

MARINE GROWTH OF WESTERN ALASKAN SOCKEYE SALMON (*ONCORHYNCHUS NERKA* WALBAUM)

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ABSTRACT

The study is based on weight, length, age and maturity data from individual sockeye salmon (*Oncorhynchus nerka*) taken by gillnets from 1956 through 1960 in the North Pacific Ocean and Bering Sea. Preliminary to estimating growth rates within and between certain marine life history stages, the effects of the following sources of variation are considered: (1) sex, maturity and winters at sea before capture; (2) continent of origin; (3) changes in size between time of capture and time of laboratory processing; (4) use of gillnets known to be selective for size; (5) area of capture; and (6) year of capture.

Seasonal increases in average body weight of Western Alaskan sockeye salmon are found to be 30 percent for 1-winter immatures during 40 days in July-August, 22 percent for 2-winter immatures during 50 days in July-August, 13 percent for 2-winter maturing fish during 40 days in May-July, and 14 percent for 3-winter maturing sockeye salmon during 30 days in May-June.

With average body weight of 1-winter immatures on August 3 as a reference, estimated long-term increases are as follows: 149 percent until July 30 the next year as 2-winter immatures, 247 percent until June 14 the next year as 2-winter maturing sockeye, and 382 percent until June 10 the second year later as 3-winter maturing sockeye. Between July 30 as 2-winter immatures and June 10 the following year as 3-winter maturing fish, average body weight of Western Alaskan sockeye salmon is estimated to increase by 94 percent.

Percentage rates are converted to total and 30-day average instantaneous rates. Also discussed is the need for future research on short-term ocean growth and natural mortality rates of Pacific salmon, particularly as knowledge of these parameters relates to rationality of fishing salmon on the high seas.

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INTRODUCTION

Growth of Pacific salmon (*Oncorhynchus* spp.) during short intervals of their life at sea has seldom been a major concern of management. So long as the stock is exploited only during maturation in inshore waters, focus is on manipulating the return to achieve reasonable balance between escapement and catch, and therefore to attain maximum yield insofar as is practicable. When maturing or immature salmon are also exploited offshore, however, short-term rates of ocean growth and mortality will fix the time and area of harvest that best approximate maximum yield from a given recruitment. Knowledge of both parameters may then become vital to management of the resource.

Parker and Kirkness (1956) and Parker (1960) were the first to publish on this balance between ocean growth and mortality in the salmon. The latter report concludes maximum yield for king salmon (*O. tshawytscha*) at current fishing intensity would be best approximated by abolishing size limits in the troll fishery, by encouraging use of non-selective gear and, through time and area restrictions, by harvesting only maturing fish. In terms of biomass, growth was believed to exceed mortality throughout the life of a brood.

In maturing Asian chum (*O. keta*) and sockeye (*O. nerka*) salmon, Taguchi (1961a, 1961b) investigated rates of growth and mortality from the time of recruit-

ment to a high seas gillnet fishery until inshore appearance of survivors on the spawning migration. That author computed higher rates for natural mortality than for growth. Therefore, he concluded offshore fishing approximates maximum yield more closely than inshore fishing.

On the other hand, Ricker (1962) inferred that oceanic harvest of maturing sockeye would yield from 6 to 40 percent less weight than inshore exploitation of the same North American stocks. Calculated weight loss from offshore fishing the year before maturity was from 50 to 65 percent. For both periods of ocean life, growth was shown to exceed the computed maximum values for natural mortality.

Growth is unquestionably the easier to estimate. Scales, or direct observations on fish size, are available from commercial or research operations at sea or ashore. Yet all methods of using the data raise problems.

In his informative review of life history studies on sockeye salmon of the Far East, Hanamura (MS) notes two causes of difficulty. First, growth differs between segments of a brood maturing in successive years; to presume that annual ocean growth is simply the difference between average size-at-age of spawners, although much data on spawners may be available, is a serious mistake. Secondly, failure to define the relationship between fish length and scale radius from data taken throughout the life span can cause observed and calculated lengths to contradict one another.

In tagging studies, necessarily hurried measurement of live releases (e.g., Parker and Kirkness, 1956; Koo, 1959) or inaccurate measurement of dead recoveries, perhaps by observers not thoroughly trained, can bias estimates of growth. While observations showing larger size at release than at recovery are commonly discarded (e.g., Koo, 1959), accuracy of remaining records is seldom known. Moreover, effects on growth from handling or from the tag itself cannot be examined in direct and simple fashion. These factors mar the intuitive appeal of successive observations on size of individual fish. Finally, the recoveries may be too few to estimate growth rates with high precision.

The present study is based on weight and length data from individual fish. A major part of the study is an effort to account for the following sources of variation: (1) sex, maturity and winters at sea before capture; (2) changes in size between time of capture and time of laboratory processing; (3) area of origin; (4) use of gillnets known to be selective for size; (5)

area of capture; and (6) year of capture.

Background material (Fukuhara *et al.*, 1962) provided means of separating Western Alaskan from Asian sockeye salmon. However, probabilities of misclassifying individual fish taken on the high seas were unknown. Therefore, it was necessary to establish certain criteria for investigating possible size differences by area of origin; if present, such differences could bias estimated growth rates for the target stock. Similarly, the theory of gillnet selection was useful in judging effects of mesh selectivity in present data. Sampling coverage imposed important limitations on evaluating effects of area and annual variations in size.

The type of data, the sources of variation, and the availability of background information led to problems or methods not commonly considered in studies of marine growth in fishes. Solutions given here are not presumed to be final. Rather, the objective is to provide a basic description of growth in weight for sockeye salmon of Western Alaska. A secondary objective is to stimulate further research on short-term ocean growth and mortality of Pacific salmon.

Various research groups at the Bureau of Commercial Fisheries Biological Laboratory, Seattle, Washington, provided data for the present study. The High Seas Salmon Research Unit collected most specimens and supplied fork lengths of fresh fish to investigate the effects of mesh selection. The laboratory of the Morphology Unit procured length, weight and maturity data. The Age Analysis Unit determined ages from scales. Data were punched on cards by the Biometrics Unit, which also provided machine processing.

For stimulating criticism of the manuscript, we wish to thank Drs. R. R. Parker and W. E. Ricker of the Fisheries Research Board of Canada Biological Station at Nanaimo, B. C., and the following scientists at the Bureau of Commercial Fisheries Biological Laboratory at Seattle, Washington: G. Hirschorn, D. D. Worlund, F. M. Fukuhara and H. H. Shippen.

COLLECTION AND PROCESSING OF SPECIMENS

Annual reports of the International North Pacific Fisheries Commission (INPFC, 1957-1961) for the years 1956 through 1960 describe the national source, area and sample size for whole sockeye salmon collected annually for the United States from the North Pacific Ocean and Bering Sea. Capture was by gillnets. Taken primarily for racial studies, these samples are

TABLE 1. Mesh size composition of gillnets used and mean effort of Japanese and United States research vessels and of Japanese commercial vessels for the years 1956 through 1960.

Country and year	Mesh size and average no. of gear units fished ¹ per set										
	2.50"	2.98"	3.25"	3.58"	4.18"	4.50"	4.77"	4.80"	4.89"	5.25"	5.37"
<i>United States research vessels</i>											
1956	3	—	3	—	—	6	—	—	—	6	—
1957	4	—	4	—	—	12	—	—	—	4	—
1958	4	—	4	—	—	12	—	—	—	4	—
1959	4	—	4	—	—	24	—	—	—	4	—
1960	4	—	4	—	—	24	—	—	—	4	—
<i>Japanese research vessels</i>											
1956	—	4	—	4	7	—	92	—	—	—	5
1957	5	—	4	—	—	15	**	—	—	5	—
1958	2	—	2	—	—	6	—	—	40	2	—
1959	4	—	4	—	—	4	—	25	25	4	—
1960	4	—	4	—	—	12	—	60	—	4	—
<i>Japanese commercial vessels</i>											
1956	—	—	—	—	—	—	—	293	—	—	—
1957	—	—	—	—	—	—	—	293	—	—	—
1958	—	—	—	—	—	—	—	293	—	—	—
1959	—	—	—	—	—	—	—	293	—	—	—
1960	—	—	—	—	—	—	—	293	—	—	—

¹ *U. S. research vessels*: Shackles—one shackle is approximately 300 feet in length. *Japanese research vessels*: Tans—one tan is approximately 300 feet in length for 2.50", 3.25", 4.50" and 5.25" meshes; for other mesh sizes it is approximately 180 feet in length. *Japanese commercial vessels*: Tans—one tan of Japanese commercial gear is approximately 180 feet in length.

** Average number of tans fished not available.

the general source of the data used herein. The data are tabulated in basic data tables, a list of which is given on page 31. Interested persons can obtain these basic data tables by writing to the authors at the Seattle Biological Laboratory of the Bureau of Commercial Fisheries (2725 Montlake Boulevard, Seattle, Washington 98102).

Table 1 gives the mesh size composition of gillnets used by year, along with mean effort per vessel of Japanese and United States research vessels and of Japanese commercial vessels. Research sections of the INPFC annual reports provide a more detailed classification by vessel, position and time.

SHIPBOARD PROCEDURES

Gillnetting and data collection procedures aboard United States research vessels changed very little from 1956 through 1960. The sequence of operations was as follows:

- (1) Gillnets were set in the evening and hauled the next morning.
- (2) During hauling, salmon were fin clipped to record direction of entry on capture (in effect after 1958). Blood samples, if requested, were pro-

vided for independent studies from live fish. Fish were then placed in bins according to mesh size of capture.

- (3) Once hauling was completed, each specimen in a catch, up to 250 fish, was saved for shipment to the laboratory. These were selected according to two separate size groups: 125 fish were taken from the large meshes (4½-inch and 5¼-inch), and 125 fish from the small meshes (2½-inch and 3¼-inch). If the total catch in a mesh size grouping exceeded 125, fish were selected randomly in proportion to the catch by mesh size within that grouping. If the total catch in a mesh size grouping was less than 125, then all fish were saved. Selection of whole fish was not influenced by their condition, except that fish without heads or tails were not retained for the laboratory. An identifying tag was placed on fish saved.
- (4) Length from tip of snout to fork of tail was read from a measuring board and recorded, and a scale sample was taken from each fish. Starting in 1960, maturity and sex were also recorded for those fish not sent to the laboratory.
- (5) Fish kept for the laboratory were immediately placed on sharp freezing plates, glazed and put

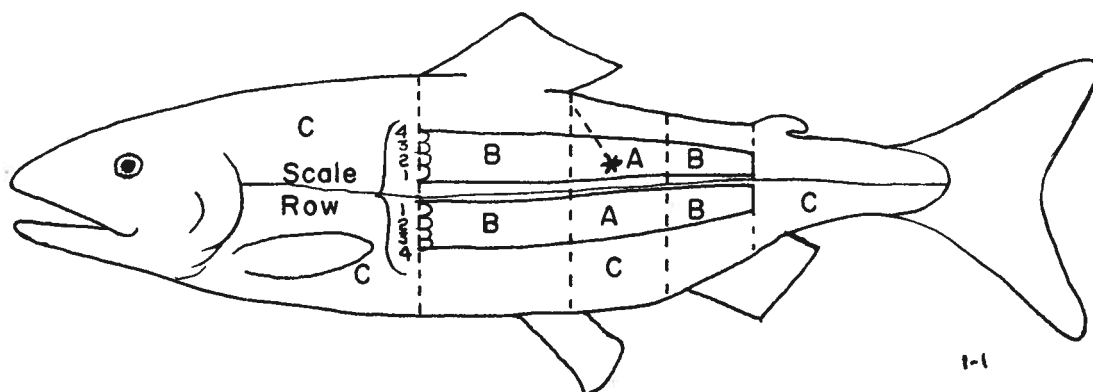


FIGURE 1. Scale sampling code used by agencies of the International North Pacific Fisheries Commission. *Note.* The asterisk denotes the preferred scale, which can be found by following the diagonal scale line from the posterior edge of the dorsal fin to the second scale row above the lateral line. "A" is the preferred area if the preferred scale is missing. "B" is the second choice area if scales in area "A" are missing. "C" areas are all other scales. Scales may be taken from either side of the fish but the left side is preferred.

in plastic bags the next day for later transport to Seattle.

Procedures differed somewhat on Japanese research vessels, but gillnetting operations and handling of whole fish sent to the Bureau of Commercial Fisheries Biological Laboratory, Seattle, Washington, were much the same as on United States research vessels. Whole fish also were collected from predesignated areas and times aboard vessels of Japanese commercial fleets. Here, salmon were tagged with an identification number, frozen, bagged and boxed for eventual shipment to Seattle. Data on fleet name, and on area, date and mesh size of capture accompanied each specimen.

Body weights of fresh fish are limited in this study to 335 records collected by the authors with a spring scale aboard a United States research vessel in 1961. The resulting relationship to weights taken in the laboratory is applied to the years 1956 through 1960.

LABORATORY PROCEDURES

Laboratory procedures for data pertinent to this study likewise changed little from 1956 through 1960. These were as follows:

- (1) *Body weight*—frozen fish, identified by the tags affixed at capture, were thawed approximately five minutes in warm water (70°F. to 80°F.) to remove the glaze. They were next placed on a table to let excess water drip off, then weighed to the nearest dekagram on a calibrated spring scale.
- (2) *Length*—various lengths on thawed fish were taken to the closest millimeter on a calibrated

drum-type machine (Thompson and Hartt, MS).

- (3) *Sex and gonad weight*—visual examination of gonads determined sex. Large or maturing gonads were weighed to the nearest gram on a calibrated beam scale; small or immature gonads, to the nearest 0.1 gram.
- (4) *Age*—the preferred scale, or one from other designated areas of the body if that scale was missing (see Fig. 1), was removed for later definition of freshwater and ocean ages and for recording of certain other data.

Only those fish processed through the laboratory have been considered here. Of the various lengths recorded in the laboratory, we used only the distance in millimeters from tip of snout to fork of tail. To examine effects of net selectivity, we also used fork lengths, as recorded at sea on United States research vessels, of some of the same fish. Winters at sea before capture were the only scale data utilized. Published studies by Godfrey (1961) and by Ishida *et al.* (1961) provided criteria for separating immature and maturing fish. In the present investigation, gonad weights above 2 and 15 grams were taken to represent maturing males and females, respectively.

EFFECTS OF AREA OF ORIGIN

The first problem was to find if sockeye salmon stocks other than the Western Alaskan were represented in the data. If so, and if Western Alaskan fish differed from them in average size, then pooling all data without regard to origin could bias estimates of growth for Western Alaskan fish. Therefore, it was

necessary to test the hypothesis of no difference in average size between origins. This required means of classifying fish in high seas catches by origin. Given acceptable criteria of classification, rejection of the null hypothesis would then require additional means of identifying individual Western Alaskan fish in order to estimate their growth. Of course, acceptance would imply this particular source of variation need not be considered further.

Fukuhara *et al.* (1962) developed a discriminant function that classifies sockeye salmon taken on the high seas as "Western Alaskan" or "Asian". Seven length-independent characters from mature fish of known continental origin were combined into a single function. A value of this function was computed for each fish used to define continental morphotypes. From overlap in the two resulting normal curves, risks of misclassifying Asian fish as Western Alaskan, and vice versa, were computed for each year of sampling. The midpoint between means was taken as a critical point for classifying individuals captured on the high seas.

That study demonstrated intermingling of continental stocks. Percentage estimates of Western Alaskan fish in high seas catches were derived by classifying individuals from the critical point of the discriminator. For the years 1956 through 1960, a later study (Landrum and Dark, MS) showed that risks of misclassification for Asian fish ranged from 24 percent to 37 percent, with an average of 29 percent; risks of misclassification for Western Alaskan fish varied from 18 percent to 24 percent, with an average of 22 percent.

On the average, then, 29 individuals from a catch of 100 would be classified as Western Alaskan if all 100 were actually from Asia; 22 from 100 would be classified as Asian if all 100 were in fact from Western Alaska. The bias in percentage estimates of intermingling is greatest in the case just given—when all individuals in a catch are from one continent. This bias vanishes when approximately one-half of the fish in a catch are from each continent. To account for incomplete separation of original morphotypes, a correction was applied (in the studies cited) to the initial classification of a high seas catch in order to estimate its true continental composition. Had separation of morphotypes been complete, of course, the risk of misclassifying an individual taken on the high seas could then be stated as 0.

Four aspects of the studies cited are of particular interest here: (1) segregation of fish by continental

origin is based on a set of characters which are independent of length, (2) risks of misclassifying individual fish are unknown, (3) average risks of misclassification are 29 and 22 percent for Asian and Western Alaskan fish, respectively, and (4) misclassified individuals increasingly compensate as intermingling increases—until the error vanishes when approximately one-half of the fish in a catch are from each continent.

In testing the hypothesis of no difference in mean size between origins, it was of first importance to group data so as to remove extraneous sources of variation. Sex, maturity and winters at sea before capture were obvious sources. Since discrimination between continents was independent of length, the effects of mesh selectivity should not influence this particular analysis. From cited classifications of individuals taken on the high seas, the present test of size by origin could be performed by using either: (1) all fish in individual catches of "pure" continental origin which were made at the same time, or (2) those fish in individual catches made at the same time but representing nearly equal mixtures of fish from both continents. Of course, combinations of these two alternatives might also be used. To be avoided, however, in view of unknown risks of misclassification for individuals, were those catches which were neither "pure" nor "nearly equal mixtures". Finally, possible bias in the outcome from any (environmental) effects on average size due to area of capture would be more likely in "pure" catches; these are (almost) by definition made in different areas, whereas catches of "nearly equal mixtures" are by definition from the same areas. Were effects of area of capture significant, to admit them as random variation seemed more reasonable than to risk their confounding the required test of differences in average size between areas of origin.

TEST OF THE NULL HYPOTHESIS

Those individuals taken between 160°30'W. longitude and 160°30'E. longitude, and which had all pertinent data on record, were classified by winters at sea before capture, and by sex, maturity, "origin" and 10-day periods, starting in May in each year from 1956 through 1960. Classification by "origin" was according to whether the value computed for an individual fish fell below or above the critical point ($Y_0=69.308$) of the discriminant function (Fukuhara *et al.*, 1962). Figure 2 shows the general area of sampling and, for later reference, its division into 1° rectangles of latitude and longitude. The 10-day periods are defined below:

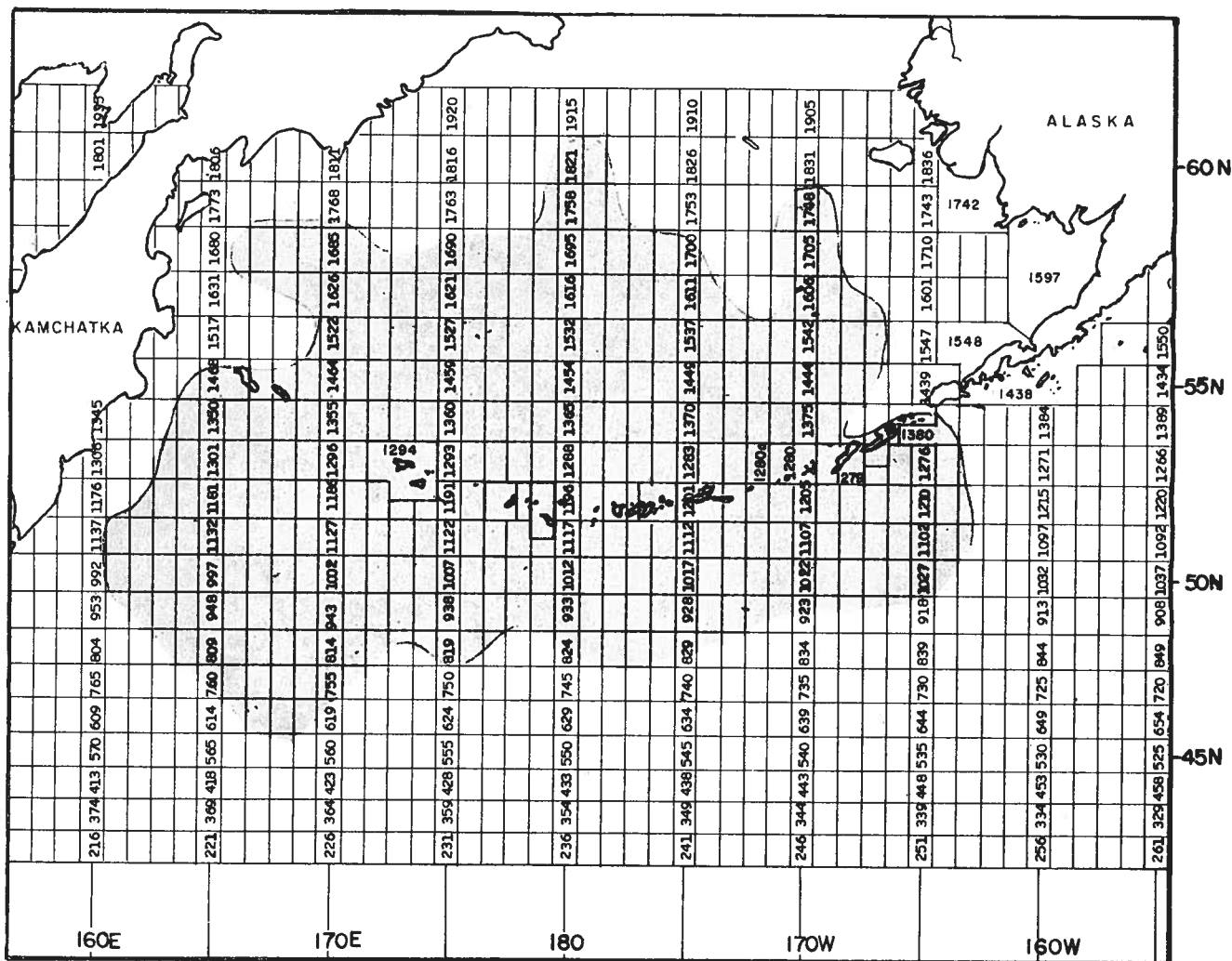


FIGURE 2. High seas statistical areas, $1^{\circ} \times 1^{\circ}$ rectangles. Shaded portion represents general area of sampling.

Period	Inclusive dates
1	May 1 to May 10
2	May 11 to May 20
3	May 21 to May 30
4	May 31 to June 9
5	June 10 to June 19
6	June 20 to June 29
7	June 30 to July 9
8	July 10 to July 19
9	July 20 to July 29
10	July 30 to August 8
11	August 9 to August 18
12	August 19 to August 28

This definition of 10-day periods was arbitrary. As it turned out, the numbers of maturing 1-winter and immature 3-winter fish taken in all periods, and of all ocean ages taken in periods 1 and 2, were too small to warrant analysis here.

Next, study of cruise patterns of the High Seas Research Unit and of results of the classification studies by Fukuhara *et al.* (1962) and Landrum and Dark (MS) showed that few catches of "pure" continental origin were made within a 10-day period. To use data from different 10-day periods would obviously introduce effects of seasonal growth into the test of size by origin. Along with possible effects of area of capture (see page 5), these considerations led us to adopt a criterion of "nearly equal mixtures". Accordingly, only those samples having from 40 percent through 60 percent Western Alaskan individuals were used to test for differences in size by origin. Where representation from a dominant area was desirable from the standpoint of large sample size or to ensure balance between the several life history groups, catches were used from only that area in order to satisfy the 40-60 percent criterion.

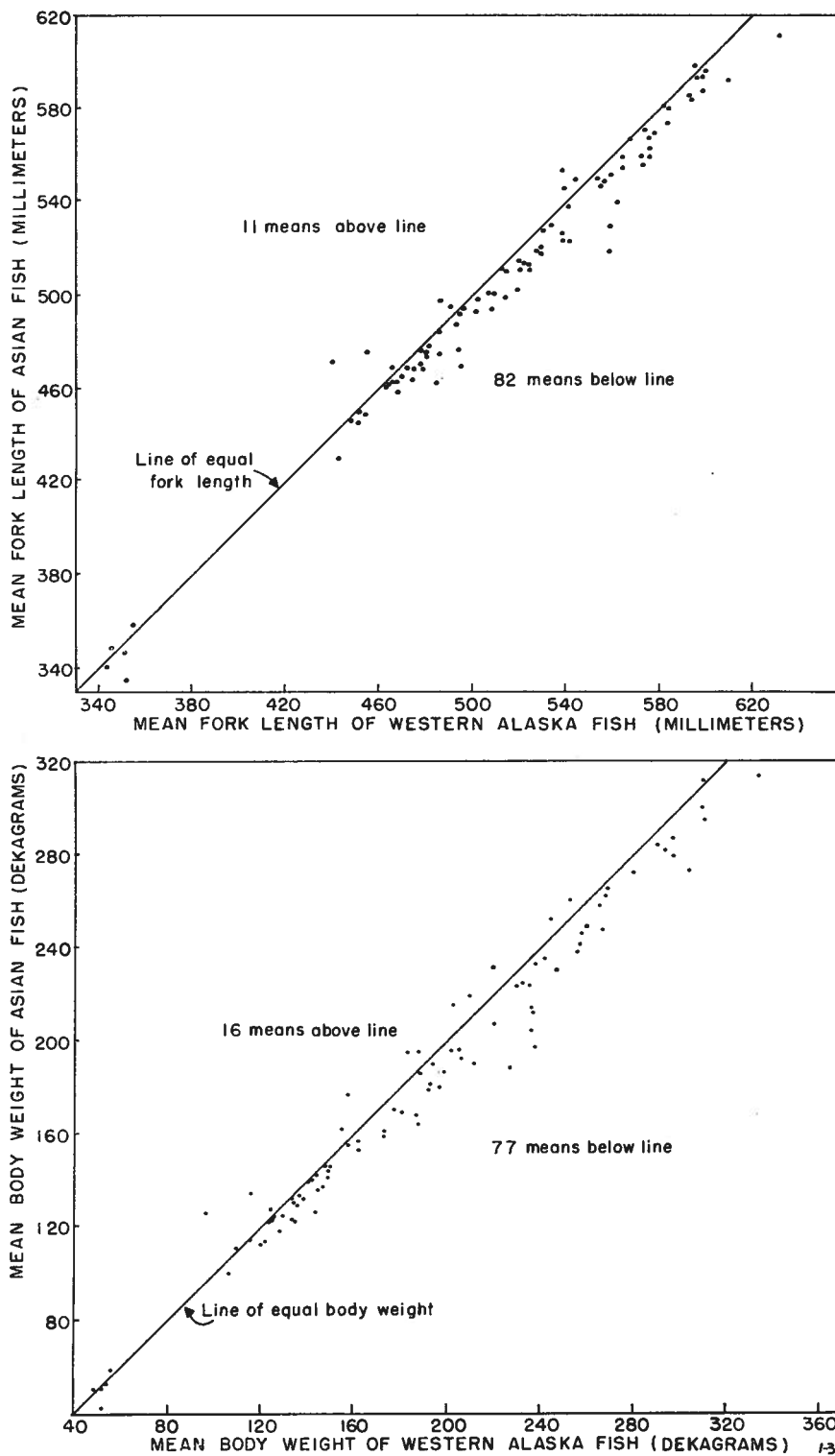


FIGURE 3. Mean length and weight of Asian and Western Alaskan sockeye salmon, relative to line of 1:1 correspondence.

TABLE 2. Test of the hypothesis of no difference in mean fork length between Asian and Western Alaskan sockeye salmon.

Test group number	Life history group ¹	Sample size	Rejection level in i^{th} test (p_i)	$\ln p_i$
1	M-I-2	46	.12	-2.207
2	M-M-2	77	.09	-2.408
3	F-M-2	32	.70	-0.357
4	M-I-2	195	.04	-3.219
5	F-I-2	83	.41	-0.916
6	M-M-3	124	.32	-1.171
7	F-M-3	448	.01	-4.605
8	M-I-1	93	.06	-2.813
9	F-I-1	107	.68	-0.386
10	M-I-2	118	.14	-1.966
11	F-I-2	164	.21	-1.561
12	M-M-3	162	.33	-1.109
13	F-M-3	456	.01	-4.605
14	M-M-2	212	.87	-0.139
15	F-M-2	549	.01	-4.605
16	M-I-2	363	.13	-2.040
17	F-I-2	447	.01	-4.605
18	M-M-3	106	.10	-2.303
19	F-M-3	123	.36	-1.022
20	M-M-2	207	.01	-4.605
21	F-M-2	223	.24	-1.427
22	M-I-2	562	.17	-1.772
23	F-I-2	519	.06	-2.813
24	M-M-3	185	.19	-1.661
25	F-M-3	656	.02	-3.912
Total		6,257		-58.177

$$C = -2 \sum_{i=1}^s \ln p_i = (-2)(-58.177) = 116.354 \text{ (with 50 degrees of freedom)}$$

$$p < 0.01$$

Explanation: To retain workable probabilities in the test:

$C = -2 \sum_{i=1}^s \ln p_i$ (a chi-square summary of s independent tests of the same null hypothesis, where p is the observed rejection level in each test and C has $2s$ degrees of freedom), the value 0.01 was substituted for highly significant differences in the i^{th} test—when $\ln p_i$ was zero to two decimals. C was significant at the 99 percent level.

¹ M—male, F—female; I—immature, M—maturing; 1, 2, 3—number of winters at sea before capture.

The 40–60 percent criterion rejected certain large catches of maturing fish taken north of the Aleutian Islands in June, particularly in 1956 and 1960. That these fish were on the spawning migration to Bristol Bay, Alaska, has been clearly demonstrated by the classification studies by Fukuhara *et al.* (1962) and Landrum and Dark (MS), and by independent tagging experiments (Hartt, 1962). Many individuals so excluded from the test of size by origin could con-

tribute, of course, to final estimates of growth.

Individual tests on data retained by the 40–60 percent criterion then took the form of separate two-way analyses of variance with disproportionate subclass number (Snedecor, 1956). Each analysis represents a different combination of one or more of these factors: sex, maturity, winters at sea before capture, or year of capture. Variables of classification are origins and periods. Expected variation from seasonal growth between 10-day periods is hence removed from comparisons of size by origin. Variability due to area of capture is retained as sampling error (see also the section entitled “Effects of area and year of capture”).

In Figure 3, the positions of means relative to the line of 1:1 correspondence reveal the tendency of Western Alaskan fish to exceed those from Asia in both length and weight. The 93 points in each portion of Figure 3 arise from the fact that two or more periods contributed to each of 25 individual analyses of variance. Of these 93 points, 82 fall below the line of equal length; 77 lie below the line of equal weight. Finally, combined results from these 25 independent tests (using the less variable length data) of the same null hypothesis into the summary of Table 2 show length differences associated with area of origin to be highly significant.

Therefore, pooling all of the high seas data would render estimates of average size too low for Western Alaskan fish. The remaining problem was how to select individuals from Western Alaska.

CRITERIA FOR SELECTING WESTERN ALASKAN FISH

Data from all areas were originally combined. A breakdown by 1° rectangles of latitude and longitude (see Fig. 2) was next imposed on these data and each resulting tabulation was treated as a sample. Given average risks of misclassification of 29 and 22 percent for Asian and Western Alaskan fish, respectively (Landrum and Dark, MS), and again recalling that risks of misclassification were unknown for individuals, the following three criteria were then adopted for selecting Western Alaskan individuals from available samples: (1) reject all samples containing fewer than 50 percent “Western Alaskan” fish, (2) use only individuals falling on the “Western Alaskan” side of the critical point of the discriminator from those samples containing from 50 percent through 69 percent “Western Alaskan” fish, and (3) use all individuals from samples containing over 69 percent “Western Alaskan” fish. An incidental rule was to reject any remaining samples with less than three fish.

After criterion (1) was applied to all available samples, the percentages of Western Alaskan fish in the remaining samples were made the basis for applying criteria (2) and (3). Weighted mean fork lengths and body weights of fish from both continents were pooled for samples to which criterion (3) applied. The resulting tabulation showed the tendency, mentioned earlier for means of test groups in Figure 3, for Western Alaskan fish to be larger than Asian fish.

It is important to distinguish once more between the earlier 40–60 percent criterion, adopted to test for size differences by origin, and the three criteria just mentioned. The latter three selected Western Alaskan individuals from the available samples, once Western Alaskan fish had been found to be larger than Asian fish. When these three criteria were applied—criterion (1) to all samples, criteria (2) and (3) to the samples remaining after application of criterion (1)—8,512 individuals remained. At least 85 percent of those in each of the four age-maturity combinations had T values in the “Western Alaskan” region of the original discriminator (Fukuhara *et al.*, 1962).

In view of the meaning and magnitudes of average

risks of misclassification, the three criteria for selecting Western Alaskan fish are believed to admit relatively few Asian fish. One qualification, of course, is that the discriminator was derived from maturing fish only (Fukuhara *et al.*, 1962; Landrum and Dark, MS).

CONVERSION OF LABORATORY OBSERVATIONS TO FRESH WEIGHT AND LENGTH

The basis for conversions is introduced here to explain why lengths and weights are not given for fresh fish, and why a weight-length relationship is not needed.

Weights of 335 fresh fish were taken in 1961 (see “Collection and processing of specimens”), but no weights for fresh fish were on hand for the years 1956 through 1960. Lengths were available from most fresh fish taken by United States research vessels and sent to the laboratory as frozen fish. United States research vessels caught 88 percent of the 8,512 individuals employed in the growth analysis, although as high as 41 percent (in 1956) were from Japanese commercial fleets in individual years. Since growth is more realistically expressed on a fresh basis, weight

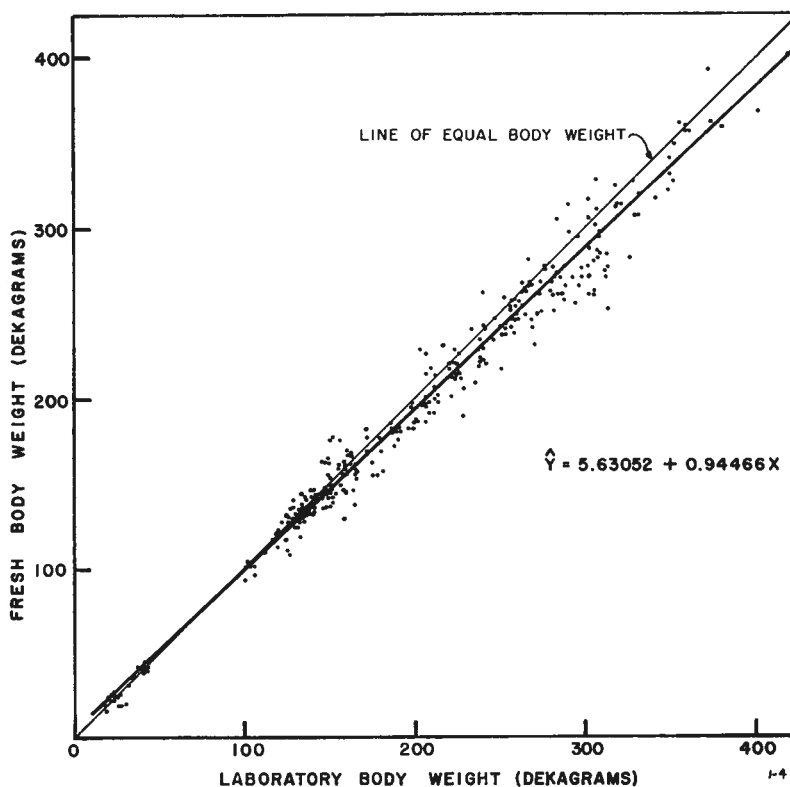


FIGURE 4. Relationship between weights of 335 fresh and partially thawed sockeye salmon collected in 1961.

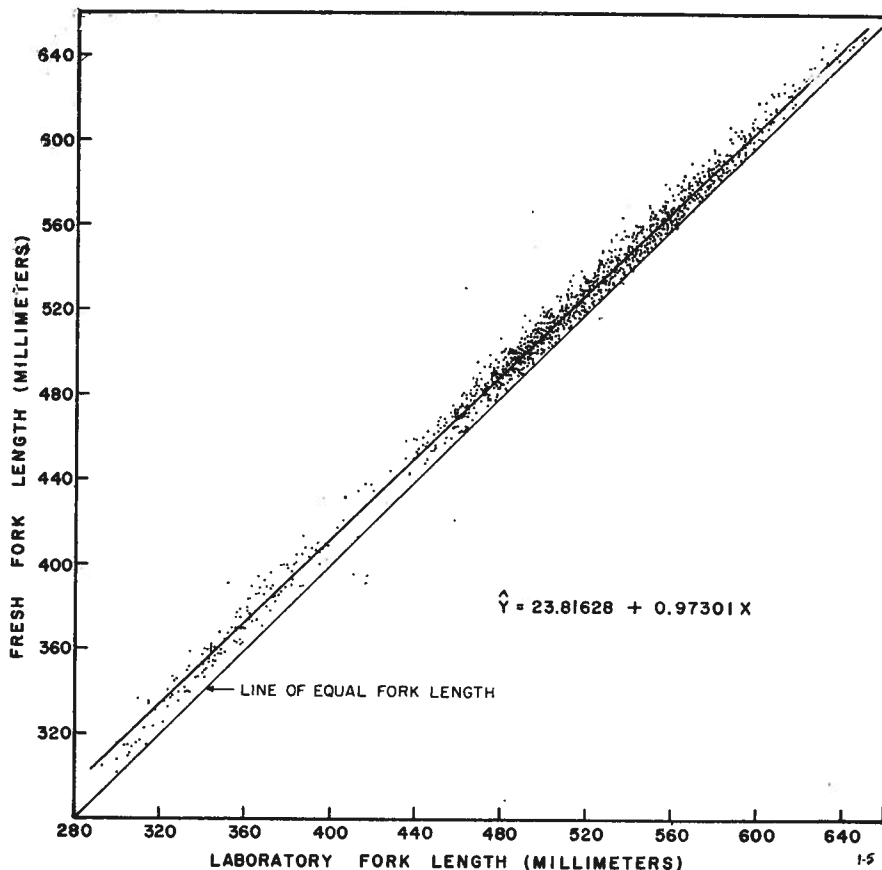


FIGURE 5. Relationship between fork lengths of 1,382 fresh and thawed sockeye salmon collected each year (except 1958) from 1956 through 1960.

records from the laboratory for the years 1956 through 1960 were converted on the basis of and were dependent on the 335 records taken at sea in 1961. The remaining question was whether to use length data taken at sea or in the laboratory.

In comparing 1,484 length records taken at sea with laboratory records from the same fish, 102 laboratory measurements (or 7%) were found to be larger. That fish shrink during freezing is common knowledge. Moreover, accuracy is harder to attain at sea than in the laboratory. Therefore, these 102 fish were discarded from analysis of the effects of mesh selectivity, details of which are given in the next section.

To the extent the above comparison of records is representative, laboratory measurements on thawed fish are likely more accurate than shipboard measurements on fresh fish in the whole body of data. A similar problem in accuracy was noted in connection with tagging experiments, where greater lengths at tagging than at recovery are commonly discarded. In the present study, it seemed reasonable to proceed

with laboratory records, then to convert only average values to a fresh basis as needed near the end of the study. Moreover, the same 1,382 observations used to examine effects of mesh selection should define quite precisely the length relationship between fresh and thawed fish. Of course, a different procedure would have been employed had weight and length observations taken at sea been available for all specimens collected from 1956 through 1960.

Figures 4 and 5 show regression lines and equations for converting mean weights and lengths to a fresh basis. Figure 4 indicates that weights of partially thawed fish were greater on the average than weights of the same fish when fresh. Changes in composition of flesh during freezing permit water uptake when fish are immersed in warm water to remove a glaze; in addition, water intake through the gullet may slightly increase the weight.¹

¹ Personal communication with Richard Nelson of the Bureau of Commercial Fisheries Technological Laboratory, Seattle, Washington.

Finally, separate treatment of weight and length avoids the need for a weight-length relationship. Note that weight gain and length loss could substantially alter the weight-length relationship that existed in the fresh fish.

EFFECTS OF SIZE SELECTIVITY BY GILLNETS

Size selectivity by gillnets is clearly a potential source of error in estimating growth. For instance, a given mesh size may select large fish from a life history group early in the season, small ones later. The resulting estimate of seasonal growth would then be too low. Other effects are conceivable on both seasonal and long-term growth rates. In present data, moreover, changes from year to year in proportions of each mesh size fished (see Table 1) tend to complicate effects of selection for size.

Readers interested in the theory of mesh selectivity are referred to papers by Olsen (1959) or McCombie and Fry (1960); its initial exposition in English by Holt (1957), while excellent, is perhaps less readily available. Recounted here is background information sufficient to clarify later analysis.

The chance of a fish being captured when swimming into a gillnet depends strongly on its girth relative to the mesh opening. Over a range of length (therefore, of girth), Holt (1957) was able to estimate selection curves, normal in shape, for each mesh size fished in a graduated series of sizes. A selection curve gives the risk of retention at any length relative to that at the mean selection length; the latter is the length at which retention is most likely for a given mesh size. By assuming no particular shape for a selection curve in advance of its estimation from catch data by fish length and mesh size, Olsen (1959) applied a more general model to Newfoundland herring. McCombie and Fry (1960) cited these and (earlier) Russian studies, and examined directly the ratio of fish girth to mesh perimeter. The latter authors then found total catch, when pooled from a series of graduated mesh sizes fishing together with equal effort and covering the length range of whitefish (*Coregonus clupeaformis*) locally available, was a representative sample of length. Still other workers have applied the basic ideas to various species.

Peterson (MS) has followed this theory in estimating, for sockeye, chum and pink salmon, selection curves for 2½-inch, 3¼-inch, 4½-inch and 5¼-inch meshes. Mesh sizes are average measured distances between opposite knots of multifilament nylon stretched taut,

United States research vessels employed these four mesh sizes from 1956 through 1960, but in varying amounts (see Table 1); recall that these vessels took 88 percent of the 8,512 fish employed in the growth analysis. Peterson (MS) then, used lengths of the same fish, when fresh, from most of the same catches to construct his mesh selection curves for sockeye salmon. He summed data separately within "spring" (May-June) and "summer" (July-August) seasons and over all life history groups within a season. A breakdown of catches by date, winters at sea, sex and maturity would have left too few fish to estimate curves with confidence.

Now the basic reason for estimating selection curves is to relate the size composition of fish in the catch to the sizes of fish in the water. The theory requires that each mesh size in a graduated series be fished with equal effort. Since United States research vessels fished differing amounts of each mesh size in various years (see Table 1), Peterson (MS) had to place catches on a per-unit-effort basis before constructing his curves. Unfortunately, we have no data adequate for testing the assumption that catch varies directly with amount of gear. That nets very rarely reached "saturation" levels in the present study is perhaps the only observation to be made on this point.

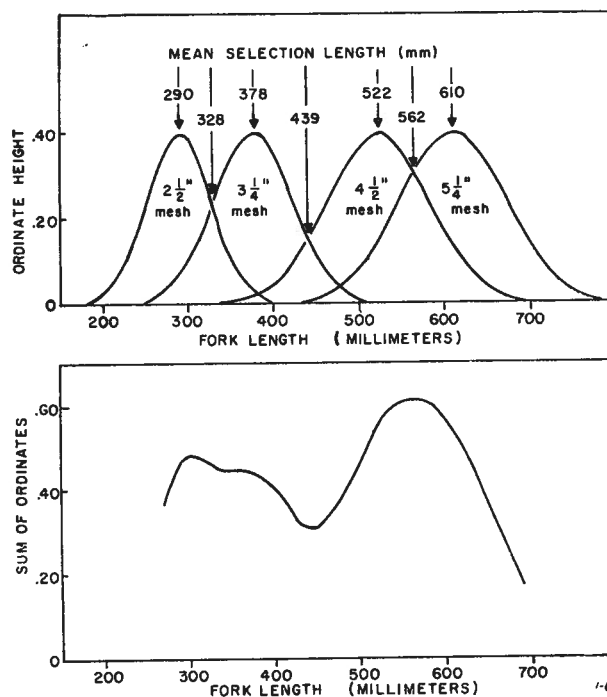


FIGURE 6. Individual and composite mesh selection curves for sockeye salmon.

TABLE 3. Ordinates of individual and composite selection curves for sockeye salmon, as constructed from average of yearly values given by Peterson (MS).

Fork length class (mm.)	Ordinates by mesh size				Sum of ordinates for composite curve
	2½"	3¼"	4½"	5¼"	
270	.342	.025			.367
280	.384	.040			.424
290	.399	.063			.462
300	.385	.094			.479
310	.345	.133	.000		.478
320	.287	.180	.001		.468
330	.220	.232	.001		.453
340	.156	.285	.002		.443
350	.104	.333	.005		.442
360	.063	.371	.008		.442
370	.036	.394	.013		.443
380	.019	.398	.020	.000	.437
390	.009	.385	.030	.001	.425
400	.004	.354	.044	.001	.403
410	.002	.310	.062	.002	.376
420	.001	.259	.085	.003	.348
430	.000	.206	.114	.006	.326
440		.156	.148	.009	.315
450		.113	.185	.014	.312
460		.078	.225	.021	.324
470		.051	.266	.031	.348
480		.032	.306	.044	.382
490		.019	.341	.061	.421
500		.011	.371	.083	.465
510		.006	.390	.109	.505
520		.003	.399	.139	.541
530		.002	.396	.174	.572
540		.001	.381	.211	.593
550		.000	.357	.252	.609
560			.324	.290	.614
570			.285	.325	.610
580			.244	.356	.600
590			.204	.379	.583
600			.165	.394	.559
610			.129	.399	.528
620			.099	.393	.492
630			.073	.378	.451
640			.052	.354	.406
650			.036	.323	.359
660			.025	.286	.311
670			.016	.245	.261
680			.010	.208	.218
690			.006	.171	.177

Mean selection lengths and standard deviations of sockeye salmon curves for a given mesh size differed little between "spring" and "summer" seasons or between the years 1956 through 1960 (Peterson, MS). Therefore, we constructed here a single curve for each mesh size. In the top of Figure 6, ordinate heights at any length show the risk of retention rela-

tive to that at the mean selection length (i.e., the mode), at which retention is most likely. The 2½-inch mesh is assumed to retain available 290-mm. fish with the same efficiency that the 3¼-inch mesh retains available 378-mm. fish. This assumption applies generally to any two adjacent mesh sizes. Also, those just mentioned retain 328-mm. fish with equal efficiency, and so forth for other lengths of intersection. Summing ordinate heights (see Table 3) for a given length class over all meshes (after McCombie and Fry, 1960) yields the composite selection curve in the bottom of Figure 6. The range of this curve corresponds to the length range of thawed fish in all life history groups.

If the theory of mesh selectivity is valid, then, and if catches may be put on the basis of equal effort before estimating selection curves under that theory, present data may be examined for effects of size selectivity by gillnets. Our procedure is: (1) to estimate the length composition of fish in the water from the composite mesh selection curve in Figure 6 and from catches based on equal effort by mesh size and then, (2) to compare this expected composition with the length composition taken by the number of shackles of each mesh size actually fished. Rejecting the hypothesis of no difference in length distributions should then provide evidence of selectivity.

SELECTION OF DATA

Table 4 identifies 28 test groups selected from samples with 50 percent or more "Western Alaskan" fish. These represent all sampled life history groups and years of sampling (except 1958); therefore, they also represent all fish lengths and allocations of mesh size by effort for U. S. research vessels (again, see Table 1). Single large catches were first chosen for these 28 test groups in Table 4. Next, catches from the same area were combined for different dates within a 10-day period. Finally, catches from different areas were pooled within a 10-day period.

Of course, all catches represented in any one test group of Table 4 are from the same composition of mesh sizes. The reason for combining dates or areas, rather than choosing only the more desirable single large catches, was to ensure balance between large samples and representation of all life history groups. While the effects of mesh size, not area of origin, are of concern here, recall none of these samples contains less than 50 percent "Western Alaskan" fish (see "Effects of area of origin"). Moreover, 19 of the 28 test groups in Table 4 were from samples containing over 69 percent "Western Alaskan" individuals.

TABLE 4. Identification of test groups selected for testing the hypothesis of no selectivity for size in data used to estimate growth.

Test group number	Life history group ¹	Year	Month and day	Period (see p. 6)	Area (see Fig. 2)	N	No. of shackles fished by mesh size			
							2½"	3¼"	4½"	5¼"
1	M-I -1	1957	8/12	11	1293	15	4	4	10	5
2	"	1957	8/11, 17, 18	11	1293	39	4	4	11	5
3	"	1959	7/13	8	1210	11	4	4	24	4
4	F-I -1	1957	8/12	11	1293	8	4	4	10	5
5	"	1957	8/11, 17, 18	11	1293	30	4	4	11	5
6	"	1957	8/9	11	1017	6	4	4	12	4
7	"	1960	7/20, 21, 23, 28	9	1119, 1205	38	4	4	24	4
8	M-I -2	1956	8/25	12	1122	46	3	3	6	6
9	"	1957	8/19, 23	12	1191	87	4	4	11	5
10	"	1960	8/14, 17, 18	11	1114	90	4	4	24	4
11	"	1960	8/20	12	1015	28	4	4	24	4
12	F-I -2	1956	8/25	12	1122	39	3	3	6	6
13	"	1957	8/19, 23	12	1191	54	4	4	11	5
14	"	1959	8/6	10	1017	46	4	4	24	4
15	"	1960	8/14, 17, 18	11	1114	66	4	4	24	4
16	M-M-2	1956	6/20	6	1542	73	3	3	6	6
17	"	1957	6/21, 22	6	1544	31	3	3	9	3
18	"	1959	6/12, 14, 15	5	1200	82	4	4	24	4
19	"	1959	6/23	6	1450	26	4	4	24	4
20	"	1960	6/20	6	1451	52	4	4	24	4
21	F-M-2	1956	6/20	6	1542	60	3	3	6	6
22	"	1959	6/12, 14, 15	5	1200	43	4	4	24	4
23	"	1959	6/26	6	1532	61	4	4	24	4
24	"	1960	6/25	6	1280	57	4	4	24	4
25	M-M-3	1957	6/18, 19	5	1542	15	3	3	9	3
26	"	1957	6/15, 17	5	1537, 1539	40	4	4	12	4
27	F-M-3	1957	6/18, 19	5	1542	67	3	3	9	3
28	"	1957	6/15, 17	5	1537, 1539	172	4	4	12	4
Total						1,382				

¹ See note 1, Table 2.

Finally, only individuals classified as "Western Alaskan" were included in the nine remaining test groups of Table 4.

Fork lengths of fresh fish were used in the analysis to follow. Of 1,568 individuals originally selected for the analysis, fork lengths recorded at sea were smaller than those recorded in the laboratory for 102 fish; the latter were discarded (see "Conversion of laboratory observations to fresh weight and length"). In addition, lengths of fresh fish were not available for 84 specimens from a large catch of June 20, 1956, made north of the Aleutian Islands in area 1542 (see Figure 2). Therefore, only 1,382 of the 1,568 individuals first selected are actually represented in Table 4.

Certain large catches of 1-winter fish taken from area 1200 (see Fig. 2) in 1959, the year of highest catches for that age group, lacked identifying infor-

mation on mesh size of capture. This is reflected in Table 4 by the few entries for 1-winter fish. The average number available for tests on 2-winter and 3-winter fish was 59. The latter seems adequate to avoid a high risk of falsely accepting the null hypothesis of no selectivity for size.

ANALYSIS OF LENGTH FREQUENCIES

Table 5 illustrates calculations performed on each test group of Table 4. Actual catch data by length class and mesh size were first adjusted to unit effort and summed over all meshes. The total adjusted catch in each length class was then divided by the corresponding ordinate of the composite selection curve (see Fig. 6 and Table 3). The latter values, when put on a percentage basis, are estimates of the length composition of fish in the water under the theory of net selectivity. Next, the estimated percentage in each length class was multiplied by total

TABLE 5. Chi-square calculations for test group 9 (Table 4), illustrating derivation of length frequencies expected under the hypothesis of no selectivity for size. Small expected frequencies are summed to exceed 5.0 in the chi-square test.

Midpoint of 10 mm. fresh fork length class	Actual catch by mesh size					Catch by mesh adjusted to common effort of one shackle ¹				Ordinate of composite selection curve (Fig. 6 and Table 3)	Comparison of observed and expected values									
	2½"	3¼"	4½"	5¼"	Total observed catch	3¼"	4½"	5¼"	Total adjusted catch		A ²	B ³	Expected	(O-E)	(O-E) ²	(O-E) ²				
																E				
460	—	—	1	—	1	—	0.091	—	0.091	.324	0.281	1.3	1.13	5.22	—2.22	4.93	0.94			
470	—	1	1	—	2	.250	0.091	—	0.341	.348	0.980	4.7	4.09							
480	—	1	3	2	6	.250	0.273	.400	0.923	.382	2.416	11.6	10.09		-4.09	16.73	1.66			
490	—	—	11	—	11	—	1.000	—	1.000	.421	2.375	11.4	9.92		1.08	1.17	0.12			
500	—	2	12	—	14	.500	1.091	—	1.591	.465	3.422	16.4	14.27		-0.27	0.07	0.00			
510	—	—	10	2	12	—	0.909	.400	1.309	.505	2.592	12.4	10.79		1.21	1.46	0.14			
520	—	2	9	3	14	.500	0.818	.600	1.918	.541	3.545	17.0	14.79		-0.79	0.62	0.04			
530	—	—	7	1	8	—	0.636	.200	0.836	.572	1.462	7.0	6.09		1.91	3.65	0.60			
540	—	—	6	1	7	—	0.546	.200	0.746	.593	1.258	6.0	5.22		1.78	3.17	0.61			
550	—	1	3	2	6	.250	0.273	.400	0.923	.609	1.516	7.2	6.26	10.70						
560	—	—	4	1	5	—	0.364	.200	0.564	.614	0.918	4.4	3.83			1.30	1.69	0.16		
570	—	—	1	—	1	—	0.091	—	0.091	.610	0.149	0.7	0.61							
											20.914						4.27			
Total catch	0	7	68	12	87												87.09			
Effort ⁴	4	4	11	5												chi-square .95(8)=15.50				

¹ Actual catch by length in each mesh, divided by effort for each mesh.

² Total adjusted catches divided by corresponding ordinate of composite selection curve.

³ Expected percentage length composition; each value in column "A" is divided by column "A" total.

⁴ Total effort in 50-fathom shackles.

actual catch to allocate the latter into numbers expected under the null hypothesis. Finally, the chi-square analysis in Table 5 shows that expected catches in each length class and in the whole distribution did not differ from actual catches for test group 9 of Table 4.

Table 6 summarizes results of similar calculations for all 28 test groups of Table 4. Only the immature 2-winter females of test group 15 gave a probability value (0.01) small enough to be significant. The summary result is far from significant (p is 0.85).

Since the composite mesh selection curve in Figure 6 shows that fish of some lengths—particularly in the range from 400 mm. to 500 mm.—are much less vulnerable than fish of other lengths, the outcome of Table 6 may at first seem surprising. Two items may be noted in this regard. First, McCombie and Fry (1960) showed for another species (*Coregonus clupeaformis*) that the total catch from all mesh sizes, provided those sizes were fished together and covered the length range of fish available, was a representative sample of length. Secondly, and perhaps a more important factor here, is the fact that a single

mesh size captured most of the fish taken from a single life history group (see Table 7). The length range covered by the composite selection curve of Figure 6 is much greater than the length range of an individual life history group. That Table 6 gave a non-significant result, therefore, is perhaps not entirely surprising.

We believe some size selectivity must occur in these data. The outcome of Table 6 would likely have been different had several life history groups been combined together. To the extent that the existing theory of mesh selection and the method used by Peterson (MS) to develop selection curves for sockeye salmon are valid, however, we conclude that size selectivity by gillnets should not seriously distort the composite picture of growth, which is the objective of the present study.

EFFECTS OF AREA AND YEAR OF CAPTURE

This picture must be assembled from certain groupings of data dictated by actual coverage in space and time; to estimate growth was not the primary purpose

TABLE 6. Test of the hypothesis that gillnets, as fished, caused no selectivity for size in data used to estimate growth.

Test group number	Life history group ¹	Rejection level in i^{th} test (p_i)	$\ln p_i$
1	<i>M-I-1</i>	0.43	-0.84
2	"	0.98	-0.02
3	"	0.89	-0.12
4	<i>F-I-1</i>	0.97	-0.03
5	"	1.00	0
6	"	0.96	-0.04
7	"	1.00	0
8	<i>M-I-2</i>	0.80	-0.22
9	"	0.83	-0.19
10	"	0.06	-2.81
11	"	0.15	-1.90
12	<i>F-I-2</i>	0.89	-0.12
13	"	0.42	-0.87
14	"	0.96	-0.04
15	"	0.01	-4.61
16	<i>M-M-2</i>	0.99	-0.01
17	"	0.96	-0.04
18	"	0.15	-1.90
19	"	0.68	-0.39
20	"	0.14	-1.97
21	<i>F-M-2</i>	0.90	-0.10
22	"	0.29	-1.24
23	"	0.70	-0.36
24	"	0.31	-1.17
25	<i>M-M-3</i>	0.33	-1.11
26	"	0.19	-1.66
27	<i>F-M-3</i>	0.92	-0.08
28	"	0.44	-0.82
Total			-22.66

Chi-square = $-2 \sum_{i=1}^8 \ln p_i = (-2)(-22.66) = 45.32$ (with $2s = 56$ degrees of freedom)

$p = 0.85$

¹ See note 1, Table 2.

TABLE 7. Summary of United States research vessel catches of sockeye salmon, 1956 through 1960, by life history group and mesh size.

Life history group ¹	Total fish	Percentage taken in each mesh			
		2½"	3¼"	4½"	5¼"
<i>M-I-1</i>	940	20	74	6	0
<i>F-I-1</i>	796	28	67	4	1
<i>M-I-2</i>	3,079	0	6	88	6
<i>F-I-2</i>	2,766	1	11	86	2
<i>M-M-2</i>	3,113	1	2	80	17
<i>F-M-2</i>	2,549	0	1	88	11
<i>M-M-3</i>	776	2	4	60	34
<i>F-M-3</i>	1,627	0	2	76	22

¹ See note 1, Table 2.

of sampling. Study of the amount of data available for each life history group demonstrated the need for combinations by time and area.

Variability in average size between areas of capture must be admitted even under a sampling survey designed for estimating growth. The fact that a life history group is broadly distributed means its members could be growing in different environments; these, in turn, could modify average size from area to area. The question is then how to weight these averages for proper representation of the entire life history group of Western Alaskan sockeye salmon. Appropriate weighting factors, however, would require a precise knowledge of relative abundance by area which is beyond the scope of current sampling effort by research vessels. When sampling is not designed for estimating growth, the alternative is to combine data from the different areas without weighting.

Area comparisons in Table 8 are, nevertheless, interesting. Of 30 individual *F* or *t* tests (*F* for three or more areas, *t* for two) on fork length of immatures, only two gave probability values below 0.05—a result close to chance expectation. On the other hand, 15 of the 45 test results for maturing fish were significant at the 95 percent level. Study of significant area differences in Table 8, of corresponding mean lengths, and of the map in Figure 2, revealed no definite geographic pattern. Maturing 2-winter and 3-winter sockeye salmon do tend to be slightly larger if sampled towards Bristol Bay, Alaska, than if sampled to the westward in the same 10-day period.

Results in Table 8 suggest that immatures, relative to maturing fish, are too young or small to grow differentially in the various physical regimes (or areas) encountered during the first year or two of life at sea. On the other hand, maturing Western Alaskan sockeye salmon evidently encounter regimes (or areas) which are in fact different; these fish are apparently now old or large enough to express inherent capacity for differential growth. More than anything, perhaps, the results of Table 8 demonstrate a need for basic inquiry into the biology of salmon growth at sea. Of particular importance is an understanding of the mechanisms governing interactions between growth, maturation and environment.

Data from different areas of capture, then, will be combined because of inexact knowledge of relative abundance in each. Also, to regard the years 1956 through 1960 as a random sample of environment-response combinations is consistent with providing a composite picture of growth from limited sampling.

TABLE 8. Sources of data and results of comparisons of average fork length by area.

Life history group ¹	Year	Period (see p. 6)	Test number	Area ² (see Fig. 2)	Sample size	Distance apart ³	Significance at .95 level	
<i>M-I-1</i>	1956	12	1	1117	18	Near	—	
				1122	11			
	1959	8	2	1210	7	Near	—	
				1276	22			
				1380	23			
				1114	36			
	1960	9	4	1200	105	Far	—	
				1119	10			
				1205	29			
				1117	9			
<i>F-I-1</i>	1957	12	5	1017	23	Far	—	
				1114	42			
	1959	9	6	1200	46	Near	—	
				1117	9			
<i>M-I-2</i>	1956	12	7	1117	9	Near	—	
				1122	52			
				1007	10			
				1017	37			
	1957	10	8	1112	30	Mixed	—	
				1017	23			
				1293	24			
				1017	27			
		12	10	1112	31	Far	*	
				1201	11			
				1017	23			
				1293	24			
	1959	7	14	t-10	69	Far	—	
				1007	20			
				t-10	69			
				1191	89			
		8	15	15	1007	20	Far	—
					1191	89		
					1007	20		
					1191	89		
1960		6	16	1205	9	Far	—	
				1690	11			
				1210	20			
				1276	22			
	8	17	17	1380	21	Near	—	
				1020	19			
				1108	17			
				1110	38			
1959	9	18	1189	24	Far	—		
			1294	52				
			1119	91				
			1205	30				
	<i>F-I-2</i>	1956	12	19	1117	20	Near	—
					1122	48		
		1957	10	20	1017	14	Near	—
					1112	31		
1017					26			
1293					31			
12			22	22	1007	29	Near	—
					1191	55		
					1017	19		
					1112	20		
12	23	23	t-22	84	Far	—		
			t-23	39				

Continued . . .

TABLE 8. Continued.

Life history group ¹	Year	Period (see p. 6)	Test number	Area ² (see Fig. 2)	Sample size	Distance apart ³	Significance at .95 level	
<i>M-M-2</i>	1959	7	25	1205	13	Far	*	
				1302	11			
				1690	8			
		8	26	1276	28	Near	—	
				1380	22			
				1191	11			
		9	27	1200	27	Far	—	
				1017	47			
		10	28	1112	25	Near	—	
				1017	47			
	1960	8	29	1110	42	Far	—	
				1189	21			
				1294	42			
	9	30	30	1119	125	Far	—	
				1205	35			
				1187	20			
	1956	4	31	1190	10	Near	—	
				1290	26			
		6	32	1542	131	Far	—	
				1122	11			
		1959	3	33	1203	28	Far	—
					1117	30		
			4	34	1126	11	Far	—
					1463	19		
			5	35	1200	95	Near	—
					1365	19		
	6		36	1288	13	Near	—	
				1454	17			
	6		37	1532	24	Near	—	
				1705	22			
	6	38	t-36	54	Far	*		
			t-37	34				
	6	39	1369	32	Near	*		
1450			33					
1960	3	40	1536	24	Near	*		
			1611	32				
	3	41	1020	29	Near	*		
			1108	49				
	3	42	1020	29	Far	*		
			1294	27				
	3	42	1108	49	Far	*		
			1294	27				
	4	43	1116	70	Near	—		
			1117	63				
5	44	1284	63	Near	—			
		1285	62					
5	45	1286	84	Far	—			
		1368	63					
6	46	1369	46	Near	*			
		1198	15					
6	46	1537	21	Near	*			
		1205	23					
				1280	37			

Continued . . .

TABLE 8. Continued.

Life history group ¹	Year	Period (see p. 6)	Test number	Area ² (see Fig. 2)	Sample size	Distance apart ³	Significance at .95 level
<i>F-M-2</i>	1955	7	47	1375	20	Near	—
				1444	34		
				1542	49		
				1540	55		
				1609	49		
				t-47	104		
				1451	63		
				t-47	104		
				1699	25		
				1107	9		
				1110	14		
				1187	34		
	1188	16					
	1290	59					
	1542	82					
	1283	14					
	1537	25					
	1542	18					
	1203	10					
	1205	12					
	1200	52					
	1365	30					
	1288	33					
	1454	15					
	1532	63					
	1369	31					
	1450	30					
	1536	32					
	1611	19					
	1705	22					
	1748	13					
	t-56	111					
t-58	35						
1020	27						
1108	22						
1116	26						
1117	17						
1284	30						
1285	33						
1286	21						
1368	76						
1369	34						
1537	10						
1611	11						
1280	59						
1375	49						
1444	40						
1542	50						
1540	29						
1609	34						
993	17						
1110	26						
1290	11						
<i>M-M-3</i>	1956	6	67	1290	11	Near	*

Continued . . .

TABLE 8. Continued.

Life history group ¹	Year	Period (see p. 6)	Test number	Area ² (see Fig. 2)	Sample size	Distance apart ³	Significance at .95 level					
<i>F-M-3</i>	1957	5	68	1542	14	Near	*					
				1537	30							
				1539	14							
	1957	6	69	1542	18	Far	*					
				1288	8							
				1544	19							
				1694	10							
				1958	2			70	940	11	Far	—
	1957	5	71	1000	22	Near	*					
				1537	109							
				1539	77							
	1957	6	72	1542	74	Far	—					
				1288	15							
				1544	33							
				1694	23							
				1958	5			74	1537	10	Far	—
									1692	19		
1958	5	74	1280	9	Near	—						
			1539	23								
1959	6	75	1369	19	Far	—						
			1616	16								

Summary of Results.

	Distance	Immature	Mature	Total
Significant	Near	0	9	9
	Mixed	0	0	0
	Far	2	6	8
	Total	2	15	17
Not significant	Near	15	17	32
	Mixed	1	1	2
	Far	12	12	24
	Total	28	30	58
GRAND TOTAL		30	45	75

¹ See note 1, Table 2.² Letter "t" followed by numerals indicates test number of pooled areas.³ Distance apart in latitude or longitude: *Near*—approximately 1-5 degrees apart; *Far*—6 degrees or more; *Mixed*—Near and Far areas tested together.

* Significant.

In this view the data for the several years would be grouped within 10-day periods to approximate seasonal and long-term growth of Western Alaskan sockeye salmon.

Here again, substantial differences in average size between years are of interest to biologists, as well as to fishermen and processors. We accordingly combined length data by areas and performed *t*-tests or analyses of variance (the latter, for three or more years, between *years* and *periods*) on the larger resulting

tabulations. Expected seasonal growth is removed from the comparisons between years, of course, while significant interactions indicate different patterns of seasonal growth for the years involved in a particular analysis of variance.

Table 9 shows 10 results for years and five for interaction, from the 14 tests, to be significant. Differences in average size between years reflect changes either in the annual growth environments or in the response of successive stock units to those environments.

TABLE 9. Mean fork lengths (mm.), sample sizes (in parentheses) and results of comparisons for years and periods, all areas within a period combined from source data.

Life history group ¹	Period (see p. 6)											Significance at .95 level	
	Year	3	4	5	6	7	8	9	10	11	12	Year	Inter-action
<i>M-I-1</i>	1957	—	—	—	—	—	—	—	—	370(65)	—	—	—
	1960	—	—	—	—	—	—	—	—	367(22)	—	—	—
	1956	—	—	—	—	—	—	—	—	—	354(29)	*	—
	1957	—	—	—	—	—	—	—	—	—	375(29)	—	—
<i>F-I-1</i>	1957	—	—	—	—	—	—	—	—	363(44)	—	*	—
	1960	—	—	—	—	—	—	—	—	348(34)	—	—	—
	1956	—	—	—	—	—	—	—	—	—	358(17)	—	—
	1957	—	—	—	—	—	—	—	—	—	368(32)	—	—
<i>M-I-2</i>	1959	—	—	—	—	488(25)	486(74)	484(69)	496(65)	—	—	*	*
	1960	—	—	—	—	462(37)	474(160)	478(121)	482(29)	—	—	—	—
<i>F-I-2</i>	1959	—	—	—	—	467(36)	470(50)	467(38)	—	—	—	*	*
	1960	—	—	—	—	449(38)	452(156)	461(160)	—	—	—	—	—
	1957	—	—	—	—	—	—	—	479(45)	—	480(126)	*	—
	1960	—	—	—	—	—	—	—	464(27)	—	476(39)	—	—
<i>M-M-2</i>	1956	511(45)	519(30)	—	—	—	—	—	—	—	—	—	—
	1959	539(71)	550(80)	—	—	—	—	—	—	—	—	*	—
	1960	521(119)	525(154)	—	—	—	—	—	—	—	—	—	—
	1957	—	—	541(42)	539(43)	—	—	—	—	—	—	—	—
	1958	—	—	548(24)	535(20)	—	—	—	—	—	—	*	—
	1959	—	—	544(134)	553(229)	—	—	—	—	—	—	—	—
	1960	—	—	524(370)	527(370)	—	—	—	—	—	—	—	—
<i>F-M-2</i>	1956	—	—	503(58)	505(141)	—	—	—	—	—	—	—	—
	1957	—	—	519(76)	526(33)	—	—	—	—	—	—	—	—
	1958	—	—	525(28)	511(36)	—	—	—	—	—	—	*	*
	1959	—	—	521(104)	523(320)	—	—	—	—	—	—	—	—
	1960	—	—	498(223)	499(372)	—	—	—	—	—	—	—	—
	1959	508(35)	522(54)	—	—	—	—	—	—	—	—	*	—
	1960	490(49)	497(51)	—	—	—	—	—	—	—	—	—	—
<i>M-M-3</i>	1957	—	593(20)	—	611(37)	—	—	—	—	—	—	—	—
	1959	—	604(24)	—	623(34)	—	—	—	—	—	—	—	—
<i>F-M-3</i>	1957	—	573(25)	570(273)	—	—	—	—	—	—	—	—	—
	1958	—	552(37)	571(32)	—	—	—	—	—	—	—	*	*
	1959	—	578(24)	579(30)	—	—	—	—	—	—	—	—	—
	1960	—	567(26)	576(39)	—	—	—	—	—	—	—	—	—
	1957	—	—	—	574(71)	574(33)	—	—	—	—	—	—	*
1959	—	—	—	585(84)	568(30)	—	—	—	—	—	—	—	

¹ See note 1, Table 2.

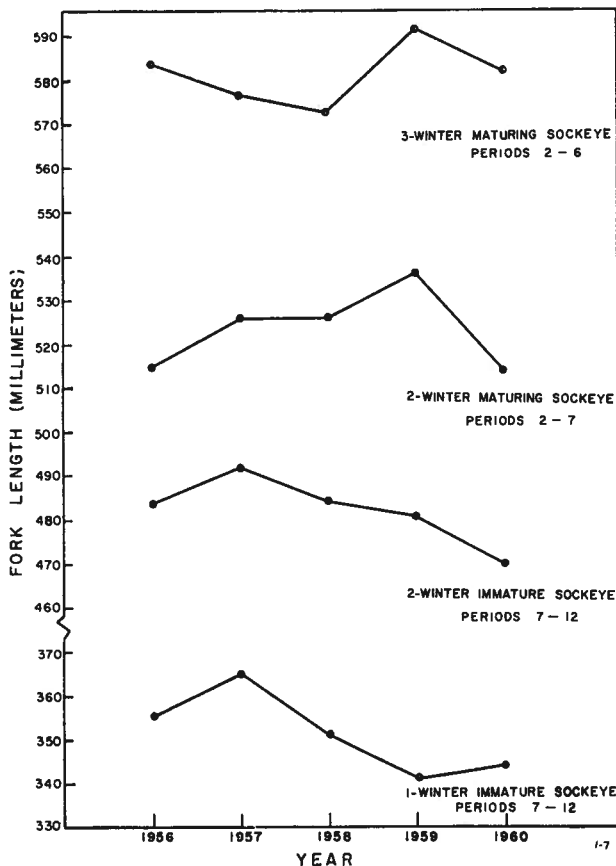


FIGURE 7. Annual mean fork lengths of Western Alaskan sockeye salmon, sexes combined, by maturity and winters at sea before capture. Means are from data pooled over 10-day periods.

Annual mean lengths in Figure 7 were computed and data were pooled for both sexes and all time periods within a year. Figure 7 demonstrates the range of length expected in Western Alaskan sockeye salmon, to the extent that the years 1956 through 1960 are a random sample of annual environment-response combinations.

COMBINATION OF DATA TO ESTIMATE GROWTH

To this stage, the analysis represents an effort to construct representative samples of mean size in Western Alaskan fish. It will be useful to review the preliminaries.

High seas sockeye salmon data were first classified by continental origin, by life history group and by time of capture. Western Alaskan fish were found to be significantly larger than Asian fish. Three criteria, believed to admit few Asian fish, were applied to available data in order to avoid this source of bias in

growth estimates of Western Alaskan sockeye salmon. Lack of weight records for fresh fish in the years 1956 through 1960, along with certain direct evidence of inaccuracy in length records for fresh fish in those years, were next noted to explain our use of laboratory data until conversions to average size of fresh fish were required to describe growth.

Catches from each life history group and allocation of mesh size by effort in U.S. research vessels, which took 88 percent of the data remaining at that stage of analysis, were found to contain no evidence of selectivity for size. Significant differences in average size of maturing fish between areas of capture were then held to be admissible in describing growth of all Western Alaskan fish. However, sampling coverage did not allow weighting these significant mean sizes to the relative abundance in respective areas of capture. Marked variations in mean size of fish in a given life history stage were then demonstrated between years of sampling. To build up samples large enough for describing, in particular, the seasonal growth, the years 1956 through 1960 were regarded as a random sample of annual environment-response combinations for Western Alaskan sockeye salmon.

Length and weight frequency data for all areas of capture and years of sampling were then summed. Numbers for some 10-day periods were judged too small to provide reliable estimates of mean size and were eliminated from further consideration. There-

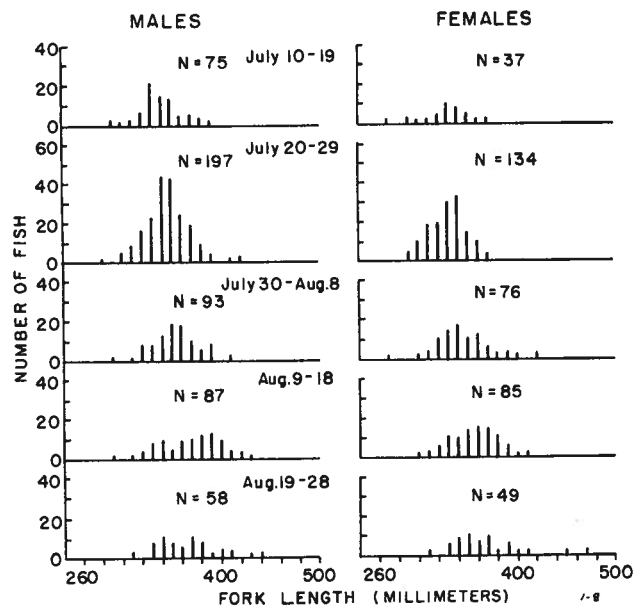


FIGURE 8. Fork-length frequencies of immature sockeye salmon taken after one winter at sea.

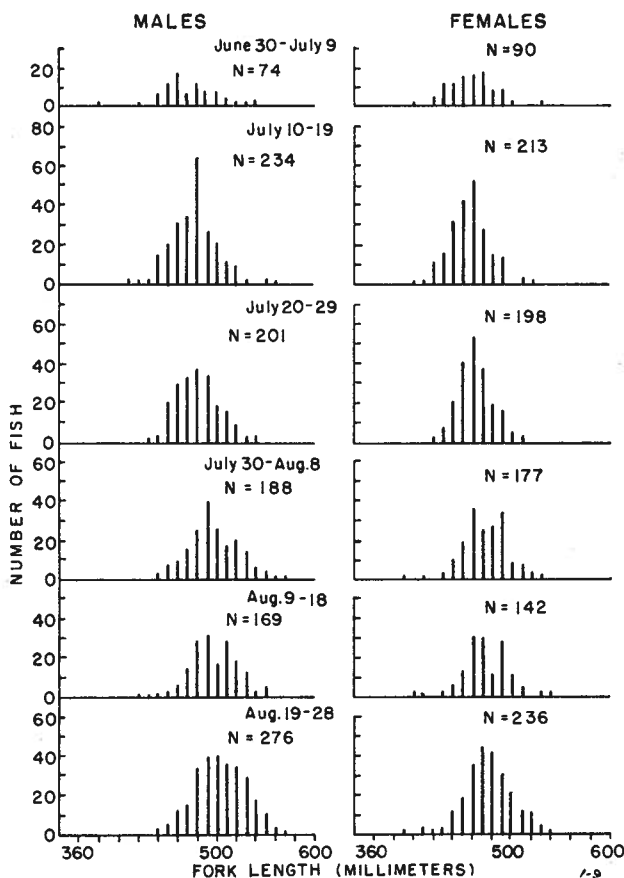


FIGURE 9. Fork length frequencies of immature sockeye salmon taken after two winters at sea.

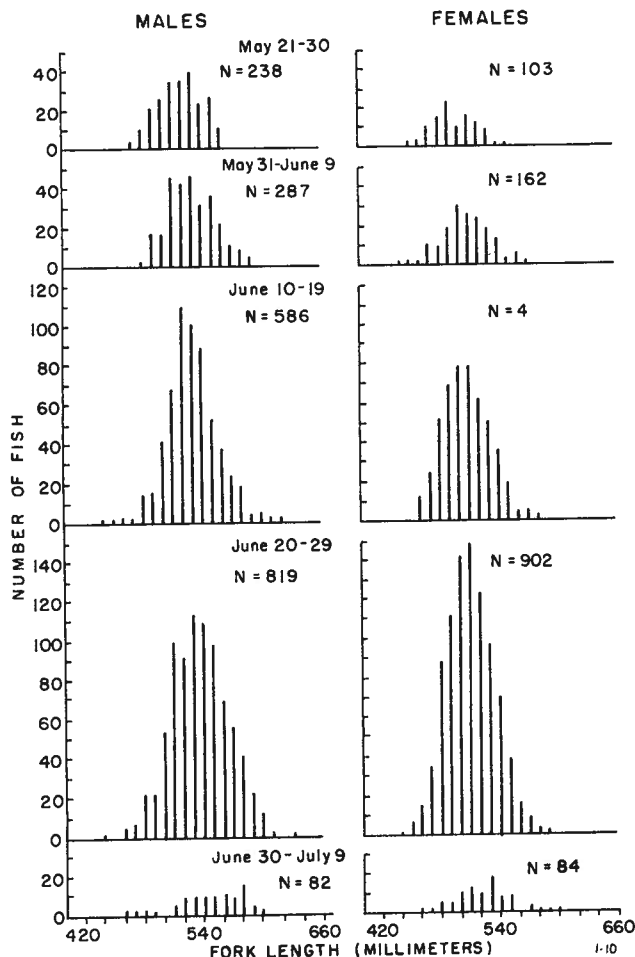


FIGURE 10. Fork length frequencies of maturing sockeye salmon taken after two winters at sea.

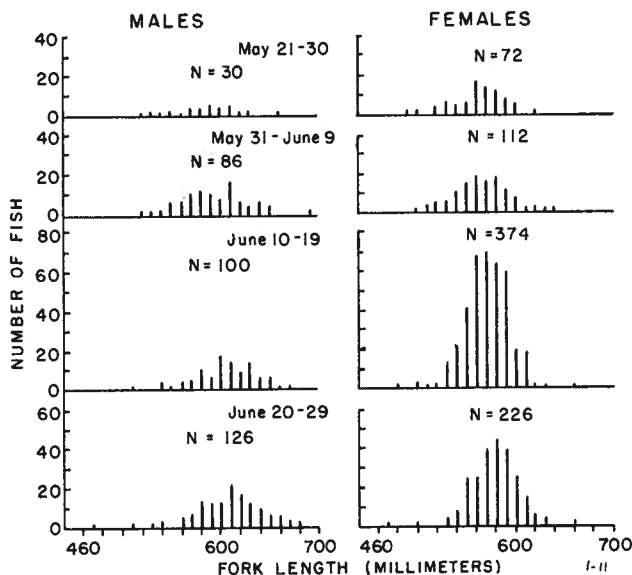


FIGURE 11. Fork length frequencies of maturing sockeye salmon taken after three winter at sea.

fore, of the 8,512 fish originally available for the analysis, only 7,967 were actually employed as a basis for growth estimates.

The following summary of numbers in each age-maturity combination gives a general idea of the relative precision to be expected in these growth estimates:

Age-maturity combination	Number of fish
1-winter immature	891
2-winter immature	2,198
2-winter maturing	3,752
3-winter maturing	1,126

Figures 8 through 15 show the composite size frequency data for estimating seasonal and long-term growth.

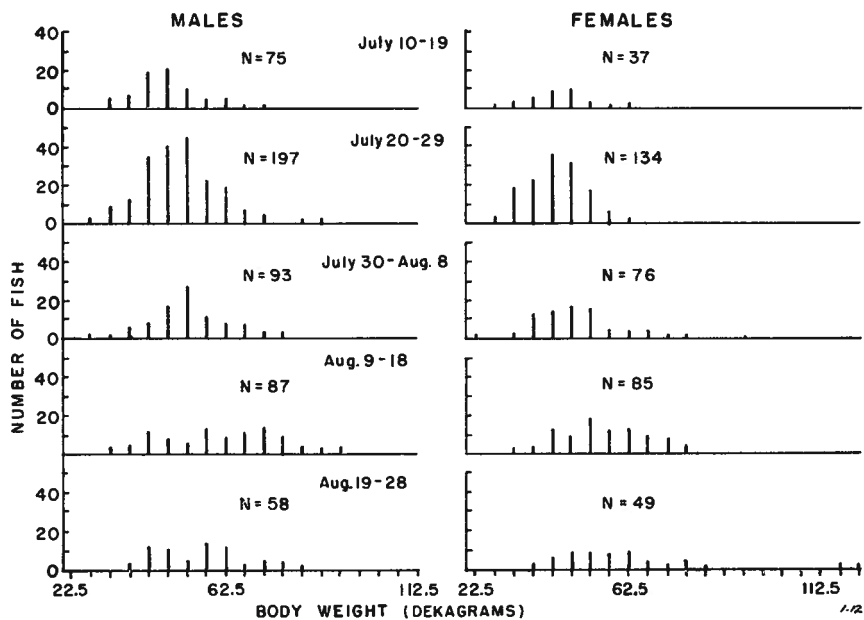


FIGURE 12. Body weight frequencies of immature sockeye salmon taken after one winter at sea.

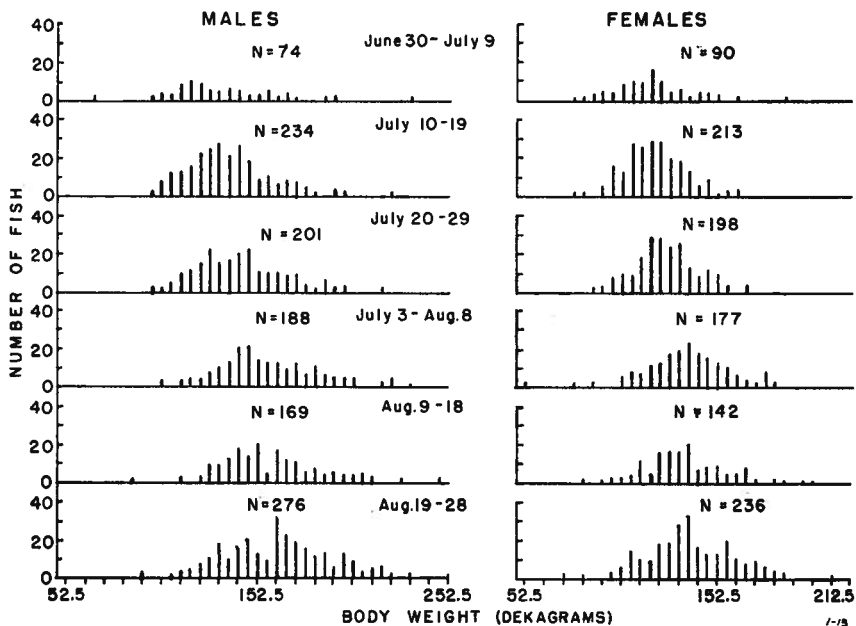


FIGURE 13. Body weight frequencies of immature sockeye salmon taken after two winters at sea.

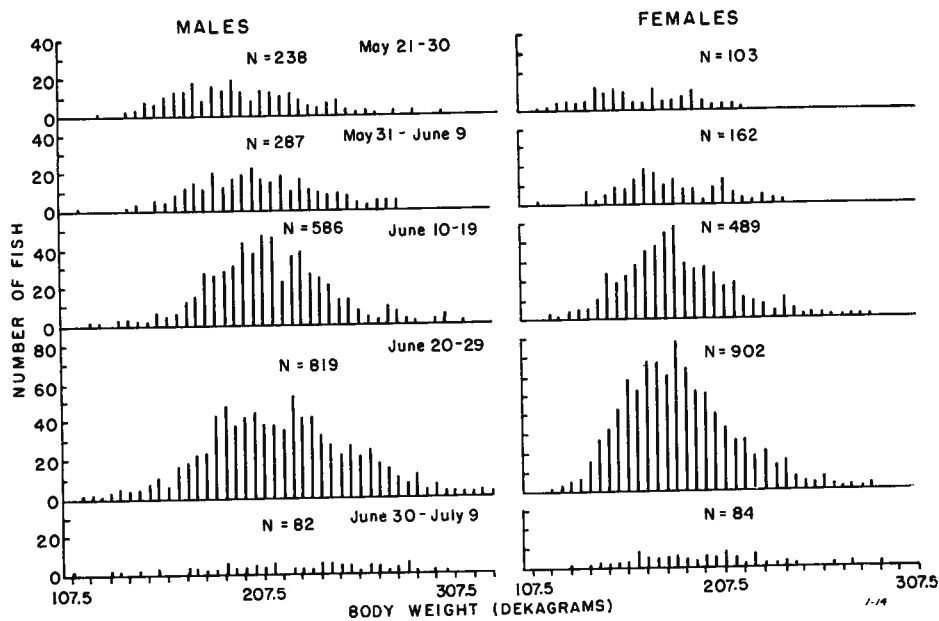


FIGURE 14. Body weight frequencies of maturing sockeye salmon taken after two winters at sea.

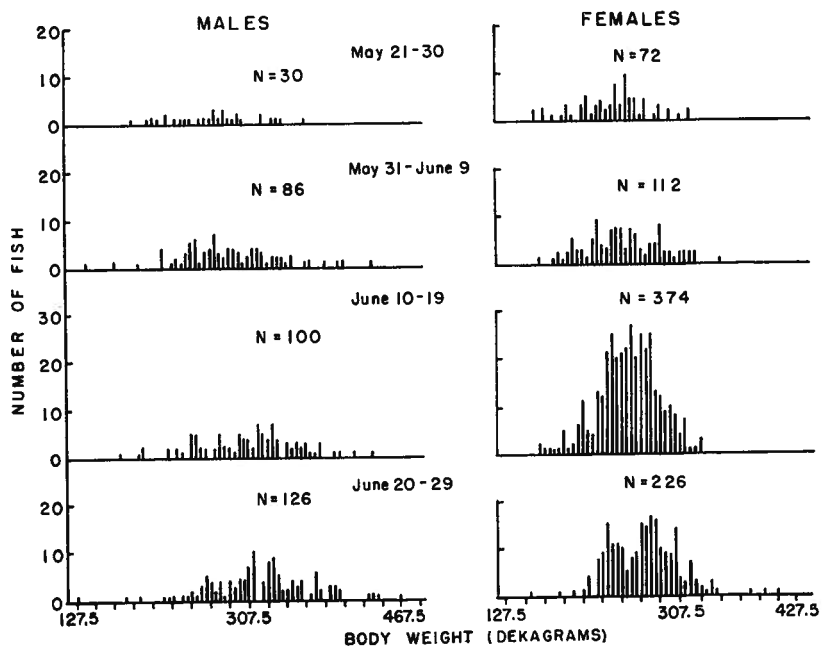


FIGURE 15. Body weight frequencies of maturing sockeye salmon taken after three winters at sea.

RESULTS

ESTIMATION OF SEASONAL GROWTH RATES

For each 10-day period and life history group, mean lengths and weights of fresh fish were next estimated by applying regressions in Figures 4 and 5 to the means of laboratory observations. Table 10 gives the resulting mean sizes of fresh fish. From the data of Table 10, Figures 16 and 17 were drawn to

TABLE 10. Estimated mean fork length and body weight of fresh fish, by 10-day periods, for each life history group (see note 1, Table 2) of Western Alaskan sockeye salmon.

Life history group	Period (see p. 6)	Mean fork length (mm.)	Mean body weight (dkg.)
<i>M-I-1</i>	8	356	50.4
	9	360	53.4
	10	368	56.2
	11	382	64.6
	12	378	60.1
<i>F-I-1</i>	8	347	46.6
	9	345	46.4
	10	359	52.0
	11	369	58.5
	12	378	61.4
<i>M-I-2</i>	7	484	131.1
	8	488	134.5
	9	491	140.5
	10	507	155.4
	11	508	156.2
	12	514	160.0
<i>F-I-2</i>	7	468	117.2
	8	468	118.5
	9	473	123.8
	10	484	134.7
	11	484	134.1
<i>M-M-2</i>	3	533	191.1
	4	540	201.8
	5	540	205.6
	6	545	210.2
	7	557	215.8
<i>F-M-2</i>	3	508	160.0
	4	520	178.0
	5	518	179.3
<i>M-M-3</i>	6	520	179.3
	7	532	188.9
	3	596	264.3
	4	602	275.8
<i>F-M-3</i>	5	612	295.3
	6	614	304.4
	3	573	232.3
<i>F-M-3</i>	4	574	240.7
	5	579	248.7
	6	586	259.3

shown time changes in mean length and weight, respectively, for each of the eight life history groups.

Growth in length could be calculated from the data of Table 10. Since growth in weight is more important in yield equations, however, the following discussion is in terms of weight rather than length. Also, the points in Figure 17 show males are heavier on the average than females. In order to estimate growth in weight for the stock as a whole, growth rates were not computed separately for each sex. Again, this could be done from the data of Table 10.

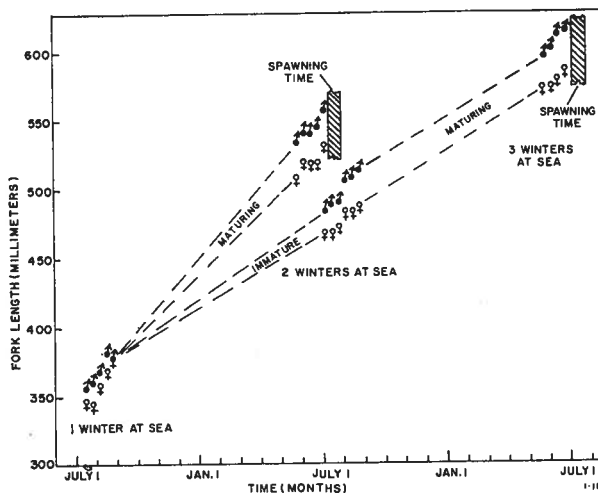


FIGURE 16. Mean fork length by 10-day period for each sampled life history group of Western Alaskan sockeye salmon. Light dashed lines indicate related groups, not linear growth, for periods not sampled.

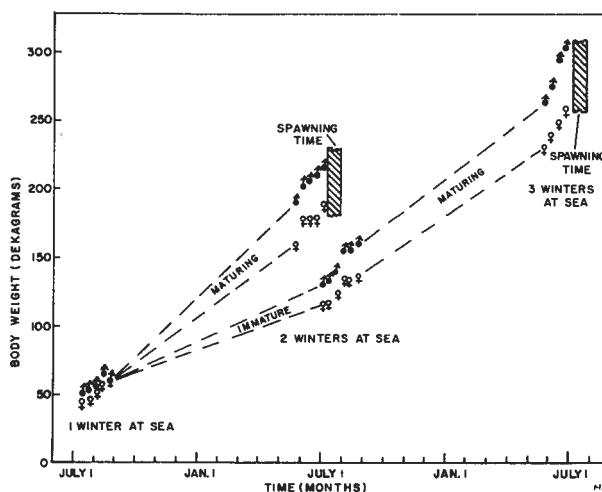


FIGURE 17. Mean body weight by 10-day period for each sampled life history group of Western Alaskan sockeye salmon. Light dashed lines indicate related groups, not linear growth, for periods not sampled.

TABLE 11. Least squares regressions of mean body weight (dekagrams) on 10-day period for each life history stage of Western Alaskan sockeye salmon. T refers to period number.

Life history stage	Regression equations
Immature after one winter at sea	$\hat{W} = 18.81 + 3.62 T$
Immature after two winters at sea	$\hat{W} = 85.26 + 5.44 T$
Maturing after two winters at sea	$\hat{W} = 161.78 + 5.84 T$
Maturing after three winters at sea	$\hat{W} = 213.62 + 11.44 T$

Two mean body weights occur in Table 10 for each 10-day period in which an age-maturity combination was sampled. For instance, mean body weights of 1-winter immatures sampled in period 8 are 50.4 and 46.6 dekagrams for males and females, respectively. The extent to which recorded numbers of each sex (see Figures 8 through 15) represent the true sex ratio in the several marine life history stages is unknown. Therefore, both such means were used without weighting for sample size in order to compute linear regressions of body weight on 10-day period for each age-maturity combination. The four combinations are referred to hereinafter as life history stages. Table 11 gives the regression equations for each life history stage; Figure 18 shows the resulting lines.

Finally, mean body weights were estimated from equations in Table 11 for the first and last 10-day periods in which a life history stage was sampled (see Table 10). These estimated means were considered applicable to the midpoints of the periods. Table 12 shows actual calculation of seasonal growth rates.

The above method of estimating seasonal growth rates—fitting straight lines to observed body weights, then converting percentage weight increases (or relative growth) to instantaneous rates—may warrant explanation. First, the appropriate growth model for longer periods than sampled here is not known, though exponential growth is commonly assumed (e.g., Ricker, 1958). Regressions of logarithm (to the base e) of body weight on 10-day period were calculated for each of the four life history stages before adopting the method of Figure 18 and Table 12. One such set of regressions¹ included weighting factors to account for the increasing variability (and hence lower precision) observed as the mean weight increased from one 10-day period to the next within a life history stage. A second set of logarithmic regressions did not contain these weighting factors. In both sets,

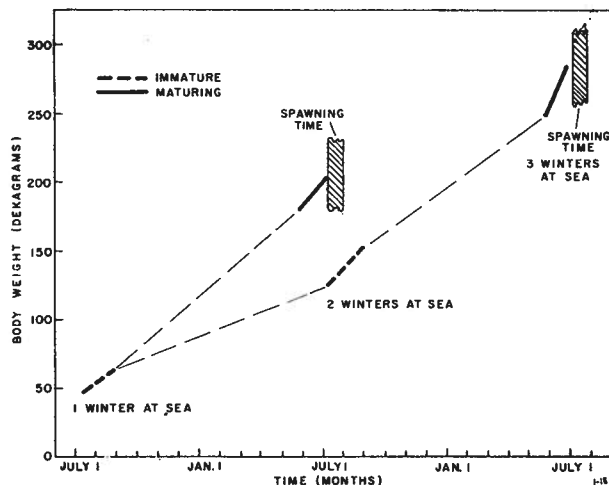


FIGURE 18. Regressions of mean body weight on 10-day period for each sampled life history stage of Western Alaskan sockeye salmon. Sexes are combined; light dashed lines indicate related stages, not linear growth, for periods not sampled.

of course, slopes of regression lines yielded estimates of instantaneous growth rates. The estimated natural logarithms of average body weight were next anti-logged to estimate actual body weights under both methods. Sums of squares of residuals between estimated and actual weights (the latter from Table 10) were then computed for the weighted exponential, unweighted exponential and arithmetic methods. No one method minimized the sums of squares of residuals for all four life history stages; had one method done so, calculations would have been shown here to more rigorously justify a choice. Moreover, total instantaneous growth rates in Table 12 were identical to the second digit for three of the four life history stages, and identical to the first digit in all four stages, with the instantaneous rates from (slopes of) logarithmic regressions. Therefore, a simple arithmetic model (Figure 18 and Table 12) was judged adequate for the present description of growth.

Obviously, a refined model for seasonal growth in Western Alaskan sockeye salmon will require extended sampling. It is not assumed in Figure 18 or Table 12 that a linear arithmetic description will suffice for other times of year in Western Alaskan sockeye salmon, or indeed for other stocks of sockeye at the times here sampled. Conversions to instantaneous rates are presented in Table 12 because of interest in yield-per-recruit computations (e.g., Ricker, 1962).

ESTIMATION OF LONG-TERM GROWTH RATES

Figure 18 indicates that long-term growth may be estimated between the following paired life history

¹ Suggested by Dr. Gerald V. Paulik of the Fisheries Research Institute, University of Washington, Seattle, Washington.

TABLE 12. Seasonal growth rates within each sampled life history stage of Western Alaskan sockeye salmon.

Life history stage	Sampling periods (inclusive dates)		Number of days between period midpoints	Estimated body weight (dekagrams) at period midpoint		Percentage increase in body weight	Instantaneous growth rates ¹	
	Initial	Terminal		Initial	Terminal		Total	30-day average
Immature after one winter at sea	8 (7/10-7/19)	12 (8/19-8/28)	40	47.8	62.2	30	0.26	0.20
Immature after two winters at sea	7 (6/30-7/9)	12 (8/19-8/28)	50	123.3	150.5	22	0.20	0.12
Maturing after two winters at sea	3 (5/21-5/30)	7 (6/30-7/9)	40	179.3	202.7	13	0.12	0.09
Maturing after three winters at sea	3 (5/21-5/30)	6 (6/20-6/29)	30	247.9	282.3	14	0.13	0.13

¹ Instantaneous growth rate, g , is defined as: $g = \log_e \left(\frac{\text{terminal weight}}{\text{initial weight}} \right)$, where e is the base of natural logarithms. See Ricker (1958) for a full explanation and for applications in fishery dynamics.

TABLE 13. Long-term growth rates between sampled life history stages of Western Alaskan sockeye salmon.

Life history stage		Midpoint of seasonal sampling, expressed as period number and date		Number of days between seasonal mid- points	Estimated body weight (dekagrams) at seasonal midpoint		Percentage increase in weight	Instantaneous growth rates ¹	
		Initial	Terminal		Initial	Terminal		Total	30-day average
Immature after one winter at sea	Immature after two winters at sea	10.0 8/3	9.5 7/30	360	55.0	136.9	149	0.91	0.08
Immature after one winter at sea	Maturing after two winters at sea	10.0 8/3	5.0 6/14	315	55.0	191.0	247	1.24	0.12
Immature after one winter at sea	Maturing after three winters at sea	10.0 8/3	4.5 6/10	675	55.0	265.1	382	1.57	0.07
Immature after two winters at sea	Maturing after three winters at sea	9.5 7/30	4.5 6/10	315	136.9	265.1	94	0.66	0.06

¹ See note 1, Table 12.

stages: (1) 1-winter immature and 2-winter immature, (2) 1-winter immature and 2-winter maturing, (3) 1-winter immature and 3-winter maturing, and (4) 2-winter immature and 3-winter maturing. Mean body weights of each of the four life history stages would be best approximated, from a statistical viewpoint, at their respective seasonal midpoints in time of sampling.

Therefore, mean body weights at midpoints of seasonal sampling were estimated from the regressions of Table 11. These means are the basis for long-term growth rates in Table 13. As in Table 12, the average 30-day instantaneous growth rates of Table

13 are not based on extrapolation from 10-day periods actually sampled.

DISCUSSION

Sampling extended only from May through August (see Table 12). This permitted no definition of growth patterns between September and April. Koo (1961) found all summer growth and, therefore, most growth in scales of chum salmon to occur between May and August; only the narrow "winter band" was deposited the rest of the year. From material collected in the Gulf of Alaska in March and April of 1962, new ocean scale growth is reckoned to start

approximately March 15 in 2-winter sockeye salmon and April 1 in 3-winter sockeye salmon¹. Yet the fish themselves grow considerably between September and April (see Figures 16 and 17). As mentioned earlier (Hanamura, MS), one cannot extrapolate scale radius to fish length over unsampled stages of life without invoking untested and perhaps inaccurate relationships. Therefore, sampling throughout the year is required to complete the growth picture begun in Figure 18.

Complete knowledge of short-term growth during the marine life of Pacific salmon may well require that at least three approaches be integrated: (1) direct observations on size of individuals, from sampling based on prior knowledge of quantitative distribution of the target stock; (2) tagging studies instituted with precise controls on quality of data; and (3) empirical definition of fish-scale relationships throughout life. Also, basic knowledge is required on endocrine and other mechanisms under genetic control and on such diverse environmental influences as food, temperature and population density.

Henry (1961) has related first-year marine growth, as estimated from scales, to the survival of Chilko River sockeye between migration of smolts and return of spawners. Not yet understood are the mechanisms by which large numbers (of Adams River fish, in the case cited) evidently depress growth independently of survival in some years, while in other years poor growth and low survival go hand in hand. Clearly, further research is needed on short-term rates of marine growth and survival.

From knowledge of total ocean mortality and total number of months at sea, Ricker (1962) calculated average instantaneous monthly mortality rates for the entire ocean life of certain stocks of sockeye salmon. From evidence of very high mortality on small fish during their first year at sea, these average monthly rates were shown to be too high for 2-winter and older fish. Growth rates, estimated from scales and weight-length relationships, permitted computation of minimum losses in stock weight from high seas fishing. As mentioned in the introduction to the present report, these losses ranged from 6 percent to 40 percent, if offshore fishing were to be conducted during the year of maturity. From 50 percent to 65 percent of the potential inshore yield from a given recruitment would be lost to high seas fishing the year before maturity.

¹ Personal communication with Kenneth H. Mosher of the Age Analysis Unit, Bureau of Commercial Fisheries Biological Laboratory, Seattle, Washington.

SUMMARY

The objective of the study was to provide a basic description of marine growth for Western Alaskan sockeye salmon. Approximately 88 percent of the specimens selected from available data were taken by gillnets fished by United States research vessels. Average mesh sizes, measured in inches between opposite knots of multifilament nylon stretched taut, were 2½", 3¼", 4½" and 5¼". Most of the remaining 12 percent of the specimens were from 4.8" Japanese commercial nets. Sampling was conducted from 1956 through 1960 in the North Pacific Ocean and Bering Sea.

Immature 1-winter and 2-winter sockeye salmon were taken mainly in July and August; maturing 2-winter fish, from late May to early July; and maturing 3-winter fish, from late May to late June. Since sampling was not designed for estimating growth, to obtain a composite picture was more feasible than to attempt separate descriptions by year and area of capture.

Body weight, length, age, sex and gonad weight data were available from whole frozen specimens sent to the Bureau of Commercial Fisheries Biological Laboratory, Seattle, Washington. The authors collected data in 1961 to put earlier laboratory records on a fresh weight basis. For the years 1956 through 1960, fork lengths of fresh fish taken by United States research vessels were also on hand, along with data on the mesh size, time and location of capture.

Background studies of the International North Pacific Fisheries Commission provided criteria for determining maturity, means of separating Western Alaskan from Asian fish and information on the selective properties of gillnets used by United States research vessels.

The following sources of variation were considered in preliminary efforts to represent average size of Western Alaskan fish: (1) sex, maturity and winters at sea before capture; (2) changes in size between time of capture and time of laboratory processing; (3) area of origin; (4) use of gillnets known to be selective for size; (5) area of capture; and (6) year of capture.

Data were combined by sex, area of capture and year of capture in order to provide estimates of seasonal and long-term growth in weight for the entire stock. Percentage weight gains were converted to total and average 30-day instantaneous rates for the four sampled stages of marine life history.

The rationality of fishing Pacific salmon on the high seas both introduces and terminates the report. Also discussed is the need for future research on short-term rates of ocean growth and natural mortality.

CONCLUSIONS

- (1) Maturing Western Alaskan sockeye salmon taken on the high seas are slightly but significantly larger, on the average, than Asian sockeye salmon taken at the same time. While indicated for all stages, this conclusion is uncertain for immatures because only matures were used to differentiate between stocks.
- (2) When each combination of sex, maturity and winters at sea is considered separately, use of graduated gillnet meshes provides substantially unbiased estimates of mean size.
- (3) Average size of maturing Western Alaskan sockeye salmon differs significantly between areas of capture. There are few such differences in mean size of immatures; here again, classification of immatures with respect to stock is uncertain.
- (4) Average size of Western Alaskan fish in a given life history stage changes considerably in different years of sampling.
- (5) Estimated total instantaneous growth in weight for 40 days in July-August is 0.26 for 1-winter immatures; for 50 days in June-August, 0.20 for 2-winter immatures; for 40 days in May-July, 0.12 for 2-winter maturing fish; and for 30 days in May-June, 0.13 for 3-winter maturing Western Alaskan sockeye salmon.
- (6) Long-term growth from the 1-winter immature stage on August 3 until the 2-winter immature stage on July 30 the following year is 0.91; from the 1-winter immature to 2-winter maturing stage on June 14 the following year, 1.24; and from the 1-winter immature to 3 winter maturing stage on June 10 two years later, 1.57.
- (7) From July 30 as 2-winter immatures until June 10 the next year as 3-winter maturing fish, Western Alaskan sockeye salmon were estimated to grow at a total instantaneous rate of 0.66.

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- E-1. Immature male Western Alaskan sockeye salmon taken after 1 winter at sea.
- E-2. Immature female Western Alaskan sockeye salmon taken after 1 winter at sea.
- E-3. Immature male Western Alaskan sockeye salmon taken after 2 winters at sea.
- E-4. Immature female Western Alaskan sockeye salmon taken after 2 winters at sea.
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- E-6. Maturing female Western Alaskan sockeye salmon taken after 2 winters at sea.
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