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RALPH P. SILLIMAN

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ABSTRACT

Comparison of the sizes of lakes and the sizes of sockeye salmon runs to Bristol Bay shows that the two variables are closely related. Birectilinear reproduction curves express quantitatively the dependence of small returns on escapement numbers and of large returns on lake capacity. Comparison of "hindcasts" from the birectilinear curves with published forecasts for 1961-67 showed that those from the birectilinear curves were closest to the actual returns. This situation changed in 1968-69. A composite of birectilinear return estimates and "probability tree" age allocations is worth considering.

INTRODUCTION

Essential to forecasting of Bristol Bay sockeye salmon (*Oncorhynchus nerka*) runs, and to salmon forecasting generally, is the establishment of a relation between the number of spawners escaping to the streams and the number of adult salmon returning to the fishery and to the streams as the progeny reach maturity. This relation is studied by fishery biologists as a topic within the more general field of stock-recruitment relations (Ricker, 1954). It would appear desirable, where possible, to have the stock-recruitment curve reflect features of the reproductive biology of the species in question, rather than simply to furnish an empirical fit to the observed data. This need holds particularly for the Bristol Bay sockeye salmon, where the empirical points have great random variability and do not closely define any type of mathematical curve.

The purpose of this report is to study the available escapement-return data for the Bristol Bay sockeye salmon and to derive curves that reflect the influence of the size of the lake on survival of young. Such curves may be useful in forecasting future runs.

THEORY OF BIRECTILINEAR APPROACH

Comparison of the sizes of the fresh-water and oceanic environments of the sockeye salmon suggests that the former may be the limiting factor to size of run. Furthermore, it seems reasonable to assume that when escapements of spawners are small the numbers of their progeny will vary with size of the escapement, as the progeny would not fully use the capacity of the stream-lake systems. When escapements are large, space or food supply or both may become limiting. This latter idea is supported by the findings of Burgner (1964), who discovered an inverse relation between numbers of fish in escapements and average weights of progeny in the Wood River Lakes. He also reported a previous finding that ocean survival is positively correlated with smolt size. Together, these findings support the thesis that survival varies with lake size, provided one adds the reasonable (in my view) assumption of some positive relation between lake area and total food supply. Rounsefell (1946) and Ryder (1965) also recognized the influence of size on productivity in north-temperate lakes by expressing production in pounds per acre. Rounsefell and Stringer (1943) demonstrated a general relation between size of alewife runs and area of lakes accessible to them.

The large sockeye salmon run of 1960 to Bristol Bay (Ossiander, 1966,[1] table 2) led to extensive studies by the Bureau of Commercial Fisheries and the Fisheries Research Institute (University of Washington, Seattle) to study the relation of the 1960 escapement to its fresh-water environment. Data reported by Burgner, DiCostanzo, Ellis, Harry, Hartman, Kerns, Mathisen, and Royce (1969) indicate that for three of the major stream-lake systems (Wood River, Kvichak River, Naknek River), the spawners seldom if ever fully use all of the available gravel. The limiting factor to survival is thus most likely the capacity of nursery lakes for juvenile salmon; this idea is supported by a comparison of lake areas and average sockeye salmon runs (table 1). No statistical analysis is required to see the close relation; the ranks of areas and runs are identical for all except the two smallest systems.

The above data support the idea that the size, or area, of nursery lakes limits the capacity of each stream-lake system to produce sockeye salmon smolts (the direct limiting factor is probably something related to area, such as food supply, rather than space itself). Under such circumstances one would

TABLE 1.--Bristol Bay lake systems, ranked by total lake area, and mean returns of sockeye salmon, 1959-68. Areas from Burgner et al. (1969); returns from Fredin et al. (1968)[1]

Lake system	Area	Return
	Sq. km.	Thousands of fish
Kvichak..........	2,889	9,867
Egegik...........	1,132	2,394
Naknek...........	790	1,884
Wood.............	425	1,680
Ugashik..........	385	1,016
Branch or Alagnak.	297	585
Nuyakak..........	279	194
Igushik..........	74	456

[1] Fredin, R. A., S. Pennoyer, K. R. Middleton, R. S. Roys, S. C. Smedley, and A. S. Davis. 1968. Information on recent changes in the salmon fisheries of Alaska and the condition of the stocks. U.S. Bur. Commer. Fish. and Alaska Dep. Fish Game, 151 pp.; App. I-9 pp. text, [55] pp. tables; App. II-[1] p.; App. III-[4] pp. figs.; [2] pp. refs.

[1] Ossiander, Frank J. (editor). 1966. Bristol Bay red salmon forecast of run for 1966. Alaska Dep. Fish Game, Juneau, Inform. Leafl. 82, 44 pp. (Processed.) A manuscript version of Informational Leaflet 82 (showing percentage age compositions omitted from the processed version) also was used in preparing the present report.

expect a curvilinear relation between escapement and return numbers to approach some asymptote related to nursery lake capacity. The actual points of such regression, however, are affected by so much extraneous variability that no specific type of curve can be discerned. As a first approximation, I decided to use a relation consisting of two straight lines. This type of curve is included in Ricker's (1954) general treatment of reproduction curves, and he later suggested its possible use for sockeye salmon (Ricker, 1958).

Data from the Naknek River demonstrate the birectilinear regression system (fig. 1). One straight line, to the left of the regression diagram, has a slope depending on the demonstrated relation between escapement and return for the smaller escapements. The other is a horizontal line representing the capacity of the nursery lake(s). Several of the regression plots for stream-lake systems of Bristol Bay conform reasonably well with the birectilinear relation (figs. 2-11).

COMPARISON WITH OTHER TYPES OF CURVES AND METHODS OF CURVE FITTING

The right-hand limb of the escapement-return curve may possibly decline after reaching a maximum, as in the recruitment curves of some marine fishes. Ossiander (1967)[2] made this assumption in the modified Ricker

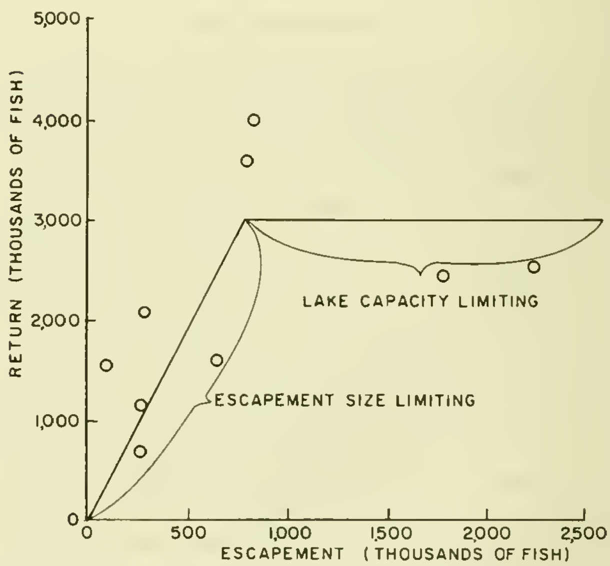

Figure 1.--Regression of return on escapement. Data on Naknek River sockeye salmon are used to show the parts of the curves (fitting methods are described later in the text) where return might be limited by size of escapement and by lake capacity.

[2] Ossiander, Frank J. (editor). 1967. Bristol Bay red salmon forecast of run for 1967. Alaska Dep. Fish Game, Juneau, Inform. Leafl. 105, 51 pp. (Processed.)

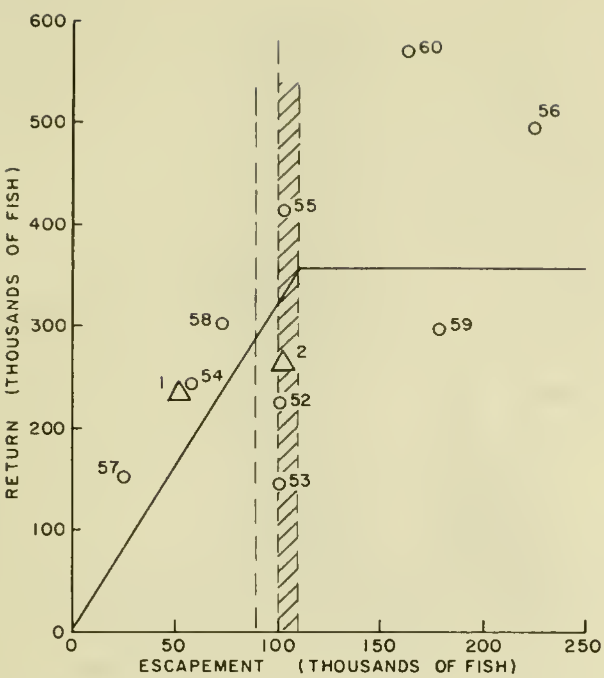

Figure 2.--Regression of return on escapement of Togiak River sockeye salmon (brood years 1952-60) with fitted birectilinear curve. Triangles indicate group means within vertical broken lines; crosshatched area indicates overlap of right-hand limb points with those used in left-hand limb. Right-hand limb represents mean of points to the right of indicated vertical line. Fitting method is described in text.

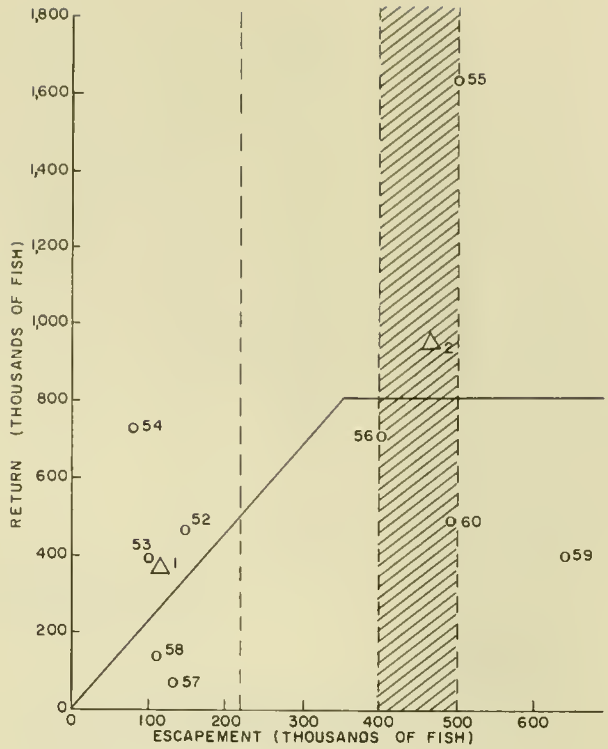

Figure 3.--Igushik River, 1952-60 (see fig. 2).

curve $R = aE^b e^{-cE}$ (where E is escapement; R is return; a, b, and c are empirical constants). In the present report, however, I am proceeding on the simple assumption that lake residence is the controlling point in the life history of sockeye salmon and that control is exerted as an upper asymptotic ceiling imposed by some factor related to lake size.

Fitting the birectilinear curve by the group mean method used herein had the undesirable feature of being somewhat subjective; therefore it seemed useful to try an objective method such as that of Quandt (1958), which I applied to the Naknek River data. The "break" occurred at about the same place as with the group mean method. The slope of the right-hand limb, when passed through the origin, was 3.47 compared with 3.80, and the difference was not significant by the t test. Likewise the slope of the right-hand limb did not differ significantly from zero, and its mean (3126) was not significantly different from that of the group mean fit (2983).

The Quandt method requires use of all possible "breakpoints" between the two straight lines, which would involve calculating as many as 24 separate regression lines for some streams. In view of the lack of significantly different results when I used this method on data from the Naknek River, I did not apply the Quandt method to data from other streams.

RETURN "HINDCASTS," 1958-67

Some idea of the utility of the birectilinear curves may be gained by comparing "hindcasts" for a series of years with the recorded returns for the same years. I have used data from official documents to make this comparision for 10 recent years.

Empirical Data

I obtained data from a number of sources. Escapements by stream system for 1944-63 were from Ossiander, 1967 (see footnote 2). Returns by stream system for various brood years in 1944-60 and total returns ("actual runs") for 1958-67 were from Ossiander, 1966 (footnote 1), 1967 (footnote 2), and 1968.[3] Estimates of average age at return were from Ossiander, 1966 (footnote 1). Published forecasts were from Royce (1961, 1962);[4,5] Tait

[3] Ossiander, Frank J. (editor). 1968. Bristol Bay red salmon forecast of run for 1968. Alaska Dep. Fish Game, Juneau, Inform. Leafl. 123, 14 pp. (Processed.)

[4] Royce, William F. (editor). 1961. Forecast of Bristol Bay red salmon run in 1961. Alaska Dep. Fish Game, Memo. 1, 9 pp. + [12] pp. figs. and tables. (Processed.)

[5] Royce, William F. (editor). 1962. Forecast of Bristol Bay red salmon run in 1962. Alaska Dep. Fish Game, Juneau, Inform. Leafl. 14, 23 pp. (Processed.)

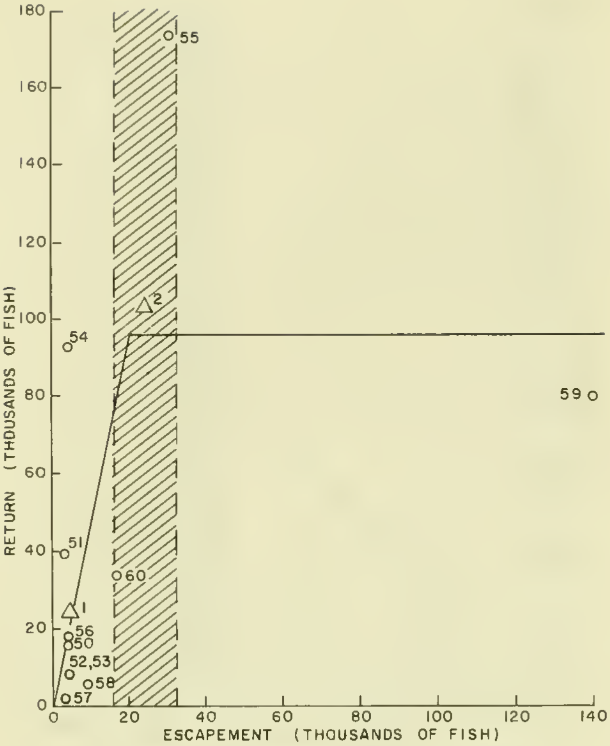

Figure 4.--Snake River, 1950-60 (see fig. 2).

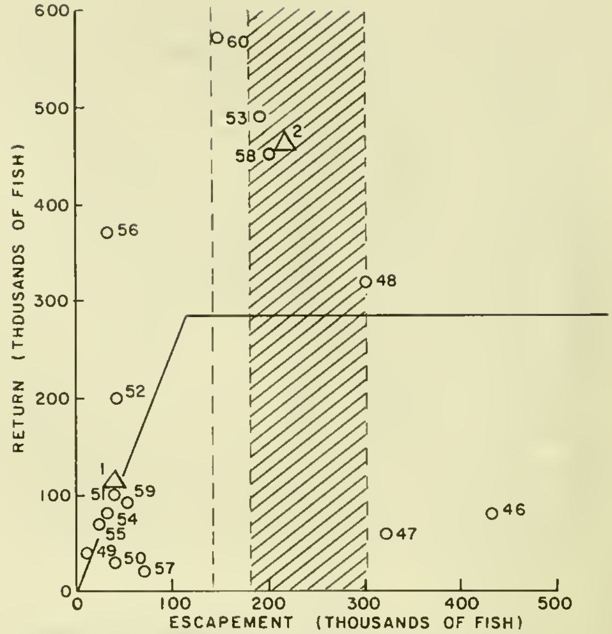

Figure 5.--Nuyakuk River, 1946-60 (see fig. 2).

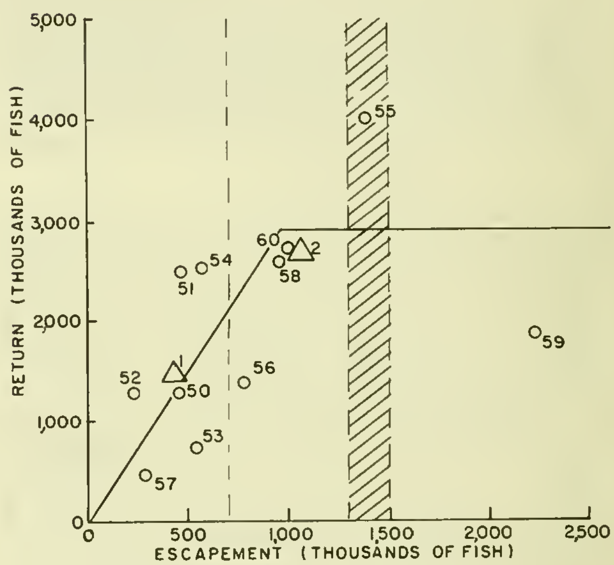

Figure 6.--Wood River, 1950-60 (see fig. 2).

(1963);[6] and Ossiander, 1964,[7] 1965,[8] 1966 (footnote 1), 1967 (footnote 2).

Birectilinear Regressions

Regression diagrams were plotted for 10 of the stream-lake systems tributary to Bristol Bay, including all those with major sockeye salmon runs (figs. 2-11). The distribution of points on several of these figures suggests conformity in some degree to the birectilinear regression surface postulated above and illustrated for the Naknek River (fig. 1). Such regressions were therefore approximated by two straight lines for each system, wherein the ascending left-hand line was defined by three points: the origin and two group means. The line, fitted by inspection, was made to pass through the origin and to have about equal deviations from the two group means. The right-hand level line was set at the mean of the group of points to the right of those included in the two group means (for the Kvichak River, the single point 1960 determined the level of the right-hand line). Some of the points selected for the right-hand and left-hand limbs overlapped. In figures 2 to 11, points of separation between group means are indicated by vertical broken lines and overlaps by cross-hatched areas.

Although selection of the points for the group means was somewhat subjective, I attempted to reduce the subjectivity by setting up the following criteria:

1. No overlap of escapement ranges for the two left-hand group means.

[6] Tait, Howard D. (editor). 1963. Forecast of Bristol Bay red salmon run in 1963. Alaska Dep. Fish Game, Juneau, Inform. Leafl. 23, 13 + [9] pp. (Processed.)

[7] Ossiander, Frank J. (editor). 1964. Bristol Bay red salmon forecast of run for 1964. Alaska Dep. Fish Game, Juneau, Inform. Leafl. 39, 43 pp. (Processed.)

[8] Ossiander, Frank J. (editor). 1965. Bristol Bay red salmon forecast of run for 1965. Alaska Dep. Fish Game, Juneau, Inform. Leafl. 59, 22 pp. (Processed.)

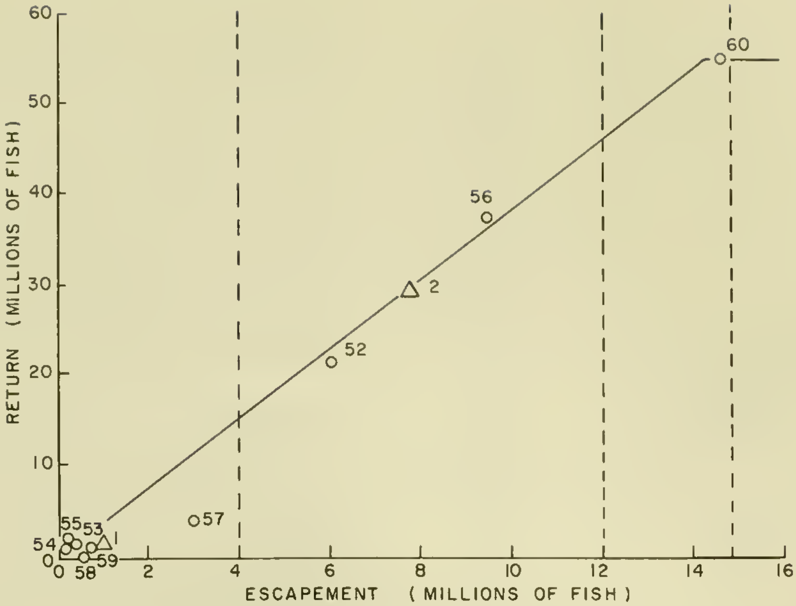

Figure 7.--Kvichak River, 1952-60 (see fig. 2).

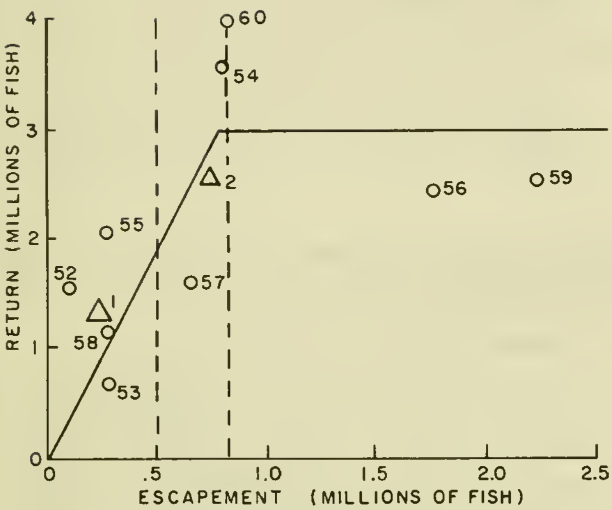

Figure 8.--Naknek River, 1952-60 (see fig. 2).

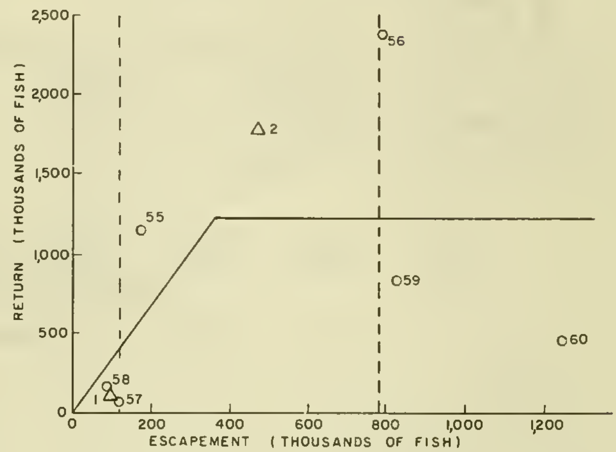

Figure 9.--Branch or Alagnak River, 1955-60 (see fig. 2).

2. Distribution of points for group means should approximate normality in horizontal and vertical directions. In some diagrams the small number of points made this approximation rather sketchy, as with means based on two or three points.

3. The group of points for the right-hand level line must include those for all escapements above the selected minimum.

A log-log regression of right-hand limb levels on lake area (fig. 12, $r = 0.86$, $P<0.01$) revealed a strong relation, which indicates that lake area provides a ceiling to return size, as suggested earlier.

Computation of Returns

Once the birectilinear regressions had been fitted, the remaining computations were simple. Total returns that corresponded to escapements for each brood year were read directly from the graphs (figs. 2-11) for the birectilinear curves. These total returns were then allocated among the several return years according to the average age at return for each stream system. Addition of appropriately lagged returns from 3 or 4 brood years completed the hindcast for each year and stream-lake system.

Individual system hindcasts were summarized (table 2) by addition for each year. No regressions were calculated for two groups of

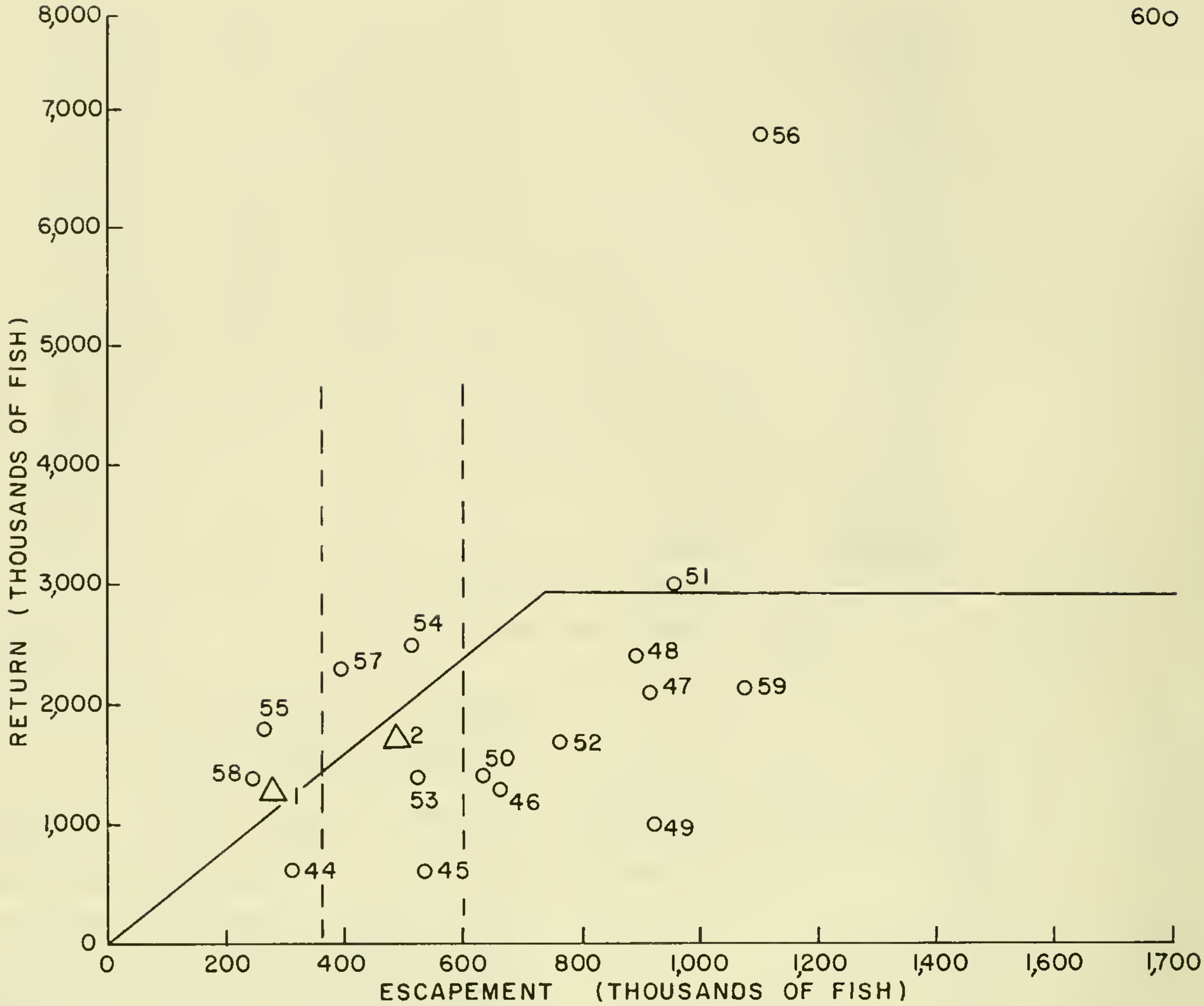

Figure 10.--Egegik River, 1944-60 (see fig. 2).

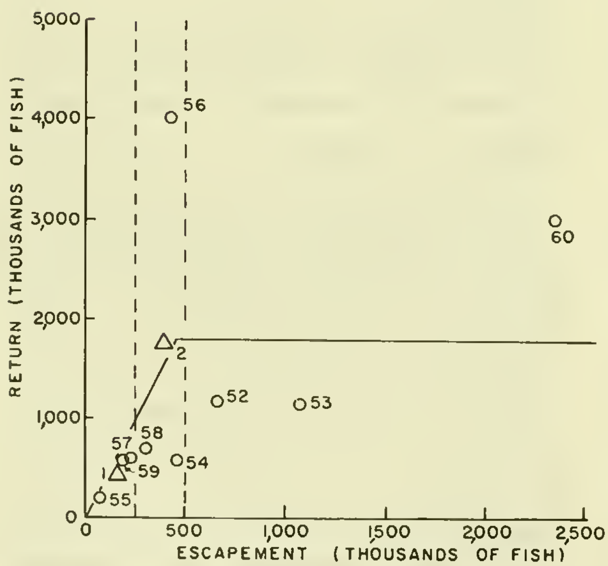

Figure 11.--Ugashik River, 1952-60 (see fig. 2).

streams with small runs: the Nushagak-Mulchatna and north side of Alaska Peninsula. Mean returns for several years were used here, as in Ossiander (footnote 1). Escapements that corresponded to Branch or Alagnak return years 1958-60 were not available; therefore, I substituted the mean returns from 1955-62 escapements.

Comparison of Hindcasts, Published Forecasts, and Actual Runs

Plots of hindcasts and actual runs (table 2, fig. 13) reveal some rather large discrepancies. The most serious of these was in 1964-65 and resulted primarily from the unusual age pattern of the return from the 1960 escapement to the Kvichak system. The huge 1965 Kvichak return was almost entirely 5-year fish (Royce, 1965).[9] Thus the return from the 1960 brood

[9] Royce, William F. 1965. The Bristol Bay sockeye run in 1965. Univ. Wash., Seattle, Coll. Fish., Fish. Res. Inst. Circ. 239, 7 pp. (Processed.)

year was almost entirely age 5, as contrasted with the normal pattern of about 50 percent 4-year fish (Ossiander, 1966--see footnote 1). Improved forecasting of age at return is outside the scope of this report but is treated at length in Ossiander (footnote 2).

Coefficients of determination (r^2) for correlations of "hindcasts" and published forecasts with actual returns measure the amounts of variation in actual returns (1961-67) that are accounted for by each type of estimate. The values of r^2 for the birectilinear hindcasts and published forecasts were similar (0.46 and 0.39, respectively). The advantage, if any, lies with the birectilinear estimates.

It is only fair to note, in considering the above comparison, that the computational techniques underlying the published forecasts were materially improved during 1961-67. In particular the "probability tree" of Ossiander (footnote 2) achieved much more accurate allocation of estimated returns among return years than the average age distributions used earlier (and also used here). Preliminary data indicate that published forecasts for 1968 and 1969 were closer to the actual runs that would have been predicted by the birectilinear approach. Runs for 1967-69 were all small, however, and it remains to be seen which method will be superior for large runs such as those of 1960 and 1965. Use of the estimated returns from the birectilinear curves and the allocation from the probability tree might represent a valuable combination of methods.

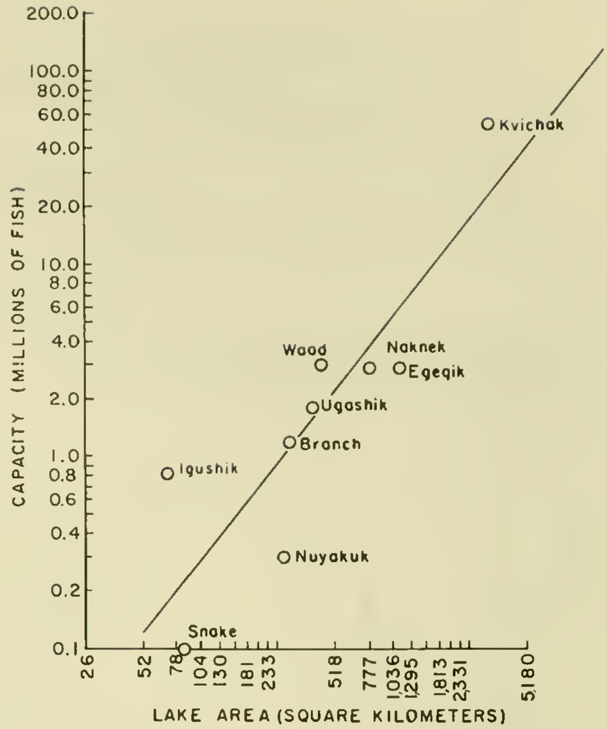

Figure 12.--Regression of capacity on lake area. Right-hand limbs are from figs. 2 to 11; lake areas from Burgner et al. (1969). Lines are least-squares fits. Lake areas were from a prepublication version of Burgner et al.; minor corrections were made in the published version, but they would have no significant effect on the fitted curve.

TABLE 2.--"Hindcasts" (estimates and actual numbers) of Bristol Bay sockeye salmon in thousands of fish, by use of birectilinear curves, 1958-67

Stream system	1958	1959	1960	1961	1962	1963	1964	1965	1966	1967
Togiak	287	234	332	283	138	256	352	346	271	211
Igushik	230	327	747	695	337	375	753	778	539	135
Snake	19	67	46	17	32	76	86	46	16	64
Nuyakuk	225	77	50	99	192	241	170	256	180	144
Wood	1,634	2,389	2,545	1,517	2,046	2,836	2,900	2,030	2,127	2,329
Nushagak-Mulchatna[1]	49	49	49	49	49	49	49	49	49	49
Kvichak	1,774	524	18,924	21,616	7,462	2,489	29,285	30,906	13,813	5,517
Naknek	1,172	2,294	1,786	2,459	2,373	1,648	2,533	2,767	1,878	2,402
Branch/Alagnak	[2] 605	[2] 605	[2] 605	664	382	888	1,169	638	351	534
Egegik	2,319	1,958	1,560	2,289	1,893	1,365	2,408	2,937	2,876	2,917
Ugashik	1,770	1,688	675	1,350	998	1,108	956	1,590	1,525	1,198
North side Alaska Peninsula[3]	1,408	1,408	1,408	1,408	1,408	1,408	1,408	1,408	1,408	1,408
Total	11,492	11,620	28,727	32,446	17,310	12,739	42,069	43,751	25,033	16,908
Actual run[4]	7,974	15,278	42,645	26,274	12,266	8,617	13,386	63,055	20,656	12,526
Published forecasts[5]	--	--	--	22,000	19,900	15,600	17,800	28,970	32,654	15,726

[1] For Nushagak-Mulchatna used mean 1956-65 from Ossiander, 1966, table 15 (see text footnote 1).
[2] For Branch or Alagnak, 1958-60, used mean return from 1955-62, escapement Ibid., tables 19, 20.
[3] For north side Alaska Peninsula, used mean 1956-65, Ibid., table 26.
[4] Actual run, 1958-65 from Ibid., table 1; 1966 from Ossiander, 1967, App. table 22 (see text footnote 2); 1967 from Ossiander, 1968, App. table 2 (see text footnote 3).
[5] From Royce, 1961, 1962 (see text footnotes 4, 5); Tait, 1963 (text footnote 6); and Ossiander, 1964, 1965, 1966, 1967 (see text footnotes 1, 2, 7, 8).

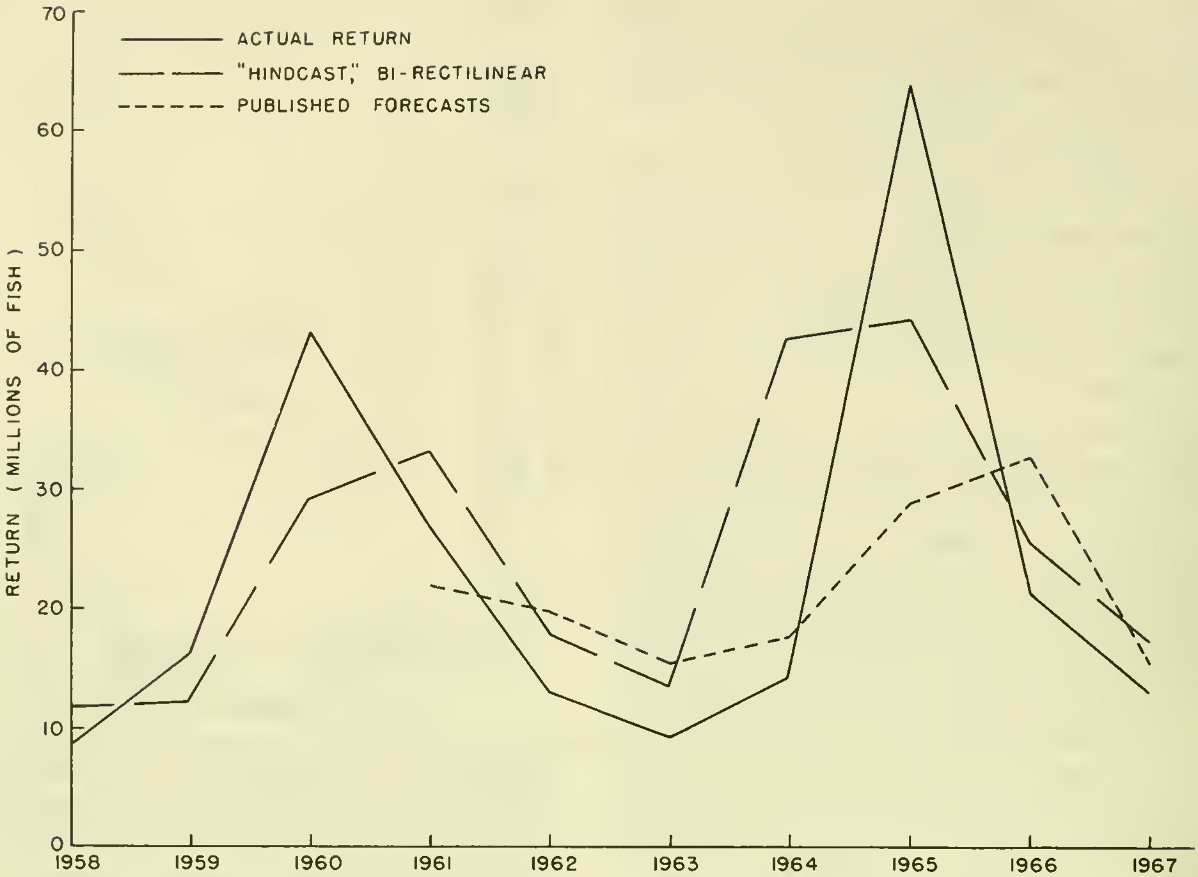

Figure 13.--Comparison of "hindcast" values and published forecasts with actual Bristol Bay returns, 1958-67.

SUMMARY

1. A close relation between return and lake size can be demonstrated for Bristol Bay sockeye salmon runs.

2. A birectilinear recruitment curve can be used to express the dependence of returns on escapement size for small escapements and on nursery lake capacity for large escapements.

3. The subjective features in fitting the birectilinear curve can be eliminated by using the Quandt "all possible breakpoint" approach. This method is extremely laborious and produced results for the Naknek River not significantly different from those obtained with the fitting method used herein.

4. Utility of the birectilinear curve in forecasting was studied by comparing "hindcasts" with published forecasts and actual runs. The coefficients of determination for hindcasts and published forecasts were about the same (0.46 for the birectilinear; 0.39 for the published forecasts). Recent improvements in published forecasts have overcome the advantage of the birectilinear approach for the small runs of 1967-69; the issue remains unresolved for larger runs such as those of 1960 and 1965.

5. Use of estimated returns from the birectilinear curves with the "probability tree" age allocations of Ossiander might provide a valuable composite method.

ACKNOWLEDGMENTS

Reynold A. Fredin, Donald D. Worlund, Richard C. Hennemuth, and Frank J. Ossiander of the Bureau of Commercial Fisheries, and Robert L. Burgner and Donald Rogers of the Fisheries Research Institute of the University of Washington reviewed my manuscript. Their suggestions have resulted in substantial revisions but they cannot be held responsible for any errors of fact or interpretation.

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