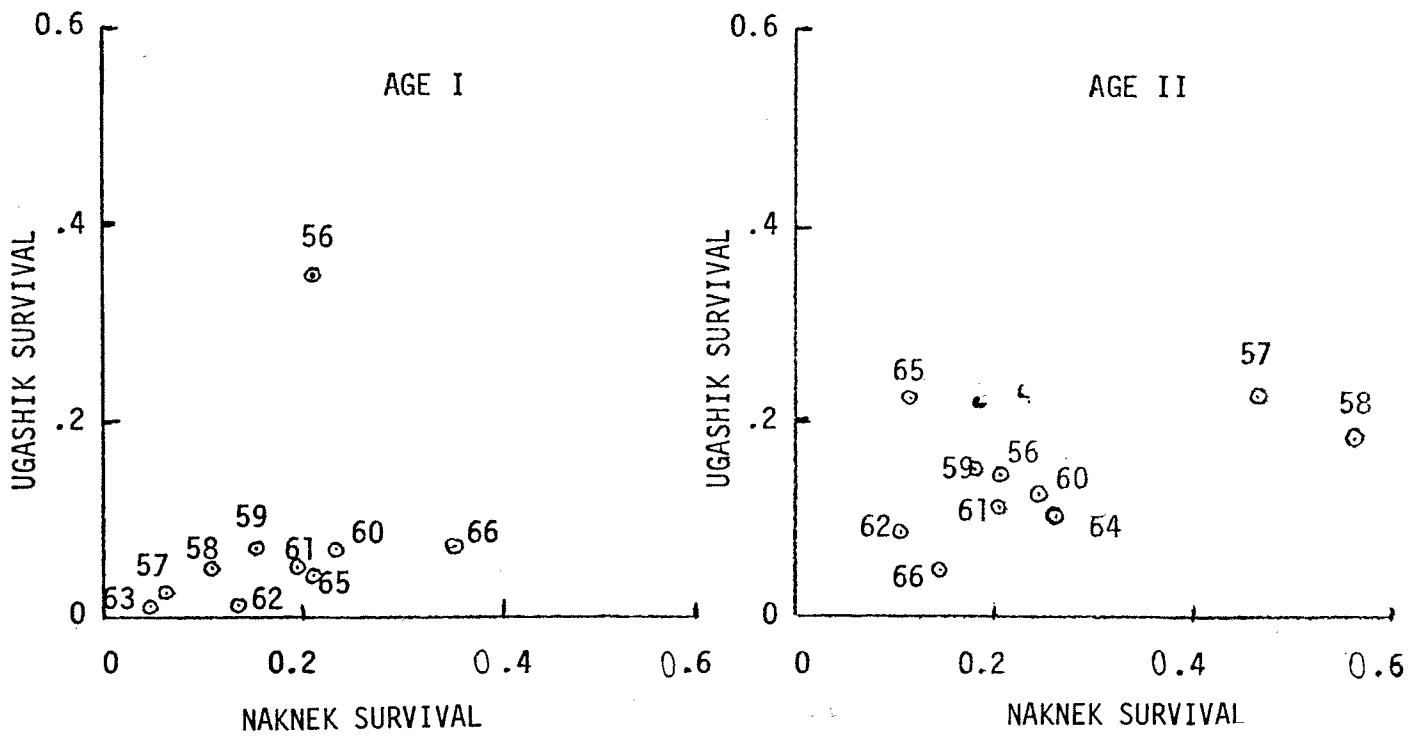
Figure 29.--Ocean survival rates of Naknek and Ugashik smolts of either age I or age II, migrating seaward in the same year. (Brood years are indicated.)
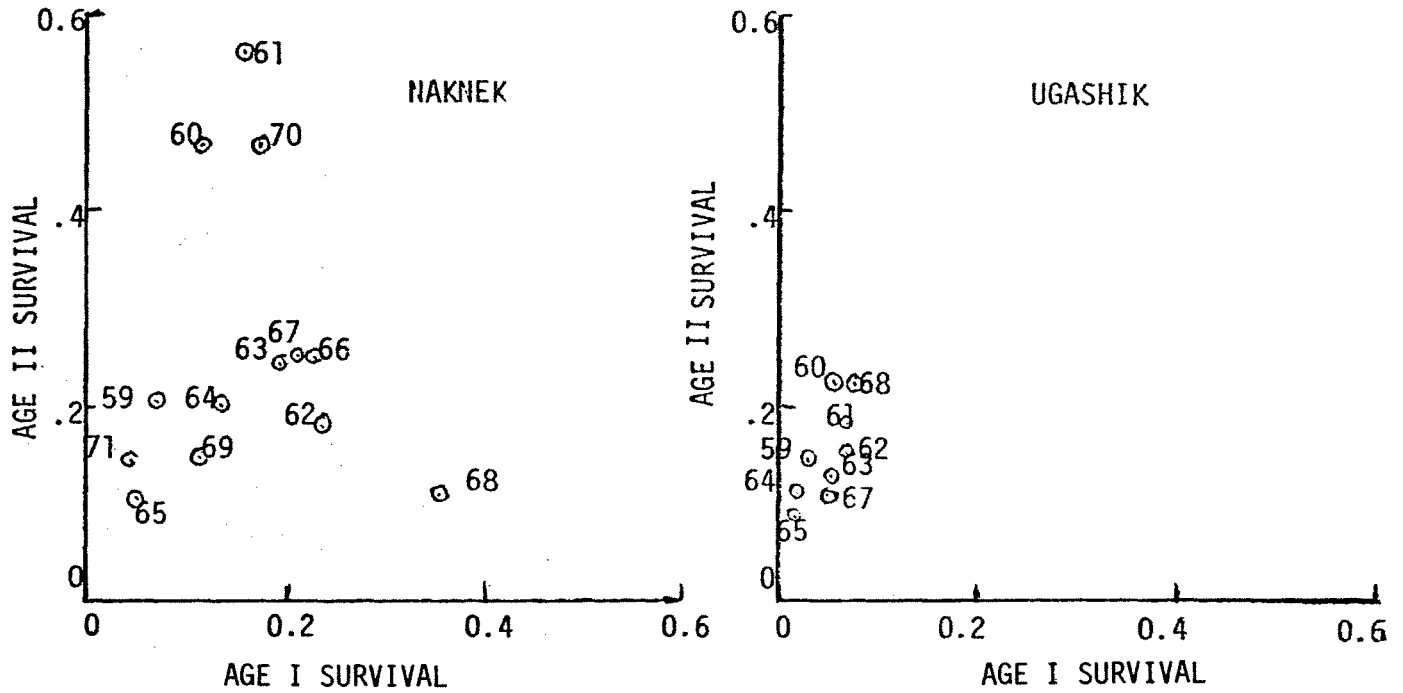
Figure 30.--Ocean survival rates of age I and age II smolts of either system, Naknek or Ugashik, migrating seaward in the same year. (Years of migration are indicated.)

Perhaps this timing of the migrations is the basis for the observed correlations.

Although the correlations between Naknek and Ugashik broods of age I or age II are not statistically significant, the low power of the test because of the small number of paired observations may be the cause rather than an actual absence of association. Time series of the survival estimates (Figures 31 and 32), especially those of age I, are evocative of a positive association between systems. Further, the survival rates of age I smolts may cycle with the interval between minima of 6 yr. No evidence for a similar quasi-periodicity occurs in the time series for age II smolts. The period in age I survival rates, if a cycle exists, agrees with the ocean temperature cycle in the North Pacific.

Total Survival

Finally, an analysis of survival from potential egg deposition to returning adult has been performed using equation (24) (Tables 34 and 35). Smolt information is ignored. Total returns including Japanese high seas catches again are considered as the returning adults. Survival declines detectably with increasing potential egg deposition in the Naknek system (Table 34); in the Ugashik system, the regression is not significant (Table 35). These results are consistent with earlier findings which indicated (1) freshwater survival is density-dependent in the Naknek system, but does not change detectably with the seeding densities observed in the Ugashik system; and (2) ocean survival is density-independent for Ugashik smolts of both age groups as well as age I Naknek smolts, but not for age II Naknek smolts.

PRODUCTION ESTIMATES AND ESCAPEMENT GOALS

Production estimates can be derived from the foregoing survival analysis. The estimated relationships of average survival rate between life stages, as related to numbers in the initial stage, are transformed to a production function. Products of expected survival with numbers in the initial stage relate expected survivors at the later stage to numbers in the initial stage. Confidence bounds on production are developed in a similar fashion from confidence bounds on survival rate. Such functions allow determination of the optimal numbers of eggs or smolts needed to maximize surplus production of adults available to the fishery. We calculate these production functions for each system and utilize them to develop management recommendations.

Production functions relating total returns and potential egg deposition will be biased upwards. Total returns include high seas catches; these in turn include immature sockeye salmon, some of which would not survive to return as adults. Therefore, estimates of production are reevaluated using inshore returns. Either analysis would be affected by mixing of eastern stocks in eastern catch districts because of resulting errors in estimates of inshore returns to river of origin. Therefore, management recommendations from the preceding are considered in light of production functions relating number of smolts and potential egg deposition.

To begin, the expected total returns from potential egg depositions over the ranges experienced in either system have been computed using the estimated expected survival rates from egg to returning adult including high seas
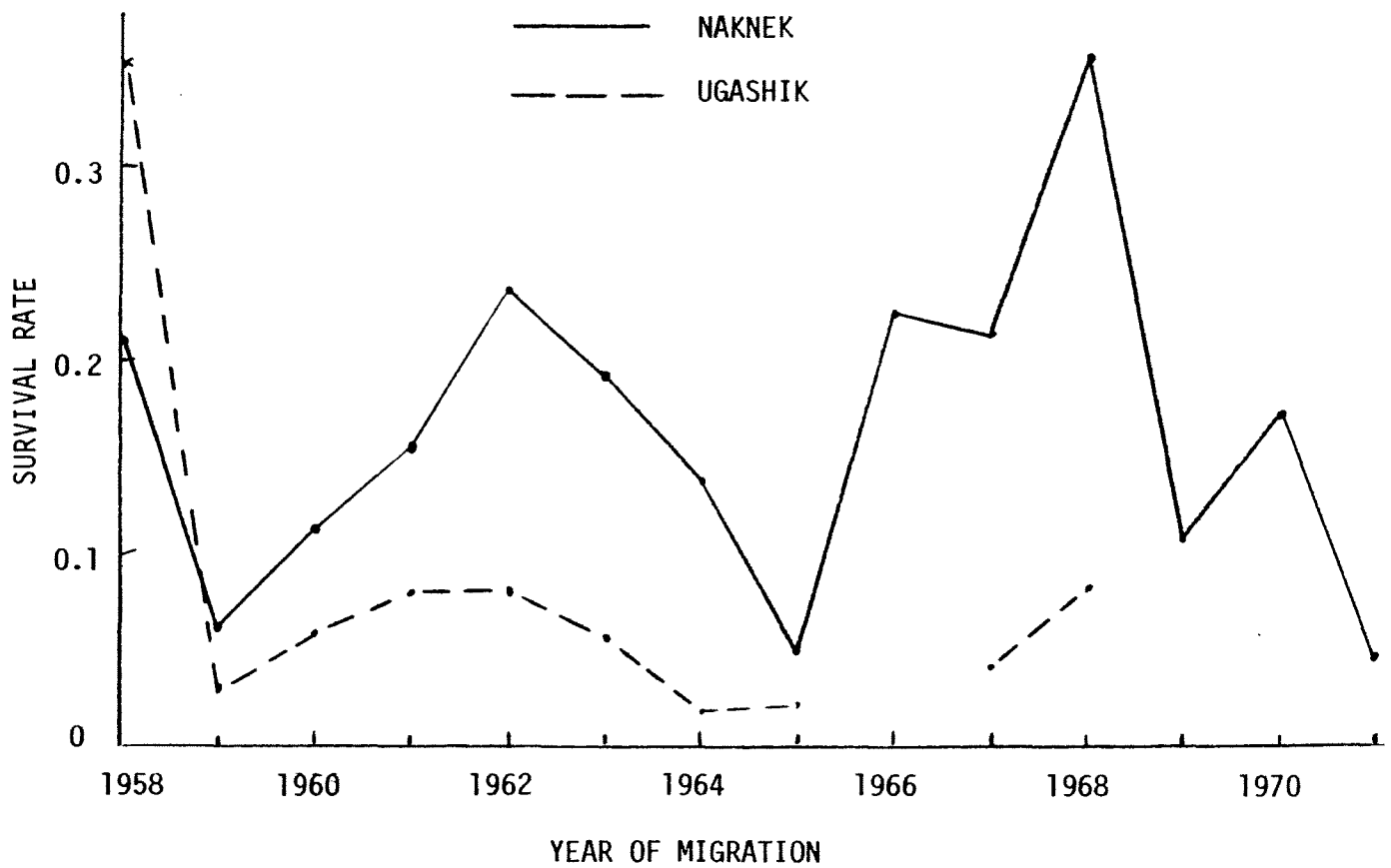
Figure 31.--Ocean survival rates of age I smolts of Naknek and Ugashik by year of seaward migration.
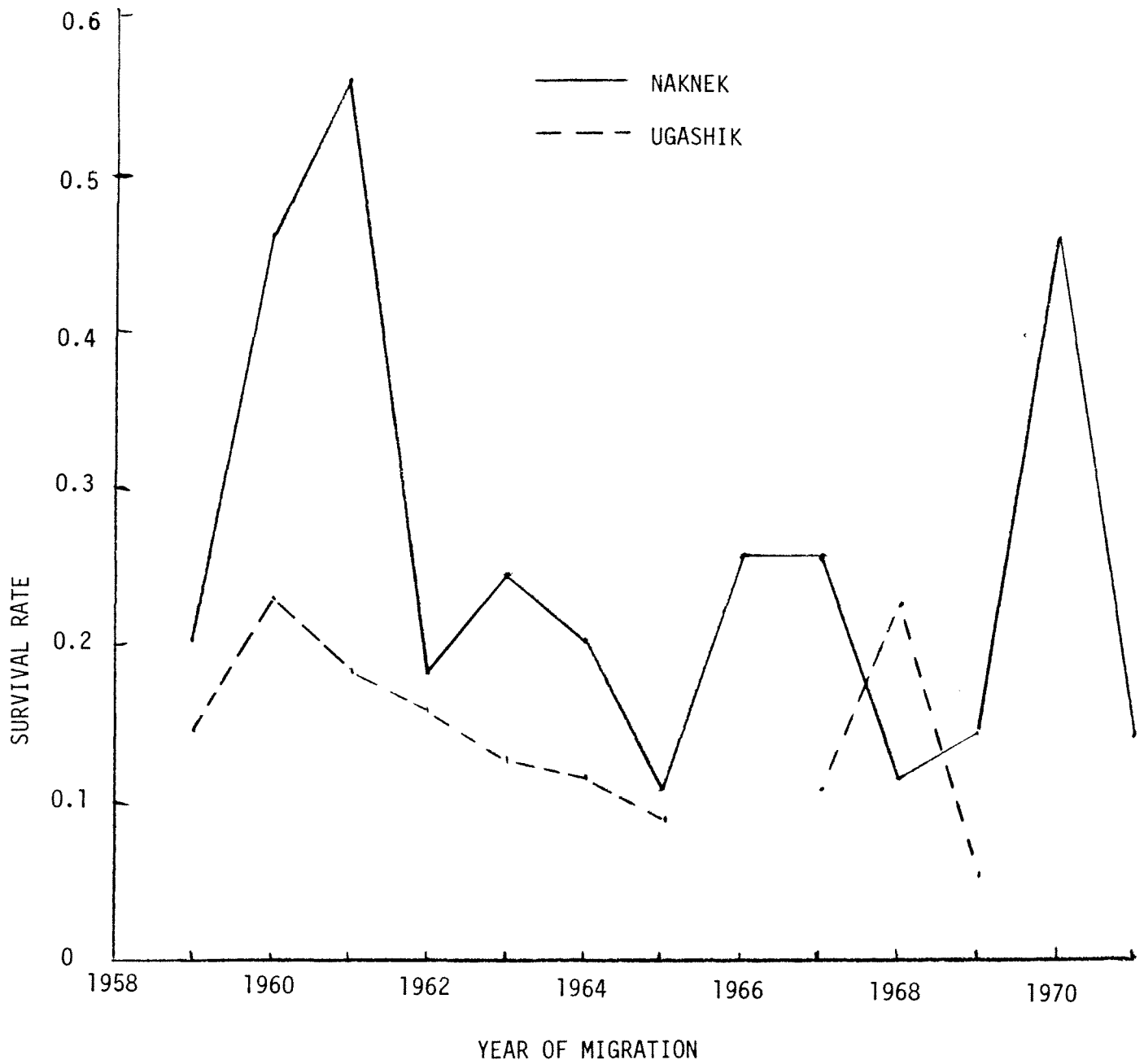
Figure 32.--Ocean survival rates of age II smolts of Naknek and Ugashik by year of seaward migration.

Table 34. Regression analysis of total survival from egg to return for Naknek broods, 1956-68.

Source	df	SS	MS	F
Mean	1	0.19264	0.19264	<1
Regression	1	1.75059	1.75059	7.35*
Error	11	2.61817	0.23802	—
Total	13	4.56140	—	—

*--Regression significant at 5%.

Table 35. Regression analysis of total survival from egg to return for Ugashik broods, 1956-68.

Source	df	SS	MS	F
Mean	1	2.38470	2.38470	2.65
Regression	1	0.04167	0.04167	<1
Error	11	9.90757	0.90069	—
Total	13	12.33394	—	—

catches (Figures 33 and 34). Expected survival is assumed to be density dependent. Confidence limits for expected and individual brood returns were computed from confidence limits for equation (24) by algebraic retransformation.

Replacement lines (see Figures 33 and 34) relate adult returns with their potential egg deposition. The slope of the replacement line is estimated as the inverse of the average potential egg deposition per spawner (Table 3) for either system. The critical values of potential egg deposition developed below are transformed to equivalent numbers of spawners using the replacement lines. The excess of expected returns over the replacement line is the expected surplus for harvest from the progeny of a parental generation in order that potential egg deposition by the progeny equals that of the parents.

In the Naknek system, the maximum production of total returns is estimated to be 2.4 million at a potential egg deposition of 2,250 million, or 1.2 million spawners. In the Ugashik system, the corresponding maximum occurs beyond the range of observed potential egg depositions. We have not computed the maximum condition for the Ugashik system, but know the estimate of maximum production exceeds 2.8 million; further, the estimated potential egg deposition to achieve this production exceeds 4,500 million eggs, or 1.9 million spawners. Although these maxima are of interest for comparative purposes, they indicate only upper limits of escapement goals for managing the fishery. Escapement goals are better determined by study of surplus production.

In the Naknek system (Figure 33) the surplus is greatest, approximately 1.4 million fish, at a potential egg deposition of about 1,500 million corresponding to roughly 0.8 million spawners. In the Ugashik system (Figure 34), expected returns are very imprecisely known above seedings of 2,000 million eggs. Further, the estimated surplus production varies only slightly over a very broad range of potential egg depositon. Surplus production is estimated to be greatest, 1.2 million fish, at about 3,000 million eggs corresponding to 1.3 million spawners. While the estimated surplus production in the Ugashik system does not increase beyond this level, several large seedings at and above 3,000 million eggs or 1.3 million spawners would be needed to better define the relationship; expected returns could be seriously overestimated or underestimated at high seeding densities (see 95% confidence bounds for expected returns), and estimated surplus production would correspondingly be in error.

When inshore returns are used in place of total returns in the preceding analyses, changes in critical values are slight. In the Naknek system, maximum production falls by 0.4 million down to 2.0 million, achieved at the same potential egg deposition of 2,250 million or 1.2 million spawners. In the Ugashik system the maximum again occurs beyond the range of observed potential egg deposition. We know the estimate of maximum production exceeds 2.7 million and that the potential egg deposition to achieve this production again exceeds 4,500 million eggs or 1.9 million spawners.

In the Naknek system surplus production is maximized again at 0.8 million fish; these are expected to produce a harvestable inshore return of 1.1 million fish. In the Ugashik system the optimum escapement is 1.4 million, slightly higher than before, which should produce a harvestable surplus of 1.0 million.

Figure 33.--Total returns and potential egg deposition in the Naknek system. (Brood years are indicated.)

EXPECTED RETURNS

95% CONFIDENCE BOUNDS ON INDIVIDUAL RETURNS

95% CONFIDENCE BOUNDS ON AVERAGE RETURNS
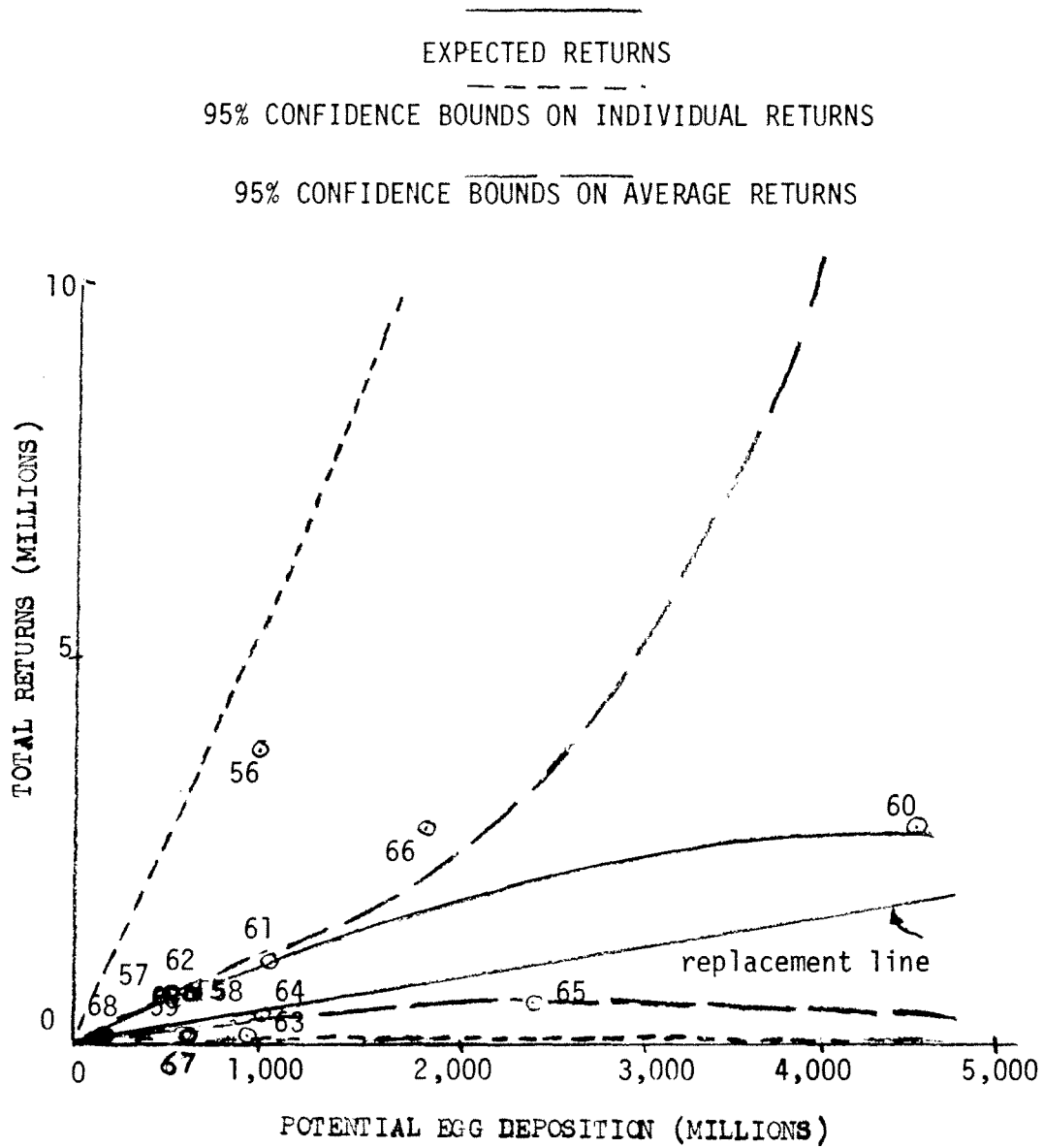
Figure 34.--Total returns and potential egg deposition in the Ugashik system. (Brood years are indicated.)

The preceding analyses of production could contain errors due to mixing of returns in catch districts. Smolt production analysis reflects on the problem of ascertaining escapement goals while circumventing, in part, the potential influence of mixing. Provided ocean survival is not affected by numbers of smolts, the potential egg deposition which maximizes smolt production will also maximize production of adults. Previous analyses of ocean survival found no effect of initial numbers of smolts in the Ugashik system, nor for age I smolts of the Naknek system. However, age II Naknek smolts probably suffer mortality rates which increase with initial numbers. If so, the escapement which maximizes Naknek smolt production is only an upper limit to that which produces maximum adult returns.

Surplus production of adults can only be evaluated from a smolt production function if ocean survival is known. Estimates of ocean survival depend on adult returns. Therefore, smolt production analysis cannot resolve the problem of optimum escapement for maximum surplus production of adults without reference to adult returns. However, an upper limit for that escapement can be found. The escapement which maximizes smolt production can be no less than that which is optimal provided ocean survival does not increase with increase in smolts. No evidence for such improvement of ocean survival was detected.

Production functions relating smolt production and potential egg deposition have been estimated for each system (Figures 35 and 36). In the Naknek system the duration of freshwater residence did not influence freshwater survival appreciably; however, in the Ugashik system this factor appeared equal to potential egg deposition in explaining variation of freshwater survival. Therefore, production functions for three levels of the holdover rate--0.0, 0.5, and 1.0--have been developed for Ugashik smolts. A production function for Ugashik smolts omitting the holdover rate has also been developed but not illustrated.

Maximum smolt production in the Naknek system is estimated to be 13.1 million at a potential egg deposition of 2,500 million eggs or 1.3 million spawners. Maximum smolt production in the Ugashik system depends on holdover rate. If all smolts are age I, maximum production is estimated as 31.9 million at a potential egg deposition of 3,250 million eggs or 1.4 million spawners. If the freshwater holdover rate is 0.5, the maximum is estimated as 19.7 million at 3,500 million eggs or 1.5 million spawners. Finally, if only age II smolts are produced, the maximum declines to 9.3 million at 3,500 million eggs or 1.5 million spawners. When the holdover rate is omitted, maximum production is estimated to be 22.3 million smolts at 3,000 million eggs or 1.3 million spawners.

The surplus production of smolts can be evaluated from the smolt production function if ocean survival is assumed known. Surplus production of smolts are those in excess of the number needed to produce as adults the same number of eggs as their parents. To simplify, knowledge of the relationship of ocean survival of age II smolts and their numbers in the Naknek system is omitted in the replacement line. Information concerning the possible influence of holdover on smolt production in the Ugashik system is ignored as well; a new production function is developed (not illustrated), based on a fitted relationship between freshwater survival and potential egg deposition only. Estimated replacement lines (not illustrated) for smolt production have slopes
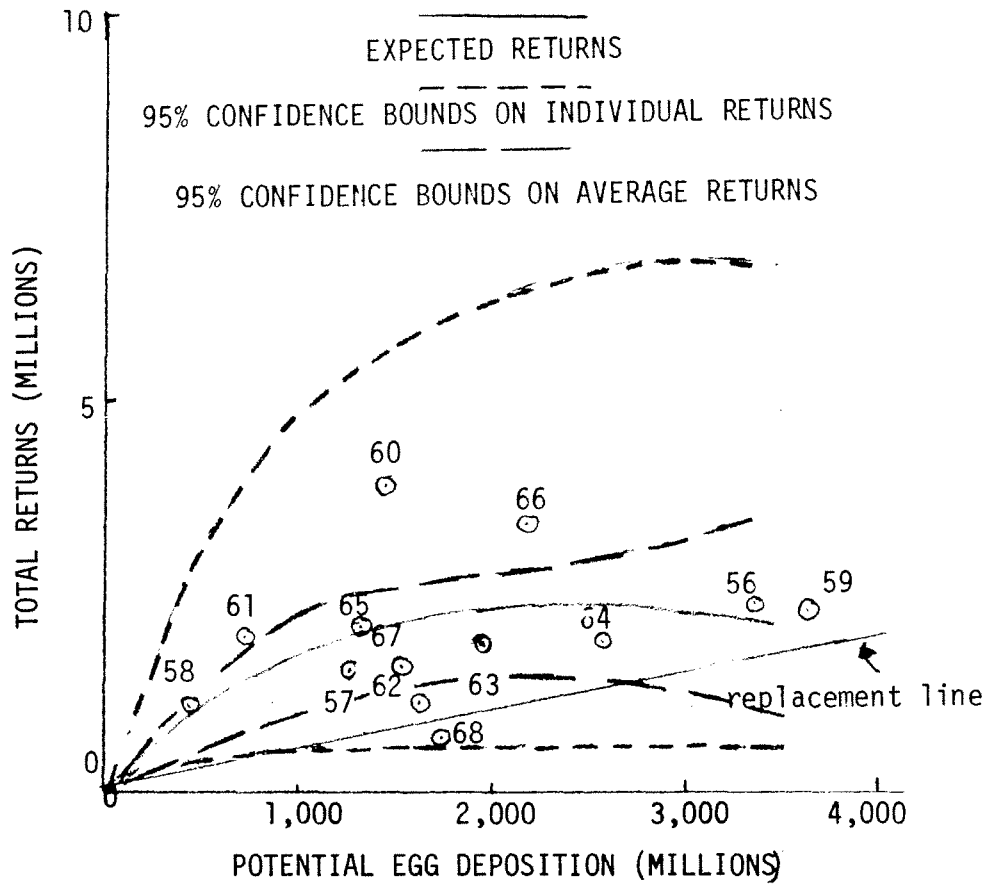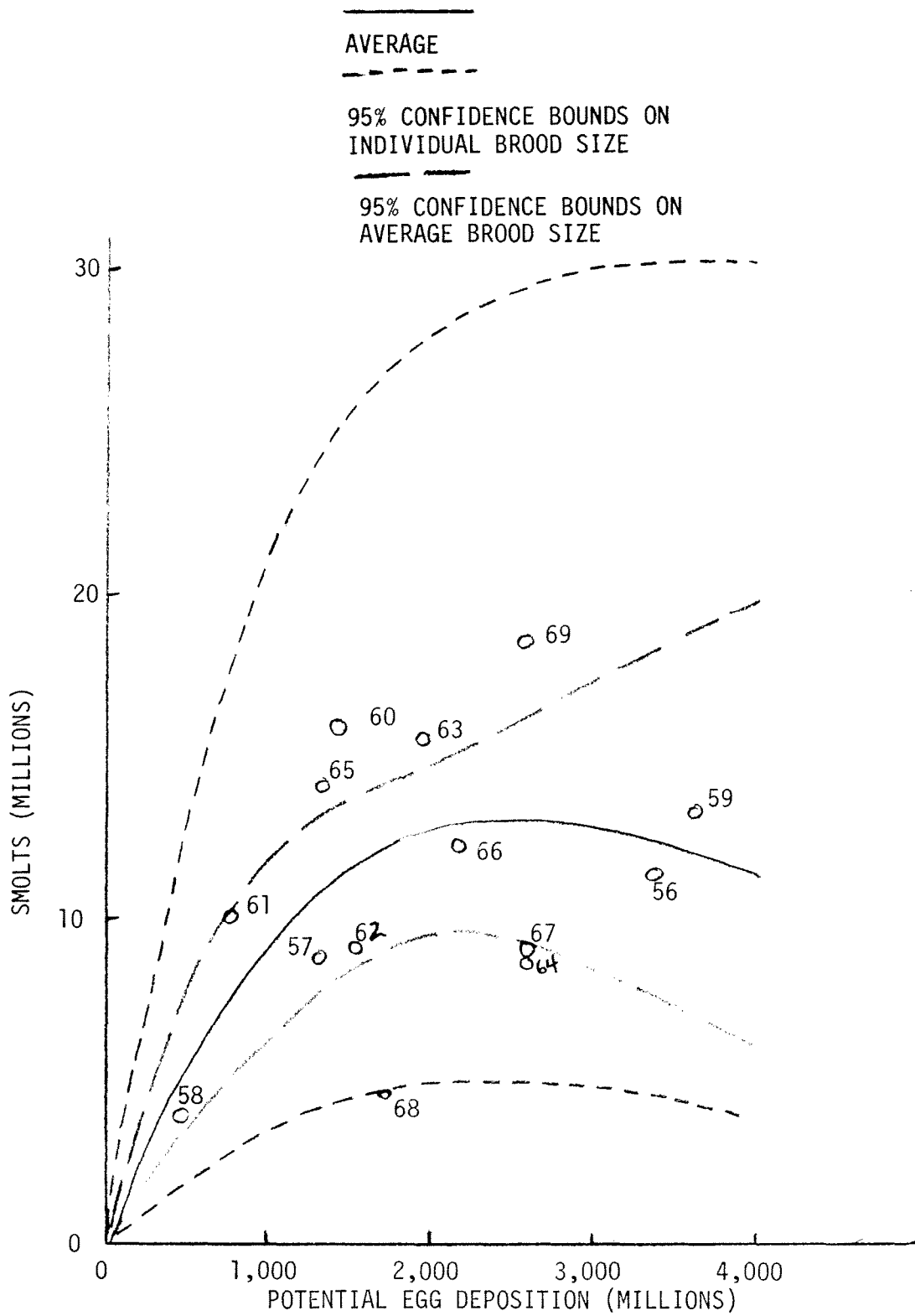
Figure 35.--Smolt production and potential egg deposition in the Naknek system. (Brood years are indicated.)
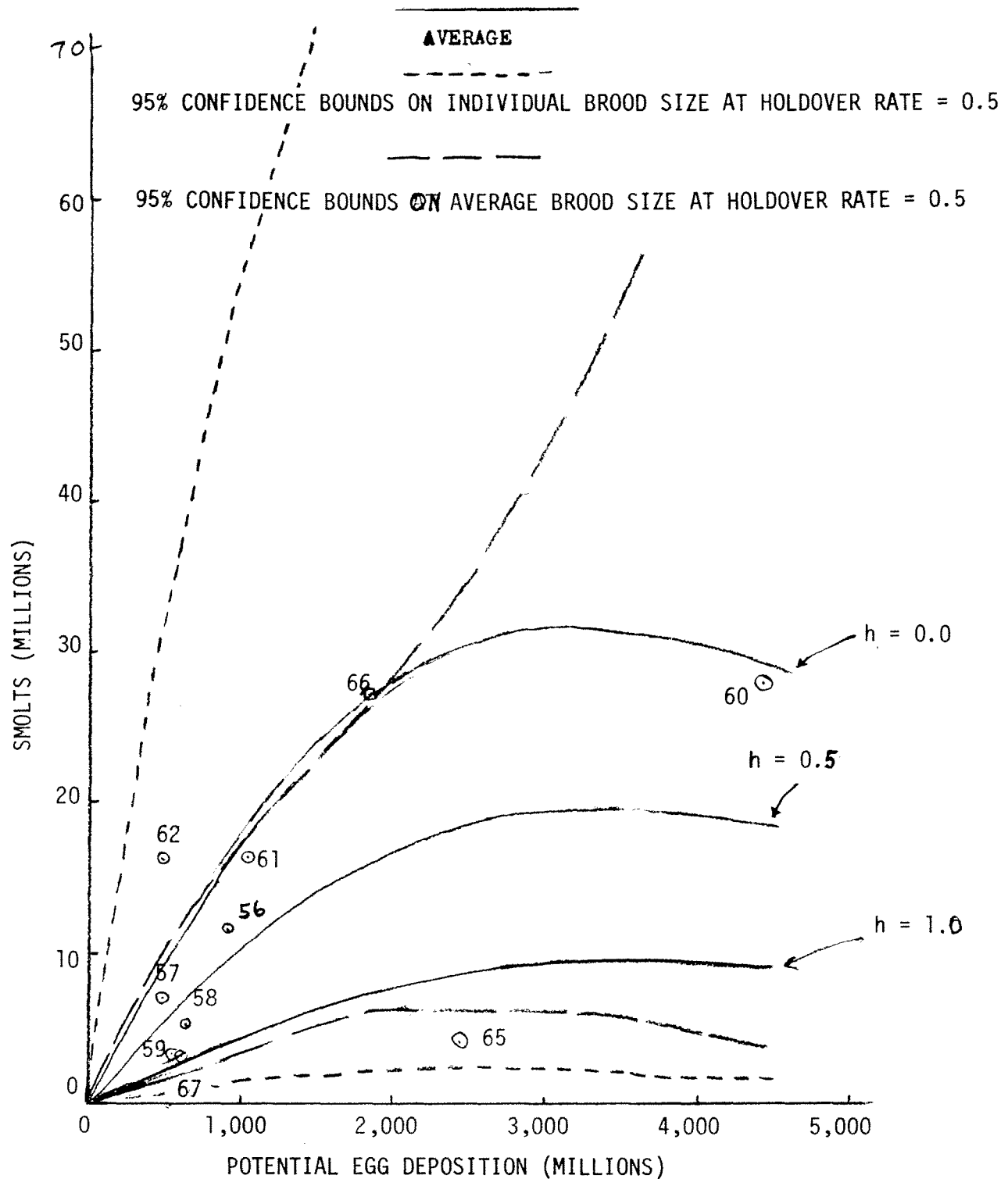
Figure 36.--Smolt production and potential egg deposition in the Ugashik system for three freshwater age compositions (h): h = 0, all smolts are age I; h = 0.5, half of the smolts are age I and half are age II; and h = 1.0, all smolts are age II. (Brood years are indicated.)

equal to the inverse of the product of average potential egg deposition per spawner (Table 3) and average total marine survival of smolt broods disregarding freshwater age (Table 27). Under these simplifications the maximum surplus smolt production in the Naknek system is estimated to be 7.5 million at an escapement of 0.9 million. In the Ugashik system, the maximum, 13.0 million, occurs at 1.0 million spawners.

A survey of critical values from production analyses based on total returns, inshore returns, and smolts (Table 36) shows negligible differences in management recommendations based on total and inshore returns; further, critical values from smolts are more consistent with those from the adults, either total or inshore returns, in the Naknek system. In the Naknek system the maximum production of smolts and adults is estimated to occur at 1.3 million escapement and 1.2 million escapement, respectively. The escapement maximizing adult production should be somewhat less than that maximizing smolt production in view of the dependence of ocean survival of age II smolts on their numbers. The production of total returns from age II Naknek smolts is estimated to be maximal from 8.5 million smolts (Figure 37); the number surviving depends on their ocean age composition. If inshore returns are used, a maximum occurs again at 8.5 million age II smolts. A production of 8.5 million smolts is estimated to occur from roughly 500,000 spawners. This value is the smallest escapement maximizing adult production. If no smolts hold over, the value of 1.3 million spawners maximizes both smolt and adult production. Other escapements maximizing adult production based on smolt analyses lie between these extremes and depend on the holdover rate.

Surplus smolt production in the Naknek system is estimated to be maximal at 0.9 million escapement. Surplus production of adults, either total or inshore returns, is maximized at 0.8 million spawners, agreeing well with the smolts.

Critical values for Ugashik sockeye salmon are less consistent. The maximum production of smolts is estimated to occur at escapements from 1.3 to 1.5 million, depending on the particular analysis (Table 36). Both total adult and inshore returns are estimated to be maximal from escapements in excess of 1.9 million. In view of the absence of a relationship between ocean survival and numbers of smolts, the maximizing escapements should be equal. The discrepancy between smolts and adults may occur for either of two reasons: (1) inaccuracy in estimation of maximizing escapements; or (2) catches in the Ugashik district, which are considered Ugashik returns, contained greater numbers of fish of other origins than the numbers of Ugashik fish intercepted in other districts. The confidence bounds for expected adult returns and expected smolt production (Figures 34 and 36) graphically show the extreme imprecision of our estimates. Net errors in allocation of catches are more difficult to evaluate, though considering Ugashik adult returns are a small fraction of the total return to eastern Bristol Bay systems, errors could favor Ugashik returns.

The surplus production of smolts is estimated to be maximal at an escapement of 1.0 million, 0.3 million or 0.4 million less than the escapements estimated to maximize surplus total or inshore returns, respectively.

FORECASTING

Forecasting of adult returns is inaccurate because of unexplained variation in survival and maturity schedules. Variation of survival in fresh water can be

Table 36.   Critical values (in millions) from production analysis.

	Maximum Production			Maximum Surplus Production		
	Production	PED	Escapement	Surplus	PED	Escapement
Egg to total return						
Naknek	2.4	2,250	1.2	1.4	1,500	0.8
Ugashik	2.8[a]	4,500[a]	1.9[a]	1.2	3,000	1.3
Egg to inshore return						
Naknek	2.0	2,250	1.2	1.1	1,500	0.8
Ugashik	2.7[a]	4,500[a]	1.9[a]	1.0	3,250	1.4
Egg to smolt						
Naknek	13.1	2,500	1.3	7.5	1,750	0.9
Ugashik						
h=0.0	31.9	3,250	1.4	—	—	—
h=0.5	19.7	3,500	1.5	—	—	—
h=1.0	9.3	3,500	1.5	—	—	—
h omitted	22.3	3,000	1.3	13.0	2,250	1.0

[a]Maximum occurs beyond the range of observed potential egg deposition. Computations were not extended to locate the maximum.
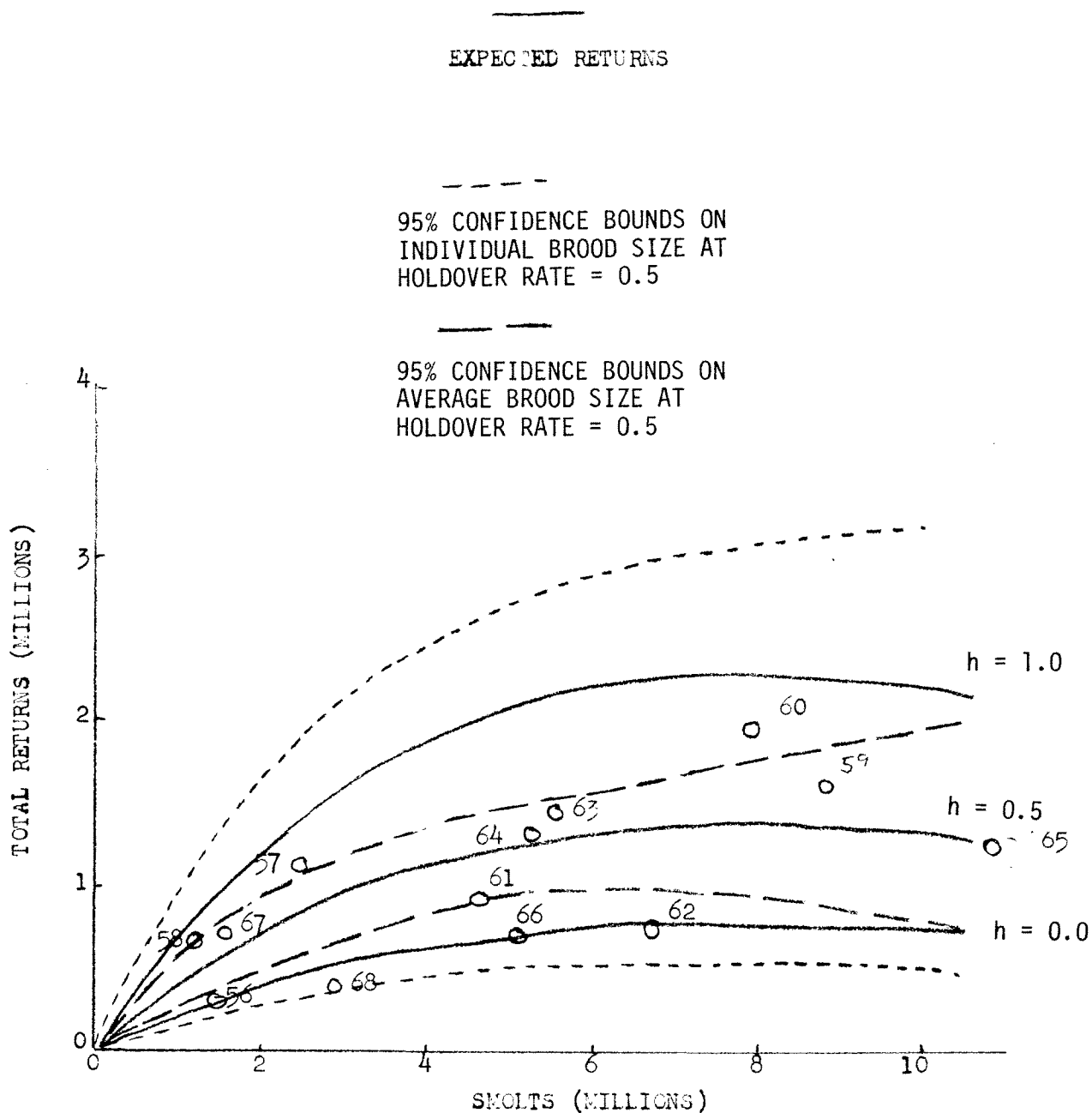
Figure 37.--Relationship between numbers of age II smolts and total returns from them--Naknek system. (Brood years and expected returns at three levels of duration of ocean residence (h) are indicated by lines: h = 0.0, all fish mature after 2 years; h = 0.5, 50% of fish mature after 2 years and 50% mature after 3 years; h = 1.0, all fish mature after 3 years.)

eliminated by counting smolts. The resultant increase in the precision of forecasting can be roughly assessed. Underlying variation in logarithm-transformed survival from egg to adult consists of two additive components-- freshwater and marine variation--assuming independence of random survival variations in the two environments for any brood. Regression analysis of survival from egg to total return produced the following estimates of underlying variation: Naknek, 0.23802; Ugashik, 0.90069 (Tables 34 and 35). Regression analysis of freshwater survival produced the following estimates of underlying variation: Naknek, 0.15915; Ugashik, 0.53376 (Tables 25 and 26). Therefore, the percentage of total variation in survival accounted for by the freshwater phase is estimated to be 67% and 59% for the Naknek and Ugashik systems, respectively. If inshore returns are used in place of total returns, the percentages decline to 61% and 56% for the Naknek and Ugashik systems, respectively. We can eliminate slightly more than half of the error variance in forecasts by counting smolts; however, immense variation remains.

To predict total returns from a group of smolts, the freshwater age and the numbers are valuable. Although marine survival probably depends on duration of ocean residence, the relationships are too imprecisely known to quantify the effect. Except for age II smolts of the Naknek system, marine survival is probably independent of initial numbers. Forecasting of total returns can be done by use of estimated relationships between total returns and numbers of smolts migrating from the streams. Such relationships based on lognormal variation in numbers of survivors are illustrated together with corresponding 95% confidence bounds for individual returns (Figures 37 through 40). Forecast total returns must be allocated to ocean age to make season forecasts. Parent and progeny ocean age composition are correlated (Table 21) and such relationships could be used (Figure 41). Confidence bounds for specific numbers returning from a given group at a given ocean age would be considerably broader than those obtained by applying the forecast ocean age proportion to the confidence bounds for total returns. The unexplained variation in marine survival is so great that the exercise of computing the actual and broader confidence bounds for returns by ocean age from numbers of smolts and ocean age composition of parents is futile; the range of forecasts would be of little value to management or industry.

Some attempt to explain the variation in marine survival beyond this study must be made if we are to forecast returns to either of these river systems with useful accuracy. If the low correlations for estimates of marine survival among groups of smolts migrating to sea in the same year reflect actual correlations of marine survival (Figures 29 and 30), substantial improvement in forecast accuracy for individual river systems by use of physical environmental measures appears improbable. Seemingly, the environment must be monitored as the smolts progress along their migration route on time and spatial scales of much finer resolution than in the past. Managers of such a program would need to select parameters for measurement in anticipation of their merit for explaining survival. Inclusion of important variables for measurement in the program is problematical; quantification of underlying relationships of the variables to survival would depend on substantial data accumulations, requiring long-term execution of the program before realizing the benefits.

An alternative program based on hatchery-reared pink salmon fry as survival indicators for sockeye salmon smolts may become feasible. Pink salmon, as
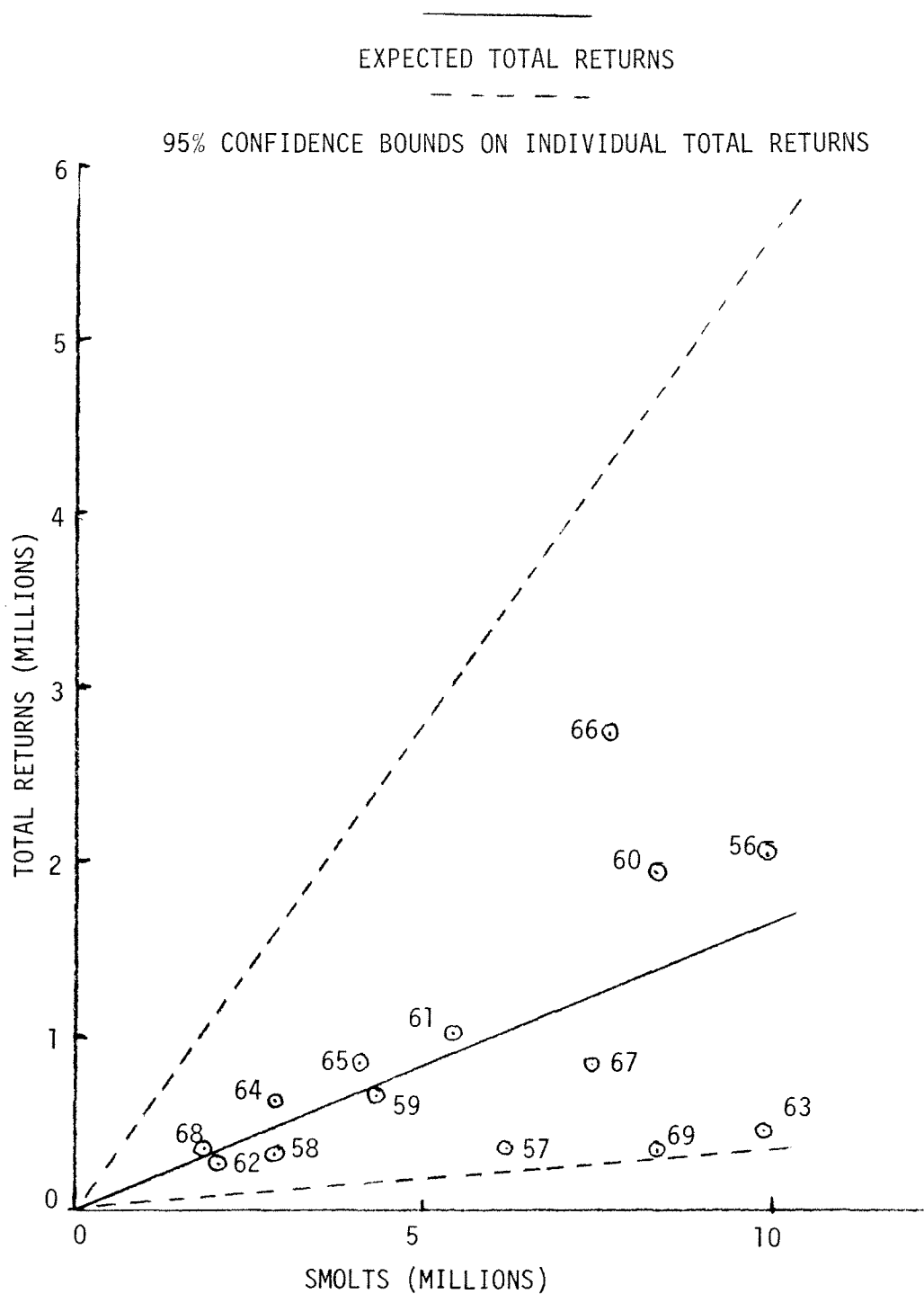
Figure 38.--Relationship between number of age I smolts and total returns from them--Naknek system. (Brood years are indicated.)
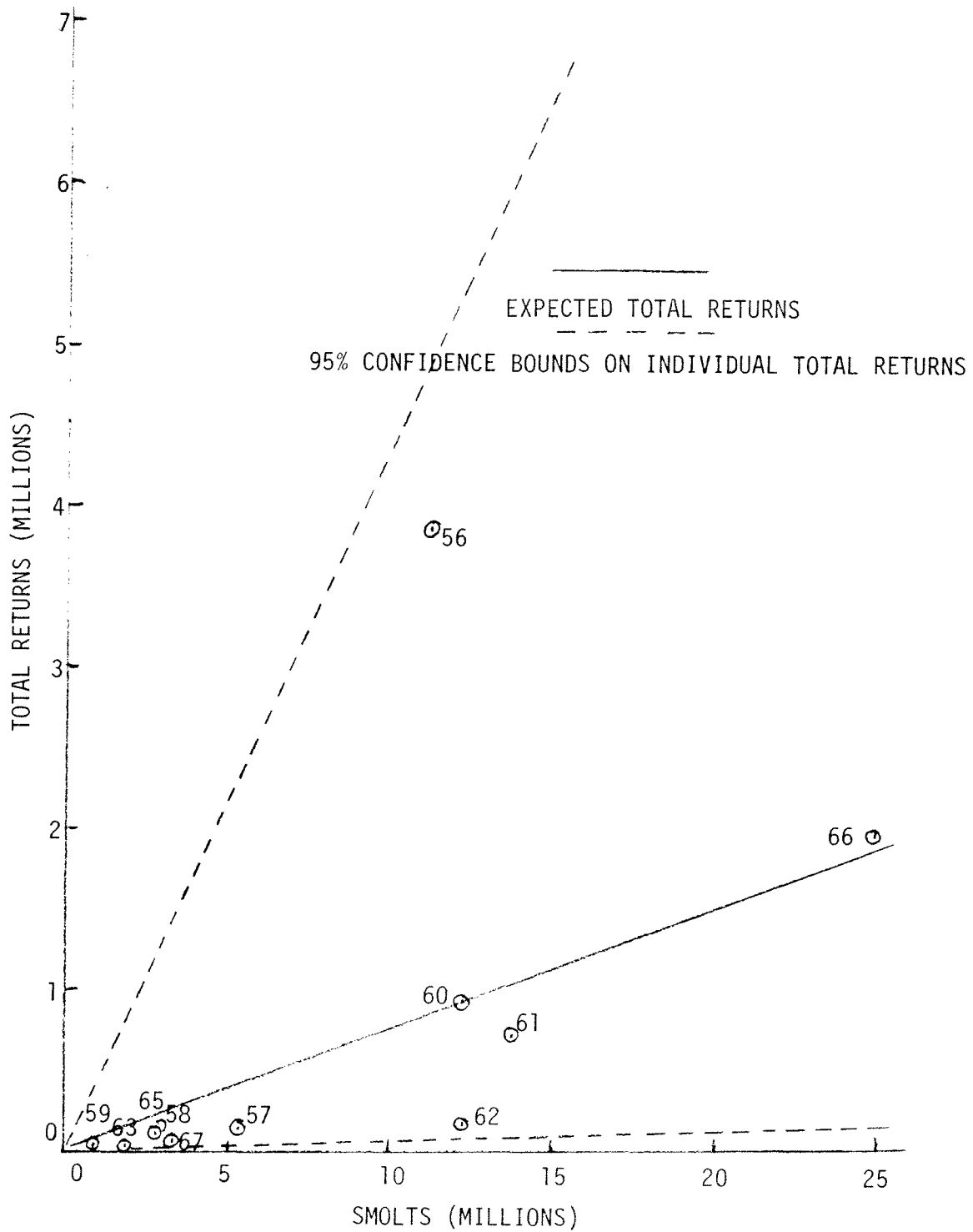
Figure 39.--Relationship between number of age I smolts and total returns from them--Ugashik system. (Brood years are indicated.)
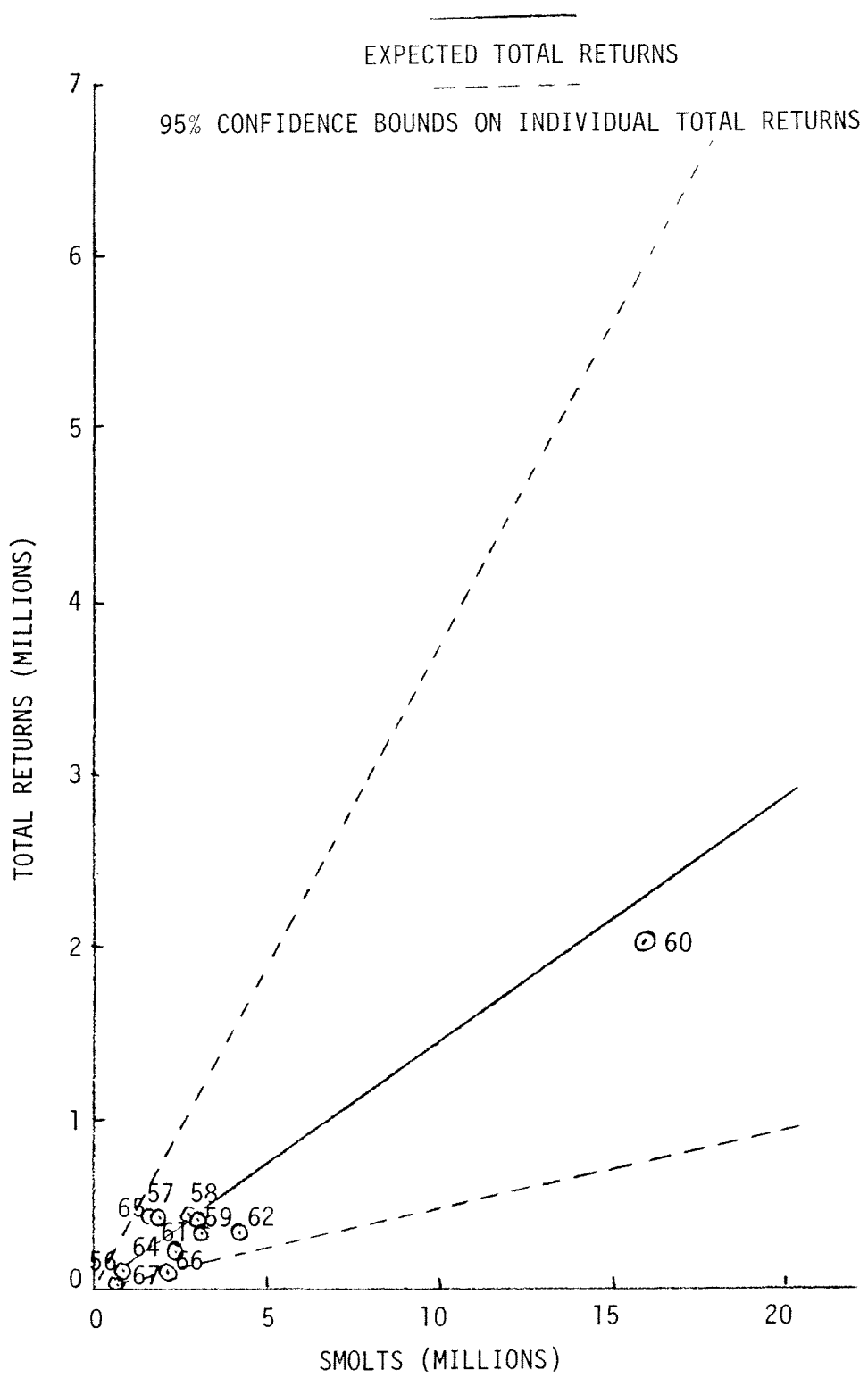
Figure 40.--Relationship between number of age II smolts and total returns from them--Ugashik system. (Brood years are indicated.)
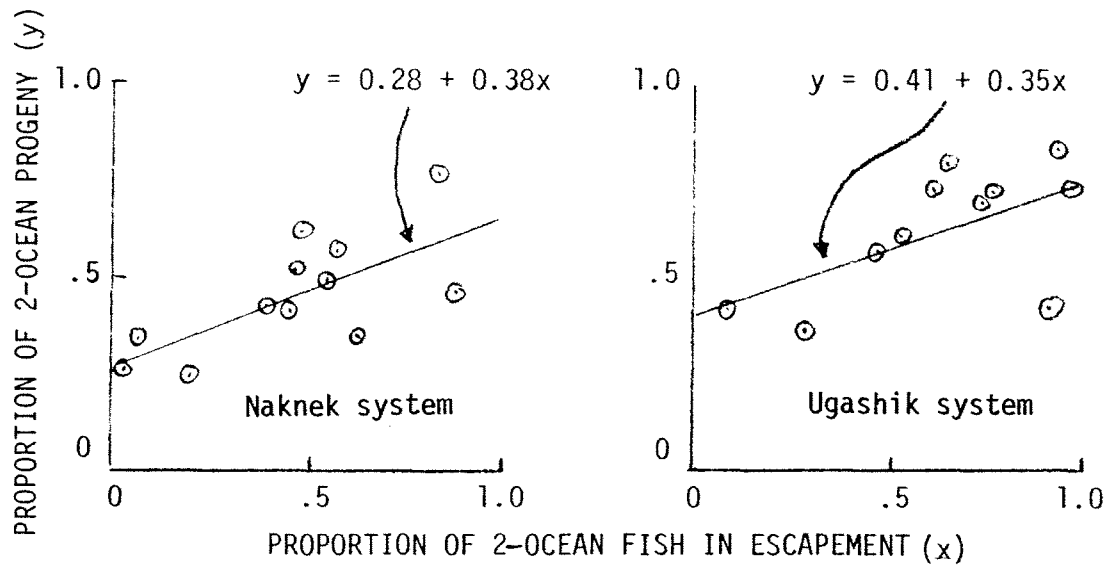
Figure 41.--Proportion of parents and progeny which spent 2 years at sea in Naknek and Ugashik systems. (Brood years and least squares linear relationship are shown.)

well as chum (Oncorhynchus keta) and silver salmon (O. kisutch), are suspected of migrating along roughly the same route within Bristol Bay as sockeye salmon smolts (Straty and Jaenicke 1971). Pink salmon feed on at least some plankton organisms in common with sockeye smolts and avoid other organisms shunned by sockeye salmon (Straty and Jaenicke 1971). The adults would return a year in advance of the 2-ocean sockeye and two years before the 3-ocean sockeye, possibly providing early measure of estuarine conditions the preceding spring.

SUMMARY

As part of an effort to obtain information on which to base management and forecasting of sockeye salmon in the Bristol Bay region of Alaska, the National Marine Fisheries Service began in the late 1950's long-term studies of the stocks of two river systems--Naknek and Ugashik. These systems, each supporting substantial populations of sockeye salmon, lie on the Alaska Peninsula and enter the eastern side of Bristol Bay about 150 km apart. The Naknek system is the larger, 790 km^2 compared to the 385 km^2 of the Ugashik system, and the more complex, seven basins to the two of the Ugashik system.

Sockeye salmon of either of these systems nearly all spend 1 or 2 yr in fresh water, age I and age II, respectively; and 2 or 3 yr in the ocean (2-ocean or 3-ocean, respectively). Therefore, four specific age types predominate--4_2, 5_2, 5_3, and 6_3--corresponding to the four possible combinations.

As major efforts of the studies, smolt migrations, adult escapements, and catches were monitored. Numbers, size of individuals, and age types were recorded as well as sex of adults. When such information is joined with that on fecundity, histories of freshwater and marine survival rates and age and size compositions of broods are obtained. Our study reviews and refines much of the basic monitoring information and then synthesizes the findings, particularly as they reflect on production and forecasting of sockeye salmon.

The first three sections deal with spawnings, smolt migrations, and returning adults. Fecundity samples are examined first with an eye to their use in estimating potential egg deposition; however, these fecundity analyses are important in their own right in establishing the first of many differences in basic population parameters between stocks of these systems. Analyses of covariance of fecundity-length relationships reveal the following: (1) variation in these relationships occurs among years of return for Ugashik females, at least for 2-ocean females; such variation cannot be detected for Naknek females; (2) 2-ocean Naknek females have greater fecundity at a given length than 3-ocean females; such a difference between ocean ages is not evident for Ugashik females; and (3) average fecundity of Ugashik females exceeds that of Naknek females over the most common lengths.

Fecundity-length relationships estimated are next used with the estimates of numbers, length, age, and sex compositon of escapements to compute potential egg deposition in either system for the years 1956 to 1969, inclusive. For the Naknek system these estimates ranged over eightfold from 450 million to 3,610 million eggs. On the other hand, Ugashik potential egg deposition ranged over 28-fold from 155 million to 4,488 million eggs. The 14-yr average in the Naknek system was 1,877 million, about 1.65-fold the corresponding average

of 1,139 million in the Ugashik system. On the other hand, average egg deposition per spawner, disregarding sex, in the Ugashik system exceeded that of the Naknek by about 1.2-fold. The Ugashik system's advantage occurs for several reasons: (1) Ugashik females tend to have more eggs than Naknek females of the same length; (2) average length of Ugashik females is nearly always greater than Naknek females in the same year of return; and (3) the proportions of females in Ugashik escapements averaged higher than in Naknek escapements.

Smolt migrations were monitored for numbers, age, and size. Migrations are partitioned by days, time within days, and river width since smolt numbers are known to vary tremendously within these classifications. Lattice samples of these three-dimensional strata and ratio estimation to expand lattice estimates for incomplete coverage of time and width are used to estimate total migrations and characteristics of the migrations--freshwater age composition, length, and weight.

Average smolt migration from the Naknek system over 15 yr is 10.5 million; in the Ugashik, the average for 12 yr adequately monitored is 10.8 million. Variation of migrations is much greater in the Ugashik system, ranging over 22-fold from 1.3 million to 29.5 million smolts; in the Naknek, the corresponding range is less than 6-fold, from 3.4 million to 18.6 million smolts.

Next, the information from monitoring programs of adult sockeye salmon in catch and escapements is considered in order to estimate returns from the smolt migrations.

Adult sockeye salmon of eastern Bristol Bay originate from the Kvichak, Alagnak, Naknek, Egegik, and Ugashik rivers. Associated with these rivers are three catch districts: Naknek-Kvichak, Egegik, and Ugashik. In order to evaluate ocean survival, catches of these districts must be assigned to the river of origin. Previous tagging studies demonstrate some mixing of eastern stocks in eastern catch districts. However, under the interpretation given these results by others, Ugashik and Egegik stocks would be caught in their respective districts with negligible interceptions elsewhere. Kvichak, Alagnak, and Naknek stocks would be mixed in the Naknek-Kvichak district; previous analyses allocated catches in this district to river of origin in proportion to their abundance in escapements to the three rivers.

An attempt is made in this study to quantify the mixing problem, using catch and escapement information of the monitoring program. A mathematical representation of the escapement, fishing, and sampling processes is developed. The model contains fourteen parameters, including encounter rate coefficients (quantifying for each stock--Naknek, Kvichak-Alagnak, Egegik, and Ugashik--the probability a member encounters gear), mixing coefficients (quantifying probability that a salmon caught from a specific stock was taken in a particular district), and selection ogive parameters (quantifying the selective properties of gill nets). The model is fitted by generalized least squares to the catch and escapement information. Fittings are computed both with and without statistical weighting to account for stochastic error, and solutions are both restricted and unrestricted. Numerical estimates of parameters indicate: (1) Egegik and Ugashik stocks usually were more likely to encounter gear than Kvichak and Naknek stocks in the years examined;

and (2) greater proportions of Egegik and Ugashik stocks stray than do Naknek or Kvichak stocks. In terms of absolute numbers, however, straying may be greater in the other systems, particularly the large Kvichak stock. The findings are viewed circumspectly because of difficulties encountered in fitting the data and sometimes widely varying estimates under differing fitting approaches. Results are not considered sufficiently reliable to allocate catches to river of origin. Allocations from previous studies are used in subsequent analyses of ocean survival. These allocations do agree with the first of the previous conclusions; Egegik and Ugashik stocks were generally exploited at a higher rate than Kvichak and Naknek stocks.

Having reviewed piecemeal the basic information from the monitoring programs, we begin our synthesis. Historical time series of numbers and age compositions of escapements, smolt production, and adult returns are discussed at length in view of certain quasi-regular recurrent variations evident in most. Temporal regularity in magnitude of numbers escaping is indicated in either system. Local maxima occur in 1959 and each 5 yr thereafter in the Naknek system; in the Ugashik system a similar sequence lags that of the Naknek by 1 yr. Freshwater and ocean age compositions of spawners in the two systems vary in synchrony. In addition, ocean age compositions of spawners of either system have recurrent minima in the proportions of 2-ocean fish at 5-yr intervals--1961, 1966, and 1971.

Estimated smolt production from the Ugashik system peaked in the broods of 1960 and 1966; these maxima are reflected in total returns, i.e., inshore returns and Japanese high seas catch of the broods. Estimated smolt production from the Naknek system peaked in 1960, 1963, and 1965; only the 1960 peak is clearly reflected in the total returns.

Age composition at the smolt stage is estimated both from smolt migration estimates and their age compositions and from estimates of total returns and their age compositions. Holdover rate is the proportion of individuals of a brood which migrate to the ocean at ages greater than the one-year-olds, the earliest migrants.

Holdover rates estimated from smolt sampling vary in good agreement with corresponding values from total returns in the Ugashik system but not in the Naknek. Comparing systems, holdover rates based on total returns are in closer agreement among broods than those from smolt sampling. Temporal regularity in holdover rates from total returns are evident in either system; minima occur at 5-yr intervals--1956, 1961, and 1966. Holdover rates based on smolt sampling are consistent with this recurrent variation in the Ugashik system but not in the Naknek. The discrepancy in the Naknek system occurs either because of sampling errors in smolt migration estimates or variations in ocean survival rates--which is responsible is not known.

Ocean age compositions of total returns from broods show temporal regularities. Proportions of Naknek broods returning as 2-ocean fish have recurrent minima at 5-yr intervals for 1956, 1961, and 1966 broods. Corresponding proportions in the Ugashik system were locally minimal in 1961 and 1966; however, the 1956 Ugashik brood had a high proportion in contrast to the same brood from the Naknek system. Although similarities in the time series of these proportions are evident between systems, the series are not closely correlated.

Average weights of smolts of the two major freshwater ages from the Naknek system vary in good accord with year of seaward migration. Weights of age I and age II smolts migrating in the same year are more positively related than those of the same brood migrating in different years. Variations in size of Naknek smolts are probably primarily due to environment in the lakes immediately preceding the spring migration; previous studies show much of annual variation in size to occur at this time.

In the Ugashik system, average weights of age I smolts vary little and these smolts are small as compared to their Naknek counterparts. Average weights of age II Ugashik smolts are variable and comparable in size to age II Naknek smolts. Nonetheless, weights of age I and age II migrants from the Ugashik system in the same year of migration are positively related, although so are those of the same brood which migrate in different years.

Average weights of either age I or age II smolts from the Naknek and Ugashik systems migrating in the same year are not correlated. Therefore, if environmental influences are responsible for variations in Ugashik smolt size, these factors either are not common to or exert different influences on freshwater growth in the two systems. Local influences induced by varying numbers of young sockeye salmon in the lakes seem unimportant to growth in either system. Ugashik smolts migrate earlier than Naknek smolts and probably fail to realize much early springtime growth in lakes; such may account for the small size of the age I smolts. Local differences in lacustrine springtime growing conditions between systems, and especially differences in migration times of smolts of the two stocks, probably account for the poor correspondence in average weights of Naknek and Ugashik smolts.

Age compositions of parent and progeny generations are compared next to ascertain rules of age inheritance if a genetic basis exists. Among the four major age types, only proportions of 5_2 fish of parent and progeny generations are significantly correlated, and this relationship is positive as expected if age is inherited. The sample correlation coefficients from 5_3 fish, although not statistically significant, are also positive but not as large in either system. The sample correlation coefficients are negative in either system for 6_3 fish as well as for 4_2 fish of the Naknek system; these ages do not seem heritable.

Freshwater age composition, disregarding ocean age, and ocean age composition, disregarding freshwater age, are compared between generations. Both freshwater and ocean age compositions of progeny of either system appear related to ocean age compositon of parents, but weakly related, if at all, to their parents' freshwater age composition. If a genetic basis exists, 2-ocean parents tend to produce 5_3 progeny, and 3-ocean parents tend to produce 5_2 progeny.

Partial correlation analyses are used to determine the direction of influence, if any, of freshwater growth on duration of residence in either fresh water or the ocean. Parent age compositons are held fixed in the analysis. Freshwater duration is measured by the holdover rate--the proportion of smolts of a brood which migrate seaward at age II or later rather than age I. Ocean duration is measured by the proportion returning as 2-ocean fish. Freshwater growth is measured as the average weight of smolts of either age group at migration. Testing of statistical significance of sample coefficients is

not attempted. Ugashik computations are repeated using Naknek smolt weights based on the rationale that these may better reflect variation in springtime growing conditions.

The direction of any relationship between holdover rate and weight of age I migrants differs between systems, but when Naknek smolt weights are substituted for Ugashik weights, the direction agrees. If the general climate of Bristol Bay influences the holdover rate in both systems similarly, it probably does so before the early spring growth occurs. If so, duration of freshwater residence increases with factors associated with later improved growth conditions.

If duration of ocean residence is influenced by weight of smolts, the association is closest for Naknek smolts and negligible for Ugashik smolts. When Naknek smolt weights are used in place of Ugashik ones, the direction and degrees of the relationships are in better accord among age groups and systems. If affected, average stay in the ocean declines when springtime growing conditions are favorable, as anticipated.

Estimates of potential egg deposition and numbers of smolts are used to estimate freshwater survival rates. Freshwater survival rates from potential egg deposition to smolt averaged higher, over 1.5-fold, but varied more in the Ugashik than the Naknek system. In the Naknek system the survival rates averaged 0.007 over a 14-yr period, ranging from less than 0.003 to more than 0.014. In the Ugashik system, the average for the 10 yr available is 0.012, and the range is from less than 0.002 to more than 0.033.

Potential sources of variation in freshwater survival rates among broods in either system are both average length of freshwater residence and density-related factors. Regression analyses of logarithm-transformed survival rates on potential egg deposition and holdover rate are performed. Only potential egg deposition in the Naknek system is statistically significant, explaining about 48% of survival rate variations. Survival rate decreases with potential egg deposition. In the Ugashik system, the relationship is also inverse, but explains only about 19% of the variations. Holdover rate is without merit in explaining variations of freshwater survival rates in the Naknek system; but in the Ugashik it explains an additional 16% beyond that accounted for by potential egg deposition. In the Ugashik system the survival rate is estimated to decline with increasing length of stay of broods.

Annual variations in freshwater survival rates of Naknek and Ugashik broods are not related. The sample partial correlation coefficient between logarithms of paired freshwater survival rates of 10 broods from these systems is negative. Variables included in addition to survival rates are potential egg deposition in either system and holdover rate in the Ugashik system. If the general climate of Bristol Bay influenced freshwater survival rates, other factors affecting survival and acting independently between systems conceal the effect.

Ocean survival rates are estimated from estimates of smolt migrations and total adult returns from these migrations. Total adult returns include some immature fish caught on the high seas which would not have survived to the inshore spawning run. Ocean brood survival of smolts of all freshwater ages combined has varied over twofold from 0.12 to 0.27 for the Naknek system;

Ugashik smolts have experienced over ninefold variation, from less than 0.04 to nearly 0.34. Ocean survival of age I smolts has averaged 0.16 in the Naknek system and 0.08 in the Ugashik. Survival of age II smolts has averaged 0.26 in the Naknek system and 0.14 in the Ugashik. On the average, Naknek smolts of either age survive roughly twice as well as their Ugashik counterparts, assuming the mixing of stocks in catch districts does not seriously bias survival estimates.

Average ocean survival of age II smolts is 1.6-fold that of age I smolts in the Naknek system; in the Ugashik, the corresponding ratio is 1.8. Presumably their greater size is responsible for some of the advantage enjoyed by the older smolts. However, among broods of either age group of each system, no improvement in survival with increasing average size is visible. Size variations among broods must be unimportant compared to other factors.

Duration of ocean residence and initial numbers are examined by regression analysis again for their possible influence on ocean mortality; each freshwater age group of either system is analyzed separately. Both initial numbers and duration of ocean residence are statistically significant in explaining variation in ocean survival of age II Naknek smolts. Survival of these smolts declines with increase in either factor. Initial numbers accounts for 39% of total variation in logarithms of the survival rates; duration of ocean residence explains an additional 20%. Apparently competition, probably for food within Bristol Bay, occurs among cohorts of these smolts.

Neither initial numbers nor duration of ocean residence is statistically significant in explaining ocean survival of the other smolts--age I Naknek smolts and age I and age II Ugashik smolts. Although not significant, duration of ocean residence explains substantial parts of variation in ocean survival of these groups, but initial numbers certainly does not.

Large-scale oceanographic conditions may be responsible for variations in ocean survival. If so, survival rates of cohorts of smolts migrating to sea in the same year should vary in accord. Four cases are considered: (1) Naknek and Ugashik smolts of age I; (2) Naknek and Ugashik smolts of age II; (3) Naknek age I and age II smolts; and (4) Ugashik age I and age II smolts. Correspondence between survival rates is positive in all cases but statistically significant in only one case--Ugashik age I and age II smolts. Ugashik smolts migrate to sea over a shorter time interval than Naknek smolts. Possibly this timing is partially responsible for the observed correspondence. Although the correspondence between Naknek and Ugashik smolts of either age is not statistically significant, time series of survival estimates for either age, especially age I, are evocative of a positive association. Further, the survival rates for age I smolts seem to vary regularly with minima at 6-year intervals. If so, this quasi-periodicity would agree with a similar phenomenon in ocean temperatures.

Survival rates from potential egg deposition to returning adult are examined by regression analysis. In this analysis smolt information is omitted. Survival rate declines detectably with potential egg deposition in the Naknek system but not in the Ugashik.

Production estimates are derived from the survival analyses. Estimated relationships of average survival rate between life stages are transformed to

obtain expected survivors. These functions allow determination of optimal numbers of eggs or smolts to maximize surplus production of adults available to the fishery. Such production functions relating total returns--inshore returns and high seas catches--and potential egg deposition are biased upwards; the high seas catches include immature fish, some of which would not survive to return as adults. Estimates of production are reevaluated using inshore returns. Either analysis would be affected by mixing of eastern stocks in eastern catch districts because of resulting errors in estimates on inshore returns to river of origin. Therefore management recommendations are considered in light of production functions relating smolt and potential egg deposition.

To summarize the production analyses we survey critical values associated with maximum production and maximum surplus production. These values are computed for either system for three cases: (1) potential egg deposition to total returns, (2) potential egg deposition to inshore returns, and (3) potential egg deposition to smolts. In the Naknek system, critical values obtained from these cases are in good agreement. Maximum production is estimated to occur at 2,250 to 2,500 million eggs or 1.2 to 1.3 million spawners, depending on the case considered. Maximum surplus production is estimated to occur at 1,500 to 1,750 million eggs or 0.8 to 0.9 million spawners. When total returns are used, maximum production is 2.4 million and maximum surplus production is 1.4 million; when inshore returns are used the values are 2.0 million and 1.1 million, slightly lower as expected.

In the Ugashik system, results do not agree as well among the cases analyzed. Production functions are determined with low precision there because of greater variation in freshwater survival rates and the concentration of observed escapements at low levels with only one or two at higher levels. Maximum production is estimated to occur at 3,000 million eggs or greater, equivalent to 1.3 million spawners or more. Maximum surplus production is estimated to occur at 2,250 million to 3,250 million eggs or 1.0 million to 1.4 million spawners, depending on the case considered. When total returns are used, maximum production is greater than 2.8 million and maximum surplus production is 1.2 million; when inshore returns are used, the values are greater than 2.7 million and equal to 1.0 million, respectively.

Forecasting of adult returns is inaccurate because of unexplained variation in survival and maturity scheules. Slightly more than half of the error variance in forecasts can be eliminated by enumeration of smolts; however, so much variation in survival in the marine phase remains, not even counting variation in maturity schedule, that the range of forecasts included in a confidence statement of a forecast would be of little value to management or industry. Use of releases of hatchery-reared pink salmon fry to monitor sockeye salmon ocean survival is suggested as a promising direction for improving accuracy of river system forecasts beyond smolt enumerations.

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FOOTNOTES

[1]Northwest and Alaska Fisheries Center Auke Bay Laboratory, National Marine Fisheries Service, NOAA, Auke Bay, AK 99821.

[2]Deceased July 1, 1973.

Appendix Table 1.--Stock encounter rate coefficients from weighted restricted fitting and standard errors of estimates, high-mixing initial guess in four river systems.

Year	Naknek	Kvichak	Egegik	Ugashik
1958	0.511(0.082)	0.579(0.032)	0.562(0.097)	0.635(0.033)
1959	0.509(0.045)	0.441(0.089)	0.417(0.089)	0.633(0.081)
1960	0.633(0.112)	0.621(0.075)	0.547(0.074)	0.577(0.211)
1961	0.076(1.391)	0.697(0.049)	0.853(0.033)	0.860(0.038)
1962	0.055(0.134)	0.436(0.030)	0.496(0.047)	0.541(0.080)
1963	0.566(0.033)	0.450(0.055)	0.337(0.053)	0.340(0.069)
1964	0.500(0.070)	0.650(0.032)	0.583(0.026)	0.664(0.048)
1966	0.096(0.169)	0.411(0.042)	0.867(0.009)	0.708(0.026)
1967	0.025(0.214)	0.415(0.030)	0.728(0.027)	0.681(0.055)
1968	0.399(0.053)	0.266(0.023)	0.679(0.034)	0.653(0.162)
1969	0.476(0.039)	0.490(0.010)	0.542(0.032)	0.401(0.373)

Appendix Table 2.--Selection ogive parameters from weighted restricted fitting and standard errors of estimates, high-mixing initial guess.

Year	μ	σ
1958	499.3(4.993)	21.15(6.737)
1959	496.1(1.613)	26.66(2.801)
1960	493.0(3.438)	26.67(3.576)
1961	498.9(3.373)	25.76(5.223)
1962	496.3(3.165)	13.10(4.448)
1963	495.5(3.661)	30.93(6.065)
1964	486.4(4.830)	22.12(2.099)
1966	488.2(3.439)	23.10(3.785)
1967	500.1(3.433)	27.43(4.703)
1968	495.4(1.929)	18.32(2.336)
1969	495.5(0.792)	28.04(1.618)

Appendix Table 3.--Mixing coefficients from weighted restricted fitting and standard errors of estimates, high-mixing initial guess, in three fishing districts.

Year and river	Naknek-Kvichak	Egegik	Ugashik
1958			
Naknek	0.706(0.112)	0.119(0.075)	0.175(0.104)
Kvichak	0.723(0.053)	0.212(0.041)	0.065(0.042)
Egegik	0.000(0.196)	0.759(0.198)	0.241(0.128)
Ugashik	0.237(0.053)	0.091(0.046)	0.672(0.066)
1959			
Naknek	0.552(0.065)	0.219(0.033)	0.229(0.034)
Kvichak	0.479(0.139)	0.263(0.071)	0.258(0.070)
Egegik	0.000(0.292)	0.571(0.170)	0.429(0.126)
Ugashik	0.492(0.140)	0.232(0.077)	0.276(0.077)
1960			
Naknek	0.858(0.375)	0.101(0.391)	0.041(0.027)
Kvichak	0.966(0.084)	0.000(0.087)	0.034(0.012)
Egegik	0.063(0.281)	0.861(0.289)	0.076(0.073)
Ugashik	0.535(0.416)	0.162(0.506)	0.303(0.208)
1961			
Naknek	0.681(5.314)	0.000(5.001)	0.319(6.206)
Kvichak	0.852(0.020)	0.139(0.020)	0.009(0.004)
Egegik	0.704(0.060)	0.291(0.059)	0.005(0.009)
Ugashik	0.494(0.113)	0.386(0.086)	0.120(0.039)
1962			
Naknek	0.572(0.811)	0.000(0.583)	0.428(1.045)
Kvichak	0.830(0.026)	0.144(0.024)	0.170(0.012)
Egegik	0.597(0.053)	0.363(0.051)	0.040(0.020)
Ugashik	0.411(0.137)	0.086(0.062)	0.503(0.151)
1963			
Naknek	0.679(0.060)	0.244(0.057)	0.077(0.028)
Kvichak	0.910(0.084)	0.000(0.085)	0.090(0.026)
Egegik	0.037(0.136)	0.773(0.122)	0.190(0.052)
Ugashik	0.174(0.135)	0.153(0.049)	0.673(0.067)

Appendix Table 3.--Continued.

Year and river	Naknek-Kvichak	Egegik	Ugashik
1964			
Naknek	0.957(0.103)	0.043(0.085)	0.000(0.054)
Kvichak	0.739(0.053)	0.153(0.049)	0.108(0.026)
Egegik	0.048(0.062)	0.784(0.059)	0.168(0.024)
Ugashik	0.412(0.082)	0.056(0.026)	0.532(0.037)
1966			
Naknek	0.919(0.651)	0.081(0.532)	0.000(0.298)
Kvichak	0.914(0.049)	0.079(0.045)	0.007(0.012)
Egegik	0.565(0.020)	0.423(0.021)	0.012(0.005)
Ugashik	0.496(0.044)	0.209(0.030)	0.295(0.034)
1967			
Naknek	0.860(3.237)	0.000(3.619)	0.140(1.303)
Kvichak	0.822(0.032)	0.139(0.031)	0.039(0.001)
Egegik	0.378(0.056)	0.552(0.053)	0.070(0.013)
Ugashik	0.426(0.108)	0.263(0.076)	0.311(0.071)
1968			
Naknek	0.791(0.082)	0.187(0.078)	0.022(0.014)
Kvichak	0.855(0.027)	0.132(0.026)	0.013(0.005)
Egegik	0.285(0.070)	0.666(0.066)	0.049(0.009)
Ugashik	0.315(0.347)	0.443(0.259)	0.242(0.154)
1969			
Naknek	0.391(0.056)	0.302(0.030)	0.307(0.028)
Kvichak	0.408(0.008)	0.296(0.004)	0.296(0.004)
Egegik	0.372(0.047)	0.380(0.032)	0.248(0.020)
Ugashik	0.000(0.940)	0.475(0.457)	0.525(0.510)

Appendix Table 4.--Stock encounter rate coefficients from weighted restricted fitting and standard errors of estimates, low-mixing initial guess in four river systems.

Year	Naknek	Kvichak	Egegik	Ugashik
1958	0.503(0.087)	0.515(0.041)	0.510(0.122)	0.526(0.055)
1959	0.501(0.043)	0.497(0.072)	0.493(0.058)	0.511(0.113)
1960	0.534(0.157)	0.490(0.087)	0.454(0.335)	0.550(0.150)
1961	0.257(0.902)	0.654(0.055)	0.824(0.043)	0.845(0.042)
1962	0.368(0.060)	0.461(0.027)	0.499(0.044)	0.518(0.084)
1963	0.520(0.036)	0.487(0.042)	0.468(0.032)	0.470(0.043)
1964	0.492(0.081)	0.555(0.057)	0.526(0.037)	0.565(0.085)
1966	0.381(0.110)	0.448(0.050)	0.817(0.021)	0.624(0.058)
1967	0.434(0.060)	0.488(0.019)	0.584(0.046)	0.527(0.089)
1968	0.399(0.052)	0.266(0.023)	0.679(0.033)	0.654(0.053)
1969	0.397(0.128)	0.453(0.024)	0.634(0.048)	0.650(0.183)

Appendix Table 5.--Selection ogive parameters from weighted restricted fitting and standard errors of estimates, low-mixing initial guess.

Year	μ	σ
1958	495.8(8.489)	26.67(11.991)
1959	495.3(2.152)	27.79(3.759)
1960	492.8(4.261)	25.88(3.900)
1961	500.0(3.675)	23.62(5.655)
1962	497.2(2.961)	17.18(4.427)
1963	494.9(3.072)	29.40(4.876)
1964	491.2(2.040)	25.13(3.371)
1966	491.6(4.241)	23.54(5.575)
1967	497.9(2.343)	28.03(3.846)
1968	495.3(1.907)	18.33(2.314)
1969	497.3(2.346)	26.09(3.607)

Appendix Table 6.--Mixing coefficients from weighted restricted fitting, low-mixing initial guess, in three fishing districts.

Year and river	Naknek-Kvichak	Egegik	Ugashik
1958			
Naknek	0.950(0.156)	0.020(0.088)	0.030(0.133)
Kvichak	0.928(0.089)	0.048(0.067)	0.024(0.059)
Egegik	0.000(0.272)	0.950(0.332)	0.050(0.198)
Ugashik	0.069(0.112)	0.036(0.082)	0.895(0.133)
1959			
Naknek	0.948(0.029)	0.025(0.023)	0.027(0.018)
Kvichak	0.952(0.029)	0.025(0.021)	0.023(0.019)
Egegik	0.000(0.197)	0.965(0.191)	0.035(0.031)
Ugashik	0.063(0.357)	0.037(0.186)	0.900(0.393)
1960			
Naknek	0.901(0.525)	0.072(0.529)	0.027(0.034)
Kvichak	0.977(0.101)	0.000(0.105)	0.023(0.016)
Egegik	0.007(0.325)	0.974(0.326)	0.019(0.051)
Ugashik	0.137(0.394)	0.165(0.435)	0.698(0.386)
1961			
Naknek	0.952(1.182)	0.002(1.203)	0.046(0.358)
Kvichak	0.857(0.025)	0.127(0.024)	0.016(0.001)
Egegik	0.701(0.075)	0.291(0.074)	0.008(0.012)
Ugashik	0.487(0.126)	0.390(0.098)	0.123(0.041)
1962			
Naknek	0.969(0.079)	0.000(0.063)	0.031(0.047)
Kvichak	0.920(0.031)	0.062(0.028)	0.018(0.011)
Egegik	0.311(0.095)	0.654(0.093)	0.035(0.019)
Ugashik	0.239(0.207)	0.050(0.090)	0.711(0.221)
1963			
Naknek	0.887(0.087)	0.080(0.079)	0.033(0.042)
Kvichak	0.982(0.076)	0.000(0.072)	0.018(0.024)
Egegik	0.000(0.073)	0.973(0.080)	0.027(0.034)
Ugashik	0.026(0.080)	0.038(0.109)	0.936(0.131)

Appendix Table 6.--Continued.

Year and river	Naknek-Kvichak	Egegik	Ugashik
1964			
Naknek	0.993(0.141)	0.007(0.122)	0.000(0.067)
Kvichak	0.881(0.103)	0.075(0.095)	0.044(0.046)
Egegik	0.028(0.090)	0.910(0.096)	0.062(0.039)
Ugashik	0.190(0.178)	0.042(0.134)	0.768(0.192)
1966			
Naknek	0.997(0.149)	0.000(0.113)	0.003(0.079)
Kvichak	0.953(0.041)	0.032(0.036)	0.015(0.016)
Egegik	0.801(0.030)	0.180(0.029)	0.019(0.011)
Ugashik	0.396(0.124)	0.159(0.056)	0.445(0.010)
1967			
Naknek	0.989(0.094)	0.000(0.091)	0.011(0.023)
Kvichak	0.935(0.019)	0.043(0.019)	0.022(0.000)
Egegik	0.219(0.123)	0.744(0.120)	0.037(0.020)
Ugashik	0.126(0.281)	0.125(0.120)	0.749(0.258)
1968			
Naknek	0.791(0.080)	0.187(0.076)	0.022(0.014)
Kvichak	0.855(0.027)	0.132(0.026)	0.013(0.005)
Egegik	0.285(0.069)	0.666(0.065)	0.049(0.009)
Ugashik	0.320(0.352)	0.440(0.262)	0.240(0.163)
1969			
Naknek	0.983(0.090)	0.000(0.086)	0.017(0.015)
Kvichak	0.959(0.006)	0.022(0.005)	0.019(0.001)
Egegik	0.433(0.104)	0.523(0.098)	0.044(0.009)
Ugashik	0.429(0.470)	0.282(0.345)	0.289(0.189)

Appendix Table 7.--Stock encounter rate coefficients from unweighted restricted fitting, high-mixing initial guess in four river systems.

Year	Naknek	Kvichak	Egegik	Ugashik
1958	0.606	0.579	0.637	0.678
1959	0.533	0.527	0.390	0.614
1960	0.653	0.541	0.436	0.454
1961	0.628	0.671	0.636	0.903
1962	0.104	0.313	0.576	0.838
1963	0.641	0.470	0.325	0.419
1964	0.252	0.698	0.590	0.494
1966	0.507	0.252	0.896	0.705
1967	0.215	0.463	0.646	0.725
1968	0.442	0.261	0.697	0.741
1969	0.453	0.487	0.565	0.239

Appendix Table 8.--Selection ogive parameters from unweighted restricted fitting, high-mixing initial guess.

Year	μ	σ
1958	502.5	21.93
1959	499.3	27.56
1960	487.3	22.77
1961	499.9	18.24
1962	490.1	16.70
1963	497.8	35.16
1964	484.9	24.05
1966	482.4	15.44
1967	507.3	20.17
1968	494.9	24.27
1969	494.7	26.94

Appendix Table 9.--Mixing coefficients from unweighted restricted fitting, high-mixing initial guess, in three fishing districts.

Year and river	Naknek-Kvichak	Egegik	Ugashik
1958			
Naknek	0.688	0.141	0.171
Kvichak	.768	.229	.003
Egegik	.000	.669	.331
Ugashik	.193	.174	.633
1959			
Naknek	.493	.253	.254
Kvichak	.532	.238	.230
Egegik	.001	.562	.437
Ugashik	.490	.216	.294
1960			
Naknek	.710	.225	.065
Kvichak	.848	.072	.080
Egegik	.000	.647	.353
Ugashik	.157	.374	.469
1961			
Naknek	.746	.250	.004
Kvichak	.823	.160	.017
Egegik	.603	.315	.082
Ugashik	.586	.342	.072
1962			
Naknek	.683	.002	.315
Kvichak	.982	.013	.005
Egegik	.570	.374	.056
Ugashik	.591	.226	.183
1963			
Naknek	.548	.416	.036
Kvichak	.862	.000	.138
Egegik	.111	.626	.263
Ugashik	.153	.328	.519
1964			
Naknek	.846	.154	.000
Kvichak	.664	.170	.166
Egegik	.179	.583	.238
Ugashik	.277	.120	.603

Appendix Table 9.--Continued.

Year and river	Naknek-Kvichak	Egegik	Ugashik
1966			
Naknek	0.657	0.266	0.077
Kvichak	.741	.015	.244
Egegik	.579	.384	.037
Ugashik	.486	.289	.225
1967			
Naknek	.662	.023	.315
Kvichak	.707	.175	.118
Egegik	.230	.725	.045
Ugashik	.393	.370	.237
1968			
Naknek	.820	.170	.010
Kvichak	.843	.144	.013
Egegik	.215	.704	.081
Ugashik	.544	.277	.179
1969			
Naknek	.389	.293	.318
Kvichak	.402	.300	.298
Egegik	.367	.386	.247
Ugashik	.001	.402	.596

Appendix Table 10.--Stock encounter rate coefficients from unweighted restricted fitting, low-mixing initial guess in four river systems.

Year	Naknek	Kvichak	Egegik	Ugashik
1958	0.537	0.530	0.553	0.575
1959	0.502	0.502	0.493	0.508
1960	0.528	0.498	0.488	0.496
1961	0.569	0.598	0.558	0.836
1962	0.408	0.460	0.517	0.754
1963	0.521	0.496	0.483	0.487
1964	0.471	0.528	0.513	0.503
1966	0.509	0.455	0.735	0.544
1967	0.475	0.496	0.523	0.532
1968	0.440	0.261	0.697	0.743
1969	0.498	0.499	0.503	0.489

Appendix Table 11.--Selection ogive parameters from unweighted restricted fitting, low-mixing initial guess.

Year	μ	σ
1958	498.2	26.22
1959	495.3	27.99
1960	493.3	26.73
1961	499.4	22.13
1962	494.7	24.27
1963	495.2	29.63
1964	493.7	27.36
1966	493.1	24.82
1967	496.4	27.37
1968	494.8	24.19
1969	495.0	27.95

Appendix Table 12.--Mixing coefficients from unweighted restricted fitting, low-mixing initial guess, in three fishing districts.

Year and river	Naknek-Kvichak	Egegik	Ugashik
1958			
Naknek	0.894	0.046	0.060
Kvichak	.912	.088	.000
Egegik	.006	.851	.143
Ugashik	.104	.090	.806
1959			
Naknek	.946	.027	.027
Kvichak	.952	.024	.024
Egegik	.000	.969	.031
Ugashik	.051	.032	.917
1960			
Naknek	.915	.062	.023
Kvichak	.969	.015	.016
Egegik	.001	.957	.042
Ugashik	.040	.051	.909
1961			
Naknek	.826	.174	.000
Kvichak	.885	.102	.017
Egegik	.329	.595	.076
Ugashik	.554	.332	.114
1962			
Naknek	.989	.000	.011
Kvichak	.945	.026	.029
Egegik	.223	.746	.031
Ugashik	.705	.237	.058
1963			
Naknek	.876	.106	.018
Kvichak	.974	.000	.026
Egegik	.018	.946	.036
Ugashik	.024	.044	.932
1964			
Naknek	.984	.016	.000
Kvichak	.930	.036	.034
Egegik	.046	.913	.041
Ugashik	.021	.031	.948

Appendix Table 12.--Continued.

Year and river	Naknek- Kvichak	Egegik	Ugashik
1966			
Naknek	0.923	0.062	0.015
Kvichak	.979	.000	.021
Egegik	.654	.323	.023
Ugashik	.138	.119	.743
1967			
Naknek	.983	.000	.017
Kvichak	.948	.028	.024
Egegik	.058	.908	.034
Ugashik	.102	.092	.806
1968			
Naknek	.823	.168	.009
Kvichak	.842	.145	.013
Egegik	.213	.706	.081
Ugashik	.547	.273	.180
1969			
Naknek	.951	.024	.025
Kvichak	.950	.025	.025
Egegik	.033	.941	.026
Ugashik	.000	.024	.976